AOS Classification Committee – North and Middle America

Proposal Set 2022-B

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No. Page Title

Remove recognition of *Loxia sinesciuris* (Cassia Crossbill) as a distinct species

Background:

The process of speciation remains highly contentious despite rapidly amassing genomic data (Mckay and Zink 2015, Ravinet et al. 2017, Wolf and Ellegren 2017, Wang et al. 2019). More than half a century ago in the early days of this discussion, Mayr (1954) emphasized the distinction between ecotypes (which we refer to as ecomorphs following current terminology (Foote 2018)) and species. An ecomorph is a regional population of a more widespread taxon that is under strong selection to adapt to a local environment but that remains connected by gene flow to the parent population (Gregor 1944, Foote 2018). According the Biological Species Concept, which remains the most widely state species concept, an ecomorph is not a species distinct from a parent population because it is not reproductively isolated (Mayr 1954, Mckay and Zink 2015).

Species concepts such as the biological species concept move from philosophical discussions to rules of operation when a checklist committee votes on whether or not a population of organisms is formally recognized as a distinct species (Remsen 2015). The AOS checklist committee recently took up the question of whether a population of Red Crossbills (*Loxia curvirostra*) with a unique call type that lives in a small area of southern Idaho should be recognized as a distinct species. The petition to elevate this population of crossbills to species status was voted down on first consideration by the committee in 2009 but was approved in 2017 by an 8 to 2 vote. The population of crossbills that lives in the South Hills and Albion Mountains in southern Idaho is now recognized as distinct from other crossbill populations at a species level and was given the name Cassia Crossbill (*Loxia sinesciuris*) (Chesser et al. 2017).

The species status of the Cassia Crossbill is significant beyond a change to the checklist of North American birds. It serves a test case for whether the hundreds of other avian ecomorphs, and potentially multiple thousands of ecomorphs across all animal taxa, should be taxonomically elevated to full species. We propose that this 6000-year-old bird population does not meet stated criteria for species designation under the Biological Species Concept. This species concept is not only the species concept followed by most avian taxonomists—it is the species concept formally adopted by the AOS checklist committee. Specifically, the committee's definition of a species comes from preface of 7th Edition of the *Check-list of North American Birds* (American Ornithologists' Union 1998). We quote below this official species statement by the AOS checklist committee because this statement frames the discussion that follows:

"The Committee strongly and unanimously continues to endorse the biological species concept (BSC), in which species are considered to be genetically cohesive groups of populations that are reproductively isolated from other such groups. According to the BSC, geographic isolation leads to genetic change and potentially to the reproductive isolation of sister taxa. If and when these closely related forms later coexist, reproductive isolating mechanisms such as distinctive displays and vocalizations serve to maintain the essential genetic integrity of the newly formed biological species." (American Ornithologists' Union 1998)

The process of speciation, as envisioned by Mayr and other biologists who established the biological species concept, is founded on the need for populations to exist in allopatry for long periods of time as reproductive isolation evolves (Dobzhansky 1935, Mayr 1942, 1982). This hypothesized process of speciation is clearly echoed in the AOS checklist committee philosophy reproduced above. Mayr envisioned, at a minimum, tens of millennia and more likely hundreds of thousands of years for reproductive isolation to evolve between isolated populations of birds (Mayr 1963, 2000). It certainly may occur faster for animal taxa with shorter generation time or take longer for the longest-lived animals, but there is a clear expectation that substantial evolutionary time is needed for reproductive isolation to be achieved. The reason that so much time was invoked is that the diverging populations need time to evolve fixed genetic differences in adaptive gene complexes that create dysfunction in hybrid offspring when alleles from two species are mixed (Coyne 1994, Schilthuizen 2000). The dysfunction of hybrids can be but is not required to be complete inviability or sterility of offspring. So long as the fitness of offspring is compromised, then the flow of genes is disrupted and species boundaries are maintained (Coyne and Orr 2004, Irwin 2019). To Mayr, reaching a point of hybrid incompatibility is the point at which the process of speciation is complete (Mayr 2000). Alternatively, the rapid evolution of morphological differences and very strong female mating preferences or ecological sorting could theoretically stop gene flow and establish a new species (Dieckmann et al. 2004, Nosil 2012). However, if mating patterns are all that stop the flow of genes then even a few mixed-population crosses per generation would lead to the flow of genes from one population to another and to the erosion of species boundaries (Irwin 2019). Mayr and other proponents of the biological species concept generally viewed mating patterns as a means to reinforce species boundaries (avoid mistakes leading to dysfunctional offspring), but they always come back to low performance of hybrids (post-zygotic isolating mechanisms) as the key to the disruption of gene flow and the maintenance of species boundaries (Schilthuizen 2000). Here we argue that the population of Cassia Crossbills in southern Idaho does not meet basic criteria of the biological species concept, even a biological species concept that deviates from Mayr's construct in allowing for some gene flow among populations (Coyne and Orr 2004).

Molecular data indicate that all extant populations in the Red Crossbill complex shared a common ancestor about 11,000 years before present (Björklund et al. 2013). Based on climate models and projections of how long a red-squirrel-free South Hills lodgepole pine ecosystem likely existed in Idaho, Parchman et al (2016) concluded the Cassia Crossbill lineage is about 6,000 years old. No other bird species recognized by the AOS checklist committee is proposed to have diverged within a period as short as 6,000 years. Thus, the brief existence of the population of Red Crossbills in the South Hills of Idaho necessitates that the claim that Cassia Crossbills are a distinct species is premised on a pace of speciation unprecedented in North American avian taxonomy.

New Information:

Reproductive Isolation Assessed from Assortative Pairing and Mating Preferences

One means to assess reproductive isolation is by observing the rate of between-species pairings in wild populations. In the small region of North America in which Cassia Crossbills breed, Red Crossbills from two other populations—call type 2 and 5—regularly breed in the same forests occupied by Cassia Crossbills (Smith and Benkman 2007). To assess the rate of assortative pairing between Cassia Crossbills and co-occurring Red Crossbills, Benkman and his colleagues assessed 1704 crossbill pairs and found 12 pairs that involved a bird giving the Cassia Crossbill-specific call type 9 and a second crossbill giving another call type (Benkman et al. 2009).

While the observation that less than 1% of all pairs involve birds of two call types seems like relatively strong assortative mating, crossbills from call-type populations other than the Cassia Crossbill call type made up only 7% of the crossbills in the Cassia Crossbill study area (Monthly averages: 488 call type 9; 30 call type 2; and 4 call type 5). Looking at the percent of heterotypical pairs out of all the observed crossbill pairs without considering the extremely unbalanced effective population sizes results in a bias in the interpretation of results. The number of Cassia Crossbills is not the limiting factor in determining the rate of heterotypic matings. The potential for hybrid pairings is limited by the availability of type 2 and type 5 birds. For example, if we look at the data presented in this study on a month-per-month basis, focusing on April of 2001, only four call type 2 crossbills were observed in the South Hills, and two of those birds mated heterotypically (Smith and Benkman (2007). So, in April of 2001, of the opportunities for Cassia Crossbill x type 2 pairings, 50% resulted in a heterotypic pairing. Expanding across all of 2001, only six pairings involving call type 2 crossbills were observed in total, and of those six pairings, 2 were heterotypic (33%).

Moreover, as Smith and Benkman (2007) observed: “a disproportionate number of call type 2 crossbills in the South Hills during June and July did not breed and thus could not hybridize with South Hills crossbills”. Further, assortative mating was only assessed in forests where red squirrels are absent and lodgepole pines have cone morphology that deters crossbills with smaller bills. One would presume that Cassia-type Crossbills with more specialized bills stay in habitat where they forage efficiently. Smaller-billed crossbills would tend to leave habitat where they forage inefficiently. As noted by Benkman (1987), crossbills are strong fliers and will leave their current habitat if their feeding rate is too low. Such a pattern of habitat occupancy might give the appearance of assortative mating when the assortment is primarily matching bill morphology to habitat.

Whether or not the assortment of birds by call type deviated significantly from random (Smith and Benkman 2007), non-random mating is not the core hypothesis being tested. The hypothesis being tested is that Cassia Crossbills are species under the Biological Species Concept. The core premise of the Biological Species Concept is cessation of gene flow between populations. In the case of the Cassia Crossbill, however, even with few opportunities for hybridization, we still see hybridization. This does not argue for a level of reproductive isolation that would halt the flow of genes between Cassia Crossbills and birds from other populations to a degree needed to maintain species boundaries.

The above argument also does not consider Cassia-type Crossbills hatched in the South Hills and Albion Mountains that disperse to other crossbill habitats in the region. Benkman (1999) documented that the density of crossbills in the South Hills and Albion Mountains is twenty times higher than in nearby Rocky Mountain crossbill habitat. It follows that in years when cone crops cannot support this high density of Cassia Crossbills, many Cassia-type crossbills would disperse out of the South Hills and Albion Mountains. In regions dominated by other call types, such dispersing Cassia Crossbills could tend to change call type (see below) and be very hard to detect. The effect would be to homogenize crossbill populations in the region.

Direct observations of mating preferences of Cassia Crossbills that hatched and developed in the wild also do not support significant barriers to between-population pairing. In captivity, female Cassia Crossbills were given a choice between male Cassia Crossbills or male crossbills from other call types that occur sympatrically; 17% of female Cassia Crossbills showed a preference for males from call types other than call type 9 (Snowberg and Benkman 2007). Genetic data indicate that the pairings between Cassia Crossbills and sympatric crossbills from other call types and morphologies results in substantial gene flow between populations (discussed below).

A key behavioral observation that applies to all crossbill populations is that, like other cardueline finches (Mundinger 1970, 1979), Red Crossbills match their call types to be more similar to their mates, including switching from one call type to another (Groth 1993, Keenan and Benkman 2008). A bird of call type 2 was observed to copy the Cassia Crossbill call type of its mate (Benkman et al. 2009). Cassia Crossbills have a somewhat distinctive bill shape relative to other crossbills, but bill shape is not diagnostic because there is substantial overlap in bill dimensions with other populations (Benkman et al. 2009). The call type is discretely different, and call type is the diagnostic characteristic of the Cassia Crossbill (Benkman et al. 2009), just as plumage pattern diagnoses many species of birds. Crossbills that switch call types are literally changing their species identity because an individual bird cannot be confidently assigned to a species by either morphology or genotype (more on genotype below). Summers et al. (2007) stated the implications of learned call types in consideration of the species status of Parrot and Scottish Crossbills: “If individuals can change their calls, then calls cannot be used to diagnose a species.”

Post-zygotic Reproductive Isolation

If pre-zygotic isolation is incomplete, perhaps post-zygotic isolation is strong enough to retain the integrity of crossbill ecomorphs across space and time. The best data on the fitness consequences of pairing between crossbill call types comes from studies of North American crossbills, but not Cassia Crossbills. Snowberg and Benkman (2007) used estimates of the heritability of bill shape based on data on Scottish Crossbills (Summers et al. 2007) and fitness of bill shapes in different environments based on rates of acquisition of seeds from cones to simulate expected fitness outcomes of pairings between crossbills of call types 2 and 5. Their model estimated a fitness increase of approximately 12% for female crossbills of call types 2 and 5 if they paired assortatively by call type versus if they mated randomly and if their offspring remained in the habitat to which the female parent was best adapted. One could reasonably expect similar outcomes of simulations run using data on Cassia Crossbills versus other crossbill call types. This could be taken as evidence for reasonably strong post-zygotic selection against “hybrid” offspring, although the fitness of hybrid crossbills has not been measured in nature. Moreover, there may be mitigating factors that would make such post-zygotic selection ineffective in isolating populations.

The loss of fitness that was inferred from models would only occur if individuals remained in their mother’s optimal habitat and only during years of relative food scarcity. In years of relative food abundance, crossbills of Call types 2 and 5 become more common in the Albion Mountain and South Hills, and Parrot Crossbills and Scottish Crossbills invade areas that typically only host Red Crossbills, presumably because food abundance makes foraging inefficiencies less important. Crossbills are famously nomadic with individuals moving to find regions where they can feed efficiently (Benkman 1987). Thus the fitness of a "hybrid" crossbill would be less—and likely much less—than the maximum fitness loss calculated in the Snowberg and Benkman (2007) and Benkman (2003) models. Indeed, it was estimated that as little as a 0.2 mm change in bill depth away from the optimal trait value would be associated with as much as a 20% decrease in "relative" survival (Benkman 2003). However, the biological significance of this estimation may have certain limitations, as it is only a relative estimation of survival (standardized to 1) based on the exponential relationship between predicted survival and feeding efficiency. Moreover, field measurements of survival were limited: birds that were recaptured in subsequent years (1-3 years after initial banding) were classified as survived, while birds that were not recaptured were classified as deceased (Benkman 2003). Using this method, 64% of the initial birds banded were assumed to have died, but clearly migration to a new region would also cause birds to not be recaptured. With varying cone crops potentially leading to varying levels of migration, in every generation there would be substantial gene flow into and out of the Cassia Crossbill population, and this predicted gene flow is evident in the relative lack of structure in crossbill genomes.

Crossbill genetics

There is no dispute among systematists that all populations of Red Crossbills are recently diverged from a common ancestor. Molecular data indicate that all extant populations in the Red Crossbill complex shared a common ancestor about 11,000 years before present (Björklund et al. 2013, Parchman et al. 2018). The Red Crossbill complex includes the three populations elevated to species status by checklist committees—Parrot Crossbill, Scottish Crossbill, and Cassia Crossbill—as well as several distinctive populations in southern Europe and nine call types in North America (Parchman et al. 2018). Based on climate models and projections of how long a red-squirrel-free South Hills lodgepole pine ecosystem likely existed in Idaho, Parchman et al. (2016) concluded the Cassia Crossbill lineage is about 6000 years old. Thus, the brief existence of the populations of Red Crossbills in the South Hills of Idaho necessitates that the claim that Cassia Crossbills are distinct species is premised on a pace of speciation with little precedence in avian taxonomy.

A predicted outcome of poor reproductive isolation is gene flow and lack of genetic distinctiveness of a population. Initial studies based on both mitochondrial and nuclear gene sequences failed to find divergence in mitochondrial genomes or fixed differences in the nuclear genomes in comparisons of Cassia, Scottish, Parrot, and Red crossbills (Questiau et al. 1999, Piertney et al. 2001, Parchman et al. 2006). After assessing divergence in both nuclear and mitochondrial genes in crossbills from throughout Eurasia and North America and including Cassia Crossbills, Questiau et al. (1999) concluded "Morphological differentiation … shows the possibility of rapid local adaptation to fluctuating resources … without necessarily promoting the development of reproductive barriers between morphs." Similarly, Pachman et al. (2006) concluded that their analysis "did not separate individuals from the eight call types in the red crossbill complex, consistent with recent divergence and ongoing gene flow." In both the Questiau and Parchman et al. papers, the genetic data indicated substantial on-going gene flow with other crossbill populations, consistent with incomplete reproductive isolation from behavioral data. These assessments of lack of species-level genetic structure in ecomorphs of the Red Crossbill were made using the same sort of molecular tools that allowed for genetic discrimination of other avian species, including closely related sister taxa (Avise and Zink 1988, Johnson and Cicero 2002, Tavares and Baker 2008).

As a follow-up to earlier genetic analyses, Parchman et al. (2016) compared almost 240,000 single-nucleotide polymorphisms (SNPs) isolated from 230 individual crossbills drawn from all North American call types including Cassia Crossbills and found evidence of genetic structure among North American crossbill populations (Parchman et al. 2016). A principal components analysis (PCA) of genetic data from the 9 North American call types that included over 18,000 SNPs indicated that individuals from the Cassia Crossbill population fell in an isolated cluster along the primary axis of variation (PC1, 11.4%). In a broader phylogenetic analysis, assessment of 238,615 SNPs indicated that Cassia Crossbills formed a monophyletic group. Finally, it was observed that Cassia Crossbills harbor more genomic loci with locus-specific Fst values greater than 0.8. (Fst is an estimate of genetic differentiation.) These results were interpreted as evidence that there is little gene flow between the crossbills inhabiting the South Hills and other crossbill populations. However, there must be caution when drawing inference about the degree of reproductive isolation in comparisons using such large numbers of SNPs. Beaumont (2005) stated the challenge succinctly: "… it might be that, what are called 'species' consist of several regions in the genome that, by virtue of their phenotypic effects, are under strong disruptive selection and/or subject to assortative mating, and thus have high Fst; whereas the remainder of the genome is exchanged relatively freely among populations and has lower Fst". This statement of concern seems to fit locally adapted crossbills very well.

We first consider the phylogenetic tree construction. The monophyly of the Cassia Crossbill population is supported with 90% bootstrap confidence, suggesting robust model support for the population clustering as a unique group. However, in this analysis, call type 6 also showed monophyly, albeit with much lower support. Call type 6 individuals have the largest bill size of North American populations surveyed (akin to the relative larger size of the Parrot Crossbill in Europe) and are considered nearly allopatric with only small overlap to other crossbill populations (Parchman et al. 2016); yet call type 6 crossbills are not recognized as species.

PCA's mathematically reduce data into series of values (scores) that represent axes of variation in the original data. The scores are partitioned into principal components (PC1, PC2, … PCn) that represent some component of the variation in the original variables that is then interpreted to be a 'caricature' of the individuals in the dataset. With genomic analyses, interpreting PC scores is difficult because of the complexity of genetic data. In the PCA of crossbill populations, the Cassia Crossbill population clustered on its own along the first axis of variation (PC1 explaining 11.4% of the variation in SNP data) (Fig. 2 in Parchman et al. (2016)). However, we have no clear understanding of what this axis of variation means in the original trait space (i.e., the original SNP data and the genetic traits it represents) (Chong et al. 2018), For this reason, caution is advised in estimating selection on traits based on PCA scores alone (Conner 2007). Despite these challenges, it was also assumed that the second axis of variation from the crossbill PCA (PC2 explaining 2.4% of the variation in SNP data) roughly represented bill size because some of the crossbill populations clustered roughly in descending order of bill size along this axis (Parchman et al. 2016). Call type 6 clustered on its own at the most extreme end of this component. Again, this result was not interpreted to mean call type 6 was genetically distinct from the rest of the population, despite the assumption that selection on bill size is the primary driver of genetic isolation among the crossbill ecomorphs. Cassia Crossbills clustered in the center with the rest of the ecomorphs along this second axis of variation. From the PCA analysis we can, therefore, conclude only that certain components of variation in the SNP data place Cassia Crossbills in their own cluster.

An admixture proportion analysis also showed genetic structure among populations. This analysis used the PCA scores mentioned above to assign the genomes of individuals to a specific number of ancestral groups. The number of potential groups can be varied to simulate *k* number of ancestral populations to which an individual may be assigned. When the admixture proportion analysis of the 9 crossbill ecomorphs returned that the Cassia Crossbill individuals clustered to a single ancestral group, no matter the number of assumed ancestral populations, it was interpreted to indicate strong support that Cassia Crossbills were much more genetically distinct than other populations (Fig. 3 in Parchman et al. (2016)). However, this approach also comes with limitations, and care must be taken not to overinterpret results. The methods used to estimate group assignments in this case were based on a model that is equivalent to a no-admixture model (Parchman et al. 2016). In this type of model, each individual is assumed to be derived exclusively from one ancestral population. This approach was taken with the crossbill data to ensure the model could successfully run (Parchman et al. 2016); however, it also means that the possibility of multiple and historical admixture events are not considered. Indeed, admixture analyses may fail to detect admixture in individuals based on the number of ancestral populations included in the model, as the model seeks to parsimoniously match individuals to the preset number of ancestral populations specified (Lawson et al. 2018). It is best to not interpret admixture analyses as models of population divergence but rather as comparisons of individuals (Lawson et al. 2018). In the most robust model of the crossbill admixture analysis, 5 ancestral populations fit the data the best, and this model showed call type 5, 6, and Cassia Crossbill individuals clustering in their own ancestral populations (Parchman et al. 2016). However, we cannot conclude from this analysis that call types 5, 6, and Cassia Crossbills have diverged as species from other populations; we can only conclude that when a model tries to bin individuals from the modern crossbill populations into *k* = 5 ancestral groups, type 5, 6, and 9 individuals most parsimoniously fit in their own groups based on the model-relative levels of admixture among the individuals sampled.

When it came to the actual estimation of population divergence, genome-wide and locus-specific estimates of differentiation among crossbill ecomorphs told conflicting stories. Fst values were used as a means to estimate the level of differentiation between the nine call types (Parchman et al. 2016). Fst is a descriptive statistic (between 0 and 1) that differentiates between groups based on variation in allele frequencies. It depends both on the differentiation among populations and genetic diversity within populations, such that lower diversity within a population leads to larger Fst values. Summarized simply, larger Fst values represent higher levels of differentiation between populations, while lower values represent low levels of differentiation (Holsinger and Weir 2009).

There is no exact cut-off as to what constitutes an Fst value indicative of species-level divergence. However, there exist rules of thumb that has been adopted by population geneticists. In general, Fst values above 0.15 indicate fairly robust levels of differentiation (lower gene flow), and Fst values below 0.05 indicate very little genetic differentiation (higher gene flow) (Hartl and Clark 1997, Frankham et al. 2002). For added context, Fst values for SNP data among human populations averages around 0.1 (Holsinger and Weir 2009). Recently, a survey across more than 60 population and species pairs found that Fst values below 0.2 reliably indicated populations with ongoing gene flow across their entire genomes (Roux et al. 2016). In comparison, the genome wide Fst values estimated among the crossbill ecomorphs averaged only between 0.011-0.035 (Fig. 5A) (Parchman et al. 2016). The median genome-wide Fst value of Cassia Crossbills compared to all other crossbill populations was just under 0.025. This result indicates high levels of gene flow and some interbreeding despite the assumption that there is high reproductive isolation (Smith and Benkman 2007). As noted above, this matches genetic data from Scottish, Parrot, and Common crossbills, which also show low genetic differentiation (in mitochondrial neutral markers; Piertney et al., 2001). Moreover, this observation also comes in spite of the fact that the Cassia Crossbill population should be prone to inflated genome-wide Fst values because of their small population size (Holsinger and Weir 2009).

The observation of low genome-wide Fst values was offset by fact that Cassia and call type 6 crossbills had a greater number of loci-specific Fst values that were very high (greater than 0.8) compared to the rest of the crossbill populations (Fig. 5B in Parchman et al. (2016)). This result was interpreted to indicate that Cassia Crossbills and call type 6 crossbills had more loci (median for Cassia Crossbills: ~15; median for type 6: ~10) that were highly differentiated compared to the other crossbill populations, and that these loci drove the isolation of Cassia Crossbills along the first axis of variation in the PCA (see above). Indeed, a significant correlation between locus-specific Fst values and the first PCA axis was found only when Cassia individuals were included in the correlational analysis. Moreover, Cassia Crossbills were found to have the lowest levels of within genome diversity among the populations (Fig. 7 of Parchman et al. (2016)). Despite these observations, estimates of genetic distance between populations did not correlate with population beak depth, the proposed driver of ecological speciation in the Cassia crossbill (Fig. 4B of Parchman et al. (2016)). Considering crossbills are nomadic, this could perhaps be explained if offspring from matings between Cassia Crossbills and other populations are capable of moving out of the South Hills to find food, as is the case with most crossbills (Smith and Benkman 2007, Benkman et al. 2009), thus minimizing the cost to mismatched pairings. It is also possible that there is too much natural variation in bill size (Groth 1993) among crossbill populations to form a strong correlation with the genetic data.

