A Practical **Subspecies Taxonomy** for North American Birds

EDITOR'S NOTE: Supplementary materials, including the suggested new subspecies taxonomy and Tables S1–S5, are online at aba.org/north-american-birds/pyle2025a

Peter Pyle
Fort Bragg, California
ppyle@birdpop.org

Subspecies, designated by trinomials (scientific names with a third name appended to the genus and species), represent phenotypically diagnosable taxonomic units below the rank of species (Mayr et al. 1953, Mayr 1963). For example, the Nuttall's subspecies of White-crowned Sparrow is designated as *Zonotrichia leucophys nuttalli* and the Gambel's subspecies as *Z. l. gambelii*. Traditionally, avian subspecies have been separated based on plumage and morphology, although other delineating factors to assess the validity of taxa can include vocalizations (Rheindt and Ng 2021), behavior (Sibley 2011), and genetic differentiation (Patten and Remsen 2017, Winker 2021). Avian taxonomists have used as a guideline the calculation that 75% of individuals within a subspecies must be separable from 99% of those of another subspecies to be considered valid (Amadon 1949; hereafter, "the 75% rule"). Adhering to the 75% rule is calculable for morphometrics, but for plumage differences, it can be subjective and challenging due to variation in feather patterns and color by age, sex, and feather wear, in turn, as related to variable molting regimes (Rising 2007, Howell 2012). Despite the 75% rule being misapplied by some taxonomists (cf. Patten and Unitt 2002; Patten 2010, 2015; Remsen 2010), it can be considered a useful metric, one that is perhaps equally as valid as applying $p = 0.05$ as a cutoff for significance in statistics.

Even when applying this standard guideline, however, subspecies recognition based on morphometrics and plumage

Figure 1 ■ **Subspecies initially described 1760–2012 and recognized by Clements et al. (2024) that are considered valid and invalid following this analysis. Three subspecies originally described by Linnaeus (1758) in addition to all nominate subspecies are not included (see text).**

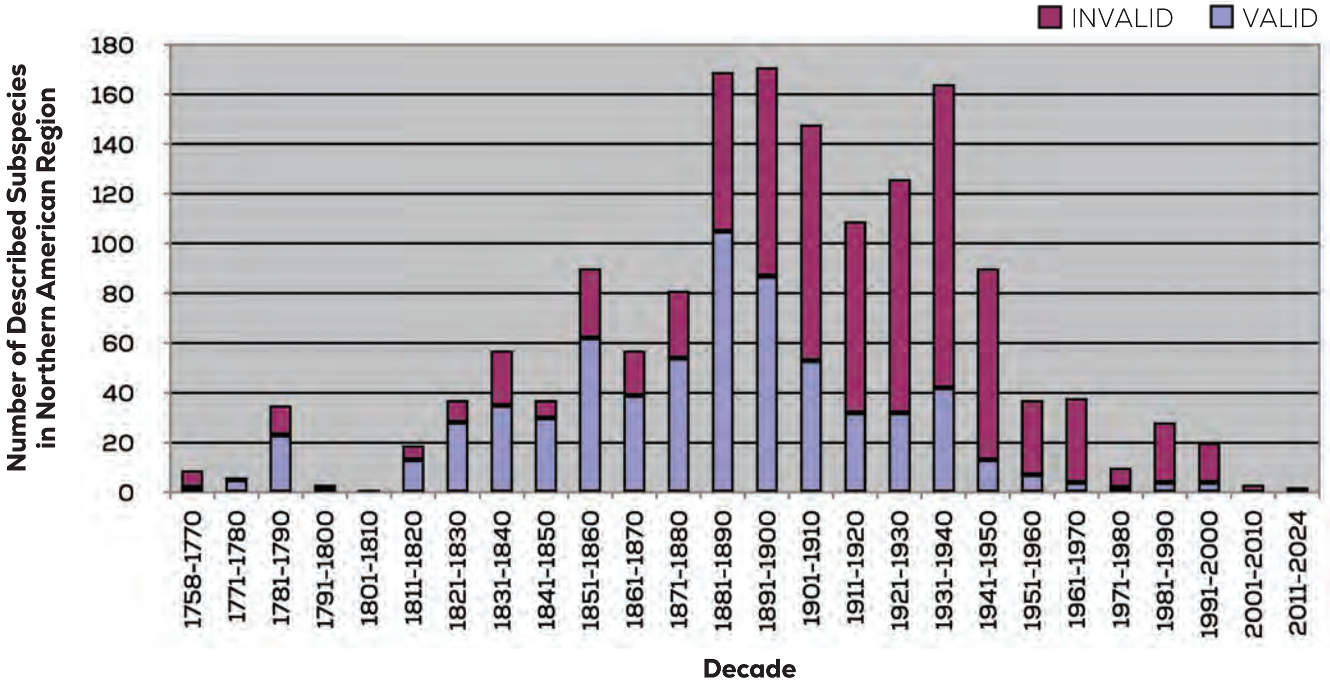


Figure 2 ■ [CLOCKWISE FROM TOP LEFT] Examples of previously recognized subspecies of Bushtit (*Psaltriparus minimus*) that have been synonymized here based on weak variation; e.g., those in which described differences generally do not approach the 75% rule. For comparative purposes, all images are of females (as sexed by iris color; Pyle 2022a) taken in fresh formative or basic plumage in Oct–Dec. a) *P. m.* "*saturatus*". King Co, Washington. 4 Nov 2018; b) *P. m.* "*californicus*". Sacramento Co, California. 21 Nov 2022; c) *P. m. minimus*. Monterey Co, California. 23 Oct 2022; d) *P. m.* "*melanurus*", San Diego Co, California. 31 Dec 2018. *Photos cropped for enlarged presentation and used by license agreement from the Macaulay Library © Ryan Schain (a, ML121987451), Kevin Thomas (b, ML505961561), Michael German (c, ML496915191), and Larry Edwards (d, ML132254901).*

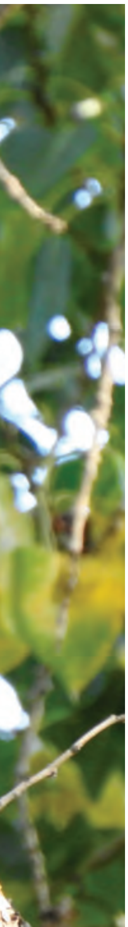
has been fraught with inconsistencies; these include descriptions based on too few data, weak differentiation that does not adhere to the 75% rule by any calculation, extensive individual variation that obscures overall diagnoses, and broadly clinal variation in measurements or plumage patterns that prevents marking precise boundaries between named subspecies (see Wiens 1982, Haig and Winker 2010, Winker and Haig 2010, James 2010, and associated commentaries for details). Many bird species are migratory or undergo short-distance movements, which result in increased genetic flow between populations through natal dispersal and vagrancy. Complications can result from subspecies being named based on hybrid swarms between species (e.g.,

