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Rigor and Species Concepts

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Rigor and Species Concepts.—Within a review of work on avian vocalizations by affiliates of his own institution, Remsen (2005) turned his attention to the debate over species concepts. This topic is very controversial and has strong advocates on both sides. Thus, readers should take literally Remsen's warning that "this is not the place for another review of species concepts…." Readers will recognize that his "review" does not present a balanced overview of the principal issues in the debate, owing to Remsen's allegiance to the biological species concept (BSC). It is also important to address controversial issues constructively. Here, I respond to his concerns and criticisms and illustrate my opinion that the BSC continues to be a poor choice for organizing our knowledge of biodiversity.

The debate in a nutshell.—Remsen believes that if two taxa, diagnosed by some phenotypic or genotypic data, can interbreed to some (unspecified) degree, they must be classified as the same species. This is the crux of the BSC. Under the phylogenetic species concept (PSC), diagnosably distinct taxa with independent evolutionary histories are considered species regardless of whether they are reproductively isolated from other phylogenetic species. Adoption of one or the other concept leads to major differences in our understanding of avian species diversity.

Importance of interbreeding.—Remsen perpetuates the notion that advocates of species concepts other than the so-called "biological" species concept (Mayr 1963) consider the phenomenon of reproductive isolation unimportant. In particular, he remarks that "proponents of the PSC [phylogenetic species concept] explicitly denounce the use of interbreeding in classification" (Remsen 2005:406). This does a disservice to the papers he cites, because readers unfamiliar with them will assume incorrectly that he has understood and reported their content accurately and not out of context. Advocates of the PSC have always acknowledged that interbreeding occurs among individuals of the same species, but its existence (actual or presumed) does not justify uniting taxa that are otherwise diagnosable. There is good reason for this, because the ability to interbreed is an ancestral condition (Rosen 1979).

In modern systematics, one does not unite taxa based on their shared possession of an ancestral condition. Apparently because he does not like the outcome, Remsen has decided to ignore this part of phylogenetic systematics and use his own rules. Advocating that we discard this fundamental rule will ensure that nonsister taxa are united by their joint possession

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of ancestral (sympleisomorphic) conditions; this is not accepted at any level of taxonomic organization. For instance, classifying the Baltimore Oriole (*Icterus galbula*) and Bullock's Oriole (*I. bullockii*) as conspecific because they hybridize creates a nonsensical taxon, as they are not sister taxa (Freeman and Zink 1995). Other than Remsen's incorrect assertion that the recognition of such paraphyletic taxa would be an infrequent occurrence under the BSC, Remsen has no solution to this problem created by, and exclusive to, the BSC. Supporters of the BSC have not answered this question since Rosen (1979) first pointed it out: if non-sister taxa hybridize "freely," are they the same biological species, to the exclusion of other, more closely related taxa that are reproductively isolated? Under the BSC version advocated by Remsen, the answer is yes, which places more importance on the potential future outcome of current interbreeding rather than on, perhaps, tens of thousands of years of genetic isolation. To Remsen, this is preferable to a classification that accurately reflects evolutionary history. I fail to see rigor in Remsen's method.

Allopatric populations.—It has been noted numerous times that the BSC provides little basis for judging the species status of allopatric populations. Advocates of the BSC such as Remsen (2005:407) acknowledge this problem: "As for the well-known problems of the BSC in classifying allopatric populations…." This is an important issue, because it is likely that most avian diversity arose as a result of allopatric differentiation. Using a species concept that is not objective in allopatry therefore makes little sense. Remsen suggests that a solution to this problem is the protocol of Isler et al. (1998, 2005), which identifies a set of vocal attributes that characterize antbird taxa known to be reproductively isolated, and then uses them as a benchmark for allopatric forms. Remsen (2005) believes that this approach will codify the long-standing notion that one can make "rigorous" guesses as to whether allopatric populations are reproductively isolated. This may work for a few groups after intensive study (indeed, the Isler et al. [1998] study took many years to complete), but it offers no more than approximate guidelines, not an actual set of rules, and it will be group-specific. Also, suboscines are a special case, because their vocalizations are innate; Remsen's guidelines may not be applicable to the more than 4,000 species of oscine passerines, let alone to other orders for which the genetic–innate contribution to songs is unknown. Application of Remsen's method to the Golden-winged Warbler (*Vermivora chrysoptera*) and Blue-winged Warbler (*V. pinus*) may be instructive. These two species use the same vocalizations in allopatry as they do in sympatry, where they interbreed extensively. Thus, there is no reason to maintain them as separate species. However, they are morphologically distinct, and the American Ornithologists' Union (AOU) check-list committee, which like Remsen strictly follows the BSC, classifies these phylogenetic species as separate biological species. Here, apparently, tradition takes precedence over rigor.