Even though tests for an ecological driver of genetic differentiation were not significant, it was concluded that selection on a small number of loci, regardless of very low differentiation across the genome, was sufficient to support the hypothesis that the Cassia Crossbill is a recently diverged species. Again, this same interpretation was not imparted on call type 6 crossbills despite their high Fst values at specific loci. This conclusion was based on the assumption that differentiation of small regions of the genome is sufficient for speciation (Nosil et al. 2009, Parchman et al. 2016). However, heterogenous selection across the genome can also raise genome-wide differentiation and increases the association between phenotypic adaptation and genome-wide genetic distance (Nosil et al. 2009), neither of which have been observed in the crossbill populations (Parchman et al. 2016). We do not agree that differentiation at a small number of specific loci in the face of on-going gene flow is sufficient to diagnose species, especially if differentiation is driven by selective sweeps and reduced within-population diversity (Cruickshank and Hahn 2014).

Fitting crossbill observations to species concepts

When Benkman and colleagues proposed that the Cassia Crossbill population was a new species of bird, laying the groundwork for the vote by the AOS Checklist Committee, they invoked the Biological Species Concept as their criteria assessing the species status of crossbills (Benkman et al. 2009). In the introduction to their paper, Benkman et al. (2009) vacillate a bit in invoking the Biological Species Concept by saying they followed a Biological Species Concept that permits a degree of gene flow (citing Coyne and Orr 2004). Indeed, many bird species widely considered to meet the criteria of the Biological Species Concept show evidence of gene exchange with other taxa (American Ornithologists' Union 1998). But these other avian species are divergent in morphology or behavior, and they show significant divergence from sister taxa in mitochondrial and nuclear genes. As Coyne and Orr (2004:30) stated, biological species cannot be "distinct at only a few loci but freely exchange genes in the rest of the genome". By any stretch of the Biological Species Concept, the Cassia Crossbill should not be recognized as a distinct species because species identity cannot be diagnosed with certainty by morphology; individuals can change the call type that is purported to diagnose the species; there is incomplete reproductive isolation between Cassia Crossbills and other taxa leading to a substantial flow of genes; and, individuals assigned to the Cassia Crossbill population are not genetically distinct from other crossbill populations at a level that discriminates other populations of birds recognized as species.

Cassia Crossbills are also not species under the Mitonuclear Compatibility Species Concept (Hill 2017). This species concept defines a species as a population with a uniquely coadapted set of mitochondrial and nuclear genes (Hill 2016). Cassia Crossbill do not show significant divergence in mitochondrial genotype from other North American Red Crossbill populations (Questiau et al. 1999; Piertney et al. 2001), so there is no potential for uniquely coadapted mitonuclear genotypes.

Are Cassia Crossbills species under the Phylogenetic Species Concept? This species concept defines species as diagnosable, independently evolving lineages. There is a stronger argument to be made for Cassia Crossbills being Phylogenetic Species than Biological Species. The problem here may be diagnosability. A diagnosable trait should be a fixed difference between individuals in two populations. Call type or alarm calls are proposed to be among the most reliable diagnosable traits in crossbills (Edelaar 2008), but the fact that individuals learn call types and can change call types within a lifetime, makes us reject a species status for these taxa even under the Phylogenetic Species Concept. If we accept these crossbill populations as species then we have to accept that, within a lifetime, an individual can change species identity.

We propose that Cassia Crossbills are not a distinct species under any species concept. Ecomorphs like Cassia Crossbills are fascinating examples of local adaption, but they are not species.

Recommendation:

Remove recognition of *Loxia sinesciuris*, the Cassia Crossbill, as a distinct species and subsume the Cassia Crossbill population into *Loxia curvirostra*, the Red Crossbill.

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Date of Proposal: 15 October 2021

External Comment on Proposal 2022-B-1

I write in response to the Cassia Crossbill (*Loxia sinesciuris*) proposal Hill and Powers (hereafter H&P) submitted to you. H&P recently published an opinion piece of a similar nature in the *Journal of Avian Biology* (available early online as of this writing). I submitted a response with three co-authors to the *Journal of Avian Biology*, which is available as an attachment. Much of what I state below is lifted from our manuscript; it might be easier to simply read the (albeit longer) manuscript although it doesn't follow as closely the organization of H&P's proposal. The manuscript also contains all the references listed below. Below I try to focus on the most relevant mischaracterizations and misinterpretations in H&P. I address the sections in H&P in sequence under their "New Information" although this is a misnomer because no new information is presented, and more recent "New" information since the Cassia Crossbill was recognized is ignored.

"Reproductive Isolation Assessed from Assortative Pairing and Mating Preferences"

As H&P state in the first paragraph of this section, 12 (0.7%) of 1704 breeding pairs over 6 years were mixed. H&P then state in the second paragraph that although this "seems like relatively strong assortative mating" they claim it isn't. H&P state "Looking at the percent of heterotypical pairs out of all the observed crossbill pairs without considering the extremely unbalanced effective population sizes results in a bias in the interpretation of results." Thus, they choose to ignore the first two rather strong premating isolating barriers: habitat isolation and reduced immigrant fecundity (their contribution to total reproductive isolation is between 0.877 and 0.984 depending on the call type comparison where 0 represents panmixia and 1 is complete reproductive isolation [Table 2 in Smith and Benkman 2007]; see next paragraph). Combined, these two reproductive isolating barriers result in few non-Cassia Crossbills remaining and attempting to breed because they have difficulty competing for lodgepole pine seeds with the locally adapted Cassia Crossbill (see accompanying manuscript for a fuller discussion). Instead, H&P focus on the pattern of pairing by the two call types (types 2 and 5) that occur regularly in the area and breed in very low numbers in the South Hills.

However, focusing exclusively on the proportion of the breeding individuals of the rare ecotypes (types 2 and 5) that form mixed pairs is misleading. It has long been recognized that an individual is more likely to hybridize when conspecifics are rare because of the difficulty of finding a conspecific mate (Hubbs 1955, Mayr 1963, Grant and Grant 1997). Consequently, those interested in measuring behavioral and reproductive isolation account for asymmetries in the abundance of the sexes of each species (e.g., Rolán-Alvarez and Caballero 2000, Pérez-Figueroa et al. 2005). H&P suggest we ignore such asymmetries in abundance when stating "Looking at the percent of heterotypical pairs out of all observed pairs without considering the extremely unbalanced effective population sizes results in a bias in the interpretation of results." However, Smith and Benkman (2007) employed such corrections when estimating behavioral isolation. The difference is that H&P would emphasize, for example, that one of three Type 2 individuals, among hundreds of Cassia Crossbills, is paired with a heterospecific, whereas the more telling result for reproductive isolation is that so few Type 2 stay and successfully breed, and that the other two Type 2 paired assortatively. Given that Type 2 females usually choose the one male out of hundreds that is of their own call type is striking, especially if there are costs associated with finding mates (Irwin 2020), and consistent with the very strong estimated behavioral isolation (0.980 to 0.988; Smith and Benkman 2007). When we use the widely accepted Coyne and Orr (1989) method (as modified by Ramsey et al. 2003) for estimating total reproductive isolation, where 0 equates to panmixia and 1 equates to complete reproductive isolation, we found that premating reproductive isolation averaged 0.999 over 6 years (estimated as in Smith and Benkman [2007] but including an additional 4 years of data from Benkman et al. 2009).

In the third and fifth paragraphs of this section, H&P speculate that we miss hybridization because Cassia Crossbills commonly wander away from the South Hills. However, Cassia Crossbills don't commonly if ever wander away. None of the over 3000 Cassia Crossbills color-banded in the South Hills since 1997 has been detected outside the South Hills. In contrast, two of the ~60 red crossbills categorized as Type 2 captured and color-banded in the South Hills have been subsequently photographed elsewhere (Benkman 2017; CWB unpubl. data). Furthermore, there are no recordings of Cassia Crossbills from outside the South Hills or Albion Mountains (the Albions are the other range in which Cassia Crossbills occur) in massive citizen science databases such as eBird or Xeno-canto despite high interest among birders in recording crossbill vocalizations (Young and Spahr 2017). These observations indicate that Cassia Crossbills have not been detected outside the South Hills and Albions because they rarely, if ever, leave (contra the speculation by H&P). In the accompanying manuscript we provide background on the Cassia Crossbill that explains the biology for why they are so sedentary.

In the sixth paragraph, H&P refer to the results of mate choice experiments by Snowberg and Benkman (2007) to argue that they "do not support significant barriers to between-population pairing." Eighty-three and 82 percent of estradiol-implanted female Cassia and Type 2 crossbills, respectively, showed a preference for conspecifics when given a choice between two males, one of each of these two taxa matched for differences in body and bill size, and coloration. These are strong preferences ($P \leq 0.0005$) but not as strong as might be expected from our measures of behavioral isolation in the field (Smith and Benkman 2007). However, the males in the experiments were not singing, and thus Snowberg and Benkman (2007) examined preference in relation to contact calls only (which was the intention; females were primed to breed, but males weren't). However, Cassia Crossbills have distinctive songs (Porter and Smith 2020), and we strongly suspect that (1) females also prefer the song of their father, (2) song is unlikely to switch even occasionally between types, and (3) song undoubtedly plays an important role in mate choice and promotes assortative pairing beyond that based on calls alone.

In the seventh and last paragraph of this section, H&P discuss call modification. We note that we have recently documented striking divergence in the contact calls (those we use to categorize crossbills into call types) between Cassia Crossbills and Type 2 over a 20-year period due to population-level changes in Cassia Crossbill calls (Porter and Benkman 2019). This population-level call divergence has been caused by adults subtly modifying their calls over time to be more distinctive from the calls of Type 2 and by offspring learning their calls from their parents (Keenan and Benkman 2008, Porter and Benkman 2019). Individual Cassia Crossbills may modify their calls to be more divergent from the calls of Type 2 to reduce heterotypic flocking, which lowers feeding efficiency (Smith et al. 1999, Porter and Benkman 2019). Call divergence in turn has resulted in Cassia Crossbills more likely to land in response to playbacks of calls representative of contemporary calls than of those representative of 20 years earlier. In contrast, Type 2 are more likely to ignore playbacks of contemporary than older calls of Cassia Crossbills (Porter and Benkman 2019). This should lead to stronger assortative flocking by call (Smith et al. 2012), which is important because crossbills flock year-round and choose mates from within flocks (Newton 1972, Nethersole-Thompson 1975). We should expect therefore that behavioral and total reproductive isolation increase as assortative flocking increases, which is exactly what we have found for types 2 and 5 (Porter and Benkman, in press). Thus, the already high levels of premating reproductive isolation for Cassia Crossbills measured in 2001–2006 may have increased as their calls have diverged further. Importantly, we would not expect to see such striking divergence in calls if call learning was an unreliable inheritance mechanism as suggested by H&P. Instead, these results provide support that sexual imprinting and learning can facilitate assortative mating and speciation, consistent with previous work (Irwin and Price 1999, Grant and Grant 2009, Verzijden et al. 2012, Turbek et al. 2021).

Although call learning and modification have an overwhelmingly positive influence on call divergence (Porter and Benkman 2019), we found that three of 844 birds initially giving Cassia Crossbill calls gave a categorically different call (a call that we categorized as Type 2; we have never found instances of call switching between Cassia Crossbills and Type 5) in a subsequent year (Porter and Benkman 2019). That is, 0.36% of the birds that we initially categorized as Cassia Crossbills changed their calls to that of another species (hereafter call switching). This is a smaller percentage than in an earlier study of many fewer birds over a shorter time period (Keenan and Benkman 2008; 1 of 79 individuals [1.27%]). Moreover, the rarity of call switching in the field is consistent with laboratory studies showing that, although crossbills can modify subtle features of their contact calls, they rarely switch call types (Sewall 2009; H&P cite Groth [1993] as if Groth documented call switching behavior, but he did not). We agree with H&P that phenotypic plasticity for any trait used to categorize species is a problem, and a potentially insurmountable problem for taxonomists if the bar is that every individual must be unquestionably categorized based on phenotypic characters. Nonetheless, our long-term field studies suggest that the vast majority (>99%) of Cassia Crossbills can be reliably identified based on their unique contact calls. The more important question is whether occasional call switching might cause us to underestimate the occurrence of hybridization and most importantly result in the "substantial gene flow" claimed by H&P.

Observed levels of call switching cause us to underestimate the frequency of hybridization only slightly. To estimate by how much, assume that a Cassia Crossbill lives on average 3 years (Benkman and Porter 2020), breeds in each of two years following hatching, and switches its call only after its first time breeding with a heterospecific (Keenan and Benkman 2008). If individuals that changed their calls by their second year of breeding did so to match the calls of a heterospecific mate in the first year and remained paired during the second year (Keenan and Benkman 2008), then this would cause us to misidentify 0.36% of the individuals during their second year of breeding. Thus, over the average individual's breeding lifetime of two years we would misidentify on average 0.18% of the pairs as assortative when in fact they were disassortative. This would act to increase the occurrence of mixed pairs from 0.7% to 0.9%.

“Post-zygotic Reproductive Isolation”

H&P discuss estimates of extrinsic postzygotic reproductive isolation from Snowberg and Benkman (2007). Extrinsic postzygotic isolation is likely to be important given the ecological differences and strong divergent selection between Cassia and Type 2 crossbills (Benkman 2003). Snowberg and Benkman (2007) estimated the expected differences in offspring survival from random matings relative to assortative matings for types 2 and 5; annual survival is an excellent surrogate for fitness in longer lived species such as birds (Crone 2001). We found that offspring from random matings (homotypic matings equally likely as heterotypic matings) had a 12.4% lower expected rate of survival than those from assortative matings. The implication is that the depression in hybrid offspring survival would be double that expected for offspring from random matings (or about 25% lower than offspring from assortative matings). Thus, selection against hybrids is twice as large as H&P suggest. We have no reason to believe that the depression in survival would be less for offspring from Cassia Crossbills mating with Type 2, given that Cassia Crossbills and Type 2 are similarly divergent in bill morphology as are Types 2 and 5. If anything the depression in hybrid fitness should be even greater because Cassia Crossbills differ in other ways such as being sedentary. Such a reduction in hybrid fitness (25%) is considerable because any reduction in hybrid fitness over 10% might by itself eliminate most gene flow (Irwin 2020). Thus, if extrinsic postzygotic isolation is even half as strong as estimated by Snowberg and Benkman (2007), the combination of pre- and postzygotic reproductive isolation would prevent little if any gene flow (Irwin 2020).

H&P claimed that this was “the maximum fitness loss calculated in the Snowberg and Benkman (2007) and Benkman (2003) models.” It was not. It was simply the average expected based on a quantitative genetic model of inheritance and empirical relationships between bill structure and feeding performance, and bill size and estimated relative survival. H&P question this estimate because “it is only a relative estimation of survival (standardized to 1)” but given that we are estimating a percent reduction in survival, a standardized measure of survival is appropriate. It is also what is used to model gene flow in common population genetic models (Wright 1943, Irwin 2020). Although H&P do not provide an explanation for why our estimate of selection against hybrids is necessarily overestimated nor do I understand what H&P envision are “mitigating factors that would make such post-zygotic selection ineffective in isolating populations”, I agree that such analyses would benefit from more direct estimates of hybrid fitness.

“Crossbill genetics”

First paragraph of this section: Not that this matters, but the statement that “Molecular data indicate that all extant populations in the Red Crossbill complex shared a common ancestor about 11,000 years before present” is wrong. The crown age of red/common crossbills is >200,000 years (Brock et al., unpubl. data) and the time of divergence for nearly all extant population-level lineages has not been estimated. In addition, whole genome resequencing of 90 genomes from Cassia, type 2, and type 5 crossbills indicates that the Cassia Crossbill diverged ~16,000 years ago (CI of 4000-25,000 yrs.; Brock et al., unpubl. data); this is longer than we suggested in Parchman et al. (2016).

In the second paragraph of this section, H&P discuss work prior to Parchman et al. (2016) based on either a very short sequence of mtDNA or many fewer genetic markers, and one study (Piertney et al. 2001) that does not include Cassia Crossbills or any North American crossbill. That comparable analyses discriminate between "other avian species" isn't particularly relevant given that they wouldn't discriminate between many recently diverged species (e.g., Turcek et al. 2021).

The following eight paragraphs in H&P pertain mostly to the results in Parchman et al. (2016), which were included in the proposal I originally submitted to recognize the Cassia Crossbill. I stand by the interpretation that the data show that Cassia Crossbills are genetically distinct and monophyletic with little evidence of introgression. The first two of following three paragraphs are general comments concerning H&P's discussion, and the third paragraph below is more specific to the analyses and interpretation in Parchman et al. that H&P contest.

We reiterate that the Cassia Crossbill likely began diverging from Red Crossbills in the very recent past (Parchman et al. 2016). Moreover, there is no evidence in the history of conifers in the region and the biology of crossbills to suggest there was a period of geographic isolation as Cassia Crossbills diverged (Smith and Benkman 2007, Parchman et al. 2016, Benkman and Young 2020). Consequently, genome-wide divergence is expected to be limited if simply because of incomplete lineage sorting (which H&P ignore), even if reproductive isolation was complete. While summary metrics of differentiation and divergence should not be overinterpreted, we find it striking that estimates for both relative (F_{ST}) and absolute (Dxy) genomic differentiation/divergence between Cassia and types 2 and 5 are comparable in magnitude to those found in other rapid radiations driven by strong ecological and/or sexual selection (Cassia vs Type 2/5: $F_{ST} = 0.016/0.019$, Dxy = 0.004, Parchman et al. 2016, Brock et al. unpubl. data; Iberian seedeaters: $F_{ST} = 0.006$, Turbek et al. 2021; Lake Malawi cichlids: Dxy = 0.002, Malinsky et al. 2018; Lake Kivu cichlids: $F_{ST} = 0.04$, Dxy = 0.003, Brock and Wagner in prep.; Lake Saka cichlids: $F_{ST} = 0.012$, Bezault et al. 2011).

Furthermore, it is widely appreciated that F_{ST} is not a useful indicator of gene flow as the most common approach for converting F_{ST} into units of migration (Nm) uses Wright's Island Model (Wright 1931) and consequently makes a number of assumptions unlikely to hold in natural populations (Slatkin 1985, 1987, Whitlock and McCauley 1999, Holsinger and Weir 2009). The value of F_{ST} for most estimators depends strongly on within population or species diversity (Whitlock and McCauley 1999, Holsinger and Weir 2009). Thus, high F_{ST} estimates can reflect large divergence, reduced within population or species diversity variation, or both (e.g., Cruickshank and Hahn 2014). In addition, F_{ST} often varies substantially across the genome, as background selection, recombination rate variation, gene density as well as other components of genomic architecture will influence the 'local' genomic effective population sizes and the rate of lineage sorting and divergence (Cruikshank and Hahn 2014, Stankowski et al. 2019, Matthey-Doret and Whitlock 2019). Indeed, Parchman et al. (2016) did not apply analyses to infer migration or the demographic context of divergence for Cassia Crossbills. In contrast, H&P argue that the small value of F_{ST} "indicates high levels of gene flow and some inter-breeding despite the assumption that there is high reproductive isolation (Smith and Benkman 2007)." We note that Smith and Benkman (2007) did not assume high reproductive isolation as indicated by H&P. Smith and Benkman (2007) measured it.

Three analyses of >18 000 SNPs in Parchman et al. (2016) are consistent with our measures of little contemporary hybridization and gene flow, contra H&P. The principal components analysis (PCA) of genotypic variation reveals that Cassia Crossbills are discrete and widely separated from the different ecotypes of North American red crossbills along the first PC (Fig. 2 in Parchman et al. 2016). These results indicate that Cassia Crossbills are fully identifiable based on clustering patterns in analyses of genotypic data, contra H&P. Such "genotypic clusters" is the type of criterion Mallet (1995) argued delimits sympatric species and indicates that despite occasional hybridization there is little introgression. Otherwise, we should have detected individuals between the well-separated genotypic clusters in the PCA, as has been found when such analyses have been conducted in hybrid zones where hybrids and backcrossed individuals occur (e.g., Mandeville et al. 2015). This would be the case even if elevated divergence across a small fraction of the genome was contributing to variation in principal components. Moreover, these results indicate that few individuals have been misidentified because of call switching (contra that expected based on the assumptions of H&P). Ancestry-based analyses with entropy (a model similar to that of Structure [Pritchard et al. 2000] that accounts for genotype uncertainty in high throughput sequencing data [Gompert et al. 2014, Shastry et al. 2021]) further suggest limited if any evidence for admixture between Cassia Crossbills and the other ecotypes (Fig. 3 in Parchman et al. 2016). Lastly, phylogenetic analyses of the same data indicate that Cassia Crossbills are reciprocally monophyletic with a bootstrap support of 90% (Fig. 1 in Parchman et al. 2016) and recent whole genome resequencing work also strongly supports Cassia Crossbills as monophyletic with respect to types 2 and 5 (Brock et al., unpubl data).

Final comments

H&P state that "Benkman et al. (2009) vacillate a bit in invoking the Biological Species Concept by saying they followed a Biological Species Concept that permits a degree of gene flow." Although we do not know why invoking such a concept implies vacillation, interestingly, Coyne and Orr (2004:33) noted examples where Mayr (1963), whom H&P rely so heavily on, "wavered" between whether or not complete reproductive isolation was necessary. Indeed, with increased application of genomic data at the population and phylogenetic levels, the prevalence of hybridization has become increasingly appreciated across different groups of taxa (e.g., Mallet et al. 2015, Osborne et al. 2016, Taylor and Larson 2019, Bemmels et al. 2021, Linan et al. 2021). Furthermore, H&P seem to insist that specific reproductive isolating barriers (i.e., intrinsic postzygotic isolation) are necessary for speciation to occur (see Rabosky and Matute 2013 for evidence that intrinsic postzygotic isolation is unrelated to speciation rates in birds), whereas most recognize that a diversity of reproductive isolating barriers can reduce gene flow between diverging lineages (Dobzhansky 1937, Coyne and Orr 2004, Kopp et al. 2018, Irwin 2020). Finally, it is obvious that Cassia Crossbills are not representative of the tempo or geographic mode of bird speciation and may have more in common with speciation in many phytophagous insects (Smith and Benkman 2007, Porter and Benkman, in press). Indeed, the requirement that crossbills adhere to the typical model of bird speciation – extended and slow divergence in allopatry, then a gradual increase in sympatry if reproductive isolation and ecological divergence allow (Price 2008, Weir and Price 2011) – and to assume all speciation must meet the same criteria (e.g., initial long periods of allopatry, F_{ST} values > 0.2, divergent mtDNA, intrinsic postzygotic isolation), seemingly underlies many of H&P's problems with accepting the evidence that Cassia Crossbills are a separate reproductively isolated evolutionary lineage.