Figure 3 [COUNTERCLOCKWISE FROM TOP LEFT] **Examples of previously recognized subspecies of Great Horned Owl (*Bubo virginianus*) that have been synonymized here. In this case, variable morphometric and plumage characteristics throughout the species's range were judged to preclude diagnoses according to the 75% rule. Several of these synonymized taxa may show plumage polymorphism that has been misapplied in subspecies diagnoses. All images are from Apr to Oct to better ensure they represent local breeding populations of this short-distance migrant species: a) *B. v.* "*saturatus*" (a known locally breeding individual). Marin Co, California. 14 Oct 2018; b) *B. v.* "*subarcticus*" or "*lagophonus*" (darker plumage). Weyburn, Saskatchewan. 2 Jul 2018; c) *B. v.* "*subarcticus*" or "*lagophonus*" (paler plumage). Carmichael Village, Saskatchewan. 15 Sep 2021.; d) *B. v.* "*pallescens*". Maricopa Co, Arizona. 16 Jul 2021; e) *B. v.* "*virginianus*" (at nest), Jefferson Co, Kentucky. 10 Apr 2021; f) *B. v.* "*mesembrinus*". Sololá, Guatemala. 24 Sep 2019. *Photos cropped for enlarged presentation and used by license agreement from the Macaulay Library © Douglas Hall (a, ML118964051), Annie McLeod (b, ML106269751), Jody Wells (c, ML369917011), Cindy Krasniewicz (d, ML441449281), Lee Payne (e, ML325210011), Josue de León Lux (f, ML180013131).***

see Johnson et al. 2024 regarding American and Black oystercatchers). There is also a need for multi-factorial comparisons of museum series in fresh and worn plumage to ensure correct subspecific identifications are based on valid intrinsic differences rather than environmental effects (Rising 2007). Many currently accepted subspecies taxonomies suffer from "historical inertia", largely repeating initial classifications from the 1940s or earlier, without further consideration or critical analyses (Remsen 2005, 2010). In the *Birds of the World* (2024) series, for example, there is frequent indication that the subspecies of polytypic North American species require critical re-evaluation.

While genetic differentiation may hold promise in delineating subspecies (James 2010, Ruegg et al. 2021, Miller et al. 2023), it has thus far been applied rather indiscriminately (Patten and Remsen 2017), and in many analyses, genotypic delineation has not corresponded with subspecies boundaries based on morphometrics and plumage (Ball and Avise 1992; Zink 2004; Zink et al. 2005, 2013; Pruett et al. 2008; Yeung et al. 2009; Ross and Bouzat 2014; DeRaad et al. 2019; Davis et al. 2021; Roeder et al. 2021); see also Cicero and Johnson (2006), Phillmore and Owens (2006), Patten (2010), Howell (2012, 2024), Patten and Remsen (2017), Cardena and Zapata (2021), Winker (2021), and Howell et al. (2025) for additional discussion on genetics and subspecies taxonomy. Likewise, variation in vocalizations and behavioral traits may be more plastic and/or shaped more by environmental variables than those of plumage and morphology (Morton 1975, Hunter and Krebs 1979, McCracken and Sheldon 1997), confounding adequate delineation of species and subspecies boundaries (see also Howell 2012, Pyle 2012). Finally, a robust understanding of variation in these traits across bird populations often suffers from inadequate data.

For my *Identification to North American Birds* series (Pyle 1997, 2008, 2022a), I summarized subspecies diagnoses for species that breed in Canada and the continental U.S. using an integrative evaluation of plumage and



morphology. In 1997, I simply followed the latest appraisals for the recognition of subspecies and became aware of inconsistent methods for diagnosis by different taxonomic authorities. By 2008, I had made an attempt to apply a standardized method of evaluation to subspecies recognition, and I synonymized some previously recognized subspecies (e.g., among those of California Quail, Red Knot, and Least Tern; see the Supplementary Tables files for scientific names). Subsequently, by 2022, I had applied a stricter and more comprehensive methodology (Pyle 2022a:19-20), thoroughly re-evaluating subspecies diagnoses through incorporation of past and current literature, specimen re-examination, morphometric data from banding stations, and examination of images at the Cornell Lab of Ornithology's Macaulay Library (ebird.org/media/catalog). I concluded that (a) many recognized subspecies could not be diagnosed according to the 75% rule and/or (b) their diagnoses had disregarded clinal differences among populations. I thus proposed (Pyle 2022a) that numerous subspecies recognized (by, e.g., Clements et al. 2024) in North America were not practically separable from a phenotypic standpoint. Here I summarize these findings, give primary factors for which I considered subspecies invalid, and propose updated taxonomies. My goal is to provide a baseline for further study, in the form of standardized and objective subspecies taxonomies which attempt to apply the 75% rule to variation in morphometric data and plumage appearance. I present this taxonomy and additional results in Supplementary Tables S1–S3.

Methods

I evaluated subspecific validity based on plumage and morphology for 724 species of native birds treated in the *Identification Guides* (Table S1), species which breed or occur regularly in North America north of Mexico, excluding 19 introduced species treated in those guides. I expanded my evaluations to subspecies of these species that occur in the entirety of North America (including Middle America and the West Indies), in the area covered by the American Ornithological Society's *Check-list* (American Ornithologists Union 1998). I did not evaluate most "extralimital" subspecies of these species, i.e., those occurring strictly in South America, Eurasia, Africa, Australia, and/or the Pacific Basin, although I list nominate subspecies that are restricted to those regions and, for some extralimital subspecies, I propose monotypy for the species as a whole, re-evaluating the validity of extralimital subspecies. I used the species and subspecies recognized by Clements et al. (2024; hereafter "Clements") as a baseline for consideration, including some changes in species and subspecies taxonomy since the *Identification Guides* (Pyle 2008, 2022a) were published. I did not seek to recognize subspecies not currently listed by Clements. I use the word "synonymy" in the traditional sense, recognizing that my evaluation is based solely on plumage and morphology, and that true "synonymization" must also include integration of other factors, such as genetic distances and, possibly, variation in vocalizations and behavioral traits. Such "integrative taxonomy" is frequently applied to evaluation of species vs. subspecies limits (e.g., Howell et al. 2025).

Literature incorporated for this analysis included works cited in the *Geographic variation* accounts in the *Identification Guides* (Pyle 2008, 2022a) and in updated "Systematics" sections of *Birds of the World* (2024) as of May 2025. For species treated by Pyle (2008), I revisited all pertinent literature and consulted recent papers and updated *Birds of the World* accounts, further synonymizing some subspecies that were treated as valid in that guide. I visited 16 major museum specimen collections and examined over 100,000 specimens while summarizing and revising subspecies accounts for the *Identification Guides* (see Pyle 2008: *ix*–*x* and 2022a:*x* for a list of these collections and acknowledgments). For many species, I revisited the collections at the California Academy of Sciences in San Francisco and the Museum of Vertebrate Zoology in Berkeley, California, to further evaluate plumage and morphological variation for this analysis.

