PATTERN, PROCESS, AND RIGOR MEET CLASSIFICATION

Author: Remsen, J. V.

OVERVIEW

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J. V. Remsen, Jr.[1]

Museum of Natural Science, Foster Hall 119, Louisiana State University, Baton Rouge, Louisiana 70803, USA

That closely related, sympatric bird species have different voices has been known since the earliest days of ornithology and was presumably known to early humans. Indigenous peoples routinely distinguish similar-looking species by vocal differences. On the other hand, age, sex, individual, and ecological differences in vocalizations are also known, in addition to regional dialects, which themselves may change through time. So, the critical question is: how different must vocalizations be to represent barriers to gene flow? In terms of speciation models, how divergent must vocalizations be to facilitate reproductive isolation?

To address this question, Isler et al. (1998) compared vocal characters between eight pairs of syntopic antbird (Thamnophilidae) species to search for objectively definable differences in vocalizations associated with an absence of gene flow. They studied congeners, presumed sister species in many cases, having both minimal plumage differences and superficially similar primary vocalizations. Their goal was to determine whether closely related taxa ranked as species by any criterion showed common patterns of vocal differences. They analyzed all available vocalizations in a species' repertoire and quantified spectrographic differences between homologous vocalizations in each species to generate an objective index of diagnosability for each character. From those comparisons, they determined that no single character was diagnosably different in all eight species pairs, but that within each pair, the members were diagnosable in at least three characters of the primary song ("loudsong") or calls. The broader goal of Isler et al. (1998) was to establish an objective framework for taxonomic ranking of allopatric antbird taxa. Their strategy was to take their findings from known "good" species and apply them in a comparative framework to the thorniest problem of the Biological Species Concept, the ranking of allopatric taxa (Mayr 1942). This methodology allows an objective, reproducible classification of allopatric thamnophilid taxa (e.g. Krabbe et al. 1999; Isler et al. 2001a, b, 2002; Isler and Isler 2003; Whitney et al. 2000).

A severe test of their system is the appropriately christened Variable Antshrike (*Thamnophilus caerulescens*), which shows extreme geographic variation in color, with a dramatic change in male plumage from mostly black to gray-and-white within 400 km in Bolivia. Although Cory and Hellmayr (1924) considered the Bolivian populations to represent three distinct species, subsequent classifications from Peters (1945) to Zimmer and Isler (2003) have treated the entire complex, from Peru to Argentina, as a series of subspecies-level taxa constituting one biological species because of the step-clinal nature of plumage variation; the nature of contact between adjacent subspecies, however, has never been studied. Because the taxa are not allopatric, but parapatric, and levels of gene flow can be measured and compared with vocal diagnosability, the Variable Antshrike provides a test of the Isler-Whitney classification scheme.

In this issue of *The Auk*, Robb Brumfield and Mort and Phyllis Isler (Brumfield 2005, Isler et al. 2005) present their analyses of genetics and vocalizations of the Variable Antshrike across the steep geographic gradient of plumage types in Bolivia. They analyzed recordings from 154 individuals and sampled mitochondrial DNA (mtDNA) from 126 individuals within that gradient, a remarkably rigorous sampling regime. Their composite findings represent the most detailed assessment of fine-scale geographic variation in a tropical bird, perhaps surpassed only by work on the White-bearded Manakin (*Manacus manacus*) complex (e.g. Parsons et al.

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[1]E-mail: najames@mail071.lsu.edu

403

1993, Brumfield et al. 2001, McDonald et al. 2001). Briefly, vocalizations and mtDNA show concordant patterns of transition between parapatric taxa, and those patterns are, in turn, concordant with plumage patterns. In other words, each plumage-based subspecies of *T. caerulescens* differs slightly in its genetic and vocal characters; nonetheless, a comparison of the geographic extremes reveals no species-level differences in vocalizations, as defined by the criteria of Isler et al. (1998).

Isler et al. (2005) have also shown, for the first time, that vocal characters can vary clinally in a suboscine passerine and that this variation parallels a step-cline in plumage characters. Even within a subspecies, vocalizations vary between sample points in a manner consistent with points along a cline. That finding provokes questions concerning the pattern and mechanism of inheritance of vocal characters in suboscines, especially as to whether songs are inherited as a single character or as a series of separate characters each with its own genetic basis. From the practical standpoint of assessing species limits in suboscines by comparing vocalizations, the message is clear. Broad geographic sampling is required to assess questions of species limits, and, as with other kinds of geographically variable characters, it is not acceptable to compare vocalizations from distant localities and then assume that they represent a taxon as a whole, much less the intervening localities.

