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COMMENTARY

Biological species and taxonomic species: Will a new null hypothesis help? (A comment on Gill 2014)

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ABSTRACT

In his article "Species taxonomy of birds: Which null hypothesis?", Gill (2014) recommended that we might apply our growing knowledge of avian speciation more effectively, particularly to avian taxonomy and the definition of species. Specifically, Gill (2014) suggested that committees on avian nomenclature should operate under a new null hypothesis for species designation: Genetically and phenotypically distinct taxa would be considered full species, a priori, in the absence of any natural tests of reproductive isolation (i.e. sympatric populations) or additional evidence of possible isolating barriers. There are several useful aspects to this suggestion. However, in this Commentary, I present a number of issues that suggest that such a proposal may be premature. More generally, I recommend that unless a more compelling argument is made for altering the status quo, it seems prudent for nomenclature committees to continue to use the best available evidence to make informed decisions about the extent of reproductive isolation between putative avian species.

Keywords: speciation, species concepts, taxonomy

Espèces biologiques et espèces taxonomiques: Une nouvelle hypothèse nulle aidera-t-elle? Un commentaire sur Gill (2014)

RÉSUMÉ

Dans son article "Taxonomie des espèces d'oiseaux: Quelle hypothèse nulle?" Gill (2014) recommande que nous appliquions plus efficacement nos connaissances grandissantes sur la spéciation aviaire, particulièrement en ce qui a trait à la taxonomie aviaire et à la définition d'espèce. Plus précisément, Gill (2014) suggère que les comités sur la nomenclature aviaire devraient opérer selon une nouvelle hypothèse nulle de désignation des espèces. Cette hypothèse stipule que les taxons génétiquement et phénotypiquement distincts seraient a priori considérés comme des espèces à part entière, en l'absence de tests naturels d'isolement reproductif (i.e. populations sympatriques) ou de preuves additionnelles de barrières d'isolement potentielles. Il existe plusieurs aspects utiles dans cette suggestion. Toutefois, je présente dans ce commentaire un certain nombre de questions qui suggèrent qu'une telle proposition pourrait être prématurée. Plus généralement, à moins qu'un argument plus convainquant soit émis pour changer le statu quo, il semble plus prudent que les comités de nomenclature continuent d'utiliser les meilleures preuves disponibles pour prendre des décisions éclairées sur l'étendue de l'isolement reproductif entre les espèces aviaires présumées.

Mots-clé: concepts d'espèce, spéciation, taxonomie

In his article "Species taxonomy of birds: Which null hypothesis?", Frank B. Gill (2014) acknowledged numerous advances, over the past several decades, in our understanding of the process of species formation in birds and in other taxa (Coyne and Orr 2004, Price 2008). Gill (2014) recommended that we might apply this new understanding of speciation in birds more effectively, particularly to taxonomic designations and the definition of avian species. Specifically, Gill (2014:151) suggested that committees on avian nomenclature should operate under a new null hypothesis for species designation, asserting that "distinct and reciprocally monophyletic sister populations of birds exhibit essential reproductive isolation and would not interbreed freely if they were to occur in sympatry." In essence, this means that genetically and phenotypically distinct taxa would be considered full species, a priori, in the absence of any natural tests of reproductive isolation (i.e. sympatric populations) or additional evidence of possible isolating barriers. Distinct, allopatric populations have been a challenge for avian taxonomy, as discussed previously (e.g., McKitrick and Zink 1988, Helbig et al. 2002, Sangster 2014), and there are several useful aspects to adopting a new null hypothesis that is centered on an a priori assumption of reproductive isolation. In particular, it provides the promise of having a more efficient and objective metric for identifying avian species. Here, I address two questions with regard to Gill's (2014) proposal. First, will taxonomic divisions made under such a proposal actually reflect species-level differences? Second, are there relevant benefits of such a proposal that justify changing the status quo for nomenclature committees?