Banding data on bird captures, collected by the Institute for Bird Populations' Monitoring Avian Productivity and Survivorship (MAPS) Program (DeSante et al. 2025), on wing length (chord) and mass (>2.1 million records), were examined to assess morphometrics for subspecies in which size was considered a delineating factor. I summarized data from over 576,000 capture records (Table S4) for 114 polytypic

Figure 4 ■ **[TOP TO BOTTOM OPPOSITE PAGE, THEN TOP TO BOTTOM THIS PAGE] Examples of two previously recognized subspecies of Western Gull (*Larus occidentalis*) that have been synonymized here based on clinal variation, e.g., the 75% rule might apply to extremes in the species' geographic range, but variation appeared to be broadly clinal between these extremes, precluding identification of subspecies boundaries. Selected images were limited to those in shade (e.g., under foggy conditions) to reduce the effects of lighting and angle on perceived upperpart color in photographs. Clements et al. (2024) indicate that the boundary between the purported darker southern subspecies (*L. o.* "*wymani*") and the paler northern subspecies (*L. o.* "*occidentalis*") occurs in the vicinity of Monterey Bay, California, but examination of Macaulay Library images indicates that variation in plumage is broadly clinal throughout California. If anything, Western Gulls become noticeably paler in Oregon, perhaps due to broad hybridization with the paraphylectic Glaucous-winged Gull (Bell 1996; see also Howell and Dunn 2007 for a good discussion). All images were taken May–Jun (to standardize effects of plumage wear and bleaching) at or near breeding colonies: a) Ensenada, Baja California. 13 Jun 2017; b) Ventura Co, California. 6 Jun 2023; c) San Francisco Co, California. 20 May 2022; d) Humboldt Co, California. 28 Jun 21; e) Coos Co, Oregon. 23 May 2018; and f) Pacific Co, Washington. 27 May 2020. *Photos cropped for enlarged presentation and used by license agreement from the Macaulay Library © James Maley (a, ML68166061), Grigory Heaton (b, ML610347463), Andrea Nale (c, ML456962961), Chris Conard (d, ML352319691), Carsten Sekula (e, ML494355911), and Mark Vernon (f, ML102571281).***

species with at least 20 captures, ranging from 20 capture records for three species to >50,000 records for eight species and up to >133,000 records for Song Sparrow. I used polygons, of approximately 1° resolution, as defined by latitude and longitude, to assess previously recognized subspecies boundaries. For many subspecies, I further examined subsets of these data to evaluate whether variation in measurements could be clinal, mindful that intermediate measurements are expected in narrow intergradation zones between valid subspecies (Mayr and Ashlock 1991).

To further assess plumage variation, I examined tens of thousands of images cataloged in the Macaulay Library (cf. Pyle 2022b for use of this collection to study birds). To assess the strength of described plumage delineations, I filtered images according to Canadian province, Mexican or U.S. state, county for large states such as California, Arizona, and Texas, and country for Central America and the West Indies, and I consulted images from specific regions within these geographic areas as needed. For resident populations, I restricted the date span to Oct–Dec for cataloged images to compare the fresh plumages of subspecies. For migratory species, I filtered the date span to Apr–Jun or May–Jun to restrict images to birds presumed on breeding grounds of the described subspecies. I carefully considered the effects of angle and lighting in images to assess variation in color tones and plumage patterns (cf. Pyle 2022b); the very large sample sizes of images for most subspecies allow a comprehensive control of these factors. I am fully aware of how variation in plumage wear may affect comparisons of individuals during breeding seasons, but for migratory species, there is no choice, due to mixing of subspecies on non-breeding grounds. These comparisons thus come with the assumption that wear rates will be about equal in individuals, with anomalously worn (or fresh) birds during these periods excluded from consideration.

I examined trends in subspecies validity according to the year in which the subspecies was originally described. I scored each subsumed subspecies for three potential reasons for synonymization: (1) weak variation, i.e., I concluded that the variation described did not approach the 75%