Submitted by: Craig W. Benkman

Date of Comment: 9 November 2021

Recognize the genus *Ramosomyia* for "*Leucolia*" *viridifrons* (Green-fronted Hummingbird) and "*L.*" *violiceps* (Violet-crowned Hummingbird)

Effect on NACC:

This proposal would replace the generic name *Leucolia*, as interpreted by Stiles et al. (2017), based on Elliot (1879), with *Ramosomyia*. Bruce and Stiles (2021) demonstrated that *Leucolia* was unavailable in the combination designated by Elliot (1879) due to a different, prior type species designation by Gray (1869).

Background:

The revised interpretation was partly influenced by a detailed study of the works of George R. Gray (1808-1872) of the British Museum, particularly his *The Genera of Birds* (1844-1849), by one of us, *cf.* Bruce (in press). The relevant details can be found in Bruce and Stiles (2021).

Bonaparte (1850) proposed the generic name *Leucippus* for a group of species, the first listed being *Trochilus fallax* Bourcier, 1843, which was designated the type species by Gray (1855). The remaining species in *Leucippus* were transferred to other genera according to the genetic data of McGuire et al. (2014) by Stiles *et al.* (2017), leaving *Leucippus* monotypic. *Leucolia* Mulsant & E. Verreaux, in Mulsant et al. (1866: 175) was originally listed with twelve species, the first listed being *fallax*. Gray (1869) subsequently designated *Trochilus fallax* as the type species of *Leucolia*, which he listed as a synonym of *Leucippus.* Elliot (1879) subsequently listed *Leucolia* as a synonym of *Uranomitra* and tentatively suggested *Cyanomyia viridifrons* Elliot, 1871, as its type species.

This was followed by Stiles *et al.* (2017) for the clade including *C. viridifrons*, *C. violiceps* Gould, 1859, and *C. wagneri* (Phillips, 1966). However, the synonymy of *Leucolia* with *Leucippus* was clearly established by Gray (1869; Art. 70.2 of ICZN 1999). A new name was required for this clade, for which we proposed *Ramosomyia* Stiles & Bruce, 2021 (in Bruce & Stiles 2021), with the same type species and included species (*viridifrons, violiceps, wagneri*).

Therefore, the genus-group name *Ramosomyia* Stiles and Bruce, 2021, applies to *Cyanomyia viridifrons* Elliot, 1871, its designated type species, which had been erroneously designated (with a "?") as the type species of *Leucolia* Mulsant & E. Verreaux, 1866, by Elliot (1879).

Recommendation:

We strongly recommend a YES vote for this change of generic name.

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Submitted by: Murray D. Bruce and F. Gary Stiles

Date of Proposal: 3 November 2021

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[1] Publication was anticipated earlier this year but currently is imminent.

[2] This proposal does not affect the currently accepted English names for these species.

Transfer *Myrmeciza zeledoni* (Zeledon's Antbird) to *Hafferia*

Background:

Myrmeciza has long been considered a heterogeneous genus (Isler et al. 2013), but a revision was only recently published. Following production of a comprehensive time-calibrated phylogeny of the Thamnophilidae (Bravo et al. 2012), Isler et al. (2013) analyzed the available morphological and vocal data in the context of the phylogeny and recommended transferring most species then placed in *Myrmeciza* to 11 other genera. In 2020, following SACC, we approved the transfer of NACC species *M. exsul* to *Poliocrania* and *M. laemosticta* to *Sipia*. However, SACC's decision on NACC species *M. zeledoni* and two closely related extralimital species, *M. fortis* and *M. immaculata*, was unclear: they transferred these species to *Hafferia,* but the votes seemed to indicate more support for a transfer to an expanded *Percnostola*. This issue was reconsidered in SACC Proposals 884 and 884x (see https://www.museum.lsu.edu/~Remsen/SACCprop884.htm).

New Information:

Bravo et al. (2012) concluded that species traditionally placed in *Myrmeciza* in fact form eight clades that, except for Clades G and H (which may or may not be sisters), are not sister to clades consisting of other *Myrmeciza* species (see Figure 1 on the next page). The subject of this proposal, *M. zeledoni*, belongs to Clade H.

Clades G and H are sister taxa in the phylogeny, but this node is very weakly supported. Likewise, the nodes delineating the successive sister taxa to Clade G + H, which are *Percnostola* Cabanis and Heine 1860 and *Pyriglena* Cabanis 1847, are weakly supported. A reasonably well-supported node (bootstrap support >70%) is reached only by adding the sister to G + H + *Percnostola* + *Pyriglena*, which is *Gymnocichla* Sclater 1858. Various methods of dealing with this circumstance were proposed in the SACC proposal, including (1) transferring all species in the larger clade, including *Gymnocichla*, to *Pyriglena*; (2) transferring all species of *Myrmeciza* in G + H to *Percnostola*; and (3) placing all species in Clade G in *Akletos* Dunajewski 1948 and all species in Clade H in the new genus *Hafferia* Isler et al. 2013. Isler et al. (2013) recommended the latter (see Figure 2 below), and their second choice was the second alternative above (the *Percnostola* option). They favored separate genera for G and H primarily because of the morphological dissimilarity of species in G and H relative to species of *Percnostola*. However, *Akletos* nor *Hafferia* are much younger than the other genera recognized by Isler et al. (2013), and neither is diagnosable morphologically, whereas an expanded *Percnostola* is diagnosable relative to *Pyriglena* and *Gymnocichla* (Donegan 2012).

More recently, Harvey et al. (2020) sequenced UCE data for almost all species of suboscine birds, including all species relevant to this issue. In their tree (Figure 3), *Hafferia* is sister to *Percnostola* whereas *Akletos* is sister to *Gymnocichla*. According to the Harvey et al. (2020) phylogeny, option 2 above (transferring all species in G + H to *Percnostola*) would create a paraphyletic *Percnostola*, so this option is not recommended. Thus, the options are to transfer all species of *Gymnocichla*, *Hafferia*, *Akletos*, and *Percnostola* to *Pyriglena* (option 1 above) or

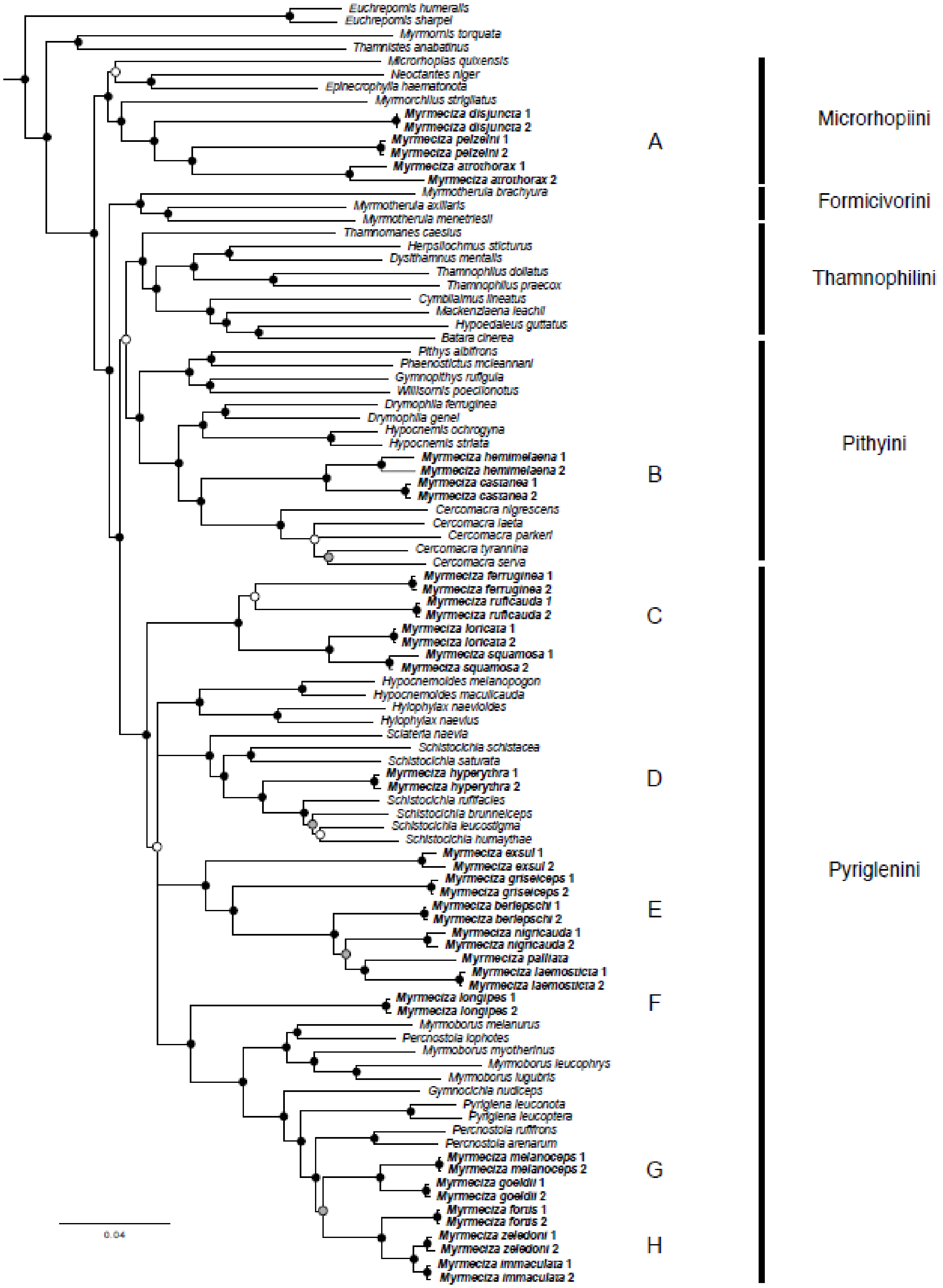

Figure 1. Maximum likelihood tree showing paraphyly of *Myrmeciza*, from Isler et al. (2013), based on Bravo (2012). Circles at nodes represent bootstrap support: > 70% (black), 50-70% (gray), < 50% (white).

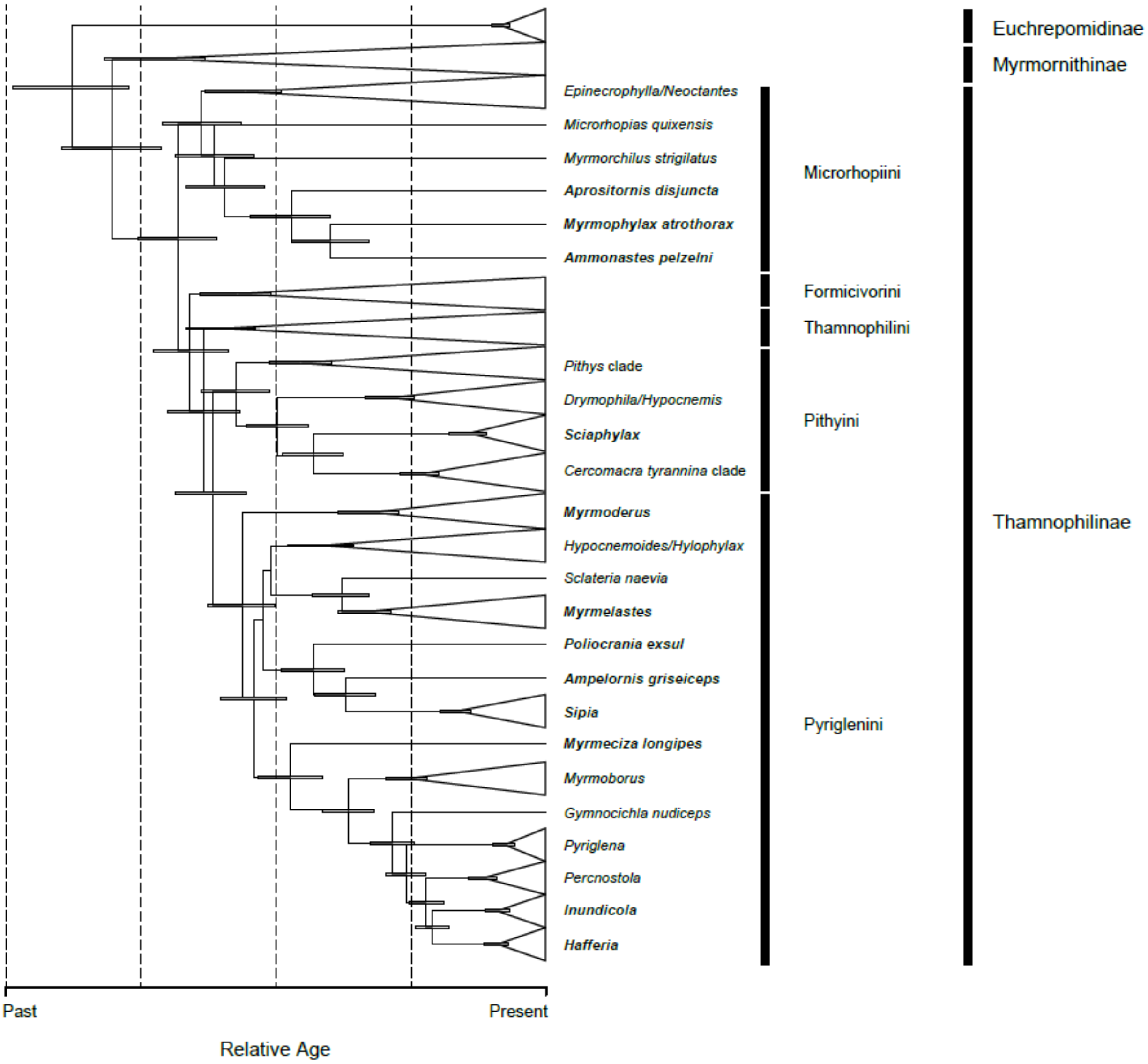

Figure 2. Time-calibrated tree showing recommended taxonomy for former members of *Myrmeciza*, slightly modified from Isler et al. (2013).

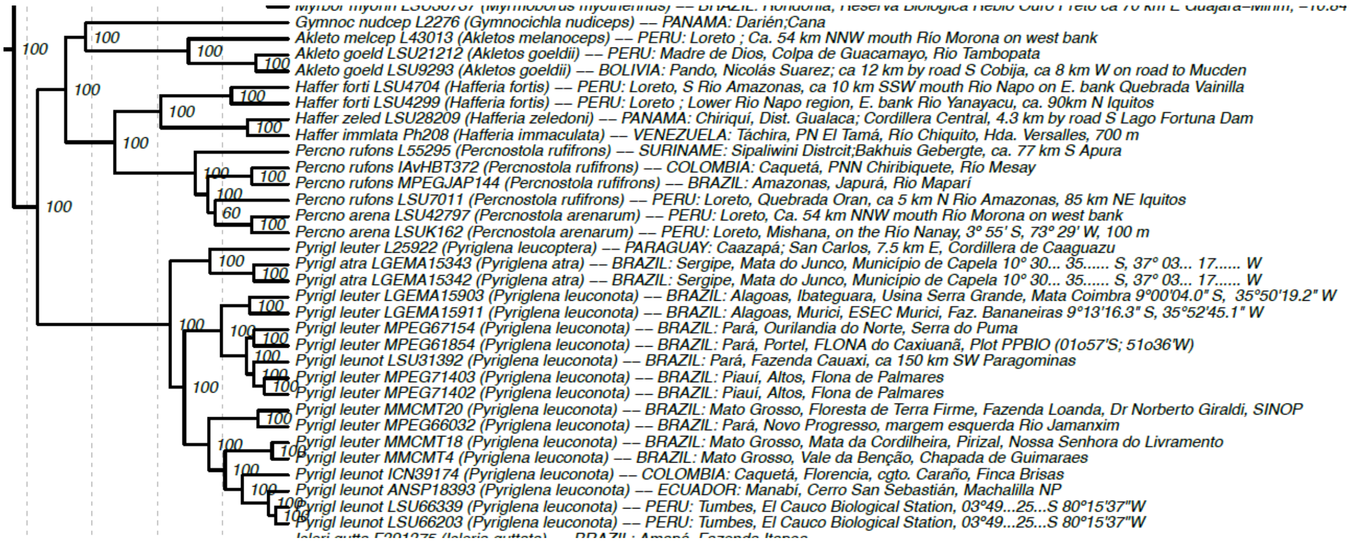

Figure 3. Relevant section of the UCE-based phylogeny of Harvey et al. (2020), showing the sister relationship of *Hafferia* and *Percnostola*.

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to recognize *Akletos* for all species in clade G (these species are extralimital to the NACC region) and *Hafferia* for all species in clade H, including *M. zeledoni* and two extralimital species (option 3 above).

Recommendation:

I recommend that we follow SACC and transfer *M. zeledoni* to *Hafferia*. SACC's vote on Proposal 884x was unanimous in favor of retaining *Hafferia* and *Akletos* (option 3) rather than transferring species in these genera to an expanded *Percnostola* (option 2). Although option 1 (transfer of *Hafferia*, *Akletos*, *Gymnocichla*, and *Percnostola* to *Pyriglena*) was not formally considered in Proposal 884x and some SACC members expressed support for this option in addition to option 3 in their comments on Proposal 884, Kevin Zimmer's comments make a good case that an expanded *Pyriglena* would be an excessively heterogeneous genus in terms of morphology and vocalizations.

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Submitted by: Terry Chesser

Date of Proposal: 30 November 2021

Votes and Comments from SACC on Proposal 884x:

Comments from Jaramillo: “NO. I am hesitant to create these large genera that are heterogenous. There is likely a better intermediate option, but until that idea is brought forward, the above is my vote. Also I am taking into account the notes given by Bravo in the associated proposal.”

Comments from Stiles: “NO, in anticipation of future events/proposal(s).”

Comments from Lane: “NO. Given Gustavo Bravo's comments and the need for a new proposal if we include *Gymnocichla*, I will change my vote to NO. In any event, the branch nodes may be deep enough that these clades are too old to consider congeneric?”

Comments from Claramunt: NO. *Hafferia* and *Akletos* should not be merged into *Percnostola* given the position of *Gymnocichla*.”

Comments from Pacheco: “NO. In view of Gustavo's comments, in the previous proposal, I understand that a highly heterogeneous genus is not the best arrangement for now. It is opportune to change my vote to no.”

Comments from Zimmer: “NO. Based upon the publication of the new data set by Harvey et al. 2020, and the additional comments by Gustavo Bravo, I change my vote on this to NO. I was willing to live with this change before we knew that the resulting grouping would be paraphyletic with respect to *Gymnocichla*, and that we would have to fold all three genera into *Gymnocichla*, which has priority. I’ve never been a fan of overly heterogeneous genera, and this proposed one (expanded *Percnostola*) was already verging on borderline for my taste without rolling them all into *Gymnocichla*. I would consider that move a bridge too far. I would prefer to keep all 4 genera separate until such time as conflicting new data comes along.”

Comments from Robbins: “NO, for reasons stated in the proposal.”

Votes and Comments from SACC on Proposal 884:

Comments from Stiles: “Especially after rereading Donegan's piece and noting the depth of the nodes in question, I agree that option 3 (uniting *Akletos* and *Hafferia* under *Percnostola*) is the best option.”

Comments from Areta: “YES. I think that merging all in *Percnostola* is a good option. In my original vote, I also mentioned that putting all in *Pyriglena* is also appealing to me, based on plumage and vocalizations. Both options satisfy me.”

Comments from Claramunt: "YES. I think it makes sense to merge these three genera. In particular, *Hafferia* and *Akletos* species are very similar and would fit in the same genus comfortably. The two *Percnostola* (sensu stricto) species are somewhat different but overall, I favor an expanded *Percnostola* over an atomized classification with 3 genera and very few species in each."

Comments from Robbins: "YES to merging *Hafferia* and *Akletos* into *Percnostola*, and I agree with Nacho, I would be fine with placing all three of these in *Pyriglena*."

Comments from Zimmer: "YES. As Isler et al. made clear in Proposal #682G, this option would at least ensure that paraphyly is avoided. Donegan's points regarding the lack of diagnosable characters distinguishing *Percnostola*, *Hafferia*, and *Akletos* are well taken – eye color goes out the window when you consider the gray-eyed minor subspecies of *P. rufifrons*, and most of the other characters are even less consistent or impressive – the three genera, as currently constituted, are probably better regarded as representing three different superspecies. And, if we could live with the *Schistocichla* group being considered part of *Percnostola* (as we did for a long time), we should certainly be able to welcome *Hafferia* and *Akletos* into the fold. However, unlike some others on the committee, I would balk at extending this logic toward the end of folding these three genera + *Gymnocichla* into an expanded *Pyriglena*. It would be defensible on genetic grounds, but looking for the most inclusive and most heterogeneous monophyletic group possible is antithetical to my concept of what a genus should be. None of the species currently included in *Percnostola*, *Hafferia* or *Akletos* approaches the complexity of the vocal repertoire found in any of the species of *Pyriglena*, all of which have equally complex social structures centered related to their habitual ant-following habits. And, although an approach to *Pyriglena* can be seen as regards group congregation over ants, vocal complexity, and stereotypical tail movements within both *Gymnocichla* and *immaculata* + *zeledoni*, each of these three taxa (not to mention *fortis, melanoceps* and *goeldii*) has obvious morphological distinctions that would make them outliers with respect to *Pyriglena*. *Pyriglena*, as currently constituted, is very homogeneous with respect to morphometrics, eye color, presence, and prominence of interscapular patches, male plumage, voice (across multiple different types of calls as well as loudsongs), social structure, and overall ecology. The various species differ most obviously in the female plumage, and even there, all of the various taxa are more similar to one another than any of them are to females of *nudiceps, fortis, melanoceps, goeldii, immaculata, zeledoni, rufifrons*, or *arenarum*."

Comments from Lane: "YES. Since we are still not yet 'settled' in a relatively final taxonomy of the Thamnophilidae after what has been nearly Earth-shaking change, why not make last tweaks before it is set and dried? Just by going over vocalizations, I hear enough similarity between members of *Percnostola* (sensu stricto) and *Akletos* to see that these two are quite similar. *Hafferia* is a bit more distinct, but the bulk and shape of its members are similar enough to *Akletos* that it doesn't result in a particularly heterogeneous assemblage... and I appreciate having to memorize fewer generic names!"

Comments from Jaramillo: "YES – The differences seem marginal between these three taxa; it makes sense to lump them under *Percnostola*. But to retain *Pyriglena* as separate."

Comments from Pacheco: “YES. It seems that lumping *Percnostola*, *Hafferia* or *Akletos* in a single genus as a good solution.”

Comments from Remsen: “NO. The just-published phylogeny by Harvey et al. (2020 Science) indicates that *Gymnocichla* is part of this group thus forcing us to reconsider.”

Additional comments from Robbins: “NO. I agree that the proposal should be modified (or create a new one) to include the new molecular data.”

Comments from Gustavo Bravo: "I read carefully this proposal to expand *Percnostola* to include *Hafferia* and *Akletos* and I decided to contribute my two cents. I'd like to start by highlighting that I still favor the treatment that Mort Isler, Robb, and I put forward in 2013, whereby those genera are best treated separately. The problem with the proposed treatment – *Percnostola* + *Hafferia* + *Akletos* in an expanded *Percnostola* – is that different types of loci and different types of analyses yield different topologies, likely suggesting that our available data and phylogenetic tools are not capturing fully the historical complexity at the base of that clade. In Harvey, Bravo et al (2020), we basically conducted two kinds of analyses – concatenation vs coalescence – and they produced conflicting results using the same data in this part of the phylogeny. These two methodological frameworks have fundamental differences in their assumptions and how they treat data (not dwelling into those details here), and such differences must not be taken lightly if we are aiming at having a stable classification that reflects evolutionary history to the best of our capacities. I personally think that coalescent-based analyses are more robust – which by the way do not conflict with this proposal – but given the incongruence, I think that we need further analyses with a more restricted sampling aiming at resolving the base of this clade. I know that this requires extra efforts causing delays in taxonomic decisions, but that is simply how things go: The more data, the more heterogeneous and conflicting signals.