It is also important to recall that under the BSC, the amount of hybridization required to indicate species status differs from authority to authority. There are no quantitative predictions from the Isler et al. (1998) protocol that would indicate whether allopatric taxa were 94%, 80%, or 99% likely not to interbreed, and then what would the investigator do to assign species limits? Thus, rather than analyze vocal characters directly as is done under alternative species concepts, Remsen offers a recipe for guessing the reproductive inclinations of allopatric populations to assess their biological species status. Again, this approach is not rigorous to modern practicing systematists.

Variable Antshrike and classification.—Remsen (2005) reviews Brumfield's (2005) study on mitochondrial DNA (mtDNA) variation in part of the range of the Variable Antshrike (*Thamnophilus caerulescens*). Brumfield discovered three main historical groupings (subspecies) of mtDNA haplotypes, and some introgression, but did not make recommendations about species limits. Remsen (2005:406) remarks nonetheless that:

> 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.

This characterization is incorrect. First, no classification portrays levels of gene flow, whether it is ongoing, and which taxa are involved (and to

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what degree). Second, besides the discovery of historical isolation and some recent gene flow, Brumfield's most important discovery was that *T. c. paraguayensis* and *T. c. dinellii* were sister taxa. A PSC classification would include three species ordered to reflect the hierarchy implied in the mtDNA tree; this information does not exist in the BSC classification.

Savannah Sparrows.—Remsen criticizes the mtDNA study by Zink et al. (2005) of the Savannah Sparrow (*Passerculus sandwichensis*) that reported the existence of a reciprocally monophyletic clade in Baja California (Norte and Sur), Sonora and southern California, two clades in the rest of the range, and a lack of support for named subspecies. Zink et al. (2005:25) concluded:

> Therefore, on the basis of these molecular data as well as morphological data (Rising, 2001), variation in plumage color and pattern (Rising, unpubl. data) and differences in vocalizations (Bradley 1977, Wheelwright and Rising 1993), we suggest that "typical" Savannah Sparrows and the salt marsh populations of Savannah Sparrow from coastal Baja California, San Diego, and Sonora be treated as separate species. Further sampling along the California coast between San Diego and Suisan Bay is required to locate the contact zone between the two major groups.

Remsen concluded that the suggested classification results in an "obvious erasure of biodiversity," because it results in inclusion of a subspecies traditionally in the northern group (which migrates south to winter) into the southern group (some of which migrate north). It is unfortunate that the evolutionary history of Savannah Sparrows is more complex than Remsen wishes. In fact, it appears that there were once three phylogenetic species but that the two continental forms have undergone secondary intergradation to such a high level as to make them not diagnosable. The mtDNA tree indicates that some part of the southern group retained an ancestral migratory habit. This should not strike fear into ornithologists and lead to pleas for retaining the BSC and subspecies. Instead, it apparently reveals an interesting case of ecological versus historical control of migration.

Remsen proposed no classification that recovers the existence of the strongly supported mtDNA clades; instead, he advocates retaining subspecies that have already been shown to be nonhistorical (Rising 2001). Thus, he would ignore significant evidence of independent histories in favor of the status quo. This is neither rigorous nor a better classification. Granted, the population on Sable Island is worthy of additional study to determine whether it is morphologically diagnosable and, if it is, it would qualify as a phylogenetic species despite lack of mtDNA support (Zink 2004).

Subspecies.—Although Remsen expresses admiration of subspecies, the failure of most northern temperate subspecies, including those of the Savannah Sparrow, to be distinct historical entities (Zink 2004) is consistent with Remsen's (2005:407) view:

> 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?

