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PERSPECTIVE

Species taxonomy of birds: Which null hypothesis?

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ABSTRACT

The polytypic species concept unites populations that theoretically could and would interbreed were the opportunity to arise. This concept places the burden of proof of reproductive incapability and species status on those claiming species or higher rank. Advances in our understanding of the nature of reproductive isolation, the genetics of speciation, the limited role of gene flow, the power of directional selection, and the dynamics of hybridization support a different null hypothesis for taxonomic decisions, one that places the burden of proof on ‘lumping’ rather than on ‘splitting’ taxa at the species level. Switching the burden of proof provides an improved conceptual basis for the recognition of many allopatric island taxa and subspecies groups that merit species status. Taxonomic revisions based on these advances predictably confirm that distinct sister populations once lumped as polytypic species are independent evolutionary lineages that exhibit essential reproductive isolation. Release from the concerns about hybridization also positions proposed species for timely taxonomic decisions. The stage is set to proactively redefine polytypic species to separate component species for the 21st century. The improved species classification will better reflect phylogeny and evolutionary status, characterize biodiversity more accurately, guide improved sampling patterns of bird populations for systematic studies, and enable informed conservation decisions.

Keywords: species taxonomy, hybridization, null hypothesis, reproductive isolation, polytypic species

Taxonomía de especies de aves: ¿Cuál es la hipótesis nula?

RESUMEN

El concepto politípico de especie une poblaciones que, en teoría, podrían reproducirse entre ellas y lo harían si se presenta la oportunidad. En este concepto, la carga de probar la incapacidad de la reproducción y el estatus de especie recae en aquellos que reclaman que a dos poblaciones debe tratarse como especies distintas o asignarles rangos taxonómicos mayores. Los avances en nuestro entendimiento sobre la naturaleza del aislamiento reproductivo, la genética de la especiación, el papel limitado del flujo genético, el poder de la selección direccional y la dinámica de la hibridación apoyan una hipótesis nula diferente para tomar decisiones taxonómicas, que pone la carga de la prueba en el agrupamiento en vez de en la división de taxones a nivel de especie. Este cambio provee una base conceptual mejorada para el reconocimiento de varios taxones alopatricos en islas y de grupos de subespecies que merecen el estatus de especie. Las revisiones taxonómicas basadas en estos avances confirman que, una vez que se agrupan distintas poblaciones hermanas como especies politípicas, tales especies son unidades evolutivamente independientes que exhiben un aislamiento reproductivo esencial. La liberación de las preocupaciones sobre la hibridación también facilita la toma de decisiones taxonómicas oportunas para las especies propuestas. Esta etapa se establece para redefinir proactivamente las especies politípicas con el objetivo de separar las especies que las componen en el siglo 21. La clasificación mejorada de las especies va a ser un mejor reflejo de la filogenia y el estado evolutivo, caracterizará la biodiversidad de manera más precisa, guiará los patrones de muestreo de poblaciones de aves para estudios de sistemática y permitirá la toma informada de decisiones de conservación.

Palabras clave: taxonomía de especies, hibridación, hipótesis nula, aislamiento reproductivo, especies politípicas

Seventy years ago, Ernst Mayr (1942, 1954, 1963) steered the species taxonomy of the world's birds onto a new course with a brilliant integration of classical *Drosophila* genetics, population genetics, and landmark studies of the systematics of island birds based on museum specimens (Futuyma 1994, Gill 1994, Bock and Lein 2005). Together, he and other leaders of the time launched the “Modern Synthesis” with a vision of polytypic species based on

population biology and genetics rather than on typology (O'Hara 1997, Birkhead et al. 2014). Mayr championed the Biological Species Concept (BSC), which portrays species as arrays of local populations that are linked reproductively through exchange of individuals and/or their gametes and progeny (Hastings and Harrison 1994, De Queiroz 2005). Under the BSC, biological species are broad and dynamic entities, or metapopulations, united cohesively by gene

flow in geographical space and in evolutionary time and isolated from other such evolutionary lineages. Thus, “biological species are genetically cohesive groups of populations that are reproductively isolated from other such groups” (AOU 1998:xiv).