“Finally, I'd like to send a cautionary note regarding similar cases in our suboscine analyses. In Harvey, Bravo et al (2020) we chose to use the concatenation-based tree for downstream analyses and to go in Figure 1 due to its more stable structure toward the base of the tree and the way it behaved with samples with high proportions of missing data, such as toe-pads. However, it doesn't necessarily mean that it is the "true" phylogeny– whatever that means – or even better than the coalescent-based tree. Hence, whenever conflicts appear, taxonomic decisions must not be made solely based on a single tree. I am aware of many more cases like *Percnostola's* across suboscines. and my advice is to move forward with caution when dealing with them. As I mentioned above, ideally, I'd like to see analyses targeted at those specific taxa before making taxonomic decisions, and that's the way I am moving forward in producing a taxonomic classification of the Thamnophilidae."

Treat *Chondrohierax wilsonii* (Cuban Kite) as a separate species from *C. uncinatus* (Hook-billed Kite)

Description of the problem:

Chondrohierax uncinatus is a widespread polytypic raptor found from central Mexico to Argentina, with 3 subspecies currently recognized (Clements 2021). The nominate subspecies is widespread throughout the continental parts of its range. The two other widely recognized subspecies are *mirus* from the island of Grenada, and *wilsonii* from Cuba. Friedmann (1934) described, as subspecies, the populations from northern and central Mexico (somewhat darker; "*aquilonis*") and the western Amazon (larger bill and broader rectrices; "*immanis*"), but neither are generally recognized. There is a confusing array of plumage variation within all taxa, including strong sexual dimorphism, distinct juvenile plumages, and a dark/melanistic morph in both adults and juveniles. There is also a white-bellied morph, at least in juveniles, that bears a strong resemblance to comparable plumages of some Forest-Falcons (*Micrastur*). Additionally, there is lots of individual variation, especially in bill size, with especially large-billed individuals originally described as a separate species ("*megarhynchus*"), now a synonym of *uncinatus* (Friedmann 1934, Hellmayr and Conover 1949).

Morphological differences among the three taxa were well described by Friedmann (1934, 1950), which are summarized here. In his key to *Chondrohierax*, Friedmann (1950) gives the main difference between *wilsonii* and the rest of the taxa as: "upper mandible pale yellowish white, inclining to bluish horn at base; feathers of upperparts with concealed white bars on their bases". Friedmann (1950) also mentions the solidly tawny nuchal collar of female *uncinatus* in contrast to the "white or pale buff [nuchal collar], barred with russet or chestnut" of female *wilsonii* (males have no nuchal collar), plus narrower barring below on *wilsonii*. Friedmann's other mainland subspecies ("*aquilonis*" and "*immanis*") are largely separated based on the shade/darkness of the overall coloration (i.e., minor differences), so although there is considerable individual variation, there are few geographic differences among continental populations. The mostly solid-yellow bill and barred vs. solid nuchal collar seem to be the most consistent characters separating *wilsonii*. The rationale used by BirdLife for splitting *wilsonii* included the smaller size and larger bill, so below I have pasted the measurements (of adult males) from Friedmann (1950) for *uncinatus*, *mirus*, and *wilsonii*:

uncinatus (n=26): wing 265-301 (285.8); tail 173-210 (191.1); culmen from the cere, 27.0-35.5 (31.3), one 42.0; tarsus 32.0-37.0 (35.1); middle toe, without claw, 28.0-35.0 (31.1 mm.).
mirus (n=3): wing 250-265 (257); tail 165-182 (172.7); culmen from base of cere, 28-32 (30); tarsus 30-38 (34.5); middle toe, without claw, 25 mm.
wilsonii (n=2): wing 240-244; tail 177-178; culmen from cere, 35.5-37.5; tarsus, 29-30; middle toe without claw, 26-27 mm.

These size differences seem minor to me, and given that bill size especially is known to vary drastically among individuals within *uncinatus*, I don't think these are reliable species-level characters. The wing length does appear to be significantly shorter in *wilsonii*, however.

Taxon *wilsonii* was described as a species by Cassin (1847), and considered as such by most authors (e.g., Peters 1931, Friedmann 1934, 1950, Bond 1940) until it was lumped with *uncinatus* by Amadon (1960). Amadon (1960) cited considerable individual variation in bill size in *uncinatus* (Hellmayr and Conover's justification for lumping *megarhynchus* with *uncinatus*) to suggest that the difference in bill size between *wilsonii* and the *uncinatus* was insufficient for species status. Friedmann (1934) also listed the concealed white barring on the back as a character for separating *wilsonii*, but Amadon (1960) noted that this can be shown by immature plumages of *uncinatus*. Amadon (1960) also suggested that the mostly pale maxilla of *wilsonii* may not be a species-level character, as *uncinatus* shows a pale mandible and that this pale coloration can extend onto the maxilla. However, this pale coloration on the maxilla of *uncinatus* is largely restricted to the lower part of the cere. Therefore, Amadon's primary justification for lumping *wilsonii* was that differences in bill size and in the hidden white bases to the dorsal feathers were shown by other taxa of *Chondrohierax*, and that bill coloration alone was insufficient to split *wilsonii*. (Many thanks to Frederik Brammer for tracking down the Amadon paper.)

Later authors (e.g. AOU 1983, Howard and Moore 1991, Clements 2007, Clements et al. 2021) consistently treated *wilsonii* as a subspecies of *uncinatus* (following Amadon 1960), until BirdLife International, using the Tobias yardstick criteria, elevated *wilsonii* to species status with the following rationale: "Until recently was considered conspecific with *C. uncinatus*, but trend now widespread to accept species status: differs on account of all-yellow bill (3); larger bill (at least 1); barred collar (2); smaller overall size (at least 1). Molecular evidence has been interpreted as supporting this split (Johnson et al. 2007)." Note, however, that the bill lengths of *wilsonii* and *uncinatus* overlap (see measurements above). The IOC list split them based on morphological differences and modest mtDNA divergence.

New information:

Very little. Results from a genetic study (Johnson et al. 2007) were the basis for NACC proposal 2007-B-4 to split *wilsonii* from *uncinatus*, which did not pass (votes were 5-4 in favor, falling short of the 2/3 needed for acceptance): (https://americanornithology.org/wp-content/uploads/2020/02/2007-B.pdf and comments https://americanornithology.org/nacc/current-prior-proposals/2007-proposals/comments-2007-b/). As far as I can tell there has been no additional work on the genus that is relevant to taxonomy. No recordings of the taxon are known, nor is the voice described in any texts that I can find. A single in-life photo of the bird has been published but is of too poor quality to be relevant for this proposal (page 23): https://www.aba.org/themencode-pdf-viewer/?file=https://www.aba.org/birding_archive_files/v42n1p22.pdf#zoom=page-fit

The taxon is critically endangered, or possibly extinct, with very few sightings in recent years, despite focused surveys (Gallardo and Thorstrom 2019, BirdLife International 2021). It may now be restricted to a remnant population in the mountains of the far east of the island (Gallardo and Thorstrom 2019). Its declines are attributed to loss of habitat, loss of its main prey item (snails), and persecution due to the mistaken belief that it hunts game birds. This doesn't have any bearing on the taxonomy, but the lack of data makes a decision on species status difficult. Thankfully, there is a small series of specimens, which combined with the detailed descriptions of Friedmann (1934, 1950; see above) can help with the decision. I do suggest that the committee read the (short) 2007 proposal and comments linked to above.

Jacob Saucier has been gracious enough to photograph some of the series of specimens housed at the USNM, and Marco Rego photographed a single specimen housed at the LSUMZ, which are pasted below. These include photos of *wilsonii*, *uncinatus*, and *mirus*, although the USNM specimen of female *wilsonii* is unfortunately rather faded. In all photos, note the pale bill and narrower but more extensive barring below of *wilsonii* in comparison to *uncinatus*/*mirus*. The LSUMZ *wilsonii* specimen is labeled as a male, but the brown dorsum, narrow tail bars, and barred nuchal collar all suggest it is a female (or perhaps a subadult male). The USNM male *wilsonii* has an unbarred nuchal collar and is grayer above. In looking at these photos, it appears that both sexes of *mirus* show an unbarred tawny nuchal collar, whereas this character is only found in females of *uncinatus*. The specimens of *wilsonii* that show a nuchal collar do have this area barred rather than unbarred tawny, although the coloration of this region in the female USNM specimen is too faded to assess the original color.

USNM males: *wilsonii* left, *uncinatus* right.

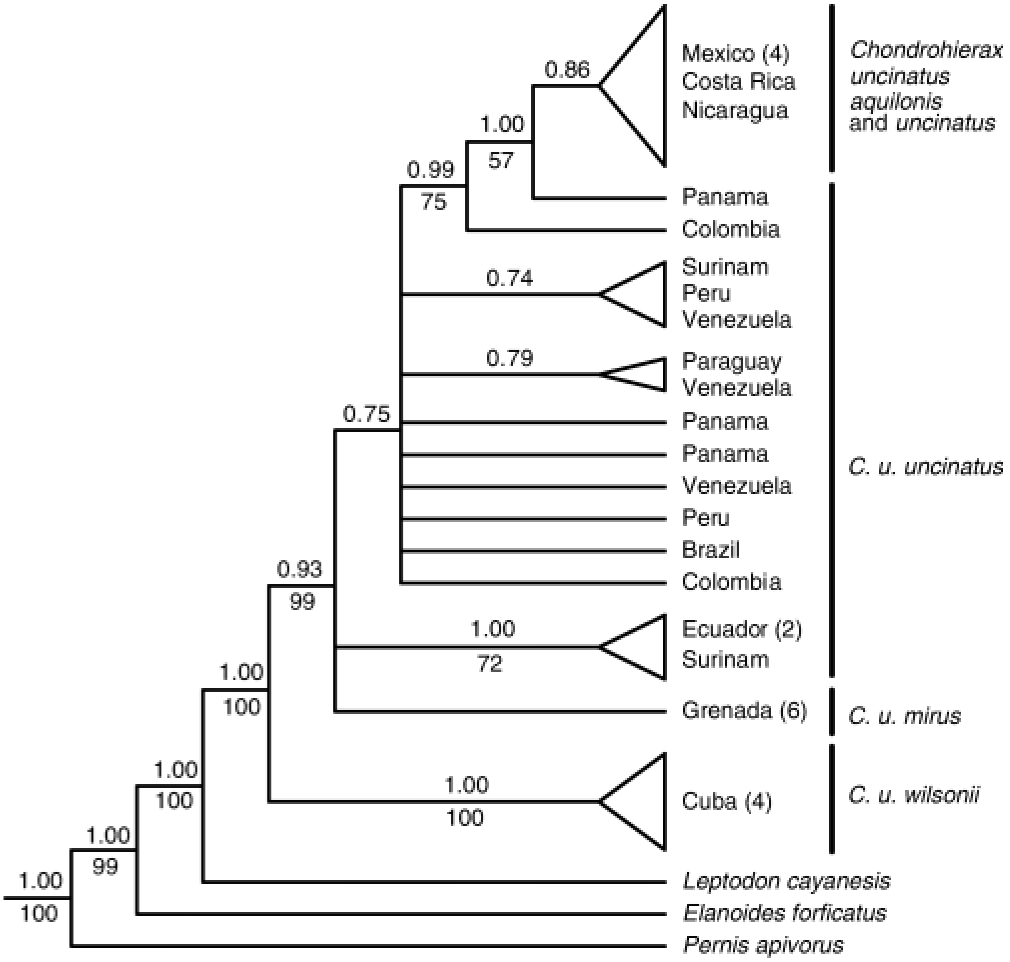
LSUMZ specimens: *wilsonii* on left (labeled as male, possibly a female or subadult male), female *uncinatus* on right.

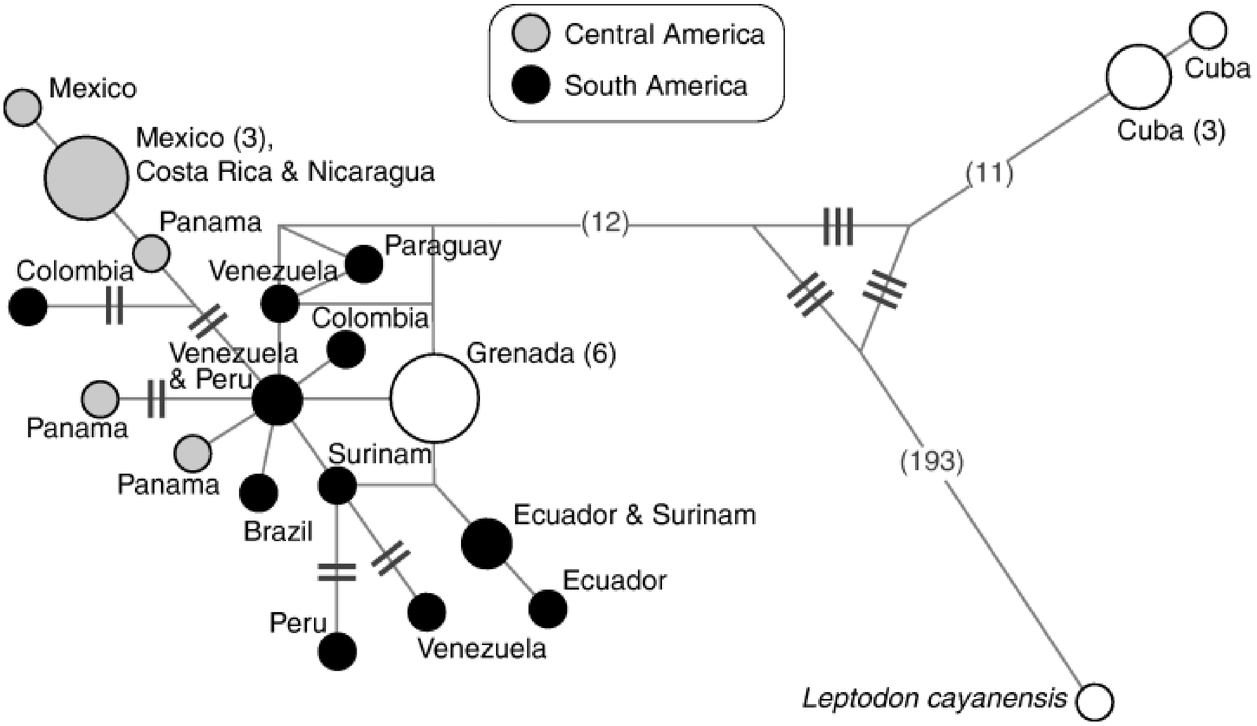
USNM females: *wilsonii* on left, *uncinatus* on right.

USNM specimens: two male *uncinatus* (darker bird from Mexico, typical male from Colombia) on left, typical female *uncinatus* on right.

USNM specimens: male *mirus* on left, female *mirus* on right.

Although the results from Johnson et al. (2007) have been voted on by the committee previously, I have pasted the main results below for reference. That study used two mitochondrial genes, cyt-b and ND2 (so all the standard gene tree/species tree caveats apply), but did find that *wilsonii* was sister to the remainder of *Chondrohierax* and 1.8-2.0% divergent, with a divergence time estimate of 400,000-1.25 million years. The Grenada taxon *mirus* was largely undifferentiated from continental populations (nominate *uncinatus*). The phylogeny and the haplotype network are included below. Node support values in the phylogeny are from maximum parsimony (above branches) and Bayesian (below branches) analyses. Unfortunately, Johnson et al. (2007) estimated migration rates between North and South American populations of *uncinatus*, but not between *uncinatus* and either of the insular taxa. However, those migration rates within *uncinatus* were close to zero (albeit with broad confidence intervals), perhaps suggesting that there is low connectivity even within continental populations.





Effect on AOS-CLC area:

Splitting *wilsonii* from *uncinatus* would result in one additional species for the AOS area.

Recommendation:

The genetic differences between *wilsonii* and *uncinatus*/*mirus* are rather borderline regarding species status, especially given that it's only two mitochondrial genes, so in my opinion are not very informative either way. The morphological differences do seem quite pronounced for a raptor, however. The combination of the solid yellow bill of *wilsonii* and differences in the pattern of the nuchal collar and width and extent of the barring below, all give *wilsonii* quite a different appearance. Plus, there is rather little geographic variation within the remainder of *Chondrohierax*, making *wilsonii* the morphological outlier within the genus. I recommend a **YES** on splitting *wilsonii* and *uncinatus*.

The English name of Hook-billed Kite could stay with *uncinatus*, given that *wilsonii* is a peripheral isolate. The name Cuban Kite is appropriate for *wilsonii*.

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

Date of proposal: 9 December 2021

Treat *Accipiter chionogaster* (White-breasted Hawk) as a separate species from *A. striatus* (Sharp-shinned Hawk)

Background:

Sharp-shinned Hawk (*Accipiter striatus*) is a widespread small raptor found throughout North America, Central America, the Caribbean, and parts of South America. There are 10 subspecies recognized by most authorities, which are usually divided into 3 main "groups." 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 3 groups, with northern "*striatus*," white-breasted "*chionogaster*," and rufous-thighed *"erythronemius*." Of the four main global checklists, the IOC Checklist currently recognizes four species in the Sharp-shinned Hawk species complex, including *Accipiter striatus*, *A. chionogaster, A. ventralis,* and *A. erythronemius* (Gill et al. 2021), where they follow the treatment of Ferguson-Lees and Christie (2005). The other checklists treat the complex as a single species.

New Information:

There is very little "new" information to shed light on this complex. In comparing *chionogaster* to the "northern" group, the main difference is in plumage of adults, with *chionogaster* having clean white underparts with some light buff on the tibial feathers, compared to the rich rufous to orange barring on the underparts of northern birds. Central American *chionogaster* tends to also be darker above, being described as "sooty to fuscous black" compared to "gray to grayish blue" (Bildstein et al. 2020). The juvenile plumage of *chionogaster* has similarly pale underparts, and is very lightly streaked below compared to northern subspecies (Storer 1952).

Although *chionogaster* is significantly different in terms of plumage compared to the widespread and migratory *velox* subspecies of North America, subspecies *suttoni* and *madrensis* of Mexico (mountains of Chihuahua, Sonora, south to Veracruz; and Sierra Madre del Sur in Guerrero and Oaxaca, respectively) are intermediate between *velox* and *chionogaster*. As such, the underparts of *suttoni* are paler than those of *velox*, and *madrensis* is paler than *suttoni*. This geographic pattern could suggest that *chionogaster* is just the pale extreme of a cline (Storer 1952, Bildstein et al. 2020). Although the distribution of *chionogaster* is separated from *madrensis* by the Isthmus of Tehuantepec, an important biogeographic barrier, Storer (1952) suggested that the paleness of *madrensis* could be the result of introgression from *chionogaster*, which influenced his decision to consider *chionogaster* conspecific with *striatus*.

Subspecies *chionogaster* is extremely similar to northern birds in terms of size. Dickey and van Rossem (1938) reported the only difference between *chionogaster* and northern *velox*, which is sympatric with *chionogaster* during the winter, as the slightly longer bill and longer middle toe of *chionogaster* (Jenner 2010); northern *velox* and *chionogaster* overlap in measures of wing length and tail length (Storer 1952). In a supertree generated by Mindell et al. (2018), *chionogaster* was sister to nominate *striatus*, with very short branch lengths. However, only three subspecies were sampled in this tree. In a recent study by Catanach et al. (2021), UCEs were used to study the systematics of Sharp-shinned Hawks, with a focus on Caribbean taxa. In this study, which included representatives of *chionogaster*, *velox* (widespread North American subspecies), *ventralis* (mountains from Venezuela to Bolivia), and *erythronemius*, *chionogaster* was found to be sister with strong support to *velox*, with these two sister to *ventralis*. These three subspecies were in turn sister to the clade of Caribbean taxa (Catanach et al. 2021). However, since the focus of this study was on the Caribbean taxa, additional work is needed to further clarify the relationships of the taxa from North America, Central America, and South America, especially to address the potential for gene flow between these phenotypically variable and geographically widespread groups.

In a study of *chionogaster*, Jenner (2010) described various aspects of life history of this subspecies, including its breeding biology, molt patterns, and descriptions of vocalizations. The post-juvenile molt (preformative molt of Howell et al. 2003) of *chionogaster* in Honduras and El Salvador was completed in most individuals before the breeding season in their second calendar, meaning that birds acquired adult plumage before their first breeding season in their second calendar year; this same molt in northern Sharp-shinned Hawks begins near the start of the breeding season in their second calendar year (Bildstein et al. 2020). The early progression of molt in *chionogaster* perhaps contributed to the higher proportion of first-year breeding compared to other taxa (Jenner 2010). The courtship display of *chionogaster* was described as similar to that of other species of *Accipiter*, though some birds would rock back and forth in the air such that the white underparts seemed to be prominently displayed. If prominently displaying the white underparts is an important aspect of the courtship display, it could represent a potential pre-mating barrier (Jenner 2010). Courtship began in October, and the breeding season lasted for about 9 months in Honduras and El Salvador; importantly, courtship and pair formation at these two locations occurs before most northern migrant Sharp-shinned Hawks (*velox* subspecies) arrived in the area, suggesting that there is a form of temporal isolation between these two groups (Jenner 2010).

Recommendation:

The Sharp-shinned Hawk complex is extremely variable in terms of plumage and is widely distributed in North and South America. As others have recognized, these very distinctive taxa may represent distinct species (e.g., Sibley and Monroe 1990, Bierregaard 1994, Ferguson-Lees and Christie 2005, Gill et al. 2021). Differences in timing of molt, potential differences in courtship displays, and the timing of breeding of *chionogaster* relative to northern migrant *velox* could all represent important species-level differences. However, to date, there are no phylogeographic, population-level studies of genetic diversity within mainland taxa of the Sharp-shinned Hawk complex, which could shed important light on the status of not only *chionogaster*, but also the South American taxa. The pattern of progressively paler taxa through Mexico south to *chionogaster* is especially intriguing, and genetic data will help to resolve the relationships among these groups.

This is a borderline case, and I do think *chionogaster* likely represents a good biological species; however, I am recommending that *chionogaster* be maintained as a subspecies of

Sharp-shinned Hawk for the time being, until more data can help to further elucidate the status of this taxon.

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

Date of Proposal: 13 December 2021

Reconsider treatment of Barn Owl subspecies *Tyto alba insularis* and *T. a. nigrescens,* with a note on the distribution of *T. glaucops* (Ashy-faced Owl)

Background:

Current AOS taxonomy recognizes the Barn Owl (*Tyto alba*) as one cosmopolitan species with 28 to 32 subspecies (AOU 1998, Marti et al. 2005). The number of species and subspecies in this lineage is controversial, and there remain many outstanding questions, such as whether to follow authors who recognize three species: Common or Western Barn Owl *T. alba*, American Barn Owl *T. furcata*, and Australian or Eastern Barn Owl *T. delicatula* or *T. javanica*; see Gill et al. (2021) and NACC proposal 2018-C-13, SACC proposal 908, and references therein. In addition, a move to elevate *Tyto furcata* of Cuba, the Cayman Islands and Jamaica to species status would lead to the treatment of *T. alba* from continental North and South America and the Bahamas, Hispaniola, and Puerto Rico as *T. tuidara* (Suárez and Olson 2020).