Importance of Vocal Characters in Classification

Because vocalizations in suboscines are assumed to be inherited characters, not learned, they have been used frequently in assessing species limits and providing clues to genetic discontinuities among suboscine populations. The Isler-Brumfield study on *T. caerulescens*, with its concordance between vocal and genetic data sets, strengthens the case for their continued use in this regard.

Similar use of vocal characters in the oscine passerines has been less enthusiastic, because oscine song is learned, not inherited (as far as we know from the limited taxon-sampling so far; Kroodsma 1988, Kroodsma and Konishi 1991), and cultural transmission of song types is well documented (e.g. Grant and Grant 1996, Payne 1996). Although cultural transmission of certain aspects of oscine song complicates their analysis, dismissal of song in oscines as inappropriate for assessing gene flow ignores experimental research that reveals an innate predisposition for learning the song of the parental population despite the ability to learn other species' songs (reviewed by Baptista 1996, Baptista and Kroodsma 2001); that innate preference has also been shown to extend to the subspecies level (Nelson 2000). The existence of such a genetic predisposition is strongly predicted from the natural-history observations that oscine birds routinely learn their own species' song rather than those of syntopic species during the critical learning period. Therefore, studies of gene flow and song variation in oscines should emphasize macrogeographic patterns (again, broad sampling is indicated), and careful attention should be paid to identification and interpretation of any local variations (i.e. dialects) that could potentially cloud the picture.

Use of vocal characters as indirect measures of gene flow and species limits has several pragmatic advantages as well. In contrast to specimen-based data, vocal data can be collected easily, quickly, and with minimal bureaucratic complications or disturbance of the birds. Note that recordings should not be considered a replacement for genetic sampling, but rather an additive contribution that provides geographic texture beyond the scope of most genetic studies. For species that vocalize frequently, data can be gathered from more individual birds in a given period than with any other sort of data. A recordist can easily carry all necessary equipment anywhere, and physical and political obstacles are greatly reduced in comparison with the case of researchers seeking genetic samples. Thus, the geographic scope of vocal sampling is potentially much greater. Importantly, data can be gathered by a growing army of amateur recordists, provided that they use equipment of sufficient quality, whose data can be deposited in centralized digital archives for future analysis. For example, the Macaulay Library (formerly the Library of Natural Sounds) at the Cornell Laboratory of Ornithology archives more than 160,000 recordings contributed by hundreds of recordists; more than two-thirds of the world's bird species are represented so far (see Baptista and Kroodsma [2001] for a compilation of sound archives). Ornithology is privileged to be able to muster a coterie of amateurs

often eager to participate in a research project at their own expense because they enjoy making a contribution to knowledge, particularly to a high-interest topic such as species limits. If a researcher were to advertise that recordings were badly needed from throughout the ranges of, for example, fox sparrows (*Passerella* spp.) or spotted towhees (*Pipilo* spp.?), I predict that the response would produce a substantial contribution to the project. Additionally, recordings can be stored cheaply, duplicated and transmitted easily and without degradation from the original, and analyzed quickly and with minimal expense. Further, the nature of vocal recordings permits their experimental use in studies of species recognition and mate selection.

Use of vocalizations for delimiting species' boundaries comes with the usual difficulties of any character-based phylogenetic analysis. In particular, assessment of homologies in vocal characters among populations requires thorough knowledge of the behavioral contexts of the vocal repertoire (Schwartz 1972, Whitney 1994, Isler et al. 1998, Price and Lanyon 2002, Whitney et al. 2000). Although the lure of experimental playback trials is strong, assessment and interpretation of responses to playback are often problematic (Payne 1986; Kroodsma 1989, 1990a, b). Briefly, in some cases even crude imitations of vocalizations can generate a positive response, whereas in other cases, homotypic song can be ignored. Thus, if playback experiments are not carefully designed and carried out over repeated trials with multiple individuals at various seasons of the year, they probably should not be considered in taxonomic assessments.

VOICE AND GENE FLOW

That vocalizations play an important role in gene flow in birds comes as no surprise; that communication among individuals is partly based on voice is obvious; that different species have different voices is equally obvious, as reflected in the widespread onomatopoetic naming schemes of prescientific human societies. Studies documenting the general use of voice in mate selection and species discrimination are too numerous to cite. The direct links between vocal variation, mate selection, and gene flow, however, require more detailed studies.