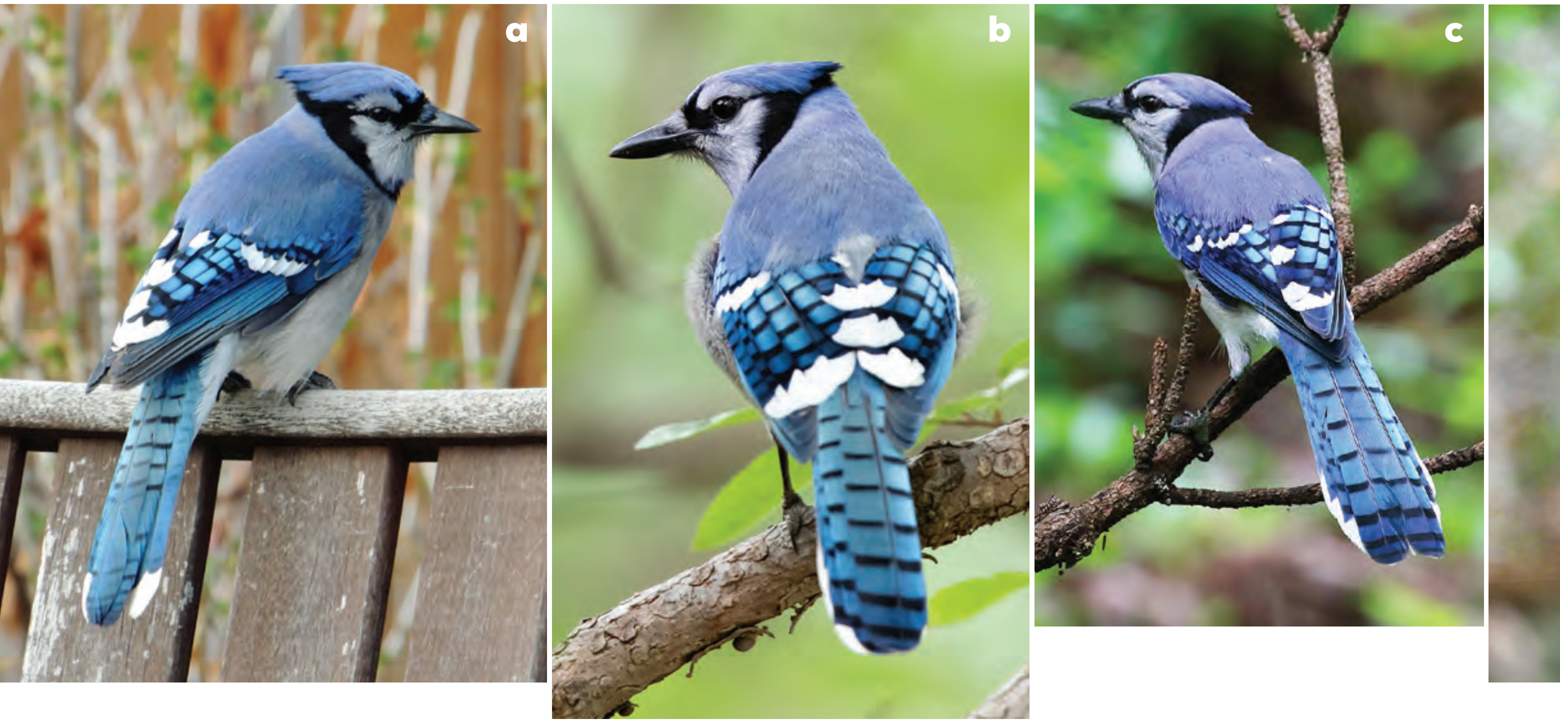


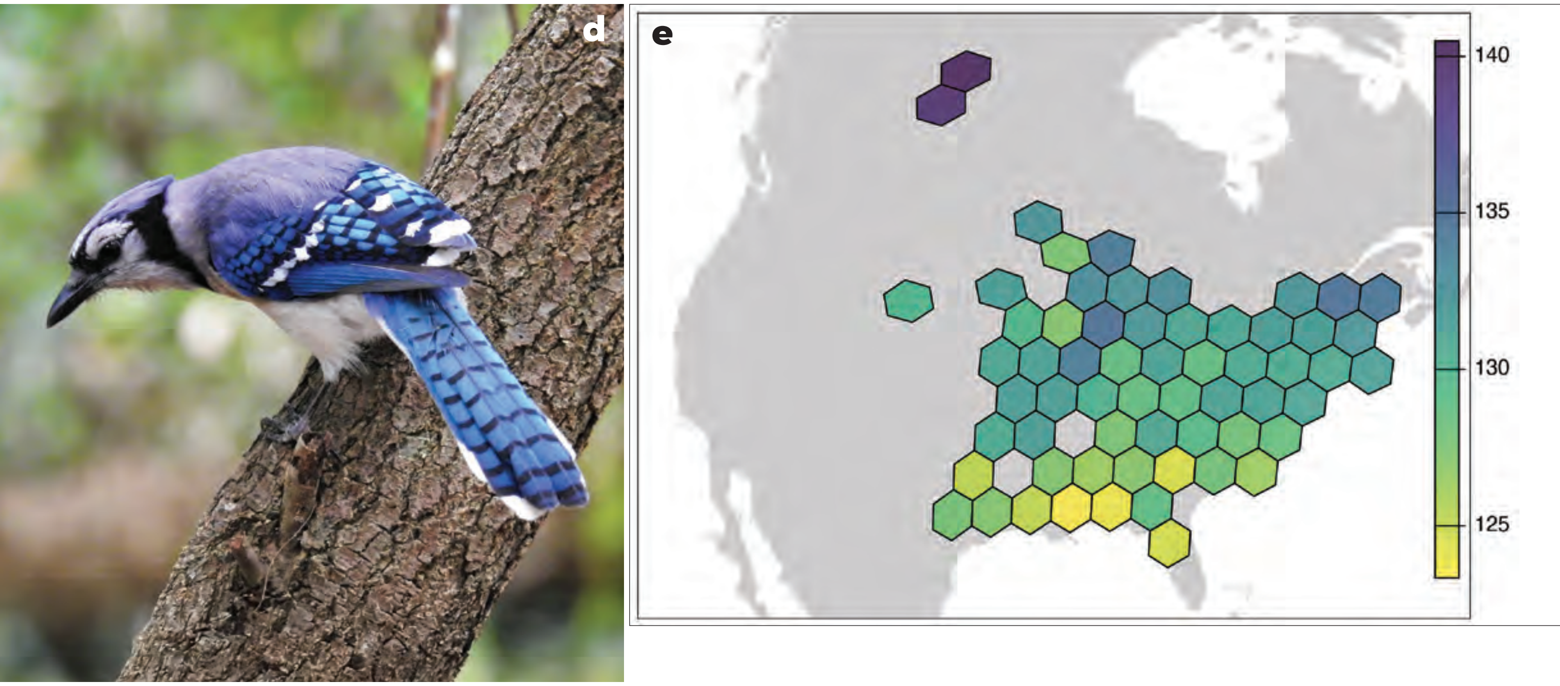
Figure 5 ■ [LEFT TO RIGHT] **Examples of four previously recognized subspecies of Blue Jay (*Cyanocitta cristata*) that have been synonymized here based on all three factors, in order of priority: clinal variation, weak variation, and variable morphometric and plumage characteristics (see also Ridgway 1904, Mengel 1965). All images were taken May–Jun to attempt standardizing effects of plumage wear and to better ensure they represented local breeding populations of this short-distance migrant species: a) *C. c.* "*bromia*". Red Deer, Alberta. 12 May 2019; b) *C. c.* "*cyanotephra*". Collin Co, Texas. 15 May 2020; c) *C. c.* "*cristata*". DeKalb Co, Georgia. 13 May 2019; and d) *C. c.* "*semplei*". PalmBeach Co, Florida. 1 Jun 2018. e) Equal-area hexagonal grid with cells (of approximately 70,000 km^2) representing mean wing chords (mm) calculated from MAPS data (see text) for each cell (minimum 3 adult [AHY] individuals) showing clinal distribution of this measure used to delineate subspecies of Blue Jay. Data parsed by province and state are shown in Table S5). A separate paper is planned using breakpoint analysis or vector machine regression with these MAPS data, to see if morphological divisions can be found that correspond with recognized subspecies boundaries of many North American subspecies.** ***Photos cropped for enlarged presentation and used by license agreement from the Macaulay Library © Ken Gade (a, ML158032491), Mike Cameron (b, ML234957621), Dan Vickers (c, ML267629661), and David Gabay (d, ML102847781).***

rule; (2) variable morphometric or plumage characteristics within subspecies ranges, i.e., actual or perceived standard deviations in variation appeared to be high, precluding diagnosis according to the 75% rule; and (3) clinal variation, i.e., the 75% rule might apply to geographic extremes among two or more described subspecies, but intergradation zones were too broad, precluding identification of subspecies boundaries. For each synonymized subspecies, I assigned a score of 2 for the primary or most influential factor, 1 for the secondary factor, and 0 for the third or least influential factor, or for inapplicable factors, such as clinal variation among allopatric subspecies (Table S3). To investigate how migratory status might have affected subspecies recognition, I scored each species as a resident (little if any migration), short-distance migrant (generally, migration within Canada and the United States), medium-distance migrant (generally, migration from temperate or Arctic North America to Middle America or the West Indies), or long-distance migrant (generally, migration from North America to South America). For species that have populations that span these categories, I chose the migratory status that reflected the majority of the population (see Table S1 for categorization).

Results

A total of 724 species that breed or occur regularly in North America north of Mexico were considered (Table S1). Years in which these species were first described (Table S1) included 1758 (138 species by Linnaeus), 1759–1800 (182 species), 1801–1850 (278 species), 1851–1900 (115 species), 1901–1950 (8 species), and 1951–2023 (2 species). The latest newly described species was Cassia Crossbill (*Loxia sinesciuris*) in 2009. Among these 724 species, 307 were considered monotypic (no subspecies recognized), and 417 were considered polytypic (two or more subspecies recognized) by Clements. Within these 417 polytypic species, Clements recognized 2,291 subspecies worldwide: 417 nominate and 1,873 additional. Once the nominate subspecies and 334 additional extralimital species (see Methods, above) were excluded, 1,539 subspecies remained that I examined for validity. Of these, I propose that 681 (44.2%) are valid, and 858 (55.8%) are invalid (Tables S1 and S2), based on phenotypic evidence and adhering, as best as possible, to the 75% rule. The number of subspecies synonymized included one subspecies for 123 species, two for 46 species, three for 50 species, and up to 14 of 27 subspecies for Horned Lark, 14 of 21 subspecies of Spotted Towhee, and all 14 subspecies (including 3 extralimital subspecies) of Great Horned Owl, which I thus propose as monotypic here (see Fig. 3).