In practice, species are split by inferences of reproductive isolation or lumped based on evidence of hybridization, phenotypic similarity, or imagined reproductive compatibility. Evolution of reproductive isolation during periods of reduced gene flow has been the foundation of geographical speciation theory. The criterion of reproductive isolation for species status, however, has broadened in recent years to include populations that exhibit “essential reproductive isolation” (AOU 1998:xiv, Johnson et al. 1999), or “substantial but not necessarily complete reproductive isolation” (Coyne and Orr 2004:30). Hybridizing sister taxa exhibit “essential reproductive isolation” when assortative mating, hybrid inferiority, or other departures from free interbreeding restrict gene flow between them. Departures from free interbreeding prove to be more prevalent and more subtle than our predecessors realized, as I review below. Taxonomic practice, therefore, must continue to accommodate advances in understanding “how properties of genomes, organisms and environments lead to restrictions in gene flow” (Harrison 2012:4).

The Biological Species Concept has long guided taxonomic practice in ornithology, despite decades of discomfort and of proposed alternatives (Cracraft 1989, Gill 1995, Johnson et al. 1999, Coyne and Orr 2004, Remsen 2005, Peterson and Navarro-Sigüenza 2006, Zink 2006). In contrast to revisions of higher-level taxonomy, the contests among taxonomic camps seem to have constrained major revisions of species limits of birds. Ornithologists, however, are not as polarized in the actual practice of taxonomy as one might think. The concept of species as independent evolutionary lineages unifies all species concepts at a primary level, even though operational criteria for delimiting lineages may differ (De Queiroz 2007). Applications of lineage concepts usually include diagnostic characters of morphology and vocalizations that contribute to essential reproductive isolation. Considerations of multiple criteria, such as diagnosability, lineage monophyly, and species recognition blend strict applications of different species concepts into an integrated practice (Payne and Sorenson 2007, Irestedt et al. 2013). Publications in avian taxonomy increasingly accommodate alternative species concepts in the same paragraph and treat different criteria as complementary rather than competitive (Tobias et al. 2010, Sangster 2009, 2013). Features of diagnosability (emphasized under the Phylogenetic Species Concept) actually prevail over assessments of reproductive isolation and the degree of difference as criteria for deciding taxonomic rank for subspecies and

species (Sangster 2013). Applications of the Biological Species Concept increasingly incorporate empirical delimitations of lineage independence, the hallmark of the Evolutionary Species Concept. Together, these factors predictably reveal that populations of birds once lumped within polytypic species are independent evolutionary lineages that qualify as species under all three concepts.

Allopatric populations, including those on separate mountains and other disjunct habitats as well as those on oceanic islands, have challenged Biological Species Concept taxonomy since its initial formulation because, among other issues, one cannot assess reproductive isolation between them (Mayr 1940, Zink and McKittrick 1995, Helbig et al. 2002, Remsen 2010, Tobias et al. 2010, Winker 2010). Whether they be Island Thrushes (*Turdus poliocephalus*) of the western Pacific or montane populations of Common Bush Tanagers (*Chlorospingus flavopectus*) of the Neotropics, differentiated “island” populations aggregate into bloated polytypic species that comprise diagnosable, independent, evolutionary lineages (Peterson 2006, Andersen 2013a). These lineages often qualify for (biological) species status, even though we can only guess whether they are reproductively isolated. The realities of reduced gene flow between “island” taxa favor an assumption of essential reproductive isolation as the default condition. In practice, the delimitation of Evolutionary Species Concept lineages converges with applications of the Biological Species Concept for these avifaunas (Andersen et al. 2013b). As a general rule, therefore, many distinct island taxa merit recognition as valid evolutionary species and biological species until new and compelling evidence is presented to the contrary (Pratt 2010; cf. Remsen 2005, 2010).

Null Hypotheses

Explicit null hypotheses add rigor and clarity to the scientific process (Popper 2002, Prum 2010). With respect to species classifications in ornithology based on the Biological Species Concept, the prevailing, usually implicit, null hypothesis is:

H₀1: Distinct and reciprocally monophyletic sister populations of birds do not exhibit essential reproductive isolation and would interbreed freely if they were to occur in sympatry.

Documentation of essential reproductive isolation, such as assortative mating or hybrid inferiority, provides a basis for the rejection of H₀1 and, in turn, the assignment of species status to divergent populations. Conversely, clinal intergradation and uncompromised introgressive hybridization support H₀1 and deny separate species status for sister populations. Distinct allopatric populations are lumped by default to await critical study and rejection of H₀1 through peer-reviewed publication and debate by

TABLE 1. Current views of major genetic and evolutionary features of speciation in birds differ from those that prevailed in the middle 20th century.