Genetic barriers to interbreeding in closely related birds are few, and fertile hybrid crosses are known between members of different genera that have presumably been separate for millions of years (Prager and Wilson 1975, Grant and Grant 1992, Price and Bouvier 2002). Clearly, premating isolating mechanisms provide the primary barrier to gene flow in birds, and it has long been known or suspected that vocalizations are the predominant premating isolating mechanism. As emphasized by Edwards et al. (2005), the study of processes generating vocal differences and the consequences of those differences on mate selection continues to be a fruitful line of inquiry.

Vocal divergence between allopatric and parapatric populations can be driven by a number of extrinsic factors, including (1) the bioacoustic properties of habitat differences (Slabbekoorn and Smith 2002, Patten et al. 2004); (2) character displacement among closely related syntopic species (Seddon 2005); and (3) consequences to sound production caused by differences in bill size and shape and body mass driven by divergence in feeding ecology (e.g. Tubaro and Mahler 1998, Palacios and Tubaro 2000, Podos 2001, Podos et al. 2004b). In addition, intrinsic individual variation, including learned cultural differences in oscines, provides the raw material for vocal divergence through drift or selection (see Podos et al. 2004a for review). Individual, local, and regional variation in bird songs has been documented in almost every bird species examined so far. The often-spectacular variation in oscines (e.g. Kroodsma and Parker 1977, Cicero and Benowitz-Fredericks 2000) challenges our abilities to measure it. Some birds are sensitive to minute differences in syllable structure (e.g. Clayton 1990) or temporal and spectral differences (Lohr and Dooling 1998 and references therein), and thus the complex variation in bird vocalizations has the potential to function as signal rather than noise.

The consequences of vocal differences to mate selection are more challenging to document. Female passerines are often, but not always, more strongly attracted to local, familiar song types than to songs from more distant populations (Searcy 1992). Conflicting results in studies of mate selection and dialect may sort out according to whether dialects reflect selection on song structure associated with differing acoustic properties in different habitats (Slabbekoorn and Smith 2002). Thus, local differences among singing males, regardless of

origin, have the potential for rapid fixation if also associated with bioacoustic advantages. For example, Patten et al. (2004) documented that female Song Sparrows (*Melospiza melodia*) are more strongly attracted to their local song type than to that of the parapatric subspecies, and that the differences in song type were consistent with predictions from habitat bioacoustics. Because boundaries between parapatric and allopatric populations are typically associated with habitat changes, the potential for habitat-mediated vocal divergence to affect mate discrimination provides a mechanism for accelerated speciation.

Given the notorious diversity of plumage patterns and colors of birds, as well as the visual acuity of birds, one might predict a major role for that diversity in driving or reinforcing population divergence. However, one can question whether plumage differences in the absence of song differences can promote reproductive isolation. Although the importance of plumage characters in mate selection is well documented, the virtual absence of data elucidating their role in speciation *per se* is striking. From classic studies that use plumage characters to index gene flow (e.g. Short 1965) to more recent studies that measure gene flow directly (e.g. Cheviron et al. 2005), the general trend is that striking plumage differences between parapatric populations with similar voices are not in themselves effective isolating mechanisms. By contrast, reproductively isolated species can be so similar in plumage that distinguishing them is difficult (e.g. Johnson 1963, Stein 1963, Schwartz 1972, Rising and Schueler 1980, Johnson and Marten 1988, Connors et al. 1993, Groth 1993, Whitney 1994, Cicero 1996, Bierregaard et al. 1997, Krabbe and Schulenberg 1997, Whitney et al. 2000, Alvarez and Whitney 2001, Isler et al. 2002, Johnson and Cicero 2002), but in all such cases, clear-cut vocal differences have provided nearly perfect predictors of premating isolation. The wealth of examples of avian cryptic species that differ primarily in vocalizations is clear testimony for the need to take vocal data into account when assessing species limits.

The "Species" Problem

The classification that Isler et al. (2005) and Brumfield (2005) recommend for the populations they studied is a single species with three subspecies under the Biological Species Concept (BSC); a fourth population, previously designated as a subspecies, was found to represent a zone of intergradation rather than a stable entity worthy of formal taxonomic recognition. This classification tells us that there are three diagnosable units but that gene flow is extensive and ongoing among the three distinct population units. Neither of the potential alternative treatments under the Phylogenetic Species Concept (PSC)—a single, highly polytypic species or three separate species—provides a comparable level of information about the evolutionary status of these populations.