For the purposes of this proposal, we defer consideration of multiple splits in the Barn Owl and instead focus on two issues concerning the Caribbean subspecies *T. a. insularis* of the southern Lesser Antilles and *T. a. nigrescens* of Dominica: (1) whether *T. insularis* should be recognized as a valid species with subspecies *T. i. insularis* and *T. i. nigrescens*; and (2) whether these taxa are best retained as subspecies, either within *T. alba* or *T. glaucops*. We also comment on the distribution of *T. glaucops* based on fossil evidence.

Hartert (1913) classified all West Indian taxa (plus others globally) as subspecies of *T. alba*, whereas Ridgway (1914) adopted a classification that elevated *T. glaucops* of Hispaniola, *T. insularis* of the Lesser Antilles, and *T. bargei* of Curacao, as well as *T. punctatissima* of the Galapagos, to species rank. Hartert (1929) once again treated those populations and others as subspecies of *T. alba* – a treatment followed by Peters (1940) that became the prevalent taxonomy for decades. The species-level distinctiveness of *T. glaucops* on Hispaniola became apparent after the continental form *T. a. pratincola* became established around 1950, resulting in sympatry of the two forms (AOU 1998, Wiley 2010, Suárez and Olson 2020). Elevation of *T. glaucops* to species status led some to question treatment of the equally distinctive form *insularis* of the Lesser Antilles, which was retained as a subspecies of *T. alba* (AOU 1983, 1998 and supplements; Sibley & Monroe 1990; Raffaele *et al*. 1998). Bruce (1999) recognized this anomaly and compromised by treating *T. insularis* as a subspecies of *T. glaucops*, and this treatment was retained by del Hoyo & Collar (2014) and subsequent updates (HBW and BirdLife International 2021). However, no other influential treatments place *insularis* and *nigrescens* as subspecies of *T. glaucops.*

Summary of the subspecific or specific treatments of *insularis* and *nigrescens*:

	Subspecies of:		
Reference	***Tyto alba***	***Tyto glaucops***	***Tyto insularis***
Ridgway 1914			x
Hartert 1913, 1929	x		
Peters 1940	x		

Sibley & Monroe 1990	x		
AOU 1998	x		
Raffaele et al. 1998	x		
Bruce 1999		x	
Keith et al. 2003	x		
König & Weick 2008			x
Dickinson & Remsen 2013	x		
del Hoyo & Collar 2014		x	
Suarez & Olson 2020			x
Gill et al. 2021	Subspecies of *T. furcata*		
Clements 2021	x		

New Information:

Suárez and Olson (2020) conducted a systematic review of the taxonomy and distribution of barn owls of the West Indies using modern and fossil museum specimens (skins and skeletons, distribution of taxa illustrated below). They compared measurements of "*T. i. insularis*" and "*T. i. nigrescens*" with *T. tuidara pratincola* (=*T. alba pratincola* of AOS), *T. furcata* (= *T. a. furcata* of AOS), and *T. glaucops* which showed *insularis/nigrescens* to be much smaller than the other West Indian taxa (see Table below with morphological measurements). Additional measurements of pelvic and pectoral elements are given in Tables 2 and 3 of their paper. They also noted that the skull of *insularis* is similar to that of *T. glaucops* but "without the well-developed, pointed supraorbital processes and with the palatines not tapered and narrowed posteriorly." These data were based on 25 specimens of *insularis* and 7 specimens of *nigrescens.* Suárez and Olson (2020) concluded that *T. insularis* should be treated as a separate species with two subspecies (*T. i. insularis* of the southern Lesser Antilles and *T. i. nigrescens* of Dominica) that show slight but consistent differences in plumage coloration; unfortunately, both were labeled *insularis* in their map.

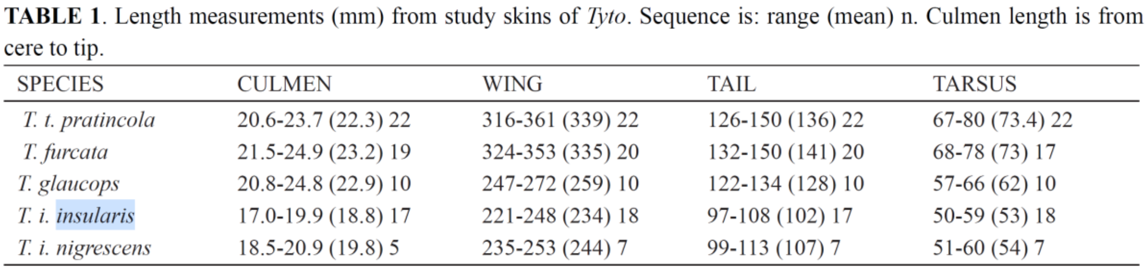

TABLE 1. Length measurements (mm) from study skins of *Tyto*. Sequence is: range (mean) n. Culmen length is from cere to tip.

SPECIES	CULMEN	WING	TAIL	TARSUS
T. t. pratincola	20.6-23.7 (22.3) 22	316-361 (339) 22	126-150 (136) 22	67-80 (73.4) 22
T. furcata	21.5-24.9 (23.2) 19	324-353 (335) 20	132-150 (141) 20	68-78 (73) 17
T. glaucops	20.8-24.8 (22.9) 10	247-272 (259) 10	122-134 (128) 10	57-66 (62) 10
T. i. insularis	17.0-19.9 (18.8) 17	221-248 (234) 18	97-108 (102) 17	50-59 (53) 18
T. i. nigrescens	18.5-20.9 (19.8) 5	235-253 (244) 7	99-113 (107) 7	51-60 (54) 7

There are no other published data to help evaluate this issue. A molecular phylogenetic study of barn owls by Aliabadian et al. (2016) had limited sampling that did not include representatives of *insularis, nigrescens,* or *T. glaucops.* In a separate molecular study, Uva et al. (2018) sampled *T. glaucops* but lacked samples of *insularis* or *nigrescens* from the Lesser Antilles. However, potentially relevant is the fact that *T. glaucops* was sister to *T. alba punctatissima* from the Galapagos, another small and relatively dark-plumaged taxon. Xeno-canto does not have any

FIGURE 1. Map of the West Indies showing the distribution of living and fossil small species of barn owls. *Tyto tuidara* is represented by the subspecies *T. t. pratincola*, **new combination**, and *Tyto insularis* by two subspecies in the Lesser Antilles: *T. i. insularis* (St. Vincent, Grenada and the Grenadines) and *T. i. insularis* (Dominica). *Tyto* sp. (fossil) from Barbuda is not indicated.

Barn Owl recordings from the West Indies, and Macaulay Library only has four recordings of *insularis* from Grenada and St. Vincent and the Grenadines, and none of *nigrescens* from Dominica*.* A quantitative vocal analysis of barn owls is lacking, and the available recordings of *insularis* and *nigrescens* are insufficient for a vocal analysis. Thus, our decision regarding species limits in these taxa would have to be based on plumage, size, and osteological evidence. We note that, in addition to recognizing *T. tuidara*, *T. insularis*, *T. glaucops*, and *T. furcata* from the Caribbean, Suarez and Olson (2020) also implicitly recognize *T. bargei* of Curacao and *T. punctatissima* of the Galapagos as species, as well as multiple additional extinct species of small and giant barn owls from the West Indies (Suarez and Olson 2015).

Additional note on the distribution of *T. glaucops*

T. glaucops is currently endemic to Hispaniola (AOU 1998). However, Suárez and Olson (2020) examined fossil material of the extinct taxon "*T. cavatica*" from Puerto Rico and reported that "all of the newer fossil material from Puerto Rico falls exactly in the range of *T. glaucops* [with regard to size]" and they "could detect no differences whatsoever between these two populations." They therefore concluded that "*T. cavatica*" is a junior synonym of *T. glaucops.*

Recommendation:

Arguments in favor of elevating *insularis*/*nigrescens* to species status (= *T. insularis*) are that (1) *insularis/nigrescens* and *glaucops* are similarly divergent from mainland American *T. alba* in plumage, (2) *insularis* is noticeably different in size from mainland American *T. alba*, (3) the initial lump of *insularis/nigrescens* (as well as *glaucops* and *punctatissima*) with *T. alba* does not appear to have been justified by Hartert (1913, 1929) or Peters (1940), and (4) *glaucops* is reproductively isolated from sympatric continental birds, suggesting that the same may be true if *insularis/nigrescens* co-occurred with continental barn owls. Thus, multiple lines of morphological/phenotypic evidence (darker plumage like *glaucops*, osteological differences [and similarities to *glaucops*], strikingly smaller size), combined with the analogous case of *glaucops* and continental birds occurring in sympatry without interbreeding, could be taken as evidence for resplitting *insularis/nigrescens* from *T. alba* – akin to the recent splits of *Melanitta fusca/deglandi/stejnegeri* and *Sarkidiornis melanotos/sylvicola* (this latter split seemingly based on some plumage differences and an unfounded rationale for lumping them in the first place). Pam and Max recommend this option.

On the other hand, an argument could be made for retaining *insularis/nigrescens* as subspecies pending genetic/genomic and ideally a quantitative vocal analysis. Furthermore, one could argue that it is premature to adopt the proposed split of *T. insularis* in light of the complexity of issues in barn owls as a whole. Carla recommends this option. If the NACC chooses not to elevate *insularis* to species, then we recommend retaining *insularis* and *nigrescens* as subspecies of *T. alba* pending evidence to support their treatment under *T. glaucops*.

With regard to the distribution of *T. glaucops*, we recommend adding Puerto Rico to the distribution of *T. glaucops* based on the fossil data.

Please vote on each of the following subproposals:

A. Recognize *T. insularis* as a species with subspecies *insularis* and *nigrescens*

B. If *insularis* and *nigrescens* are not treated as separate species, then treat them as subspecies of *T. glaucops*, transferring them from *T. alba*

C. Revise the distribution statement of *T. glaucops to* "Resident in Hispaniola. Fossil evidence suggests that it also formerly occurred in Puerto Rico (Suárez and Olson 2020)."

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Submitted by: Carla Cicero, Pam Rasmussen, and Max Kirsch

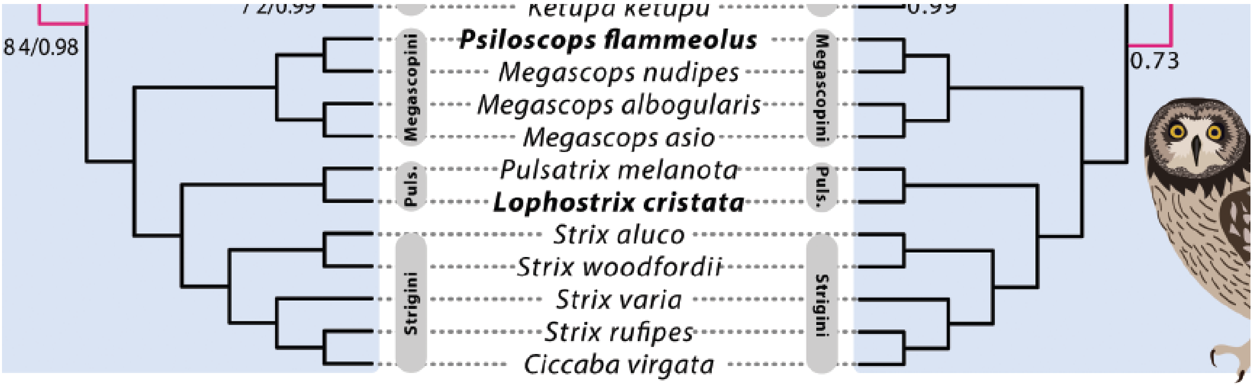
Date of Proposal: 16 December 2021

Merge *Ciccaba* into *Strix*

Background:

As Van has indicated in SACC notes (Remsen et al. 2021, footnote 15a) under *Ciccaba virgata*, many authors over the past few decades have merged *Ciccaba* into *Strix*. However, as Van noted, there has not been concrete data to make this merger even though morphological data supporting recognition of *Ciccaba* has been weak at best (Peters 1938).

Recent molecular data demonstrate that *Ciccaba virgata* is deeply embedded within *Strix* (Salter et al. 2020); below is the relevant part of their Fig. 2, which is based on UCE data. ML and Bayesian analyses are to the left, SVDquartets analysis to the right, and all unlabeled nodes received 100% support.



Although the designation of the type of *Ciccaba* is somewhat convoluted and confusing (Peters 1938), *C. huhula* is the type. Unfortunately, *huhula* was not included in the Salter et al. study. Nonetheless, given the plumage similarity among *Ciccaba*, and has been recognized for a long time, vocalizations (song and calls) among the four species that are currently in *Ciccaba* are very similar (e.g., compare *huhula* with *virgata*). Moreover, vocalizations of those four taxa are also similar to taxa that SACC recognizes as *Strix*, e.g., *S. rufipes*.

Recommendation:

Given the above I recommend that *Ciccaba* finally be officially merged into *Strix*.

Literature Cited:

Peters, J. L. 1938. Systematic position of the genus *Ciccaba* Wagler. Auk 55:179-186.

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Submitted by: Mark Robbins

Date of Proposal: August 2021 (SACC proposal), slightly modified for NACC 7 January 2022

SACC comments:

Comments from Remsen: "YES. Genetic data confirm what has long been suspected, and this merger is mandated by those data."

Comments from Lane: "Reluctantly, YES. I do like the nice, tidy group of *Ciccaba*, but I suppose one can't argue with the phylogenetic placement."

Comments from Stiles: "YES to merging *Ciccaba* under *Strix*; the morphological evidence is strong, and finally there is good genetic evidence as well for congeneric treatment."

Comments from Areta: "YES. Not so much due to the genetic data in Salter et al. (2020), but rather because support for *Ciccaba* as a separate genus is weak and vocalizations of these owls suggest a close affinity."

Comments from Pacheco: "YES. Recent genetic data provide objective data for the subordination of this group in *Strix*."

Comments from Claramunt: "YES."

Treat *Saltator coerulescens* (Grayish Saltator) as three species

Note: This is a makeover of two proposals passed by SACC. The original SACC proposal to split them was written by Boesman, and a follow-up SACC proposal on English names was written by Beck. In this proposal, Remsen combines the two original proposals and tweaks the proposal for NACC.

Effect on NACC list:

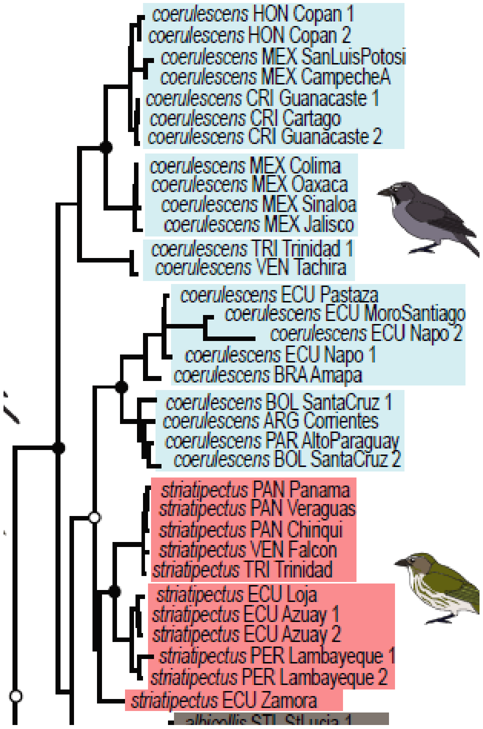
Saltator coerulescens would be split into three species, two of which occur in the NACC area.

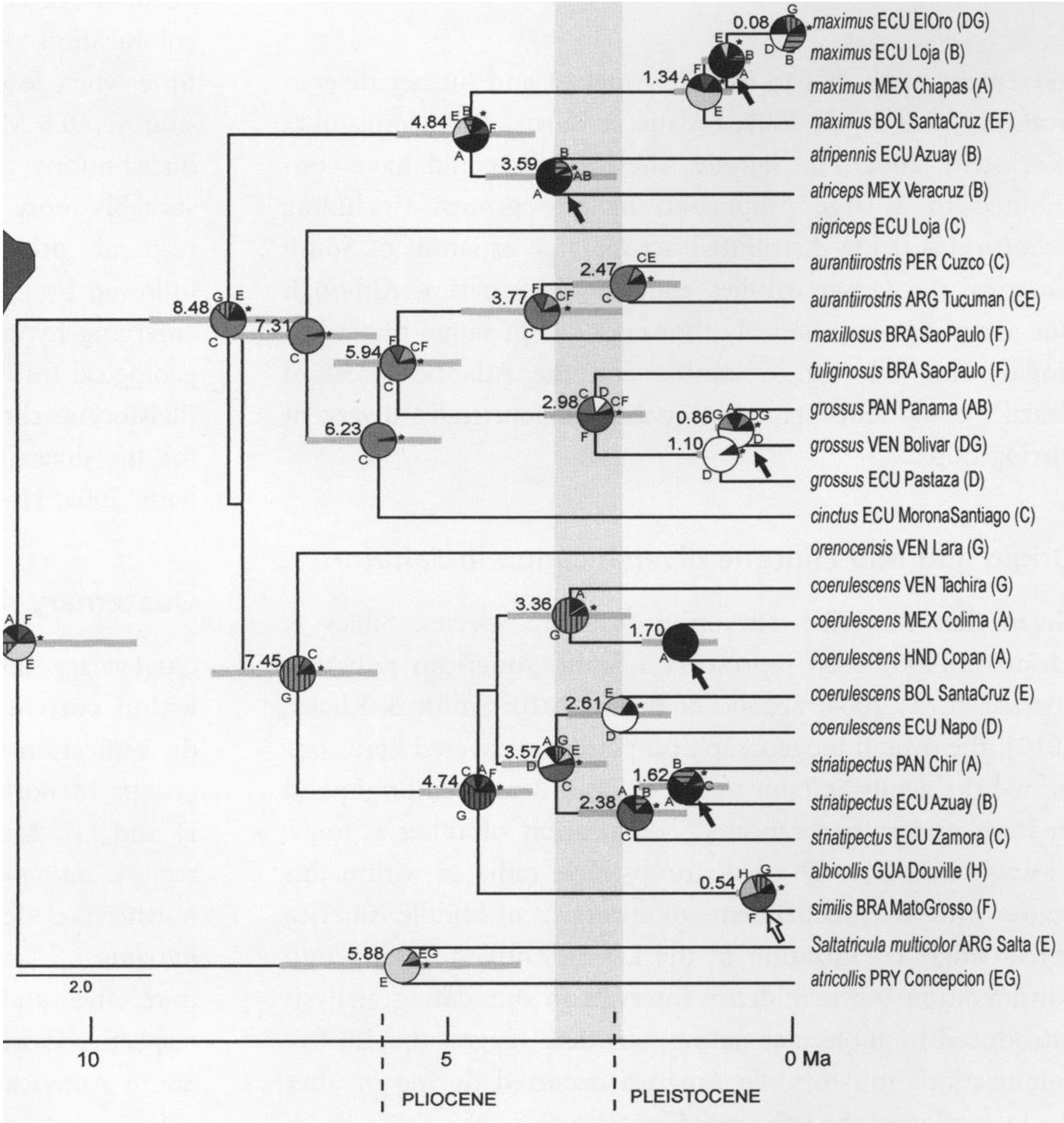
Background:

Paynter (1970) treated *Saltator coerulescens* (with 13 subspecies) as a single species ranging from Mexico to Uruguay. In his Venezuela guide, Hilty (2003) included a taxonomic note indicating that the Middle American *grandis* subspecies group may be a separate species from the nominate South American *Saltator coerulescens* group (a return to the classification of W. Deppe 1830). Hilty (2003) also mentioned that vocal differences within South America may indicate additional species. Similar suggestions were also made elsewhere (Ridgely & Tudor 2009, del Hoyo et al. 2011). In the absence of any further study, all modern taxonomies, however, continued to treat Grayish Saltator as a single species (until recently).

New information:

Genetic data: Chaves et al. (2013) presented a phylogeny of the genus *Saltator*. All presently recognized species were found to be monophyletic with the exception of *S. coerulescens*:





The Amazonian group (*coerulescens* group) was found sister to Streaked Saltator *S. striatipectus* (making the present broadly defined *S. coerulescens* paraphyletic), whereas the Middle American *grandis* group was sister to the Caribbean group of northern South America (the *olivascens* group). Divergence times were estimated to be >3 million years in both cases.

Chaves et al. (2013) pointed out that taxonomically grouping the streaked vs non-streaked taxa is in fact contradictory to his genetic findings, and recommended additional research to better understand this apparent anomaly (while putting forward as a possible hypothesis that parallel evolution leading twice to a streaked plumage may be explained by paedomorphism).

Vocal data: Boesman (2016) made a brief vocal analysis (without having learnt about the findings of Chaves et al.) and found three clear vocal groups:

- The northern (or Middle American) group (including *vigorsii, plumbiceps, grandis, yucatanensis, hesperis* and *brevicaudus*)
- The Caribbean group (including *plumbeus, brewsteri* and *olivascens*)
- The Southern (or Amazonian) group (including *azarae, mutus, superciliaris* and *coerulescens*)

The Caribbean group differs from both other groups by the lack of long, slurred notes, lack of a second song type, slower pace of stuttered song, etc. (The fact that this group lacks a whistled song is possibly an evolutionary adaptation to differ from the largely sympatric Streaked Saltator *S. striatipectus*). The Amazonian group differs from the Northern group based on a stuttered song with repeated notes (# of repeats) and a whistled song with fewer notes and upslurred ending.

These findings are very much congruent with Chaves' findings of three groups (also including the fact that the Amazonian group seems vocally closer to *S. striaticeps*).

Morphological data: del Hoyo & Collar (2016) analyzed morphological differences and concluded these were small. The northern group typically has a longer white eyebrow and more rufous-brown belly, and the Caribbean group has a more whitish central belly.

Discussion:

Although in the past two allopatric species have been suggested, it would seem that in fact three clear groups are involved (a split of Middle American vs. South American taxa would not amend paraphyly nor accommodate vocal differences, and thus despite earlier suggestions is not recommendable).

The Middle American group is allopatric, but the case of the two South American groups is more intriguing. These seem to meet both along the lower east slopes of the east Andes, and north of the Amazon delta. In both regions they are likely parapatric, but this requires further study (a situation identical to, e.g., *C. cyanoides* vs. *C. rothschildii* along the Andes, where exact boundaries and possible interaction also still need to be determined). In both contact zones, there seems to be a clear-cut (and identical) change in voice, which eliminates the possibility of some type of 'ring species' based on voice.

Since the Boesman (2016) analysis, a few additional sound recordings have been deposited online from the contact zones, further confirming the sharp vocal transition along the Andes: ML59164651 is just north of the rio Meta (at a distance of ca. 30km from XC327455!), is of the 'Caribbean group' and further indicates parapatry. (No new recordings are available from the eastern contact zone).