Feature	Assumed importance previously	Assumed importance now
Prezygotic isolating mechanisms	Minor	Major
Postzygotic isolating mechanisms	Major	Minor
Long time to reproductive isolation	Major	Minor
Natural selection	Minor	Major (directional)
Sex-linked genes/Haldane's Rule	Minor	Major
Cultural evolution	None	Major
Sexual/social selection	Minor	Major
Genetic revolution	Major	Not relevant
Founder effects and drift	Major	Minor
Gene flow cohesion	Major	Minor, selection prevails
Hybridization	Major	Minor, sometimes positive
Essential reproductive isolation of sister taxa in hybrid zones	Limited	Likely
Reproductive compatibility of allopatric sister populations	Likely	Limited, due to social and ecological selection

committees of experts. Proposals for splitting 1 species into 2 or more bear the burden of proof for rejecting H_01 , regardless of how obviously those taxa may merit species status (Remsen 2005).

An alternative null hypothesis would be:

H_02 : Distinct and reciprocally monophyletic sister populations of birds exhibit essential reproductive isolation and would **not** interbreed freely if they were to occur in sympatry.

Documentation of free interbreeding is required to reject H_02 and to treat divergent sister populations as conspecifics, whereas predictable features of lineage independence and essential reproductive isolation would support acceptance of species status. Divergent allotaxa would be treated as species by default. Proposals to retain the status of two or more distinct sister taxa as a single species bear the burden of proof for rejecting H_02 , regardless of how subjectively those taxa may have been lumped in the past.

These two null hypotheses are mutually exclusive mirror images of each other. Rejection of H_01 is tantamount to acceptance of H_02 , and vice versa. Choosing one default polarity over the other for operational purposes may seem inconsequential, but there are good reasons to do so. Specifically, advances in knowledge of bird populations and their evolution soundly reject H_01 and strongly favor H_02 as the appropriate default null hypothesis for future testing and rejection.

Advances

Taxonomic decisions are hypotheses about evolutionary relationships and reproductive compatibility of taxa (Zink 2006, Patten 2010). The species taxonomy of birds has benefited from advances in both theory and empirical research (Helbig et al. 2002, Remsen 2010, Yang and

Rannala 2010, Reid and Carstens 2012, Sangster 2013). Present understanding of the major features of speciation in birds differs from that used as a basis for formulation of the Biological Species Concept (Table 1). In 1942, little was known about the history and genetic consequences of range expansions, the roles of phylogeny and lineage sorting, the dynamics and power of social selection (including sexual selection), the nature of reproductive isolation in birds, the architecture of avian hybrid zones, or the ecology and genomics of speciation (Edwards et al. 2005, Price 2008, Ellegren 2013, Nosil and Feder 2013). Projections of monophyly, historical dynamics, lineage independence, and profiles of genetic divergence now supplement the classical character sets used in taxonomic studies. Low levels of gene flow between nonsister taxa are relatively common and are therefore a poor indicator of whether two populations should be considered conspecific. Hybridization between distinct biological species is also a widespread and prevalent phenomenon that does not threaten species status (Grant and Grant 1992, Mallet 2007, Harrison 2012).

Mayr (1942, 1963) viewed species as dynamic populations of individuals stabilized by shared coadaptive gene complexes. Special events were thought to overcome the intrinsic forces of cohesion. Advances in the empirical genetics of bird populations, however, reject the three pillars of Mayr's model of speciation genetics—genetic revolutions, founder effects, and genetic drift. These factors are not driving features of avian speciation (Coyne and Orr 2004, Edwards et al. 2005). Genetic revolutions do not overcome the assumed inertia of coadapted gene complexes and epistasis (Lande 1980). Instead, essential reproductive isolation evolves through simple, additive effects of new genes. Furthermore, founder effects and genetic drift during colonization do not drive genetic diversity or divergence of bird populations, at least to the

extent that was once assumed (Barton and Mallet 1996, Clegg et al. 2002a, Walsh et al. 2005, Price 2008, Balakrishnan and Edwards 2009). Modern theory itself imposes stringent conditions on the potential roles of founder effects and drift in adaptive innovation and radiation (Templeton 2008), but empirical support is predictably scarce (Clegg et al. 2002a, 2002b, Grant 2002, Clegg and Phillimore 2010). Models based on divergence with gene flow are replacing the geographical speciation models in general and the long-accepted allopatric speciation model in particular (Fitzpatrick et al. 2008, Harrison 2012, Winker et al. 2013). Coalescence models allow inference regarding recent histories of divergence with variable levels of gene flow (Wakeley 2008, 2010, Hey 2010) and thus deeper insight into the speciation process than was possible with classical constructs based simply on spatial distribution (Harrison 2012).