Subspecies recognized by Clements from the northern American region (i.e., Canada and the continental U.S.) were originally described between 1758 and 2012, with peaks of described subspecies occurring during the 1880–1900 and 1930–1940 spans (Fig. 1, Table S2). Three subspecies were described by Linnaeus (1758) as separate species from the nominate subspecies: the Northern Bobwhite subspecies *Colinus virginianus marilandicus* (lumped with *C. v. virginianus* here), the Golden Eagle subspecies *Aquila chrysaetos canadensis* (considered a valid subspecies here), and the Northern Mockingbird subspecies *Mimus polyglottos orpheus* (considered a valid subspecies here). Many other subspecies named during the late 1700s and early 1800s were also originally described as species, whereas others, described as subspecies, were later elevated to species status. A shift occurred around 1890: a majority of subspecies described before this year are treated as valid here, whereas a majority of those described after 1890 are synony-



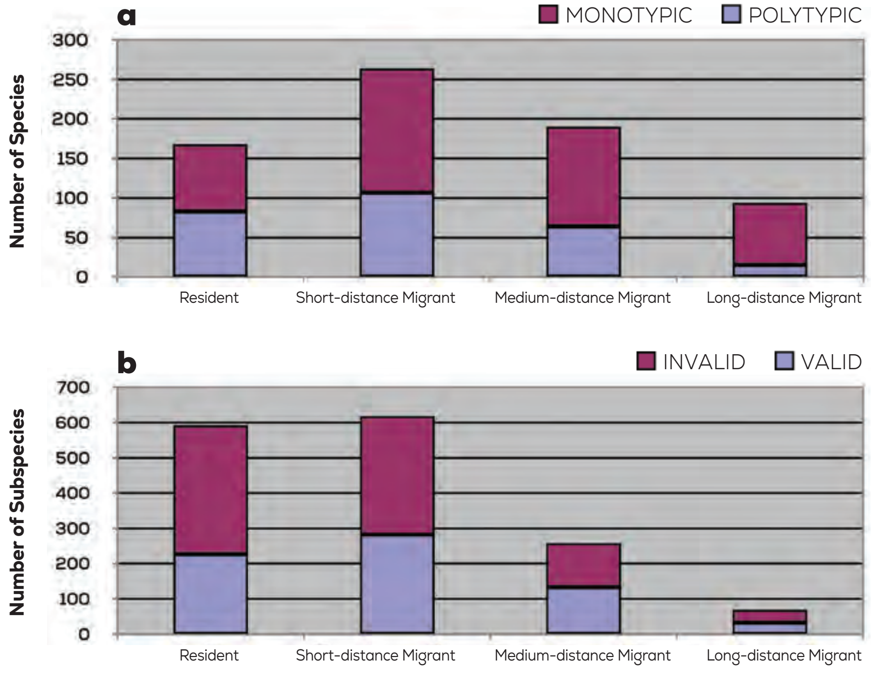


Figure 6 ■ Distribution of subspecies recognition status among surveyed birds according to migratory behavior at the species level. a) Species monotypy (as determined in this analysis) is higher for resident birds and decreases with migration distance. b) There is only a slight effect of migratory behavior on the ratios of subspecies considered invalid or valid according to the analysis herein.

mized here (Fig. 1)—e.g., 66.4% of subspecies described 1758–1890 (399 of 601) but only 29.6% of those described 1891–2012 (280 of 946) are considered valid here.

There were two instances in which species-level taxonomy was affected. I propose synonymizing the Cackling Goose subspecies *Branta hutchinsii taverneri* with the Canada Goose subspecies *Branta canadensis parvipes*, following Palmer (1976; see also Gibson and Kessel 1997, Patten et al. 2003). The type specimen of *taverneri* was collected in California (Delacour 1951), is thus of unknown breeding origin, and shows little phenotypic difference from *B. c. parvipes* (Mlodinow et al. 2008). I also propose Cassia Crossbill to be a subspecies of Red Crossbill rather than a separate species. Unique among North American taxa, nomadic subspecies of this complex have been described based to a large degree on vocalizations (call "types") rather than geographic isolation of breeding ranges (cf. Groth 1993, Hill and Powers 2021, Pyle 2022a, Clements et al. 2024), resulting in assessment of subspecies validity being difficult or impossible according to plumage and morphology. The species-level split of Cassia Crossbill was based, in part, on its reproductive isolation in Idaho (Smith and Benkman 2007, Benkman et al. 2009, Chesser et al. 2017); however, recent reports away from its breeding range, in Colorado and California (e.g. eBird checklists S145328729 and S153766446), suggest that it may be nomadic, as are other described subspecies of Red Crossbill. Here, the subspecies grouped by Pyle (2022a) are proposed as synonymized, resulting in 7 recognized subspecies of Red Crossbill in the northern American region (reduced from 11 taxa recognized in the region by Clements), and including *L. c. sinesciuris*. Subspecies taxonomy in this complex requires further study. This decision results in my evaluating subspecies among 723 rather than 724 species. Another potential decision involving different species would be for the Eurasian Wren subspecies *Troglodytes troglodytes pallescens*, which perhaps should be considered a subspecies of Pacific Wren (Pruett and Winker 2008, Pruett et al. 2017), but as Eurasian Wren is an extralimital species, this subspecies was not considered here.

For the 858 subspecies I propose as invalid, I assigned factors for proposed synonymization as being weak differences between subspecies (cf. Fig. 2), variable phenotypic characters within the ranges of described subspecies (cf. Fig. 3), and/or clinal variation in phenotypic characters (cf. Figs. 4–5), ranking the causes for each subspecies (Table S3). Weak variation was considered one of the two factors in proposed synonymy for 677 subspecies (78.9%), variable phenotypic characters was considered a factor for 547 subspecies (63.8%) and clinal variation was considered a factor for 496 subspecies (57.8%). Weighting the priority for these assessments (1st factor * 2 + 2nd factor) resulted in weak variation accounting for 36.3% (945/2604), variable characters accounting for 34.4% (896/2604), and clinal variation accounting for 29.3% (763/2604) of the reasoning for the proposed synonymizing of these 862 subspecies.

I assessed subspecies validity based on migratory status of the species (see Table S1 for categorization). The proportion of polytypic species decreased with increased migration distance (Fig. 6a), from 50.9% for residents (89/175 species), to 41.1% for short-distance migrants (109/265), to 34.2% for medium-distance migrants (65/190), to 16.0% for long-distance migrants (15/94). However, the proportion of subspecies proposed for synonymization showed only a slight trend relative to migratory status (Fig. 6b), declining with migration distance, from 62.4% for residents (368/590 subspecies), to 54.4% for short-distance migrants (388/619), to 51.5% for medium-distance migrants (123/258), to 47.8% for long-distance migrants (33/68).