Learned songs in oscine passerines call for some caution, but it should be noted that in the genus *Saltator*, several other clear-cut cases are based on vocal differences between related species pairs (and confirmed by genetics) for which prior classifications based on morphology were not always in accordance (e.g., *S. nigriceps* vs. *S. aurantiirostris*; Boesman 2016b).

Genetically, calculated time of divergence of the three groups was comparable to those between the widely accepted species pairs *S. grossus* vs *S. fuliginosus, S. atripennis* vs *S* *atriceps*, and *S. aurantiirostris vs. S. maxillosus* (all pairwise sister species). A weakness is that the Caribbean group was only analyzed by two (admittedly widely separated) samples and that Bayesian PP<0.75.

Ideally, to make this case more robust, besides more extensive genetic sampling, playback experiments could be added (although, e.g., playing the whistled song of Amazonian group to Caribbean group is in fact about the same as playing song of the sympatric Streaked Saltator, with predictable result).

Furthermore, study of the situation in the contact zones of the two South American groups would allow for a better assessment of interactions between these groups. The fact that such potential contact exists (twice) without any indication of clinal variation, on the other hand, is a strong argument absent when dealing with allopatric populations.

It would thus seem that the following viable taxonomic options exist:

- Retain the present treatment while awaiting more research, accepting paraphyly and highly divergent vocal groups within a single species
- Split the southern group, thus creating two monophyletic groups, but still having a (northern/Caribbean) species with two very distinct vocal groups
- Split into three species, all monophyletic and with distinct voice

Proposal:

A. Split *S. coerulescens* into two monophyletic species: *S. grandis* (including also *vigorsii, plumbiceps, yucatanensis, hesperis, brevicaudus, plumbeus, brewsteri* and *olivascens)* and Amazonian *S. coerulescens* (including also *azarae, mutus* and *superciliaris)*
B. If A is accepted, split *S. grandis* into two species: Middle American *S. grandis* (including also *vigorsii, plumbiceps, yucatanensis, hesperis, brevicaudus)* and Caribbean *S. olivascens* (including also *plumbeus* and *brewsteri*)

Recommendation:

SACC approved both A (7 to 3) and B (8 to 2). See the extensive comments pro and con on the issues at the SACC proposal page: https://www.museum.lsu.edu/~Remsen/SACCprop879.htm. We recommend following SACC.

English names:

The original set of English names in SACC 879 was voted down, and a new proposal (https://www.museum.lsu.edu/~Remsen/SACCprop913.htm), after several iterations, was finally passed. If anyone thinks AOS doesn't pay close attention to English names, just direct them to SACC 879 and 913; we even checked the color cinnamon against Ridgway's color swatches to make sure that was correct. The final choices were approved by fairly strong voting in a ranked-choice voting scheme that including two "guest members" (Marshall Iliff and Don Roberson):

S. grandis: Cinnamon-belled Saltator
S. olivascens: Olive-gray Saltator
S. coerulescens: Bluish-gray Saltator (extra-limital to NACC)

We recommend endorsing this slate of names (if only to avoid further machinations).

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Submitted by: Peter Boesman, Josh Beck, and Van Remsen

Date of Proposal: 8 January 2022

Recognize *Haematopus bachmani* (Black Oystercatcher) as a subspecies of *H. ater* (Blackish Oystercatcher)

Note from the Chair: This proposal is being considered concurrently by SACC. In addition to the external comment at the end of this proposal, other, sometimes extensive, comments on vocalizations and other aspects of this issue are available in the SACC votes at https://www.museum.lsu.edu/~Remsen/SACCprop931.htm.

Effect on NACC (and SACC):

This would lump the Black Oystercatcher (*Haematopus bachmani*) of Pacific-coast North America with the Blackish Oystercatcher (*H. ater*) of South America, considering the former as a subspecies of the latter.

Background:

We are revisiting this species limits issue in association with the effort to harmonize world lists, and treating *H. bachmani* as a separate species is a point of disagreement.

Oystercatcher taxonomy has been an ongoing challenge because members of the family are morphologically quite conservative. The two general plumage types, black and pied, tend to correspond to rocky versus soft shoreline specialization, respectively (Jehl 1985, Hockey 1996).

H. bachmani has been recognized as a species by the *Check-list* in every edition since the first. The ranges of *H. bachmani* and *H. ater* are entirely allopatric, so the most appropriate way to determine species limits in this case is to infer them using the classic yardstick comparative method (although it has been applied infrequently and not with the depth one might hope for today; Murphy 1925, del Hoyo and Collar 2014). Both taxa occur in sympatry with the more widespread *H. palliatus* (American Oystercatcher), and both hybridize with this pied form (*ater* and *bachmani* are of course of the black plumage type, as their English names indicate; Jehl 1985, Hockey 1996).

The taxonomic notes provided in the 6th and 7th editions (AOU 1983, 1998) mentioned that some authors had considered *H. bachmani* and *H. palliatus* (American Oystercatcher) to be conspecific; they have a hybrid zone of ~480 km in width in Baja California (Jehl 1985). It is not apparent whether the relationship between *bachmani* and *ater* has been evaluated by NACC before.

Murphy (1925:13-15) elaborated on the differences and similarities between *ater* and *bachmani* thus: For *bachmani*: “Juvenal birds closely resemble the young of *H. ater*, the feathers of the upper surface, breast, and flanks being edged with pale tawny brown. It is interesting that the down of chicks of this species is much darker than that of *H. ater* or of any other American form.” And for *ater*: “Superficially resembling *H. bachmani*, *H. ater* is widely separated from all other oyster-catchers in the form of the bill, the excessive compression of which approaches that of *Rynchops*. The distinctive character of the bill is apparent even in chicks taken from the egg. Color differences between *H. ater* and *H. bachmani* are much greater among downy young than among adults. The young of *ater* are relatively pale, only slightly darker, indeed, than those of *H. palliatus*, which they much resemble. The white area is confined to the breast, instead of covering the belly and flanks as in *palliatus*, but it is far more extensive than in *bachmani*."

As Jehl (1985) remarked, although AOU (1983) and Murphy (1925) recognized *H. bachmani* and *palliatus* as separate species, most other authors did not at that time. For example, *H. bachmani* and *H. palliatus* have been considered conspecific by Peters (1934), Friedmann et al. (1950), and Mayr and Short (1970)—all of these considered *bachmani* and *palliatus* as subspecies of *H. ostralegus*, the Eurasian Oystercatcher. This situation has changed, however, and most authorities now recognize *palliatus* and *bachmani* as separate species (checking via Avibase; https://avibase.bsc-eoc.org). Jehl's (1985) work appears to have been effective on this issue.

Peters (1934), while lumping both *palliatus* and *bachmani* in *ostralegus*, considered *H. ater* to be a separate species. Although this work does not provide any reasoning behind its taxonomic decisions (long a sore point), this could have been based on Murphy (1925) or been simply inertia; as Hockey (1996) related, in the genus in general allopatric black forms have been considered species, whereas pied forms are often considered subspecies.

In his study of the hybrid zone between *bachmani* and *palliatus*, Jehl (1985) found assortative mating, a stable (though 480-km wide) hybrid zone (after late-19th and early-20th c. disruption), and inferred selection against hybrids, leading him to conclude that the two are valid species. He surmised that the primary mechanism of reproductive isolation was likely postzygotic, focusing especially on predation on chicks of mixed pairs in which some would have plumage coloration inappropriate for their beach color, i.e., through loss of crypsis. Given the high rates of chick predation in some species (60-85%; Hockey 1996), this seems plausible.

H. ater also hybridizes with *H. palliatus*, in Argentina (Jehl 1978). Jehl (1978) described a single hybrid specimen between *ater* and *leucopodus* (the Magellanic Oystercatcher, also a pied form) that he took in Santa Cruz Province, Argentina. This latter hybridization event (*ater-leucopodus*) is uncommon compared to *ater-palliatus* crossings, which he noted occur in this area of overlap "with appreciable frequency" (Jehl 1978:346). Both the *bachmani-palliatus* and *ater-palliatus* hybrid zones should be revisited with population genetics studies to determine the degrees of introgression (given clearly incomplete isolating mechanisms), but I do not know whether such work is occurring.

New Information

There is remarkably little modern work available on *Haematopus* systematics or species limits. This is an area ripe for study.

Using mtDNA (COI) barcoding, Hebert et al. (2004) found that the difference between *H. palliatus* and *H. bachmani* was remarkably low compared with other North American bird species-level differences, and they considered that this was consistent with treating them as a single species.

Senfeld et al. (2020) also examined mtDNA (2835 bp) and found *palliatus*, *ater*, and *bachmani* to be very closely related, with *bachmani* perhaps being sister to the other two. This clade is quite distinct from *H. leucopodus*, the Magellanic Oystercatcher, another pied form as noted above.

del Hoyo and Collar (2014) lumped *bachmani* and *ater*, stating that "Race [sic] *bachmani* has normally been considered a separate species, but the two are almost identical in plumage and voice, apparently differing only in greater depth of bill of nominate *ater*. Two subspecies recognized." (p. 420). (It is worth contrasting this brief emphasis of similarities with Murphy's [1925] emphases on differences quoted above.)

Careful analysis of vocalizations is needed. Subjectively, listening to some of the recordings on xeno-canto (https://xeno-canto.org) reminds me of the mtDNA relationships: *bachmani*, *ater*, and *palliatus* are similar; *leucopodus* is different. It is perhaps no accident that these similarities and differences are reflected in the rates of hybridization where the taxa overlap. Future work is also needed to rigorously quantify morphological similarities and differences. Murphy's (1925) evaluations show some disagreement with del Hoyo and Collar's (2014) conclusions.

With neither appreciable song nor plumage differences between *ater* and *bachmani*, neither assortative mating nor the putative postzygotic isolating mechanism of strong plumage color selection favored by Jehl (1985) would likely be very effective in preventing substantial hybridization (especially given considerable levels of crossing of both with *palliatus*). I realize that such conjectures are rather unsatisfactory, but that is one of the acknowledged weaknesses of the biological species concept when asking whether allopatric forms are "different enough" to warrant recognition as full species.

Two broader issues have some relevance when evaluating this and other cases in which allopatry and the Tobias et al. (2010) criteria are in play. Although many do not like the Tobias et al. (2010) criteria, the accumulation of subsequent, independent case studies indicate that the initial use of these criteria has proven much more often right than wrong in determining species limits (Tobias et al. 2021; although see Rheindt and Ng 2021 who came to a different conclusion using a different approach). In addition, across Aves we are likely over-splitting allopatric taxa at the species level (see Hudson and Price 2014). These are generalities, probably both true. That said, each case should be rigorously examined.

Taxonomy and nomenclature:

H. ater (Vieillot and Oudart 1825; *Galerie Oiseaux*, II, p. 88, I, P1. ccxxx) has priority over *H. bachmani* (Audubon 1838; *Birds of America*, folio edit., IV, P1. ccccxxvII, fig. 1). See Murphy (1925) for discussion of the history of *ater* and its priority for that taxon. Thus, if this proposal is approved, *H. bachmani* would become *H. ater bachmani*. Murphy's (1925) study of the two supports considering *bachmani* a valid subspecies if lumped with *ater*.

Recommendation:

Based on current evidence, particularly the strikingly different phenotypes of both *bachmani* and *ater* from *palliatus* and the noteworthy levels of hybridization with that pied form, these taxa should be considered a single biological species with two allopatric subspecies-level populations. I find especially compelling that the strikingly different phenotypes of *bachmani* and *palliatus* appear to be barely limiting hybridization in a region of overlap to a level that only some authorities (us included) consider to be low enough to be full biological species. Given the remarkably close mtDNA relationships among *palliatus*, *bachmani*, and *ater*, it seems likely that the phenotypic similarities between the latter allopatric pair (including vocalizations) would be insufficient to preclude more extensive hybridization if the two were to come into contact.

The vote is in two parts.

A. Recognize *H. bachmani* as a subspecies of *H. ater*.
If A is approved, then B: Apply the English name Blackish Oystercatcher to both taxa

(as HBW-BirdLife already does).

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Submitted by: Kevin Winker

Date of Proposal: 14 January 2022

External Comment on Proposal 2022-B-9

Notes on the vocalizations of Black Oystercatcher *Haematopus bachmani* and Blackish Oystercatcher *Haematopus ater*

I compared the sonograms of the *Haematopus* species, and most look very much the same. Only in some cases of largely sympatric breeding areas of two species of the genus, there seems to be some clear vocal differentiation, e.g.

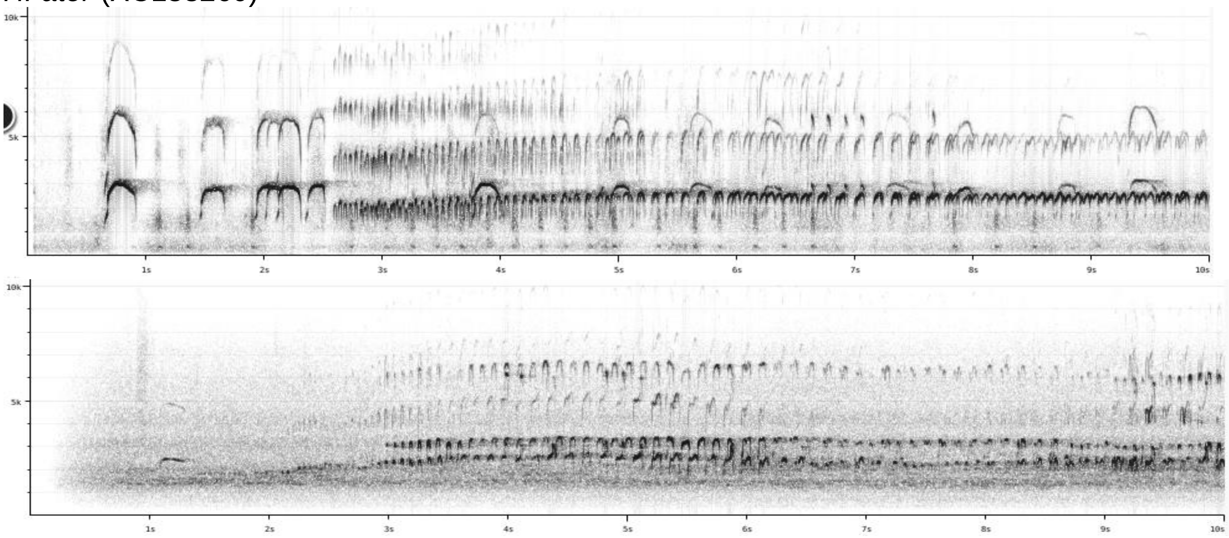
Haematopus ater vs. *H. leucopodus*: the latter has mainly high-pitched squeaky notes in its vocabulary

Haematopus finschi vs. *H. unicolor*: the latter has some more nasal notes in its vocabulary

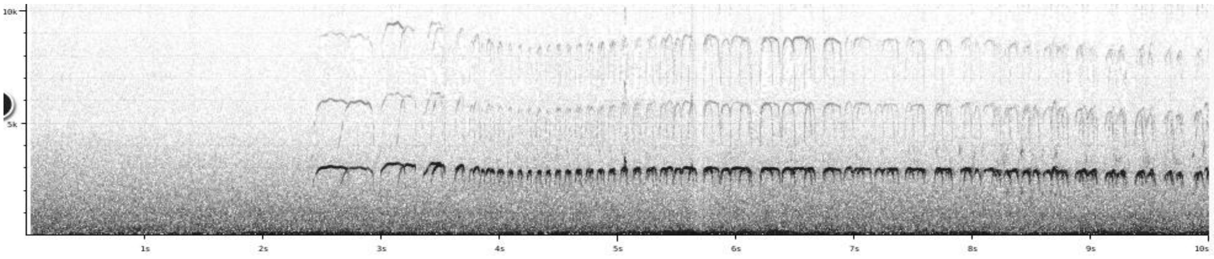
In the specific case of *Haematopus ater* and *H. bachmani* I think however <u>I have found one difference</u>! In the former the long piping trill typically uttered during display or interaction apparently always starts at the lowest frequency after which it rises in pitch for a while to remain stable afterwards. In the latter it typically starts at a high pitch after which it drops and rises a bit to remain stable afterwards.

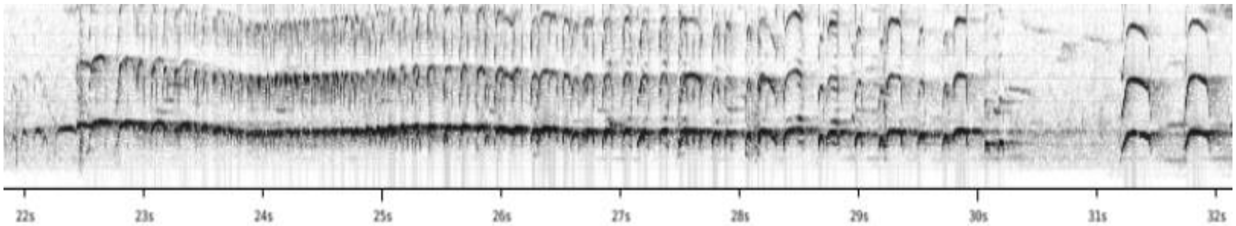
Example:

H. ater (XC188260)



H. bachmani





There aren't that many recordings in which the full series is recorded from the very start, however:

H. ater

XC: 4 recordings, all have initial rise

ML: 2 recordings, all have initial rise

H. bachmani

XC: 7 recordings, all showing the initial drop and rise in pitch

ML: I didn't listen to all 226 recordings but of the 7 I found having the piping trill, all showed the initial drop and rise.

Whether this is an important difference is hard to tell, but given the vocal variation in the genus is very limited, and given it is a vocalisation used during display and interaction, it may well be considered important. If it has to be scored for Tobias, one could define the parameter initial drop or rise in pitch, which would give a score of about 3.

A possible second difference is that *H. ater* starts the trill with very short notes which gradually increase in duration, while *bachmani* has initial longer notes which reduce in duration during the drop in frequency. I said 'possible' because one can't be sure always if the initial longer notes are from a second bird or not, but it would seem this feature holds quite well, in which case it could also be given a score of 2-3.

Submitted by: Peter Boesman

Date of Comment: 7 January 2020

Treat Caribbean Island populations of *Troglodytes aedon* (House Wren) as seven species

Effect on NACC:

This would treat seven insular endemic subspecies as species separate from continental House Wren *T. aedon.*

Background:

We (AOU 1998) currently treat all the Caribbean Island *Troglodytes* as the single species *T. aedon*, with the following note (which has a lot of material not directly relevant to the insular populations):

> "Notes.—Species limits within this complex are not well understood. Groups: *T. aedon* [Northern House-Wren], *T. brunneicollis* Sclater, 1858 [Brown-throated Wren], *T. musculus* Naumann, 1823 [Southern House-Wren], T. *martinicensis* (Sclater, 1866) [Antillean House-Wren], and *T. beani* Ridgway, 1885 [Cozumel Wren]. *Troglodytes aedon* and *T. brunneicollis* intergrade through intermediate breeding populations in southern Arizona (Marshall 1956, Phillips et al. 1964, Lanyon 1960), but intergradation between *brunneicollis* and *musculus* in an area of close approach in north-central Oaxaca has not been definitely established (Monroe 1968, Binford 1989). *Troglodytes beani* appears to be part of the Antillean *T*. *martinicensis* complex. Many or all of the distinctive Caribbean subspecies included within the *martinicensis* group may each warrant species status. Brumfield and Capparella (1996) suggested that the *musculus* group and probably the *brunneicollis* group are specifically distinct from *aedon*, but study of parapatric populations is needed to resolve species limits in this complex."

SHORT VERSION SYNOPSIS

From Remsen: Since I first saw specimens about 40 years ago, I have regarded this as the most severe case of over-lumping in the Western Hemisphere, and with the recent publication on the distinctive voices of the Cozumel and Dominica populations, I think it's time to restore species rank to these populations. Ridgway (1904) treated them all as separate species, and no convincing rationale has ever been published to change that treatment. All seven are more distinct in terms of phenotype (plumage, bill length, voice so far as is known) than an Alaskan House Wren is from one from southern South America. We have no comprehensive published summary of all of this, but I think the accumulated weight of what we do know clearly puts burden-of-proof on a single species treatment.

From Sullivan: It's rare that one has an opportunity to encounter a complex of recognized subspecies that obviously hits the observer instead as clearly distinct species. I was lucky enough to have such an occasion when I joined a trip in the spring of 2018 to explore the islands of the Lesser Antilles. On this trip I paid special attention to the House Wrens on the various islands, as I was curious to understand how similar (or different) they might be. After photographing and sound recording birds on several islands, I was convinced that they were not only strikingly different from all the mainland House Wren taxa that I was familiar with, but also exceedingly distinct from each other. While several of these taxa are recognizable as 'wrens' by voice, several were so distinct to me that I couldn't even recognize the vocalizations as clearly being part of the Troglodytidae. I recall walking a trail on Saint Vincent with renowned tropical ornithologist and Cornell Lab of Ornithology Director Dr. John Fitzpatrick and asking him what vireo was singing—we tracked the bird down and were surprised to discover that it was the Saint Vincent Wren! In addition to the distinctive voices of these birds, their appearances varied to such a degree across islands that it was hard to discern a clinal pattern: the general patterns of plumage were similar, but not in the sense of any kind of meaningful geographic cline. Some were quite rufescent, others very white-bellied with big eyebrows. All were long billed. One would expect a cline geographically to blend from one thing into the next from island to island, but the distribution of these phenotypes did not conform to those expectations. I agree that it's clear the burden of proof is on those who consider these forms to be the same species, rather than on those who consider these insular island forms to be separate species. Lastly, two of these forms are already extinct, lost to science and the world—how many more will we lose before we recognize these birds as distinct species and offer them the conservation measures they deserve?

LONG-WINDED VERSION:

Taxonomic history:

- Ridgway (1904) treated all seven as separate species:

T. beani (Cozumel Wren)
T. guadeloupensis (Guadeloupe Wren) [probably extinct]
T. rufescens (Dominican Wren)
T. martinicensis (Martinique Wren) [now extinct]
T. mesoleucus (St. Lucia Wren)
T. musicus (St. Vincent Wren)
T. grenadensis (Grenada Wren)

To be fair, Ridgway (1904) also treated the *brunneicollis* and *musculus* groups as separate species, as well as the population of coastal Yucatan as a separate species, *T. peninsularis*; we now treat *brunneicollis* and *musculus* as subspecies groups within *T. aedon* (but more on that later).

- Hellmayr (1934) continued to treat *musculus* and *brunneicollis* as separate species from *T. aedon*, but treated all seven insular taxa as subspecies of *T. musculus*, with the following rationale:

> "The Santa Lucia Wren is closely similar to *T. m. beani*, of Cozumel Island, and at the same time connects the other West Indian wrens so completely with *T. m. tobagensis* that I have no hesitation in combining this whole group under the specific term *musculus*."

Other pertinent comments:

> "*Troglodytes musculus beani* Ridgway, while quite different from *T. m. peninsularis*, of the Yucatan mainland, can hardly be told apart from *T. m. mesoleucus*, from Santa Lucia Island, by less rufescent flanks, sides of neck, and posterior upper parts. The similarity of these wrens, restricted to two widely separated islands, presents a remarkable case of parallel development."