Our understanding of reproductive isolation in birds also has advanced well beyond the ingredients of the Modern Synthesis, which emphasized postzygotic isolation. Neither genetic divergence as espoused by Mayr nor the intrinsic postzygotic barriers championed by Dobzhansky (1951) prevail as key features of the speciation process in birds. Unlike mammals and fruit flies, birds typically retain genomic compatibility, hybrid viability, and fertility for millions of years (Prager and Wilson 1975, Edwards et al. 2005, Price 2008, González et al. 2009). Complete loss of F_1 hybrid fertility in birds takes millions of years; hybrid inviability takes longer to manifest by an order of magnitude. Even nonsister species and those in different genera of ducks, fowl, hummingbirds, buntings, and others hybridize successfully. Consequently, the propensity of birds to evolve intrinsic reproductive isolation does not predict the rate at which they form new species over geological timescales (Rabosky and Matute 2013). Instead, birds speciate before they achieve hybrid sterility or hybrid inviability (Price and Bouvier 2002, Lijtmaer et al. 2003, Edwards et al. 2005).

Prezygotic incompatibilities, including those in social signals and ecology, are the primary ingredients of essential reproductive isolation in birds (Edwards et al. 2005, Price 2008). Postzygotic reduction of hybrid fitness—including disparities in courtship behavior, migration patterns, habitats, and ecological physiology, or genetic incompatibilities in backcross generations—supports the evolution of prezygotic isolating mechanisms. Sexual selection and social selection lead the speciation process in birds, mediated by cultural processes such as imprinting and song learning (Zink 1996, Paterson 1985, Carling and Brumfield 2008, Price 2008). Advances in genomics focus on the roles of sex-linked genes, including Haldane's Rule, and speciation genes that control traits such as plumage and vocalizations (Edwards et al. 2005, Wolf et al. 2010, Nosil and Schluter 2011). Mutations of regulatory and

“switch” genes bypass the hypothesized barriers of epistasis to effect significant changes in prezygotic compatibility. Local adaptive shifts to new climates, habitats, temporal cycles, and assemblages of species also may promote reproductive isolation (Funk et al. 2006, Price 2008, Schluter 2009, Nosil 2012).

Hybridization and Essential Reproductive Isolation

Regarding the interpretation of hybridization, we emphasize that a significant number of undisputed biological species of birds long retain the capacity for at least limited interbreeding with other species, even non-sister taxa (Prager and Wilson 1975, Grant and Grant 1992). Therefore, the occasional occurrence of hybridization, even between taxa that the Committee has long recognized as species, by no means diminishes the biological reality of their essential reproductive isolation. In practice, interbreeding has not been the ironclad determinate of conspecificity that some would believe. Thus, essential (lack of free interbreeding) rather than complete reproductive isolation has been and continues to be the fundamental operating criterion for species status by workers adhering to the BSC. (AOU 1998:xiv)

Advances in understanding of the speciation process, including the prevalence and consequences of interspecific hybridization among birds, reaffirm the (American Ornithologists' Union's [AOU's]) policy of dismissing narrow hybrid zones as evidence of conspecificity. More broadly, the extent and consequences of hybridization are not easily assessed. They add little value to species threshold decisions, even beyond the Phylogenetic Species Concept view that hybridization is a shared, ancestral feature (see Remsen 2005, Zink 2006 for points/counterpoints). {Note: I confine the term 'hybridization' to interbreeding between distinct taxa that actually or potentially qualify for species rank (McCarthy 2006), as opposed to broad (clinal) intergradation among populations traditionally treated as subspecies.}