Discussion

I propose that 55.8% of the subspecies recognized by Clements et al. (2024) of species that breed in the northern American region be considered for synonymization based on application of the 75% rule. This accords with an estimated 75%

synonymization based on a 95% separation theoretically proposed by Remsen (2010) and is consistent with recent recommendations for synonymization based on critical subspecies evaluations within individual North American species (e.g., Molina et al. 2000, Patten and Unitt 2002, Cicero and Johnson 2006, Rising 2007, Patten and Pruett 2009, Cicero 2020, Ross and Bouzat 2014). Weak differentiation among subspecies was the most prevalent factor in my proposed synonymization (estimated 36.3%), followed by variable phenotypic characters within subspecies (34.4%) and broadly clinal variation (29.3%). However, clinal variation was not considered for allopatric subspecies, and this proportion thus represents an underestimation of what is probably the most important factor in proposed synonymization here (cf. James 1991, Rising 2007, Ennen et al. 2014, Ross and Bouzat 2014, Donald 2021; Figs. 4–5).

Weak differentiation (according to my analysis) appears to be a most prevalent factor in the over-delineation of subspecies described after 1890 (Fig. 1), and this is not including those that have already been synonymized by Clements; e.g., many described by H. C. Oberholser and others (cf. Browning 1978, 1990). During the early and middle parts of the 20th century, avian taxonomists could amass large series of specimens from multiple collections and were able to detect small differences in biometrics and subtle differences in plumage that, while real, may have been applied over-exuberantly to naming or recognizing new subspecies (cf. Pyle 2012). Variation in plumage characters can result from adaptive responses to the environmental conditions (e.g., Bergmann's, Allen's, and Gloger's rules), resulting in phenotypic plasticity that is too localized to be incorporated in subspecies taxonomy (Donald 2021). Ratios of plumage color morphs within a population may also be misapplied to subspecies recognition (cf. Wunderle 1981, Collar et al. 2021), e.g., for subspecies recognition among Great Horned Owls (Fig. 3), Ruffed Grouse, and Common Nighthawks, but not among other North American species such as Snow Geese, Hook-billed Kites, Broad-winged Hawks, or Red-tailed Hawks. Other potentially invalid reasons for subspecies recognition include differences in alternate plumages being related to environmental conditions and timing of molt rather than being intrinsic (Pyle 2008)—e.g., for Ruddy Turnstone, Red Knot, Dunlin, and Yellow Warbler; variable topical application of pink diatomaceous pigment among Red-tailed Tropicbirds (and perhaps similarly, between Western and Eastern cattle-egrets); and over-reliance on seasonally variable coloration in bare parts (e.g., in Great Egret and White Ibis). Other results of this study indicate that gene flow prevents subspeciation to a greater extent in more migratory populations of birds, although this was recognized by previous taxonomists (e.g., Parkes 1955) and is reflected in a lower proportion of longer-distance migrant species than residents or shorter-distance migrants being proposed for synonymization here.

Avian subspecies represent important taxonomic classifications that can be used to delineate populations for conservation purposes (Haig et al. 2006). However, the lack of diagnosability for many North American subspecies can simply lead to confusion, or it may have the opposite effect for conservation, providing reasons for critics to challenge ecological restoration projects. In addition, funding to conserve subspecies may be better spent elsewhere if a subspecies does not differ substantially from other conspecific subspecies (Zink 2004). My goal with this analysis is to propose a practical subspecies taxonomy for bird species in the northern American region—one based on the visible phenotypic characters (plumage and morphology), that can be used by ornithologists, museum workers, banders, birders, and community scientists to collect more accurate data. It is important to note that differences in behavior and vocalizations have not been considered in my analyses; however, these learned traits can be more plastic than those related to measurements and plumage coloration (cf. Sibley 2011, Rheindt and Ng 2021) and were not factors traditionally considered by those defining most subspecies. Likewise, molecular data may certainly be useful for identifying genetically diagnosable conservation units through the development of genoscopes (e.g., Ruegg et al. 2018, Miller et al. 2023), but these may or may not equate with diagnosable subspecific boundaries based on phenotypic factors. This discrepancy presents an interesting future dilemma for the definition of subspecies.

Certainly, inconsistencies in my results will be found. Some subspecies proposed as invalid here will undoubtedly prove valid, and vice versa. Inconsistencies may especially occur in subspecies endemic to Mexico, Central America, and the West Indies, where diagnoses have been based, in many cases, on few specimens and inadequate supplemental data. At the broader level, some may consider my proposed taxonomy as too conservative, but, importantly, it does represent the standard application of subspecific boundaries across all taxa. In these respects, my proposed subspecies taxonomies can be used as anchor points or hypotheses for future research on variability within species or among groups of species.

Acknowledgments

I thank Moe Flannery of the California Academy of Sciences and Carla Cicero of the Museum of Vertebrate Zoology, Berkeley, for access to specimens at these collections and for discussions on subspecies. I thank the thousands of community scientists who have contributed images to the Macaulay Library and for agreeing to allowing their use and publication for research purposes; the use of the Macaulay Library and other community-science based catalogues for avian research is proving valuable and satisfying to those who contribute to such catalogs. I also thank the hundreds of banders and others who provided feedback useful on subspecies and other elements presented in *The Identification Guides* (e.g., see Pyle 2008: *ix–xi* and Pyle 2022: *ix–xiv*) and for contributing data to the MAPS program. Danielle Kaschube of the Institute for Bird Populations provided and helped me summarize MAPS data, and Morgan Tingley of the University of California, Los Angeles, helped prepare Fig. 5e. I thank Steve N. G. Howell, Michael A. Patten, Martin

Freeland, and anonymous reviewers for very helpful manuscript reviews. This is contribution # 776 of the Institute for Bird Populations.

References

Amadon D. 1949. The seventy-five percent rule for subspecies. *Condor.* 51: 250–258.

American Ornithologists' Union. 1983. *Check-list of North American Birds. Sixth edition.* American Ornithologists' Union.

Ball, R. M., Jr and J. C. Avise. 1992. Mitochondrial DNA phylogeographic differentiation among avian populations and the evolutionary significance of subspecies. *Auk.* 109: 626–636.

Bell, D. A. 1996. Genetic differentiation, geographic variation and hybridization in gulls of the *Larus glaucescens-occidentalis* complex. *Condor.* 98: 527–546.

Benkman, C. W., J. W. Smith, P. C. Keenan, T. L. Parchman, and L. Santisteban. 2009. A new species of Red Crossbill (Fringillidae: *Loxia*) from Idaho. *Condor.* 111: 169–176.

Birds of the World. 2024. Edited by S. M. Billerman, B. K. Keeney, P. G. Rodewald, and T. S. Schulenberg. Cornell Laboratory of Ornithology. birdsotheworld.org

Browning, M. R. 1978. An evaluation of the new species and subspecies proposed in Oberholser's Bird Life of Texas. *Proceedings of the Biological Society of Washington.* 91: 85–122.

Browning, M. R. 1990. Taxa of North American birds described from 1957 to 1987. *Proceedings of the Biological Society of Washington.* 103: 432–451.

Cadena, C. D., and F. Zapata. 2021. The genomic revolution and species delimitation in birds (and other organisms): Why phenotypes should not be overlooked. *Ornithology.* 138: 1–18.