> "*Troglodytes musculus tobagensis* Lawrence: Nearest to *T. m. clarus* [of Trinidad and much of eastern tropical South America], but wings longer; bill heavier; under parts whiter, the buffy tinge on chest and sides of breast being absent or but slightly suggested."

And here we see the precursor to the eventual lump of *musculus* into *aedon*:

> "As pointed out by Chapman and Griscom, the Mangrove Wren is so decidedly intermediate between *T. aedon* and *T. musculus* that one is tempted to regard these two wrens as conspecific. The only reason that prevents me from following this course is our ignorance as to the southern limits of the breeding area of the House Wren (*T. a. parkmanii*) in Mexico. It will be recollected that the range of *T. m. peninsularis* has been shown to extend along the coastal plains north to southern Tamaulipas, while Phillips (Auk, 28, p. 81, 1911) records specimens of *T. a. parkmanii* from Realito in the Temperate region of the same state, the dates between May 27 and June 13 indicating their breeding in that vicinity. These wrens may thus prove to be zonal representatives in Tamaulipas, whereby the last obstacle for their specific association would be removed. It is greatly to be hoped that definite information on their breeding ranges in Mexico will soon be supplied."

We appreciate Hellmayr's logic, and for the era (ca. 90 years ago), this is as good as it gets, and definitely an upgrade over Peters' decisions, which were almost never accompanied by any rationale. What Hellmayr is saying, based mainly on plumage, is that he sees a connection between *musculus* through *peninsularis* to *beani,* and from *musculus* to *grenadensis* through *tobagensis*; therefore, he treated the whole complex as conspecific, especially with the superficial similarity between *beani* and distant *mesoleucus*. However, if Ridgway's classification had remained intact, one can only imagine the ensuing derision if a proposal based on Hellmayr's reasoning were submitted in 2021 to reverse it. Hellmayr's logic was long before any appreciation of the significance of vocal differences in marking discontinuities in gene flow. This classification has been continued in all subsequent classifications, from Paynter in Peters (1960) through Dickinson & Christidis (2014) and including all of Bond's West Indian classifications as well as books on West Indian birds, although *beani* has been treated as a separate species by some (details below).

• Phillips (1986: " .. Known Birds …", Part 1) treated *beani* as a separate species from *T. aedon* sensu lato, without meaningful comment.

• Howell & Webb (1995) treated *beani* as a separate species from *T. aedon* sensu lato and wrote the following: "Sometimes considered conspecific with Southern House Wren, but appears closer to the Caribbean forms (species?) *musicus* of St. Vincent and *mesoleucus* of St. Lucia. Comprehensive studies of house wrens outside the USA are still needed."

• Raffaele et al. (1998: A Guide to the Birds of the West Indies; Princeton) treated them all as conspecific and did not mention voice other than "A bursting, gurgling warble unlike any other resident landbird in the West Indies; dialects vary slightly among islands."

• Brewer (2001: Wrens, Dippers and Thrashers; Yale U. Press) treated *beani* as a separate species, and wrote: "Song is somewhat similar to that of the Southern House Wren [treated as a separate species], but has some distinctive features; it is fuller and richer without trills, typically begins with a slight scolding *chih-chih,* breaks into a short rich warble which ends with a bright *wheet-wheet-wheet-wheet*, or with longer series of bright notes which may suggest Whitethroated Wren (Howell and Webb 1995); often interspersed with a persistent *wha-wha* note." Unfortunately, no information on the Lesser Antillean subspecies is presented.

• Navarro-Sigüenza and Peterson (2004) treated *beani* as a separate species, but that was based on the ESC (and thus also treated *brunneicollis* and *musculus* as separate species).

• Kroodsma & Brewer (Handbook of Birds of World Vol. 10; 2005) treated *beani* as a separate species, Cozumel Wren (but retained the equally distinctive Lesser Antillean subspecies within *T. aedon*); their family chapter did not discuss the Caribbean wrens and species limits.

• Boesman (2016) treated *beani* as a separate species and summarized his findings as follows: "… 'Cozumel Wren' *beani* differs strikingly in having a much simpler song: several grating or scratchy notes followed typically by one or two series of pure whistles, which can reach low pitches. Some examples (illustrated with multiple sonograms in the pdf version of this note): *beani,* to be compared with some typical examples of song of the 'House Wren complex'.

> "It would seem that in *beani*, after the scratchy introductory notes, the whistled phrase is limited to only two parts consisting of one or more identical whistles, which are very simple in shape. All other races in contrast typically have the scratchy introductory notes (if present) typically followed by several parts which may consist of alternating whistles, again a few scratchy notes, different fairly complex notes etc. *beani* can thus be identified based on the few different whistled notes (typically 1 to 3 different note series vs. typically 4-5, score 2-3), with notes which are simpler and purer, reflected in the note shape (score 1) and usually the lower minimum frequency. When applying Tobias criteria, this would lead to a total vocal score of about 3-4."

• del Hoyo & Collar (HBW: 2016) treated *beani* as a separate species, based largely on Boesman: "Unlike most races of *T. aedon*, song of present species differs strikingly in being much simpler, with several grating or scratchy notes typically followed by one or two series of pure, sometimes lower-pitched whistles (of different shape and fewer)." They treated the Lesser Antillean taxa as subspecies of *T. aedon* without additional comment.

Fast-forward to recent years. The Falkland Islands subspecies *cobbi* is now treated as a separate species from *T. aedon* by SACC based on voice and morphology. Despite minimal variation in plumage, evidence is growing that Ridgway's 3-species treatment of continental populations might be correct (e.g., Brumfield and Capparella 1996; Sosa-López & Mennill 2014a).

Plumage and morphology:

The variation in color, pattern, and bill length among the W.I. subspecies by any objective standard is greater than that among all the continental *aedon* (s.l.) populations. Here's a photo of LSUMZ specimens: 4 of the Caribbean taxa and 2 continentals)"


Grenada
Troglodytes aedon
grenadensis
St. Lucia
Troglodytes aedon
musicus
Dominica
Troglodytes aedon
rufescens
Cozumel
Troglodytes aedon
beani
Argentina
American Museum
of Natural History
W. H. Partridge
North America
Troglodytes aedon
aedon

What is striking is that the insular forms show more differences among each other than does a North American *aedon* from a southern South American one. Notice also that the 4 insular forms have dramatically larger bills (a frequent symptom of insular taxa, as pointed out 50+ years ago by P. R. Grant), presumably due to ecological release. (Anecdote: *rufescens* is so big and fearsome that it has been documented eating an anole; I can't imagine a continental *aedon*-type eating a lizard.)

Here are photos by Jaramillo of specimens of *guadeloupensis* from the AMNH. They are paler than *grenadensis*. Ridgway's key indicates that *guadeloupensis* was most like *rufescens* in plumage and bill length, but it had "buffy cinnamon" underparts rather than "deep rufous-cinnamon".

Below are photos of living individuals from each extant insular population.

T. beani **(Cozumel Wren)**

Cozumel Wren, 8 October 2021, Cozumel, MX. Photo by Daniel Garza Tobón. ML385855291.

More photos of Cozumel Wren:
https://ebird.org/media/catalog?taxonCode=houwre&mediaType=p&sort=rating_rank_desc&region=Cozumel,%20Quintana%20Roo,%20Mexico%20(MX)&regionCode=MX-ROO-002&q=House%20Wren%20-%20Troglodytes%20aedon

***T. rufescens* (Dominica Wren)**

Dominica Wren, 3 March 2018, Morne Diablotin NP, Dominica. Photo by Brian Sullivan. ML89359521.

Photo by Alvaro Jaramillo.

Note the extremely rich coloration; see the specimen photo above to appreciate the bill size. *Rufescens* is perhaps the most distinctive taxon in being dark and having a bright yellow mandible.

More photos of Dominica Wren:
https://ebird.org/media/catalog?taxonCode=houwre&mediaType=p&sort=rating_rank_desc&region=Dominica%20(DM)&regionCode=DM&q=House%20Wren%20-%20Troglodytes%20aedon

T. mesoleucus (St. Lucia Wren)

Saint Lucia Wren, 24 January 2014, Soufrière, Saint Lucia. Photo by Charles Davis. ML284243401.

House Wren (St. Lucia), 29 Dec. 2019, Soufrière, Saint Lucia. Photo by Ryan Zucker. ML207254501.

Note the whitish underparts and big bill size.

More photos of Saint Lucia Wren: https://tinyurl.com/mesoleucus

T. musicus (St. Vincent Wren)

Saint Vincent Wren, 12 April 2017, Saint Vincent Parrot Preserve, Saint Vincent. Photo by Frantz Delcroix (Duzont). ML60652371.

Note the whitish underparts and big bill.

More photos of Saint Vincent Wren:
https://ebird.org/media/catalog?taxonCode=houwre&mediaType=p&sort=rating_rank_desc&region=Saint%20Vincent%20and%20the%20Grenadines%20(VC)&regionCode=VC&q=House%20Wren%20-%20Troglodytes%20aedon

Here are side-by-sides of (left) *mesoleucus* (St. Lucia) and (right) *musicus* (St. Vincent):

Photos by Alvaro Jaramillo.

These two populations are most similar in overall look, as they are pale bellied. However, *musicus* is larger, and has a relatively smaller bill. The bill of *mesoleucus* is quite long and deep at the base. The buffy coloration on *musicus* is more extensive below than on *mesoleucus*. The distribution of *mesoleucus* is much more restricted, in fact of the four types still extant it is the one with the lowest population and strongest affinity to dry coastal (deciduous) forest. It is not found in wetter highland forest. On St. Vincent *musicus* can be found in towns, cities, coastal dry areas, and the edge of forest higher up in elevation. It is much broader in its habitat choice.

***T. grenadensis* (Grenada Wren)**

Grenada Wren, 30 July 2013, Saint George, Grenada. Photo by Frantz Delcroix (Duzont). ML62042621.

More photos of Grenada Wren:
https://ebird.org/media/catalog?taxonCode=houwre&mediaType=p&sort=rating_rank_desc&region=Grenada%20(GD)&regionCode=GD&q=House%20Wren%20-%20Troglodytes%20aedon

We do not have easy access to specimens of *mesoleucus* or *martinicensis*. Both were large-billed forms, separating out in Ridgway's key from *aedon*-types on bill length alone. For *martinicensis*, Ridgway said it was most like *grenadensis* but was grayish brown dorsally instead of rufescent brown, and slightly duller ventrally.

Keep in mind that congeneric *T. troglodytes* (s.l.) is now treated by NACC as consisting of at least three species based largely on vocal differences; morphological differences among the three populations (exclusive of Aleutian Is.) are much more subtle than those among the Caribbean taxa and between them and mainland *aedon*. Therefore, from the perspective of more recent data on vocal differences compared to morphological differences, the Caribbean taxa stand out as outliers in their continued treatment as subspecies … which is based on a few sentences of rationale published almost 90 years ago.

Voice:

Here are some sample recordings:

T. beani (Cozumel Wren): (I can hear *aedon*-like resemblance, but fairly different)
https://www.xeno-canto.org/166911 (by Ian Davies)
https://www.xeno-canto.org/114023 (by Gary Nunn)
https://www.xeno-canto.org/5917 (by Rich Hoyer)

T. guadeloupensis (Guadeloupe Wren) (probably extinct – I can't find any recordings online, although Jon Barlow obviously made some --- here's the sonogram from Barlow (1978) compared to a House Wren; with all appropriate caveats, it certainly looks different to me, and Barlow in fact said "To my ear the song of the Guadeloupe House Wren is the louder, richer, and more melodious of the two."

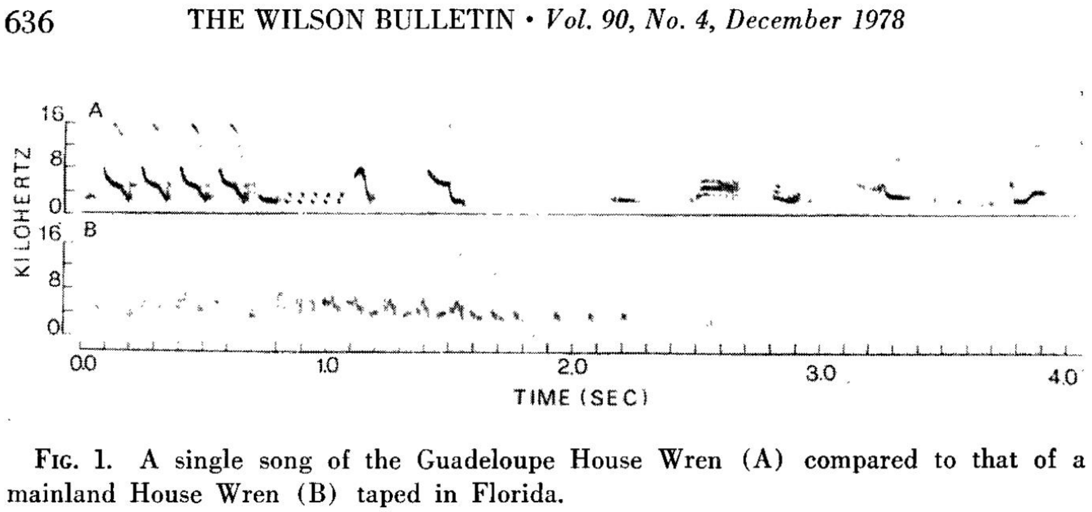


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FIG. 1. A single song of the Guadeloupe House Wren (A) compared to that of a mainland House Wren (B) taped in Florida.

T. rufescens (Dominican Wren): (I can hear some *aedon*-like pacing and elements, but generally very different; see last one especially)
https://search.macaulaylibrary.org/catalog?taxonCode=houwre6&behaviors=s&sort=rating_rank_desc (by Ted Parker)
https://search.macaulaylibrary.org/catalog?taxonCode=houwre6&behaviors=s&sort=rating_rank_desc (by Jeff Gerbracht)
https://search.macaulaylibrary.org/catalog?taxonCode=houwre6&behaviors=s&sort=rating_rank_desc (by Brian Sullivan)
https://search.macaulaylibrary.org/catalog?taxonCode=houwre6&sort=rating_rank_desc&q=House%20Wren%20(Dominica)%20-%20Troglodytes%20aedon%20rufescens (by Mark Robbins)

T. martinicensis (Martinique Wren) (extinct– I can't find any recordings or even a description of the song)

T. mesoleucus (St. Lucia Wren): this one sounds more or less like a typical *aedon*-type to me
https://search.macaulaylibrary.org/catalog?taxonCode=houwre8&behaviors=s&sort=rating_rank_desc (by Brian Sullivan)

T. musicus (St. Vincent Wren): (This one really sounds different – I have to struggle to find anything *aedon*-like in this one – and "*musicus*" is a good name)
https://search.macaulaylibrary.org/catalog?taxonCode=houwre10&behaviors=s&sort=rating_rank_desc (by Josep del Hoyo)
https://search.macaulaylibrary.org/catalog?taxonCode=houwre10&behaviors=s&sort=rating_rank_desc (by Brian Sullivan)

T. grenadensis (Grenada Wren): (The first two sound very *aedon*-like, but the third one somewhat different)
https://www.xeno-canto.org/443260 (by Kim Wetten)
https://search.macaulaylibrary.org/catalog?taxonCode=houwre11&behaviors=s&sort=rating_rank_desc&q=House%20Wren%20(Grenada)%20-%20Troglodytes%20aedon%20grenadensis (by Josep del Hoyo)
https://search.macaulaylibrary.org/catalog?taxonCode=houwre11&behaviors=s&sort=rating_rank_desc&q=House%20Wren%20(Grenada)%20-%20Troglodytes%20aedon%20grenadensis (by Larry Therien)

Jaramillo has done informal playback trials over the years on these wrens. The N is small, but he has played back to all 4 extant forms, songs of their own taxon and songs of other Lesser Antillean taxa. Despite the small N, the results were clear. Attraction to songs of other taxa was nearly always nothing, at times mild, or moderate. Attraction to songs of own taxon usually was strong, coming to the speaker, singing back, agitated and at times moderate.

Genetic data:

There are no genetic data for the Lesser Antillean wrens that we know of. Remsen continues to point out that genetic data for allotaxa have limited taxonomic application in terms of species rank unless we devolve to bar-coding rationale or reciprocal monophyly. The latter term is often used in the taxonomic literature as if it is some absolute term of great significance. In Remsen's view, it is a conditional term that requires appended caveats, e.g., "with respect to the N of loci and the N of individuals sampled", and is always one additional sample away from being falsified; further, for populations that may have had contact zones in the past, the geography of those samples must include populations from near that contact zone.

Nonetheless, genetic data in this complex would be especially interesting because the heterogeneity among the Lesser Antillean in plumage and morphology as well as their different degrees of sensitivity to human disturbance suggests the possibility of multiple independent colonization events, i.e., that they do not form a monophyletic group. The plumage similarities that led Hellmayr to posit parallel evolution between *beani* on Cozumel and *mesoleucus* from St. Lucia would be formally tested. That "we" AOU (1998) treat the Lesser Antillean taxa as a subspecies group assumes that they as a group are more closely related to each other than either is to the *musculus* group. We are skeptical. In fact, given that populations of the *aedon* group are long-distance migrants, the possibility that one or more of the Lesser Antillean forms represent an *aedon* colonization, albeit highly unlikely given near-absence of *aedon* records from West Indies, shouldn't be dismissed out of hand. Multiple *aedon* records from Bermuda show that it can cross saltwater gaps (1000 km) larger than anything it would face in the Caribbean.

Ecological data:

From the mostly anecdotal accounts in the literature, we think it is safe to surmise that all but one of the Lesser Antillean forms represented fragile populations that had diverged so far from the mainland *aedon* complex that they had "become different species". I'm (Remsen) not sure what the best term for this kind of speciation is, but the thesis is that these populations are/were in several cases essentially so different in their basic ecology that they can be considered different species.

Here's what a superficial search yielded on habitat and abundance:

• *beani* (Cozumel): Birdlife International considered it a species of Least Concern. Considered common by Sosa-López and Mennill (2013), who noted that although evidently primarily a forest bird, it also occurs in human-modified landscapes. Occurs in "urban" habitat category (MacGregor-Fors et al. 2021).

• *guadeloupensis*: (Guadeloupe): last record 1973 and presumably extinct, although Barlow (1978) noted that remote areas of rugged forested terrain could still have them. It was evidently restricted to humid forest and was always uncommon to rare; in fact, it was suspected of being extinct through much of the 20th century.

• *rufescens*: (Dominica): This one creeps around in vines in thick and moist forest more akin to a Gnatwren than a House Wren (Jaramillo, pers. obs.). Birders find it regularly – eBird's bar chart indicates that its status there in terms of "% eBird checklists" is equivalent to that of *Allenia fusca*, *Cinclocerthia ruficauda*, *Margarops fuscatus*, and other landbirds; the high count for a single list is 15 (Mark Robbins, 1987). All internet sources suggest that forests on Dominica are in better condition than elsewhere in the Lesser Antilles due to legislation.

• *martinicensis* (Martinique): last record 1896. From what little is known, it was evidently a forest bird. An 1878 quote from Ober reproduced by Hume (Extinct Birds, 2012, Helm) is quite specific on this: "An inhabitant of the woods. I have not seen it near houses or sugar mills, only in the forests of the hills, and along the borders of streams where the bushes are thick."

• *mesoleucus* (St. Lucia): of the four Lesser Antillean types still extant, it is the one with the smallest population and strongest affinity for dry coastal (deciduous) forest; it is not found in wetter highland forest (Jaramillo, pers. obs.). Ebird indicates that this wren is frequently reported. About 35% of St. Lucia is still forested (Anthony and Dornelli 2013?), although Wikipedia indicates 77%.

• *musicus* (St. Vincent): can be found in towns, cities, coastal dry areas, and the edge of forest higher up in elevation; thus it is much broader in its habitat choice than any of the other insular populations (Jaramillo, pers. obs.).

• *grenadensis* (Grenada): Wunderle's (1985) quantitative analysis of habitat preferences of birds on Grenada found that it occurred in 10 out of 10 samples in Residential habitat, more than in any other habitat, followed by Savanna (7 of 10 samples), and he did not detect it in 10 samples of Mature Lowland Forest Old Secondary Forest. Therefore, this indicates that unlike the other Lesser Antillean populations, this one is common in human-disturbed habitats and is more like a proper *musculus*-type in terms of habitat. It is not in forest, but instead in dry shrub thickets in the drier parts of the island, such as where the Grenada Dove can be found; although *grenadensis* is superficially similar to *rufescens*, it is paler below and entirely different from it ecologically (Jaramillo, pers. obs.).

The extent Lesser Antillean wrens divide into three habitat preferences, *grenadensis* and *musicus* prefer coastal dry forest, but will use edge habitat in higher elevations; they can also be found near human settlements. St. Lucian *mesoleucus* is restricted to the two larger patches of dry forest on the island and is absent from moist forest; it might be the one that is most restricted in range and population currently. Dominican *rufescens* is forest-restricted, in moist forest as opposed to dry forest, and can be found commonly in highlands; it is essentially the opposite of *mesoleucus* in habitat preference. From a single anecdote, we surmise that *guadeloupensis* was a montane forest species. The early extinction of *martinicensis* strongly suggests it was specialized on some sort of native habitat.

Our House Wren does just fine in manicured suburbs and parks as long as a nest box is available, and its tropical counterparts of the *musculus* group thrive in tropical latitude towns and villages … to the point that I'm not sure where they occurred before human arrival. In our opinion, a proper continental *musculus*-type would thrive on those Caribbean islands as well, and thus several of the insular taxa really are different species in the ecological sense. The corollary is that if the Lesser Antillean taxa were really the same species as the House Wren, they would have benefitted by human disturbance rather than be threatened by it.

Discussion and Recommendation:

For more than 30 years, Remsen has been planning to write a short paper on this group, enlisting co-authors who have actually had field experience with them, to lay out the rationale for overturning these lumps. Sullivan has independently contemplated such a paper. But it hasn't happened, and it's time, in our opinion, to move forward. Typically Remsen is the one calling for publication of all the details before making a NACC change, but in this case, the combination of lack of evidence for treating them as conspecific and overwhelming anecdotal evidence that species rank should be restored leads me to this proposal and to recommend a YES vote.

We treat the three major continental lineages as subspecies groups (*aedon*, *brunneicollis*, *musculus*) although they have been, and continue to be, treated as separate species by some, yet we treat these insular oddballs as subspecies.

Because the evidence varies for each taxon, we think voting should be on a menu basis. We recommend Yes for all except perhaps G – we are undecided on that one given its apparent vocal and ecological similarities to the *musculus* group. *Beani* and *grenadensis* seem to do just fine in human-disturbed habitats, but *beani* seems to have diverged to the level associated with speciation in wrens in terms of voice; we are less certain about *grenadensis* and worry that bundling it into a comprehensive split is not justified. Grenada also tends to have a slightly greater representation of continental taxa (e.g. *Glaucis hirsutus*, *Sporophila nigricollis*) than any other island, as might be expected from its proximity to Tobago and Trinidad.