First, hybridization by undisputed bird species is widespread (Grant and Grant 1992). Well-documented cases of it rarely invalidate species status in ornithology, with few exceptions. In one case, the Blue Goose (*Anser caerulescens*) and Snow Goose (*Anser [Chen] hyperborea*) were essentially allopatric in distribution until ~70 years ago, when their populations expanded. Now they are sympatric and behave as a single species, with extensive gene flow causing the color types to vary in frequency across much of the species' range (Mowbray et al. 2000). Ornithologists retain many separate species that hybridize

with extensive introgression. Widespread, interspecific hybridization by waterfowl (Anseriformes), usually incidental but sometimes extensive, does not threaten status as a species (Tubaro and Lijtmaer 2002, McCarthy 2006, Winker et al. 2013). Unambiguous species, such as the (introduced) Mallard (*Anas platyrhynchos*) and Pacific Black (Gray) Duck (*A. superciliosa*) in New Zealand, hybridize extensively with extensive bilateral introgression (Rhymer et al. 1994, Williams and Basse 2006), to the extent that Pacific Black Ducks are in danger of extinction in New Zealand due to genetic assimilation and ecological replacement by Mallards. No authorities consider them to be conspecific. Similar cases abound on the most authoritative regional and world bird lists.

Second, modern studies of the genetic architecture of avian hybrid zones typically reveal a lack of free interbreeding by some combination of assortative mating, subtle selection against hybrids, ecological displacement, or gene-dependent introgression (Harrison 1993). Essential reproductive isolation is the expected and default condition in hybrid zones; few sister taxa of birds interbreed freely or fuse via zones of secondary contact. Instead, hybrid zones serve as population sinks or tension zones that reflect ecological and other fitness differences among parental genotypes and their hybrid offspring (Moore and Price 1993, Wiebe 2000). Rarely also does interspecific hybridization lead to hybrid speciation, as in the Audubon's Warbler (*Setophaga [coronata] auduboni*; Brelsford et al. 2011) and Italian Sparrow (*Passer italiae*; Elgvin et al. 2011, Hermansen et al. 2011), although admittedly this phenomenon may be underestimated because of the difficulties of demonstrating it (Harrison 2012). More often, one expanding taxon eliminates the other following transient or wave front hybridization accompanied, or not, by assimilation or incorporation of some genes of the replaced taxon (Rhymer and Simberloff 1996, Rohwer et al. 2001, Gill 2004).

Third, introgression due to interspecific hybridization contributes advantageously and more extensively to speciation than was previously recognized (Dowling and Secor 1997, Rheindt and Edwards 2011). The "semipermeable" genetic architecture of hybrid zones allows free exchange of some genes and genomes, but not others that are subject to negative selection (Harrison 2012). Neutral (nuclear) genes, for example, are more likely to be introgressive than mtDNA genes due to Haldane's Rule or selection against sex-linked genes in the heterogametic sex (e.g., Carling and Brumfield 2008). Alternatively, advantageous mtDNA of one species may sweep through and replace that of the other species as a positive source of climatic adaptation (Zink and Barrowclough 2008, McKay and Zink 2010, Rheindt and Edwards 2011). Even low or episodic pulses of hybridization between divergent sister species can provide beneficial gene exchange without

fusion (Weckstein et al. 2001, Peters et al. 2013, Toews et al. 2013).

Essential reproductive isolation is the well-established prognosis for candidate species even when hybridization is reported, yet debates about species status still defer to concerns about hybridization in contact zones. For example, consider the fate of the model AOU's proposal (NACC 2009-A-2) to split the Woodhouse's Jay (*Aphelocoma [californica] woodhousei*) from the Western Scrub-Jay (*Aphelocoma californica*). It failed to achieve the two-thirds majority of votes by committee members that is required for approval. The defining question was: How much hybridization takes place between Woodhouse's Jays and California Jays in a small, but unstudied, contact zone in the Pine Nut Mountains of extreme western Nevada? The prevailing (5/12) 'No' votes focused on possible hybridization because, to paraphrase committee comments posted on the AOU's website (http://www.aou.org/committees/nacc/proposals/2009_A_votes_web.php#2009-A-2), 'what occurs in that narrow zone of contact is a critical and underdeveloped aspect of an otherwise strong case for species status.' Recent studies of the jays in the contact zone support the majority prediction of restricted introgression and species status (Gowen et al. 2012). A backlog of such cases of undecided species status awaits attention (AOU 1998, Hockey et al. 2006, Christidis and Boles 2008, Remsen 2013).

The advances in the documentation of hybridization and its consequences in birds negate its value as a primary criterion for conspecificity. The burden of proof should fall instead on the explicit definition and documentation of free interbreeding. Given today's standards, historical samples of hybrid specimens from localities of presumed secondary contact are not sufficient to judge whether two taxa interbreed freely. Required instead are field studies that fully take into account (1) subtle forms of selection against hybrids (Brelsford and Irwin 2009), (2) variable dynamics of introgression of nuclear DNA and mtDNA genes, including selection against some but not others, (3) paternity issues that cloud assessments of levels of hybridization and assortative mating based on field observations of socially paired birds (Gill 2004, Vallender et al. 2007), (4) geographical mosaics in the amount of essential isolation, (5) time lines of transient hybridization, and (6) the positive consequences of interspecific introgression between taxa that continue to be recognized as biological species.