I would add that it is, in fact, "most" northern temperate subspecies, not "many." Thus the sentiments of Wilson and Brown (1953:100) ring true half a century later: "the subspecies concept is the most critical and disorderly area of modern systematic theory." What is interesting is that Remsen has identified the culprit (p. 407): "The BSC removes these conceptual and practical problems from the all-important 'species' taxon and relegates them to the 'subspecies' level." This is an important insight—if you use the BSC, you can simply demote problems that cannot be solved to the subspecies level, where apparently they can do less damage. This will not be a rigorous solution for conservation biologists who must sometimes decide whether subspecies are distinct historical entities. This problem owes its origin to the use of interbreeding as a criterion for species status, which is not part of phylogenetic or evolutionary species.

Remsen (2005) implies that subspecies can be equated with phylogenetic species, if the former are rigorously described. There is some common ground here. In Remsen's scheme, a valid subspecies ought to be a historically significant group, diagnosable by genetic or by phenotypic characteristics, that is not

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reproductively isolated. If this were true of avian subspecies, it would be a huge step forward, but they would not be equivalent to phylogenetic or evolutionary species, because one still is forced to guess whether allopatric subspecies are reproductively isolated. The PSC applies directly to allopatric populations, and phylogenetic species are allowed to hybridize without losing their species status (e.g., as in most plant species). Importantly, hybridization would not result in the merging of two non-sister phylogenetic species, whereas the species taxonomy would be misrepresented by the BSC. We would also have to defend to others that sometimes we wish to preserve species, other times subspecies. It makes more sense to call basal taxonomic units species because they are the proper units in systematics, conservation, and evolutionary studies. Therefore, it is not true that phylogenetic species are the same as "good" subspecies.

Species limits.—Remsen (2005) concludes that the PSC does not work because one could make different decisions if, say, 99% or 100% of individuals were diagnosable. However, is this not the same situation that occurs in statistical hypothesis testing, where we accept the null hypothesis at a probability (*P*) of 0.051 and reject it at a *P* of 0.049? We have not abandoned statistical hypothesis testing because we have an arbitrary level of probability required for significance. Nor should we reject phylogenetic species as long as the sampling is sufficient. Species limits are hypotheses, no matter what concept is invoked. Nonetheless, there is no clear agreement among advocates of the PSC as to whether phylogenetic species must be 100% diagnosable. I believe that the nature of the lack of diagnosability is of interest (e.g., Zink and McKitrick 1995) and may help resolve instances in which phylogenetic species limits are unclear. Furthermore, Remsen fails to remind the reader that sampling plagues the BSC as well: what constitutes "enough" interbreeding for two taxa to be considered the same biological species varies immensely from authority to authority.

Molecular markers.—It has become fashionable to criticize studies based on mtDNA (Edwards et al. 2005). Remsen (2005) criticizes the use of mtDNA data in the Savannah Sparrow study (Zink et al. 2005), whereas mtDNA data are deemed appropriate in the Variable Antshrike. It is my opinion that the concerns expressed by Edwards et al. (2005) about the use of mtDNA data in species studies are drastically overstated. I would wager that most of the geographically structured mtDNA gene trees provide accurate information about population history. In fact, a recent analysis of 30 nuclear genes recovered the mtDNA gene tree (Jennings and Edwards 2005).

Conclusions.—Remsen's (2005) attack on the use of phylogenetics at the species level can be seen as a personal commitment to the BSC. This concept was an important advance in its time. However, the BSC is not able to deal adequately with new types of results, particularly the finding that groups within biological species have a hierarchical history. That is, unlike in the past, when we knew only that there were distinct groups within some species, we now know how they are related, owing to advances in molecular systematics. Therefore, the phenomena associated with reproductive isolation and compatibility can be studied in their proper phylogenetic context (Zink and Davis 1999), and not used to confuse or obfuscate species limits. We should recognize that lineage concepts such as the phylogenetic and evolutionary species concepts are better suited to weld together studies at the population level with those of higher taxa. Under the BSC, two sets of rules are used, which has resulted in a conceptual and methodological disconnect, and negatively affects the units used in conservation, speciation analysis, and evolutionary analyses.

The growing use of non-BSC species concepts by practicing systematists (who are often not those on checklist committees) supports the view that problems inherent in phylogenetic or evolutionary species concepts are acceptable in comparison with the greater problems caused by acceptance of the BSC, a sentiment succinctly summarized by Frost and Hillis (1990:88): "Therefore, as a working concept, the biological species concept is worse than merely unhelpful and non-operational—it can be misleading."—

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