A. *T. beani* (Cozumel Wren)
B. *T. guadeloupensis* (Guadeloupe Wren) [probably extinct]
C. *T. rufescens* (Dominica Wren)
D. *T. martinicensis* (Martinique Wren) [now extinct]
E. *T. mesoleucus* (St. Lucia Wren)
F. *T. musicus* (St. Vincent Wren)
G. *T. grenadensis* (Grenada Wren)

Note on English names:

We see no reason to deviate from the English names used by Ridgway, except Dominican should be changed to Dominica just to remove confusion with the religious order or the DR. They are already in informal use. However, the possibility of using a hyphenated group names should at least be considered. This has the advantage of setting them apart from other wrens, every one of which is called Something-Wren as well as keeping them together as a unit as a connection to former classifications; this would mean changing the cherished name House Wren to something like “American House-Wren”, so that’s a negative. But as Remsen has mentioned in previous proposals, the informal versions of these formal compound English names will be reduced to House Wren, Cozumel Wren, etc.

Submitted by: Van Remsen, Alvaro Jaramillo, and Brian Sullivan

Date of Proposal: 15 January 2022

Treat *Piaya mexicana* as a separate species from *P. cayana* (Squirrel Cuckoo)

Description of the problem:

Piaya cayana is a widespread polytypic species found from northern Mexico to Argentina, with as many as 14 subspecies recognized (Fitzgerald et al. 2020). The species is common in forested lowlands and foothills throughout its range. In Middle America, the more typical (i.e., darker) subspecies *thermophila* is found from eastern Mexico south to Colombia, but is replaced at the Isthmus of Tehuantepec by the paler western Mexican subspecies *mexicana*, which is found in the western Mexican dry forests from the Isthmus of Tehuantepec north to Sonora and Chihuahua. HBW-BirdLife split *mexicana* from the remainder of *Piaya cayana* based on plumage and slight vocal differences and their parapatric distributions, citing Navarro-Sigüenza and Peterson (2004) and Howell (2013, in litt.): "*mexicana* differs from parapatric subspecies *thermophila* of *P. cayana* in its rufous underside of tail feathers with broad black subterminal bar and broad white terminal tip vs all-black underside of tail with broad white terminal tip (3); pale grey vs smoky-grey lower belly and vent (2); much brighter rufous upperparts and paler throat (1); usually greenish-grey vs greenish-yellow orbital ring (Howell 2013) (ns1); longer tail (effect size 2.01; score 2); “somewhat different” song (Howell 2013) (allow 1); and parapatric distribution (3)."

Piaya mexicana was described by Swainson (1827), who gave the following characters (which largely mirror the differences described above): “Closely resembles *C. cayenensis* L. [=*Piaya cayana*], but the tail beneath is rufous, not black; the ferruginous colour of the head and neck is likewise much brighter.” This treatment was maintained by authors through the beginning of the 20th century (Ridgway 1916, Cory 1919), until lumped with *P. cayana* (without comment) by Peters (1940). Ridgway expanded on the differences between *mexicana*: “Resembling *P. cayana thermophila*, but colored portion of under surface of rectrices cinnamon-rufous (instead of brownish black) with a dull black area immediately preceding the white tip, general coloration much lighter, and tail relatively much longer.” Most authors since Peters (1940) have maintained *mexicana* as a subspecies of *cayana*.

Navarro-Sigüenza and Peterson (2004) use *Piaya cayana* as one of their case studies for contrasting a BSC classification (single species) with a PSC/ESC classification (two species) by splitting *mexicana*, using this rationale: “Populations along the Pacific lowlands from Sonora to the Isthmus of Tehuantepec are long-tailed, pale in coloration of the underparts, whereas the forms of eastern Mexico and Central America are shorter-tailed and darker in color. Although a narrow contact zone is present in eastern Oaxaca between the two forms, only one “hybrid” specimen is known, and the differences are maintained even in close parapatry.” The reference to the “narrow” contact zone appears to be from Binford (1989), who reported a few specimens intermediate between *thermophila* and *mexicana*: “I have seen definite intermediates from Rio Ostuta (MLZ 45402), Las Tejas (MLZ 54387), and Tehuantepec City (UMMZ 137345 and 137350), but some specimens from the last two localities are *mexicana*. Birds from Tapanatepec, Santa Efigenia, and a point 18 mi south of Matias Romero are close to *thermophila* but very slightly paler, a condition that might represent response to the drier environment rather than intergradation”, but noted that the "abruptness and apparent rarity of intergradation suggest that these two forms might be separate species; a detailed study is needed.” This, combined with the unpublished information from Howell (2013) mentioned above, appears to constitute the basis for the HBW-BirdLife split of *mexicana* from the remainder of *P. cayana.*

New information:

Very little. There are no published genetic studies of *Piaya cayana* that include samples of *mexicana*. Harvey et al. (2017) included samples of *P. cayana* from across the Amazon Basin and found that they constituted a single genetic cluster. Johnson (2021) reanalyzed these data and included one sample of *thermophilae* and one from the Atlantic forest (likely *macroura*) and found that the sample of *thermophilae* was slightly divergent from the rest (a STRUCTURE analysis gave K=2, but incompletely differentiated). Although that provides no direct information relevant to *mexicana*, it perhaps indicates that *P. cayana* (s.l.) does not show strong genetic differentiation in the face of biogeographic barriers such as Amazonian rivers, perhaps because the species prefers riverine and edge habitats in the Amazon Basin.

The primary basis for the split comes from the information provided in the introduction, i.e., Navarro-Sigüenza and Peterson (2004) and Howell (2013, in litt.). There appear to be no published analyses of plumage or song from across the distribution of *P. cayana*, or of genetics that includes *mexicana.* In looking through the specimens at the LSUMZ, the differences between the paler and longer-tailed *mexicana* and the darker and shorter-tailed *thermophila* are readily apparent (see photos inserted below), but two issues arise. First, there do appear to be a handful of intermediates from near Tehuantepec, Oaxaca, suggesting some introgression. Second, the paler overall coloration of *mexicana* is found in the other two regions where *P. cayana* is found in arid environments, the north coast of Colombia and Venezuela (ssp. *mehleri*/*circe*), and eastern Brazil (ssp. *pallescens*). In particular, the plumage similarity of *mexicana* and *pallescens* is striking, as shown in the photos below.

There appear to be no published analyses of vocal differences between taxa. In listening to recordings in the Macaulay Library, I (Oscar) am unable to find consistent differences in songs (a long series of widely spaced strident “pik” notes) or calls (a loud “chik-wraaay”). The song of *mexicana* appears to average higher pitched and more rapid than that of *thermophilae*, but some recordings of songs of *thermophilae* seem to match recordings of *mexicana*. Certainly, a formal analysis is desirable.


mexicana
intermediate?
thermophila
mexicana
intermediate?
thermophila

The following two photos show the subspecific diversity within *Piaya cayana*. From left to right are: *mexicana* (W Mexico), *thermophila* (E Mexico to Colombia), two *nigricrissa* (Pacific coast of Colombia to Peru), *mesura* (NW Amazon Basin), two *obscura* (southern Amazon Basin), *pallescens* (dry eastern Brazil), *macroura* (SE Brazil, Paraguay, Uruguay, and NE Argentina).

Below is a comparison of the two palest subspecies of *P. cayana*. Despite the similarity in overall color, note the longer tail and paler undertail (with dark subterminal bands) of *mexicana*. The long tail, however, is matched by *macroura* of southeastern South America.

Effect on AOS-CLC area:

Splitting *mexicana* from *cayana* would result in one additional species for the AOS area.

Recommendation:

We recommend a **NO** on splitting *mexicana* from *cayana* based on a lack of published studies on the group, apparent intermediates in the Isthmus of Tehuantepec, and what appears to be repeated evolution of pale plumage coloration elsewhere in the distribution of *P. cayana*. However, an argument could be made that the original lump by Peters (1940) was unjustified, as it was made without comment. However, we prefer waiting until molecular and vocal data on *mexicana* are published or at least morphometrics and color analysis.

If *mexicana* is split from *cayana*, an English name proposal should be drafted to address the new names, preferably in coordination with the SACC.

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Treat *Patagioenas albilinea* as a separate species from *P. fasciata* (Band-tailed Pigeon)

Background:

Patagioenas fasciata (Say, 1823) is a widespread species occurring from western Canada south to northwestern Argentina. Formerly placed in *Columba*, it consists of two groups (AOU 1998): *P. fasciata*, distributed from Canada south to northern Nicaragua, and *P. albilinea* (Bonaparte, 1854) in highlands from Costa Rica to Argentina. Many sources, such as the IOC checklist and Howard & Moore, recognize subspecies *monilis*, *fasciata*, and *vioscae* (an isolated subspecies in Baja California Sur) within the *fasciata* group, although other sources, such as Clements, separate two Central American subspecies from the somewhat variable *fasciata*: *letonai* of Honduras and El Salvador and *parva* of Nicaragua. Three subspecies are consistently included in the *albilinea* group: *crissalis* of Costa Rica and Panama, *roraimae* of southern Venezuela and adjacent Guyana, and *albilinea* from Colombia to Argentina.

The two groups were formerly considered separate species, e.g., by Ridgway (1916) and even Peters (1937), although Peters did remark that “[p]erhaps *C. fasciata*, *C. albilinea*, and *C. araucana* should be regarded as conspecific.” Hellmayr and Conover (1942) lumped *fasciata* and *albilinea* into the single species *P. fasciata* with the following explanation: “The *C. albilinea* group is clearly conspecific with *C. fasciata*, the Costa Rican form being, as far as coloration is concerned, in a way intermediate to the northern races.” Most subsequent sources (e.g., Goodwin 1983, Sibley and Monroe 1990, Gibbs et al. 2001, and various regional guides and global lists) have treated Band-tailed Pigeon as a single species; however, HBW-Birdlife has re-split the groups into separate species based on the following evidence:

> *P. albilinea* is “usually considered conspecific with *P. fasciata*, but [is] separable at species level on account of all yellow vs black-tipped yellow bill (2); darker grey underparts generally, with no shading to white on belly (3); wing-coverts as dark grey as mantle, not paler grey with whitish fringes, resulting in a distinct wingband in flight (2); gloss of nape and mantle green vs bronze (ns1). Subspecies *crissalis* somewhat intermediate, with undertail-coverts pale greyish-white, wing-coverts intermediate, and occasionally dusky tip to culmen.”

Band-tailed Pigeon is currently considered a single species by Howard and Moore, Clements/eBird, and the IOC list, in addition to NACC and SACC. We are considering a proposal now not because of new data, but because the difference in taxonomic treatment has brought this NACC-related issue before the IOU’s Working Group on Avian Nomenclature.

Morphology.— Size seems to shows only minor variation within *P. fasciata* (Keppie and Braun 2020), despite apparent differences in some of the photos below, and is not mentioned in the Birdlife analysis as differing between the two groups. However, plumage varies geographically, with the darkest birds in South America (*albilinea* and the similarly dark *roraimae*), somewhat lighter birds in Costa Rica and Panama (*crissalis*), and still lighter, although variable, birds to the north (*fasciata* and *monilis*). Birds in Baja California Sur (*vioscae*) have the lightest plumage, to the extent that the band in the tail is faint or lacking. Below is a series of photos of mostly male birds from the LSUMZ (the rightmost Costa Rican specimen is a female, which tend to be slightly duller). Arranged from left to right are 1 *albilinea* (Peru), 2 *crissalis* (Costa Rica), 4 *fasciata* (Honduras; Guatemala; 2 from San Luis de Potosí, Mexico), and 1 *monilis* (Oregon):

Here the dark vinaceous coloration of *albilinea* contrasts with the purplish hue of *crissalis* and the lighter purplish and white coloration of *fasciata* and *monilis*. The variability within *fasciata* is also evident, especially in the pale individual from Honduras ("*letonai*"), as is the slightly darker color of *monilis*. The same patterns are evident in the color of the pileum in the photo below:

The green vs. bronze mantle gloss is also evident in the preceding photo, although again birds from Costa Rica appear to be somewhat intermediate.

The seemingly discrete difference between the solid yellow bill of the *albilinea* group and the yellow bill with a black tip of the *fasciata* group can be seen in the side view here:

However, Wetmore (1968) noted that bill color in one of two adult female specimens from Panama (i.e., subspecies *crissalis* and the only two specimens for which soft parts colors were available) was "honey yellow, with the tip of the culmen dusky neutral gray" and a gray or dark gray (perhaps even black) bill tip is also noticeable in many photos of *crissalis* from Costa Rica in the Macaulay Library collection (many of these are juveniles but some are adults). See, for example, https://macaulaylibrary.org/asset/369692871, https://macaulaylibrary.org/asset/376900401, or https://macaulaylibrary.org/asset/252378571. A dark tip is also visible in photos of several birds from South America, such as this adult https://macaulaylibrary.org/asset/272622831 from Colombia (*albilinea*).

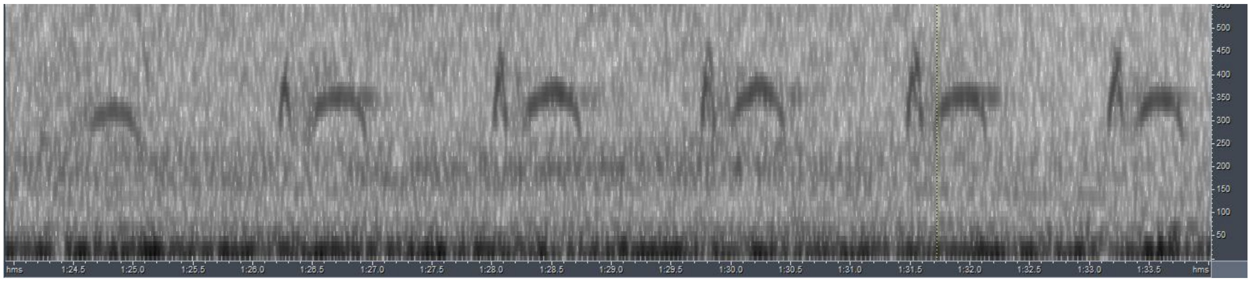
It's difficult to get a good handle on the variation in contrast of the wing coverts from the photo above; these are said to be paler with whitish edgings in the *fasciata* group, creating a wingband in flight, and to contrast with the darker back and scapulars, but it shows up better in the USNM side photo below. The Birdlife analysis notes that this character, too, is intermediate in *crissalis.*

Below are photos of male specimens from the USNM. These are again arranged from left to right in roughly south-to-north order, from *roraimae* to *monilis*, except that this series includes the isolated subspecies *vioscae* at the far right. Included are 1 *roraimae* (Guyana), 2 *crissalis* (Panama), 3 *fasciata* (Guatemala; Sonora, Mexico; Arizona), 1 *monilis* (Washington), and 1 *vioscae* (Baja California Sur). Note especially the near lack of a tail band in the specimen of *vioscae*.

And finally here are six specimens of *fasciata* from the UF collection, from left to right showing 2 from Oaxaca, Mexico: 1 ostensibly from Guatemala although the locality is not certain, 2 from Honduras (these are *letonai*, if recognized), and 1 from New Mexico (all males except the middle two birds, which were not sexed). Note the variability within *letonai* here and in comparison with the skin from LSU, which helps explain why many, including Hellmayr and Conover (1942), consider this a “questionable race”.

Vocalizations.— The typical song differs between the *fasciata* and *albilinea* groups but is largely consistent within these groups, as noted by Boesman (2015) in his comparison of their vocalizations (https://birdsoftheworld.org/bow/ornith-notes/JN100041). Nevertheless, there is variation in songs, particularly in the range of subspecies *crissalis*, that is worth exploring.

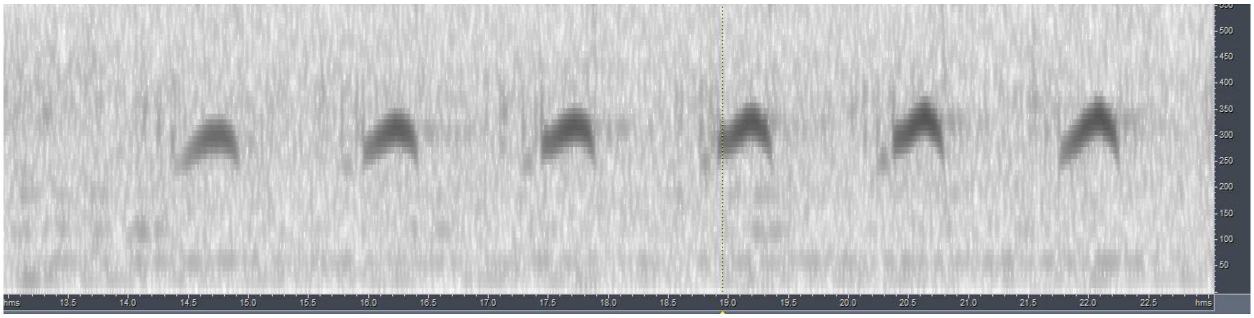
The song of the *fasciata* group typically consists of 1-2 introductory notes followed by a series of double (bi-syllabic or two note) elements. The pace of the song varies between individuals, as does the interval between the two notes of each element, but the first note always reaches higher frequency and is shorter than the second, and with a quicker rise and fall. This can be seen in this sonogram from Boesman (2015):



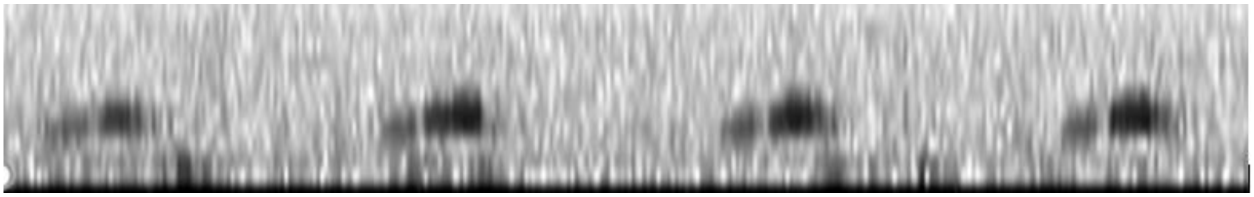
The 2-note elements have been described as “a deep, owl-like *whoo-whooo*“ (Dunn & Alderfer 2017) and the entire song as “a deep, slightly hoarse *huh whur* or *wh’hoo*, repeated 3-4x, rarely up to 13x or more, often preceded by a deep *grrrr* and at times followed by a moaning *whorr*, longer series may end with an abrupt *wu’t*” (Howell & Webb 1995). The first note reaches a higher peak frequency than does any part of the song of *albilinea* (Boesman 2015). This song occurs in more northerly populations as well as in birds recorded in the southern part of the distribution in Nicaragua (ML250647291), Honduras (ML83901331, XC323712), El Salvador (ML110064321), Guatemala (ML211589), Chiapas (XC334727 and XC221351), and Oaxaca (ML153844591 and XC623976). A recording of subspecies *vioscae* (XC21480), although largely in the background and somewhat faint, appears also to consist of the typical 2-note elements. Individuals of *fasciata* also call during display flights, giving a “grating call” (Dunn and Alderfer 2017).

The song of *albilinea* typically consists of an introductory note followed by a series of deep long notes, described as “deep, mellow cooing, *co’ oooh, co’ oooh* . . .” (Hilty 2003) repeated from two to many times. Schulenberg et al. (2007) describe this song as “a low coo with introductory note rising, but other long notes falling: *Woo uh-wooh uh-wooh*.” Boesman (2015) describes these elements as monosyllables, but he mentions one exception from Santa Marta, Colombia (XC236033), that includes a brief “hiccup” before every note. Although it’s not clear whether the two-part descriptions of the elements of the song indicate the presence of a “hiccup” or simply relate to the rising and falling parts of a monosyllable, the “hiccup” is present in several additional recordings (e.g., ML258965901 and ML257237 from Colombia; ML129476 from Ecuador). On average, the series of notes given by *albilinea* are longer and are delivered more slowly than are those of *fasciata* (Boesman 2015).

Here is an example, again from Boesman (2015), of the song with monosyllabic elements:



And here is a somewhat fuzzy example with bi-syllabic elements (i.e., with the "hiccup"), downloaded and magnified from xeno-canto (XC529591 from Colombia):



Individuals of this group also give a buzzy-screechy display-flight call, described as a "[c]hirping *dzurr* " (Fjeldså and Krabbe 1990).

Seven songs of *crissalis* are available on the Macaulay and xeno-canto websites. Three of these consist of the low-pitched series of notes typical of *albilinea*, described as "*c' cooo c' cooo*" or "*cooOOO cooOOO*" by Stiles and Skutch (1989) and "*co-oooh co-oooh*" by Ridgely and Gwynne (1989). This applies to XC274341 and ML165872 from Costa Rica and to ML172548421 from Panama. Recording XC274681 is a faster and burrier call but still within the range of variation of *albilinea*. The other recording from Costa Rica (https://macaulaylibrary.org/asset/51184), however, consists of a partial series of 2-note elements that appear to be more similar to those of *fasciata* than to those of *albilinea* (although the pace is slower than is typical in *fasciata*), and in which the emphatic long note is especially similar to the long notes of some *fasciata*. The other two recordings from Panama (https://macaulaylibrary.org/asset/302869 and https://macaulaylibrary.org/asset/302873) sound quite different from either of these: these songs consist of a series of 3-note elements, the second note shorter than the rest, and third note lower and longer, the shorter notes recalling in their brevity the clipped first note of *fasciata* songs (especially in the last song of ML302869, in which the first note has a quick rise and fall). These two recordings were made at the same time on the same date by Boesman, who put the ID certainty at 80%, presumably because of the unusual nature of the songs compared to those of *albilinea*. However, multi-note elements in the pattern "short-shorter-long" have been noted in other songs from Chiriquí, which were described by R. Ward in Ridgely (1976) as "*look for paw-paw*", supporting the identification of these recordings.

Recommendation:

Populations of *P. fasciata* from Nicaragua north to Canada (the *fasciata* group) and in South America (subspecies *albilinea*, and presumably subspecies *roraimae*, which is similarly dark-plumaged but whose voice is apparently unrecorded) appear to differ consistently and diagnosably in morphology and vocalizations. However, Hellmayr and Conover (1942) lumped these two taxa, previously considered separate species, based on the intermediacy of subspecies *crissalis* of Costa Rica and Panama. That *crissalis* is intermediate in plumage between *fasciata* and *albilinea* seems clear, and it is also intermediate, albeit to a much lesser extent, in the color of the bill tip; that is, most birds have the completely yellow bill typical of *albilinea*, but some have a dusky bill tip. Only seven recordings of *crissalis* are available: four of these feature vocalizations that sound like those of *albilinea*, but songs in the three other recordings differ from those of both groups and in some characters appear to be more like those of *fasciata*. These latter recordings were made in both Costa Rica and Panama, and birds with dusky bill tips also occur in both countries, indicating that these intermediate or aberrant character states are not restricted to a narrow zone but apparently occur more widely within the range of *crissalis.*

In my view this information, taken together, raises enough doubt concerning species status of *albilinea* for me to recommend a NO vote on separating it from *fasciata*, pending further investigation. Additional sampling and analyses of vocalizations of *crissalis*, and genomic data encompassing both *crissalis* and populations to the north and south would be especially helpful in determining the taxonomic status of *albilinea.* It's possible that *fasciata* and *albilinea* are separate species but to me there are too many unanswered questions to endorse species status at this time.

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