Gene Flow and Selection

Ornithologists loosely invoke gene flow as a criterion for conspecificity. Although sometimes significant (Kisel and Barraclough 2010), gene flow generally does not explain phenotypic uniformity at large scales, nor does it unite allopatric bird populations as cohesively as was hypothe-

sized in the Modern Synthesis. However, rigorous metrics are still needed for defining how much actual gene flow is, or is not, allowed between recognized species. Stringent theoretical conditions underpin the hypothesis that gene flow is a powerful force of cohesion; these conditions are not often manifest in natural populations (Miles and Allendorf 2002). Inadequate time to complete lineage sorting and to diverge by natural selection is responsible for many patterns of genetic uniformity that previously were attributed to cohesive gene flow or panmixia (Rheindt and Edwards 2011). Instead, speciation histories are revealed by partitioning ancestral retention of genes from estimates of current gene flow (Hung et al. 2012). Historically recent range expansions or replacements of locally extinct (sink) populations are responsible for the lack of genetic population structure of many widespread, seemingly highly mobile species (Diamond 1980, Mayr and Diamond 2001, Clegg and Phillimore 2010). Thus, populations of temperate zone species that have expanded their ranges since the last glaciations tend to be unstructured or to carry signatures of their historical refugia (Gill et al. 1993, Zink 1997, Perktas et al. 2011). Conversely, historically (more) stable, tropical bird species tend to exhibit deeper population structures than their temperate counterparts (Tobias et al. 2008). As a result, phylogeographic population structures may contradict the boundaries of classical subspecies taxonomy (Seutin et al. 1993, Avise 2000).

Many variables reduce the effective exchange of individuals among conspecific populations (potential gene flow) and consequent, or realized, gene flow, i.e. the actual incorporation of immigrant alleles into the gene pool of the recipient population (Futuyma 2009, Harrison 2012). Defined as “reduced survival of immigrants upon reaching foreign habitats that are ecologically divergent from their native habitat” (Nosil et al. 2005:705), immigrant inviability reduces realized gene flow and increases essential reproductive isolation (Grant 2002, Price 2008, Harrison 2012). Immigrants may also be disadvantaged by the physiological costs of dispersal (Harrison 2012). Among the costs, new island colonists are compromised as agents of gene flow from the source population due to reduced prospects for social integration and survival as well as for breeding with established individuals (Clegg 2009). Conversely, established predecessors have an advantage due to prior social selection and adaptations to local diseases, parasites, predators, and other “enemies” (Ricklefs 2005). Pleiotropic effects of the genes involved in ecological adaptations contribute to reduced gene flow and to essential reproductive isolation (Schluter 2009, Nosil 2012). Alternatively, mtDNA genes that directly control physiological adaptations may sweep through founding populations and be closed to future gene flow from source

populations by Haldane’s Rule (Rheindt and Edwards 2011, Ribeiro et al. 2011).

Finally, gene flow may actually advance the speciation process by increasing genetic variation in recipient populations (Irwin et al. 2001, 2005, Church and Taylor 2002, Gavrillets and Gibson 2002, Toews et al. 2013). In their studies of the potentially opposing trends of “fission” versus “fusion” in Darwin’s finches (*Geospiza* spp.), Grant and Grant (2008a, 2008b, 2010) concluded that gene flow among finch populations does not constrain phenotypic divergence. Conversely, gene flow augments genetic variation and facilitates local evolutionary divergence due to natural selection. The adaptive radiation of Darwin’s finches has occurred either despite or, perhaps, thanks to ongoing low levels of gene flow.

It follows that divergence due to natural selection and sexual selection typically trumps uniformity due to cohesive gene flow or divergence due to genetic drift (Barton and Mallet 1996, Coyne and Orr 2004, Phillimore et al. 2008, Clegg and Phillimore 2010, Seddon et al. 2013, Uy et al. 2013). Even modest directional selection for heritable traits overrides gene flow at surprisingly local geographical scales and climatic gradients (Gill 1973, Postma and Noordwijk 2005, Clegg and Phillimore 2010, Milá et al. 2010, Sly et al. 2011, Myers et al. 2012, VanderWerf 2012). New colonists of island environments are generally promptly subject to directional selection both for generic traits of island songbirds, including shorter wings and longer bills, and for new social and ecological relationships (Wright and Steadman 2012).