Although this is not the place for another review of species concepts (e.g. Sites and Marshall 2004), it is important to discuss them in the context of the *T. caerulescens* studies. Proponents of the PSC explicitly denounce the use of interbreeding in classification (e.g. McKitrick and Zink 1988, Zink and McKitrick 1995). The dismissal of lack of reproductive isolation as "illegal" for use in classification because it is a shared primitive (symplesiomorphic) "character" represents a curious view of evolution at the population level. The critical effect of reproductive isolation, or lack of it, on gene flow is so fundamental to the process of evolution at the population level that its importance requires no defense (Avise and Wollenberg 1997). Any species concept that rules out degree of interbreeding for taxon delimitation suffers an immediate disconnection from the process of divergence and eventual reciprocal monophyly. As stated by Avise and Wollenberg (1997:7754), "If concepts resembling the BSC had not existed throughout this century, in the light of modern coalescent theory and associated mulitlocus genealogical concordance principles, they surely now would demand invention."

Detailed studies of the mechanics and consequences of reproductive isolation and its absence, such as those by the Grants on Galapagos finches (e.g. Grant and Grant 2002) or by Bob Payne on viduine finches (e.g. Payne et al. 2000), provide our best views of the behavioral mechanics and processes of evolution and divergence at the population level in birds. The Isler-Brumfield papers provide yet another window into the processes that influence divergence. To deny a role for the study of reproductive isolation and barriers to gene flow in defining species, the most important taxonomic category in biological

classification, removes this critical information from the classification (Johnson et al. 1999). Further, even the PSC implicitly relies on the "outlawed" ability to interbreed freely for the spread of diagnostic character states among the individuals aggregated into minimum diagnosable units (*sensu* Cracraft 1983), and on the effects of reproductive isolation for proper diagnosis of syntopic species. Ironically, Hennig, the father of the cladistic methodology that inspired the PSC, was himself a practitioner of the BSC; he used cladistic methodology *only* for taxa that were reproductively isolated, and he provided an early outline of why incomplete lineage-sorting obstructs the definition of species using cladistic methodology (Hennig 1966).

Use of diagnosability criteria to define PSC species involves arbitrary, nonbiological decisions. Selection of any level of diagnosability, whether 100%, 95%, or 75%, creates a system of taxon-ranking that lacks a conceptual framework and is driven, to a degree, by sampling regime. For example, if the PSC diagnosability level is set at 95%—the comfortable but arbitrary convention in tests of statistical significance—two populations diagnosable at the 94% level will not be given any taxonomic standing, whereas two at 95% will be ranked as species. That difference in rankings is indefensible from a conceptual standpoint. Further, an addition of just one individual to the sample could cause the assignment of rank to waffle from "species" to no taxonomic ranking, and even measurement error could affect taxon-ranking. Additionally, diagnosability at the genetic and phenotypic level can be achieved in remarkably few generations, as in the House Finch (*Carpodacus mexicanus*) population of the eastern United States, which can be diagnosed phenotypically and genetically from western populations after fewer than 100 years of separation (Wang et al. 2003).

The BSC removes these conceptual and practical problems from the all-important "species" taxon and relegates them to the "subspecies" level. Widespread, long-standing dissatisfaction with subspecies-level designations in bird classification derives from the historical fact that most bird subspecies were described in an era when quantitative methods were unavailable to assess their validity as entities. For example, the four Bolivian populations of *T. caerulescens* were described between 1837 and 1907, before

invention of the *t*-test. Although the conceptual underpinnings of the subspecies taxon have always focused on designating discrete population units diagnosable by phenotypic characters with the assumption that they have a genetic basis (Smith and White 1956, Simpson 1961, Mayr 1969, and references therein), quantitative methodology for assessing diagnosability was lacking. In addition, individual and geographic sampling in early descriptions was often so limited that sampling bias prevented assessment of true patterns of variation. Is it any wonder, therefore, that the roster of formal subspecies, most described before the advent of statistical methods in ornithology, contains many names that refer only to arbitrary points on clines, average differences between populations, or zones of intergradation (as in *T. c.* "*connectens*" in Isler et al. 2005), rather than to discrete entities? What is needed is a quantitative reassessment of geographic variation within biological species to determine whether they contain diagnosable units. Designating the diagnosable units merges the subspecies taxon with the PSC-defined species and represents a pattern-centered level of classification, namely the terminal taxa in a phylogeny. In fact, Barrowclough's (1982) description of useful subspecies is substantively indistinguishable from Cracraft's (1983) seminal PSC definition. The only potential point of difference is whether diagnosability rests on a single character or a combination of characters; restriction to a single character state, as in many subspecies diagnoses, would make the subspecies taxon indistinguishable from PSC-defined species (*sensu* Cracraft 1983). Patten and Unitt (2002) outlined a standard methodology for reassessing phenotypic diagnosability for single characters using the traditional "75% rule," but they advocated a 95% minimum level of diagnosability for subspecies, a recommendation with which I concur. Although analyses are ongoing, the three subspecies of *T. caerulescens* studied by Isler-Brumfield almost certainly meet the 95% diagnosability criterion (R. Brumfield unpubl. data).