At least for the North and South American Nomenclature Committees (American Ornithologists' Union 1998) and the British Ornithologists' Union's Records Committee (Helbig et al. 2002), there is a strong endorsement of the biological species concept, although other concepts are also applied in practice (reviewed in Sangster 2014). In this way, avian biological species identified by these groups are unique within the current taxonomic hierarchy: Unlike other levels of organization (i.e. family or genus), biological species have a unified defining feature—reproductive isolation (Coyne and Orr 2004). It follows that much of the disagreement during debates of species "splits" or "lumps" stems from the challenge of applying hard lines to a varied and continuous process such as species formation. Gill (2014) summarized and synthesized many significant advances in our understanding of the evolution of reproductive isolation in birds. For instance, studies of artificial hybridization between divergent avian taxa demonstrate that fertilization can still be successful and, in some cases, produce viable offspring, even after many millions of years of independent evolution (Price and Bouvier 2002). This suggests a reduced role of intrinsic isolating barriers compared with premating or extrinsic postmating barriers between avian species, although more study is clearly needed (Price 2008, Rabosky and Matute 2013). In a similar vein, two recent studies have identified an unexpected positive correlation between DNA mutation rate and avian species diversity, hinting at a connection between the generation of genetic variation and species formation (Eo and DeWoody 2010, Lanfear et al. 2010).

Such novel and exciting findings reflect how quickly our knowledge of the evolution of reproductive isolation in birds is growing and changing. However, if nomenclature committees are to adopt Gill's (2014) proposal, will they be able to accurately predict the extent of reproductive isolation between avian taxa solely on the basis of reciprocal monophyly and phenotypic distinctiveness, as the proposal implies? In some cases, this is quite possible. For example, strong genetic and acoustic differences between Pacific Wrens (*Troglodytes pacificus*) and Winter Wrens (*T. hiemalis*) were well known prior to studies of a contact zone between them (Drovetski et al. 2004, Toews and Irwin 2008). In this case, differences observed between these taxa in allopatry were maintained in sympatric populations, and this information was used to identify them as two reproductively isolated species (Drovetski et al. 2004, Toews and Irwin 2008).

These types of delineations are more challenging, however, in taxa that do not show such deep levels of divergence (e.g., Pacific and Winter wrens are estimated to have diverged >4 mya; Toews and Irwin 2008). For example, studies of hybrid zones have been used to estimate possible reproductive barriers between young lineages. In the case of narrow hybrid zones, there is usually assumed to be some form of reproductive isolation between the parental taxa that maintains the width of the zone, which can also be manifested in reduced hybrid fitness (Barton and Hewitt 1985). For example, premating differences based on habitat preference and/or vocalizations have been suggested as important factors involved in maintaining the recently described hybrid zone between Townsend's Warblers (*Setophaga townsendi*) and Black-throated Green Warblers (*S. virens*) in the Rocky Mountains of western Canada (Toews et al. 2011). By contrast, broad zones of intermixing imply that isolation between taxa is weak, as is likely the case between Pacific-slope Flycatchers (*Empidonax difficilis*) and Cordilleran Flycatchers (*E. occidentalis*; Rush et al. 2009). However, aside from the well-studied hybrid populations of *Ficedula* in Europe (Qvarnstöm et al. 2010), we have few empirical tests of the important forms of reproductive isolation in avian hybrid zones. In addition, there are almost no cases in which the relevant sources of selection against avian hybrids in the wild are fully known (Price 2008).