Chesser, R. T., K. J. Burns, C. Cicero, J. L. Dunn, A. W. Kratter, I. J. Lovette, P. C. Rasmussen, J. V. Remsen, Jr., J. D. Rising, D. F. Stotz, and K. Winker. 2017. Fifty-eighth supplement to the American Ornithologists' Union Check-list of North American Birds. *Auk: Ornithological Advances.* 134: 751–773.

Cicero, C. 2010. The significance of subspecies: A case study of Sage Sparrows (Emberizidae, *Amphispiza belli*). *Ornithological Monographs.* 67: 103–113.

Cicero, C., and N. K. Johnson. 2006. Diagnosability of subspecies: Lessons from Sage Sparrows (*Amphispiza belli*) for analysis of geographic variation in birds. *Auk.* 123: 266–274.

Clements, J. F., P. C. Rasmussen, T. S. Schulenberg, M. J. Iliff, T. A. Fredericks, J. A. Gerbracht, D. Lepage, A. Spencer, S. M. Billerman, B. L. Sullivan, M. Smith, and C. L. Wood. 2024. The eBird/Clements checklist of Birds of the World: v2024. Downloaded from birds.cornell.edu/clements-checklist/download/

Collar, N. J., P. F. Donald, and G. M. Kirwan. 2021. Species, subspecies or morph– what was the Canary Islands Oystercatcher? *Ibis.* 163: 1500–1505.

Davis, K. E. C., A. E. Settlecowski, M. R. Roeder, C. Enloe, T. Virzi, M. E. Hunter, S. Woltmann, and S. S. Taylor. 2021. Range-wide population genetic analysis of Seaside Sparrows (*Ammospiza maritima*) supports at least five distinct population segments that do not align with current subspecies descriptions. *Ornithological Applications.* 123: 1–15.

Delacour, J. 1951. Preliminary note on the taxonomy of Canada Geese, *Branta canadensis*. *American Museum Novitates.* 1537: 1–10.

DeRaad, D. A., J. M. Maley, W. L. E. Tsai, and J. E. McCormick. 2019. Phenotypic clines across an unstudied hybrid zone in Woodhouse's Scrub-Jay (*Aphelocoma woodhouseii*). *Ornithology.* 136: 1–11.

DeSante, D. F., K. M. Burton, D. Kaschube, P. Velez, D. Froehlich, and S. Albert. 2025. The MAPS manual: 2025 protocols. The Institute for Bird Populations, Petaluma, CA. birdpop.org/docs/misc/MAPSManual25.pdf.

Donald, P. F. 2021. Accounting for clinal variation and covariation in the assessment of taxonomic limits: Why we should remember the 'rules'. *Ibis.* 163: 1106–1109.

Ennen, J. R., M. E. Kalis, A. L. Patterson, B. R. Kreiser, J. E. Lovich, J. Godwin, and C.P. Qualls. 2014. Clinal variation or validation of a subspecies? A case study of the *Graptemys nigrinoda* complex (Testudines: *Emydidae*). *Biological Journal of the Linnaean Society.* 111: 810–822.

Gibson, D.D, and B. Kessel. 1997. Inventory of the species and subspecies of Alaska. *Western Birds.* 28: 45–95.

Groth, J. G. 1993. Evolutionary differentiation in morphology, vocalizations, and allozymes among nomadic sibling species in the North American Red Crossbill (*Loxia curvirostra*) complex. *University of California Publications in Zoology.* 127: 1–143.

Haig, S. M., and K. Winker. 2010. Avian subspecies: Summary and prospectus. *Ornithological Monographs.* 67: 172–175.

Haig S. M., E. A. Beever, S. M. Chambers, H. M. Draheim, B. D. Dugger, S. Dunham, E. Elliott-Smith, J. B. Fontaine, D. C. Kesler, B. J. Knaus, I. F. Lopes, P. Loschl, T. D. Mullins, and L. M. Sheffield. 2006. Taxonomic considerations in listing subspecies under the U.S. Endangered Species Act. *Conservation Biology.* 20: 1584–1594.

Hill, G. E., and M. J. Powers. 2021. Ecomorphs are not species: The case of locally adapted populations of Red Crossbills. *Journal of Avian Biology.*

Howell, S. N. G. 2012. On avian subspecies: Buyer beware? American Birding Association. blog.aba.org/2012/04/sng-howell-on-avian-subspecies-buyer-beware.html

Howell, S. N. G. 2024. New field guides for Central America: purpose and perspective. *Neotropical Birding.* 34: 3–10.

Howell, S. N. G., and J. L. Dunn. 2007. *A Reference Guide to Gulls of the Americas*. Houghton Mifflin.

Howell, S. N. G., J. Vargas, S. Gómez Rosas, and L. Sietz. 2025. The Tres Marías Islands—Mexico's mini-Galapagos. *Neotropical Birding.* 36: 3–21.

Hunter, M. L., and J. R. Krebs. 1979. Geographical variation in the song of the Great Tit (*Parus major*) in relation to ecological factors. *Journal of Animal Ecology.* 48: 759–785.

James, F. C. 1991. Complementary descriptive and experimental studies of clinal variation in birds. *American Zoologist.* 31: 694–706.

James F. C. 2010. Avian subspecies: Introduction. *Ornithological Monographs.* 67: 1–5.

Johnson, O., S. M. Billerman, B. E. Hernández-Baños, D. F. Lane, P. C. Rasmussen, J. V. Remsen, Jr., K. Winker, and R. T. Chesser. 2024. Comments on the species limits of certain North American birds, Part 1. *Bulletin of the British Ornithological Club.* 144: 367–413.

Linnaeus, C. 1758. *Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis,Synonymis, Locis*. Tomus I. Editio decima, reformata. L. Salvii, Holmiae (Stockholm), Sweden.

Mayr, E. 1963. *Animal Species and Evolution*. Belknap Press.

Mayr, E., and P. D. Ashlock. 1991. *Principles of Systematic Zoology.* McGraw-Hill Book Company.

Mayr, E., E. G. Linsley, and R. L. Usinger. 1953. *Methods and Principles of Systematic Zoology*. McGraw-Hill Book Company.

McCracken, K. G., and F. H. Sheldon. 1997. Avian vocalizations and phylogenetic signal. *Evolution.* 94: 3833–3836.

Mengel, R. M. 1965. The Birds of Kentucky. *Ornithological Monographs.* 3: 1–581.

Miller, C. V., C. M. Bossu, J. F. Sarraco, D. P. L. Toews, C. S. Rushing, A. Roberto-Charron, J. A. Tremblay, R. B. Chandler, M. G. DeSaix, C. J. Fiss, J. L. Larkin, S. Haché, S. Nebel, and K. C. Ruegg. 2023. Genomics-informed conservation units reveal spatial variation in climate vulnerability in a migratory bird. *Molecular Ecology.* 109: 1–13.

Mlodinow, S. G., P. F. Springer, B. Deuel, L. S. Semo, T. Leukering, D. Schonewald, W. Tweit, and J. H. Barry. 2008. Distribution and identification of Cackling Goose (*Branta hutchinsii*) subspecies. *North American Birds.* 62: 344–360.

Molina, P., H. Ouellet, and R. McNeil. 2000. Geographic variation and taxonomy of the Northern Waterthrush. *Wilson Bulletin.* 112: 337–346.