Episodes of directional selection affect the evolution of bird populations more dramatically than was envisioned in the early days of the Modern Synthesis. In their classic studies of Darwin’s finches in the Galápagos Islands, Grant and Grant (2008a) documented the pulses of intense natural selection on the local populations. El Niño–Southern Oscillation (ENSO) cycles of drought and rainfall cause dramatic changes in seed sizes and availabilities that favor individuals of different bill sizes, which in turn affects individual vocalizations and mate choice. Like the Galápagos finches, the population of Silver-eyes (*Zosterops lateralis*) on Heron Island off northeastern Australia experiences major pulses of selection due to tropical cyclones and ENSO climate cycles (Clegg et al. 2008). In this case, pioneering Silver-eyes and their descendants responded initially to directional selection with a shift to a new optimum phenotype, followed by stabilization under generally weak directional selection.

In summary, the role of gene flow as a dominant source of cohesion in bird populations has been overestimated. Empirical data on the genetic structure of bird populations highlight the roles of historical range expansions and directional selection in defining patterns and pace of geographic variation and the potential for speciation. Bird

populations respond to directional selection at greater intensities and at more local geographical scales than was fully appreciated in the formulation of the Modern Synthesis.

The Polytypic Species Concept Revisited

Many mergers in the early days of the biological species concept were not based on strong biological evidence. We have retained the merged species because in most instances strong evidence for re-division has not been presented. (AOU 1998:xii)

The number of extant bird species recognized currently ranges from 9,721 (Dickinson 2003) to 10,507 (Gill and Donsker 2013). Dozens of species are added each year with discoveries of new cryptic species and as we chip away at the backlog of polytypic species. However, the stage is set to boldly revisit polytypic species worldwide with the goal of partitioning avian diversity consistently and comprehensively into species units that correspond more closely to their evolutionary history, current geography, and ecology. The backlog of polytypic species awaiting attention due to historical inertia is large, and the pace of taxonomic decisions—some straightforward, some difficult—is painfully slow (Navarro-Sigüenza and Peterson 2004). Proposals to separate polytypic species into component and valid species are handicapped by an inadequate workforce, insufficient modern specimen resources, stringent documentation of hallowed species status, and adherence to an obsolete null hypothesis. Can we instead move forward predictively based on the body of case studies of speciation in birds, and especially the advances of the past 30 years? Can we compile an improved working baseline of distinct bird taxa that meets approved criteria for species status based on a default prediction of essential reproductive isolation? Bird taxonomy, of course, is not the only discipline being challenged; so too is the taxonomy of other classes of vertebrates. For example, *Rana pipiens* is now 28 species (Moore 1944, Pace 1974, Hillis 1988, Newman et al. 2012) and *Plethodon glutinosus* is now at least 16 contiguous species (Highton et al. 1989).

Our “modern” classification of bird species remains rooted in morphological descriptions of new taxa that accumulated throughout the 19th century to a zenith of 18,937 (Sharpe 1909, Allen 1910). Aggregation of conspecific age and sex classes, seasonal plumages, and geographical subspecies followed the growth of museum collections and maturing of scientific ornithology from 1900 to 1940, including Robert Ridgway’s (and Herbert Friedmann’s) insightful work, *The Birds of North and Middle America* (1901–1950). But then the eager applica-

tion of a broad polytypic species concept caused wholesale lumping of similar allopatric taxa. The world list of birds shrank to a nadir of 8,616 (Mayr 1946, Mayr and Amadon 1951). In particular, Peters’ *Checklist of Birds of the World*—the cornerstone of 20th century ornithology—left a legacy of polytypic species that regrettably distorts estimates of biodiversity, speciation, and conservation status (Pratt 2010, Tobias et al. 2010).