As for the well-known problems of the BSC in classifying allopatric populations (Johnson et al. 1999), Isler et al. (1998) provided a general model for objective classification of allopatric populations. Instead of focusing directly on potential interbreeding between allopatric taxa, the Isler-Whitney model emphasizes current

levels of divergence from a comparative standpoint rather than some hypothetical future contact. Under this system, classification of allotaxa as species indicates that their degree of divergence is at or beyond that of taxa known to have reached a pivotal point in their evolution, namely reproductive isolation. That subtle but different emphasis is critical, in that it classifies taxa based on current divergence rather than some future, probably unknowable event. Helbig et al. (2002) also emphasized "comparable levels of divergence" in assigning taxon rank to allopatric populations. Continued claims that the BSC is unable to handle the classification of allotaxa (e.g. Navarro-Sigüenza and Peterson 2004) require modification.

The other major problem with the BSC, namely the occasional recognition of species that are paraphyletic, is widely perceived as an insurmountable weakness (e.g. Zink and McKitrick 1995). Although paraphyletic taxa are anathema to phylogenetic systematics at higher taxon levels, use of monophyly as a criterion for taxon-ranking at the population level is problematic. With reticulate evolution nearly inevitable among populations that are not 100% reproductively isolated, "monophyly" at this level can refer only to the most recent cycle of isolation and differentiation. Even so, from the genetic standpoint, monophyly at the population level may be unlikely or difficult to measure (Avise and Wollenberg 1997, Edwards et al. 2005), as in Darwin's finches (Zink 2002), and paraphyly at the population level may characterize many populations ranked as species (Funk and Omland 2003). The complex genetic history of most populations prior to reproductive isolation means that different genes may have different histories and produce different trees (Avise and Wollenberg 1997, McCracken and Sorenson 2005). Although classification should, of course, reflect genealogical history, the realities of population genetics make it difficult to apply phylogenetic principles at or below the species level, regardless of definition.

A recent application of the PSC merits comparison with the *T. caerulescens* study. Zink et al. (2005) analyzed the patterns of geographic distribution of mtDNA haplotypes of the Savannah Sparrow (*Passerculus sandwichensis*) over much of its broad North American range. Their data revealed three major haplotype groups; one of those they ranked as a separate PSC species (*P. rostratus* of northwestern Mexico and extreme southwestern United States) from the other two, which they treated together as the widespread *P. sandwichensis*. This two-species treatment was justified on the basis of the genetic and phenotypic distinctiveness of the *rostratus* group. Their classification denies any taxonomic standing for the large, pale "Ipswich Sparrow" of Sable Island, Nova Scotia, ranked as a subspecies (*P. s. princeps*) under the BSC, or for the San Benito Island population (*P. s. sanctorum* under the BSC), because they are not genetically distinct in terms of mtDNA. Both of those insular populations are 100% diagnosable by plumage and have distinctive ecologies (Wheelwright and Rising 1993). Furthermore, because of shared haplotypes, Zink et al.'s (2005) *P. rostratus* is a conglomerate of the large-billed, pale, northward-migrating Mexican populations (*P. s. rostratus* group under the BSC) with the smaller-billed, dark, resident populations of the Pacific Coast (*P. s. beldingi* group of the BSC; see Wheelwright and Rising 1993). The obvious erasure of biodiversity in Zink et al.'s (2005) classification suggests that taxon delimitation governed by mtDNA is not a productive line of applied research, as recently suggested by Edwards et al. (2005), who noted: "…in our opinion, maternally inherited mtDNA can never capture enough of a species' history to delimit species on its own." The mtDNA reclassification of the Savannah Sparrow provides a sharp empirical contrast to hyperbole that it is the BSC and its subspecies that threaten the proper documentation and conservation of biodiversity (e.g. Zink 2003).