Morton, E. S. 1975. Ecological sources of selection in avian sound. *American Naturalist.* 109: 17–34.

Palmer, R. S. 1976. *Handbook of North American Birds. Vol. 2. Waterfowl (Part I).* Yale University Press.

Parkes, K. C. 1955. Sympatry, allopatry, and subspecies in birds. *Systematic Zoology.* 4: 35–40.

Patten, M. A. 2010. Null expectations in subspecies diagnosis. *Ornithological Monographs.* 67: 35–41.

Patten, M. A. 2015. Subspecies and the philosophy of science. *Auk: Ornithololgical Advances.* 132: 481–485.

Patten, M. A., and J. V. Remsen, Jr. 2017. Complementary roles of phenotype and genotype in subspecies delimitation. *Journal of Heredity.* 2017: 462-464.

Patten, M. A., and C. L. Pruett. 2009. The Song Sparrow, *Melospiza melodia*, as a ring species: Patterns of geographic variation, a revision of subspecies, and implications for speciation. *Systematics and Biodiversity.* 7: 33–62.

Patten, M. A., and P. Unitt. 2002. Diagnosability versus mean differences of Sage Sparrow subspecies. *Auk.* 119: 26–35.

Patten, M. A., G. McCaskie, and P. Unitt. 2003. *Birds of the Salton Sea: Status, biogeography, and ecology*. University of California Press.

Phillmore, A. B., and I. P. F. Owens. 2006. Are subspecies useful in evolutionary and conservation biology? *Proceedings of the Royal Society, Series B.* 273: 1049–1053.

Pruett, C. L., and K. Winker. 2008. Evidence for cryptic northern refugia among high- and temperate-latitude species in Beringia: a response to Stewart and Dalén (2008). *Climatic Change.* 86: 23–27.

Pruett, C. L., P. Arcese, Y. L. Chan, A. G Wilson, M. A. Patten, L. F. Keller, and K. Winker. 2008. Concordant and discordant signals between genetic data and described subspecies of Pacific coast Song Sparrows. *Condor.* 110: 359–364.

Pruett, C. L., A. Ricono, C. Spern, and K. Winker. 2017. Island life and isolation: The population genetics of Pacific Wrens on the North Pacific rim. *Condor.* 119: 131-142.

Pyle, P. 1997. *Identification Guide to North American Birds. Part 1.* Slate Creek Press.

Pyle, P. 2008. *Identification Guide to North American Birds. Part 2.* Slate Creek Press.

Pyle. P. 2012. In memory of the avian species. *Birding.* 44(5): 34–39.

Pyle, P. 2022a. *Identification Guide to North American Birds, Part 1, 2nd Edition.* Slate Creek Press.

Pyle, P. 2022b. Examination of digital images from Macaulay Library to determine avian molt strategies: A case study on molts and plumages in eight species of North American hummingbirds. *Wilson Journal of Ornithology.* 134: 52–65.

Remsen, J. V., Jr. 2005. Pattern, process, and rigor meet classification. *Auk.* 122: 403–413.

Remsen, J. V., Jr. 2010. Subspecies as a meaningful taxonomic rank in avian classification. *Ornithological Monographs.* 67: 62–78.

Rheindt, F. E., and E. Y. X. Ng. 2021. Avian taxonomy in turmoil: The 7-point rule is poorly reproducible and may overlook substantial cryptic diversity. *Ornithological Monographs.* 138: 1–11.

Ridgway, R. 1904. The birds of Middle and North America. Part III. *Bulletin of the U.S. National Museum.* 50(3): 1–801.

Rising, J. D. 2007. Named subspecies and their significance in contemporary ornithology. *Ornithological Monographs.* 63: 45–54.

Roeder, M. F., C. E. Hill, C. S. Elphick, M. Conway, A. R. Kocek, A. Tegeler, and S. Woltman. 2021. Genetic data disagree with described subspecies ranges for Seaside Sparrows (*Ammospiza maritima*) on the Atlantic coast. *Ornithological Applications.* 123: 1–14.

Ross, J. D., and J. Bouzat. 2014. Genetic and morphometric diversity in the Lark Sparrow (*Chondestes grammacus*) suggest discontinuous clinal variation across major breeding regions associated with previously characterized subspecies. *Auk: Ornithological Advances.* 131: 298–313.

Ruegg, K. C., R. A. Bay, E. C. Anderson, J. Saracco, R. J. Harrigan, M. Whitefield, E. H. Paxton, T. B. Smith. 2018. Ecological genomics predicts climate vulnerability in an endangered southwestern songbird. *Ecology Letters.* 21(7): 1085–1096.

Ruegg, K. C., M. Brinkmeyer, C. M. Bossu, R. A. Bay, E. C. Anderson, C. W. Boal, R. D. Dawson, A. Eschenbauch, C. J. W. McClure, K. E. Miller, L. Morrow, J. Morrow, M. D. Oleyar, B. Ralph, S. Schulwitz, T. Swem, J.-F. Therrien, R. Van Buskirk, T. B. Smith, and J. A. Heath. 2021. The American Kestrel (*Falco sparverius*) genoscape: Implications for monitoring, management, and subspecies boundaries. *Ornithology.* 138: 1–14.

Sibley, D. S. 2011. Identifying subspecies by behavior–Savannah Sparrow. Sibley Guides. sibleyguides.com/2011/03

Smith, J. W., and C. W. Benkman. 2007. A coevolutionary arms race causes ecological speciation in crossbills. *American Naturalist.* 169: 455–465.

Wiens, J. 1982. Forum: Avian subspecies in the 1980's. *Auk.* 99: 593.

Winker, K. 2010. Subspecies represent geographically partitioned variation, a goldmine of evolutionary biology, and a challenge for conservation. *Ornithological Monographs.* 67: 6–23.

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

Winker K., and S. M. Haig (Editors). 2010. Avian subspecies. *Ornithological Monographs.* 67: 1–200.

Wunderle, J. M. 1981. An analysis of a morph ratio cline in the Bananaquit (*Coereba flaveola*) on Grenada, West Indies. *Evolution.* 35: 333–344.

Yeung, N. W., D. B. Carlon, and S. Conant. 2009. Testing subspecies hypothesis with molecular markers and morphometrics in the Pacific White Tern complex. *Biological Journal of the Linnean Society.* 98: 586–595.

Zink, R. M. 2004. The role of subspecies in obscuring avian biological diversity and misleading conservation policy. *Proceedings of the Royal Society of London, Series B.* 271: 561–564.

Zink, R. M, J. D. Rising, S. Mockford, A. G. Horn, J. M. Wright, M. Leonard, and M. C. Westberg. 2005. Mitochondrial DNA variation, species limits, and rapid evolution of plumage coloration and size in the Savannah Sparrow. *Condor.* 107: 21–28.

Zink, R. M., J. G. Groth, H. Vazquez-Miranda, and G. F. Barrowclough. 2013. Phylogeography of the California Gnatcatcher (*Polioptila californica*) using multilocus DNA sequences and ecological niche modeling: Implications for conservation. *Auk.* 130: 449–458.