Maintaining what we know to be wrong in the name of conservative stability is not an appropriate option. Fortunately, a new era of analysis of polytypic taxa is under way. Fully empowered studies predictably reveal distinct species that have long been buried as subspecies. Details of genetic divergence, biogeography, plumage patterns, and vocalizations provide improved criteria for species diagnosis. Recent examples include Philippine owls (Miranda et al. 2011, Rasmussen et al. 2012), Thrush-like Schiffornis (*Schiffornis* spp.) of Latin America (Nyári 2007, Remsen 2013), *Scytalopus* tapaculos of the Andes (Krabbe and Cadena 2010, Hosner et al. 2013b), and many others. Phylogenetic analyses unravel colonization histories, independent lineages, and patterns of speciation (Reddy 2008, Rheindt and Eaton 2009, Perktas et al. 2011, Sánchez-González and Moyle 2011, Andersen et al. 2013a, 2013b, Hosner et al. 2013a, Irestedt et al. 2013). Rigorous sets of evolutionary lineages replace the original projections of reproductive isolation and evolutionary independence. Differences between sympatric, congeneric species in morphology and vocalizations, supplemented by DNA divergences, help us to calibrate new thresholds of species status (Isler et al. 1998, Helbig et al. 2002, Tobias et al. 2010, Amei and Smith 2013). The revised classifications, which in the New World will resurrect the insights of Robert Ridgway and other giants on whose shoulders we stand, better reflect phylogeny and evolutionary status, more accurately define biodiversity, guide improved DNA sampling patterns of bird populations, and enable informed conservation management (Peterson 2006, De Queiroz 2007).

Maintaining the criteria and publication process for managing descriptions of newly discovered cryptic species of antpittas and tapaculos, among others, is an ongoing and vital process that continues strong traditions. At the other end of the spectrum, however, are famously bloated polytypic species such as the Horned Lark (*Eremophila alpestris*; 42 subspecies) and Island Thrush (*Turdus poliocephalus*; 51 subspecies). In 1 such case, the 15 allopatric subspecies of the Variable Dwarf Kingfisher (*Ceyx lepidus*) of western Pacific islands are morphologically distinct and genetically more differentiated (2.6–6.8% based on ND2 sequences) than 2 closely related sister species. All are eligible for species rank (Andersen et al. 2013b). Similarly, the island populations of the Red-bellied Pitta (*Erythropitta erythrogaster*) may comprise 17

or more species (Irestedt et al. 2013). Regionally, the avifauna of the Philippine islands is rich in classical polytypic species that arguably are among the most overlumped in the world (Peterson 2006, Collar 2011, Brown et al. 2013). The region's bird list grew slowly at first from 450 species (Delacour and Mayr 1946) to 572 (Kennedy et al. 2000), but renewed fieldwork supplemented by DNA analyses of speciation and historical biogeography is fragmenting species complexes into their components. Both recent discoveries of new species and revisions of polytypic species have added dozens of species to this avifauna in the last 10 years, with many more to come (Sánchez-González and Moyle 2011, Rasmussen et al. 2012, Andersen et al. 2013a, 2013b, Hosner et al. 2013a, 2013b).

How then can we proceed boldly as a discipline of taxonomic progress, not taxonomic inflation (Sangster 2009)? Improved standardization and transparency of species taxonomy, informed by current research, is essential (Helbig et al. 2002, Remsen 2005). Advances in our knowledge of birds, however, favors acceptance of essential reproductive isolation and lineage independence as default expectations in the practice of species taxonomy. Acceptance of this strongly supported proposition would move aside the anchors of hybridization analysis and classical deference to possible gene flow. Most importantly, we would be able to take command of the legacy of polytypic species that distorts the taxonomy of birds. Yes, defaulting to H_0 will occasionally produce splits that will be reversed upon further study, but occasional, correctible oversplitting is preferable to continuing the inertia and inappropriate lumping of valid bird species.

Adoption of this working proposition will accelerate the inventory of species to a needed new baseline founded on consistent application of consensus-based metrics of species taxonomy within an improved framework of a unified species concept and an informed null hypothesis. Taxonomic decisions must be independent of their applications in research and conservation. Accordingly, species recognized via the proposed default hypothesis will be more useful on average for current research than are today's recognized species, which tend to obscure variations that evolutionary biologists, ecologists, behaviorists, and conservation biologists find interesting and important. From a purely practical standpoint, changing the null hypothesis will shift priorities to studies of the genetic architecture of speciation instead of continuing to confirm predictions of essential reproductive isolation. Finally, and best of all, conservation priorities will be based on an improved foundation of avian diversity, genetics, and evolution (Rojas-Soto et al. 2010). The birds themselves will benefit from one small paradigm shift that embraces the advances in ornithology that Ernst Mayr himself

spearheaded 70+ years ago. The remaining birds of the world deserve no less.

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