On the other hand, Zink et al.'s (2005) version of the PSC, namely that taxa require unique mtDNA haplotypes, would seem to be an extreme version of the PSC. First, such an approach is at the mercy of its sampling regime. As noted by Brumfield (2005), if his population samples and geographic scope had been more similar in size to many mtDNA studies, Brumfield would have considered each of the three subspecies of *T. caerulescens* to be reciprocally monophyletic. Second, a PSC approach that assumes that genetic population structure is more complex than is revealed by mtDNA gene trees would presumably give species rank to populations diagnosable by plumage and morphology as well, including *princeps*, *rostratus*, *sanctorum*, and possibly other populations within the *rostratus* and

beldingi groups. These three populations, minimally, would certainly be classified as subspecies under the BSC (and careful study will almost certainly reveal that *rostratus* is a valid species under the BSC). Many interior continental populations previously given subspecies names would likely lose those formal designations. Although most are not diagnosable in terms of morphometrics (Rising 2001), coloration in those populations has not been analyzed; nonetheless, most of the named taxa probably represent points in clinal variation, not discrete entities (Wheelwright and Rising 1993).

FUTURE DIRECTIONS

The Isler-Brumfield studies so far do not include the geographical extremes of *T. caerulescens*. Even blacker populations extend to northern Peru, 1,500 km farther north, and gray populations extend to northeastern Argentina, 1,100 km farther southeast; additional isolated subspecies occur even farther away, in extreme eastern Brazil. Will studies of these and intermediate populations reveal a continuation of clinal variation in genetics and vocalizations as well? Once the extremes are sampled, will the level of differentiation in vocalizations meet the Isler-Whitney criterion for species rank? The latter speciation-by-distance result would produce the equivalent of a "ring species" (e.g. Irwin and Irwin 2002, Irwin et al. 2005), but without closure of the ring, the geographic connection that produces parapatry at the extremes.

The Isler-Whitney model for comparative analysis of vocalizations for taxon-ranking works well for a major bird family, the Thamnophilidae. Their approach, namely the quantitative comparisons of vocal differences between sympatric pairs of congeners, sister species whenever possible, should be feasible for other families of birds in which vocalizations play a role in mate selection and, therefore, gene flow. The feasibility of these models should be explored in oscine passerines and nonpasserines, not just suboscines. More generally, with appropriate phylogenetic comparisons, assessment of levels of divergence in any phenotypic characters among closely related sympatric species can provide a conservative scheme for taxon-ranking of allopatric populations based on comparisons with the minimum levels of divergence shown by syntopic species. Given what we know so far, the most robust schemes are likely based on vocalizations, at least for most bird groups. Increased funding and support for recordists' fieldwork, for sound archives, and for incorporation of vocal sampling into genetic sampling studies will greatly facilitate such analyses.

For populations whose level of divergence falls below species-level criteria, assignment of subspecies rank would then depend on measures of diagnosability such as those defined by Patten and Unitt (2002). Unfortunately, a complete re-evaluation of described subspecies is a daunting effort, so massive that the American Ornithologists' Union (1998) Checklist Committee has been unable to complete it for North and Middle American birds after more than 20 years of work. The alternative, compiling lists of taxa that are apparently diagnosable but without providing supporting documentation, as in Navarro-Sigüenza and Peterson's (2004) compilation of PSC species for Mexico, relies on a "trust us, we've looked at the specimens" approach, the lack of rigor of which recalls the heyday of the antiquated "Peters Checklist" method. Likewise, applying PSC rank only to highly differentiated populations that may be species under the BSC without also making an honest, thorough search for all minimum diagnosable units is not an appropriate application of the PSC (Johnson et al. 1999). The *Handbook of the Birds of the World* series edited by Josep del Hoyo et al. (Lynx Edicions, Barcelona) has generated comments on the diagnosability of thousands of subspecies, but that project's format permits only cursory summaries of those largely qualitative taxonomic judgements. Recent attention to conservation of biodiversity could catalyze quantitative, comprehensive overhauls of subspecies taxonomy, but because this type of research is applied rather than conceptually oriented, it is unlikely to have a broad appeal among frontline researchers, but rather will more likely proceed on a case-by-case basis as needs or opportunities arise (e.g. Pruett et al. 2004). Alternatives are needed. Meanwhile, we can only hope for more examples like the Isler-Brumfield papers, which combine intensive population sampling of multiple characters with rigorous analyses to study the processes governing gene flow and the patterns that it generates.

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