Aside from artificial hybridization studies, we also have very little information regarding the levels of reproductive isolation between allopatric forms within currently recognized species, sometimes referred to as subspecies or allospecies (Price and Bouvier 2002, Price 2008, Gill 2014). There have been some efforts to use objective yardsticks for diagnosable species-level traits in avian groups, generated from phenotypic differences observed between "good species" in sympatry and then applied to parapatric or allopatric groups (Tobias et al. 2010). However, measuring the efficacy of these metrics is challenging, mostly because it is difficult to assess the extent of reproductive isolation between allopatric groups in natural settings. One possible solution, given previous research implicating vocalizations as an important barrier to gene flow in birds, is controlled study of male and female behaviors following heterotypic song playback (e.g., Irwin et al. 2001, Greig and Webster 2013). Such studies can offer important insights into possible premating barriers, at least those based on vocalizations, even for allopatric groups. Although a finding of little or no response to song playback can be indicative of reproductive barriers (e.g., Benites et al. 2014), equally aggressive responses are generally inconclusive (McKitrick and Zink 1988). In general, however, there has not been a broad application of playback studies, particularly between allopatric groups. Such studies also have important limitations, namely that researchers must assume that female preference is correlated with male responses and that responses might change when combined with visual stimuli.

It has also been noted that many of the model systems in the field of avian speciation—including flycatchers (*Ficedula*; Qvarnström et al. 2010), warblers (*Phylloscopus* and Parulidae; Price 2008, Rabosky and Lovette 2008), buntings (*Passerina*; Carling and Brumfield 2009), sparrows (*Passer*; Trier et al. 2014), and crossbills (*Loxia*; Smith and Benkman 2007)—are biased toward temperate regions, which could also be said more generally of our knowledge of avian evolutionary and natural history (Tobias et al. 2008). Importantly, is the evolution of reproductive isolation in tropical avian systems similar to that in temperate-zone systems? The evidence indicates that the evolution of reproductive isolation may take much longer in the tropics than in temperate avian taxa (Weir and Schluter 2007, Price 2008), and the mechanisms of divergence may differ. For example, it has been suggested that constraints on song evolution may differ at high and low latitudes (Weir et al. 2012) and that environments may be harsher in temperate regions, both of which could influence the evolution of possible isolating barriers (Botero et al. 2014). In addition, within many species in the tropics, there are deep genetic divisions between phenotypically similar yet allopatric groups, a pattern much less common in temperate regions (Martin et al. 2010). Do these represent reproductively isolated populations/species? In some cases this is likely, but more information is clearly needed, particularly in the tropics, and understanding latitudinal variation in the evolution of reproductive isolation is an exciting and ongoing area of research (Martin et al. 2010, Botero et al. 2014).

A central point is that we still have much to learn about the important reproductive barriers between incipient avian lineages. In emphasizing reproductive isolation, Gill (2014) may be overconfident in our current ability to predict the extent of isolation between putative bird species without thorough study. An important alternative question is whether we require a strict coupling of reproductive isolation and taxonomy, at least at the species level, as some have questioned (e.g., Sangster 2014)? If fully applied, Gill's (2014) proposal would likely result in many taxa that are not reproductively isolated. While possibly cumbersome for ornithologists, this is unlikely to affect most basic research endeavors in avian systems, even those doing speciation research. However, is there a benefit of such a proposal, aside from possibly being more efficient at naming putative species? From a purely practical perspective, Gill (2014) argued that delimiting species in such a way may be more useful for clarifying patterns of diversity for comparative work or conservation applications. A counterargument can also be made: Most relevant applications of taxonomic designations appear to be well suited to incorporating information below the species level. For instance, comparative studies can include analyses with both named species and distinct phylogroups, representing possible species, and test whether patterns change significantly with or without their inclusion (e.g., Weir and Schluter 2007). While these methods still have their challenges and require refinements (Tobias et al. 2008), they emphasize the possibilities of performing comparative analyses with varying levels of taxonomic information. Gill (2014) also noted the conservation implications of splitting additional species. However, at least in the United States and Canada, federal legislation recognizes listing and management designations for taxa below the species level, including evolutionarily significant units (Moritz 1994, COSEWIC 2011). This is not necessarily true in other jurisdictions, which can have important implications for defining units of conservation on a global scale. In this case, however, it seems more appropriate for these jurisdictions to work toward recognition of within-species variation as opposed to letting policy differences drive a utilitarian argument for changing taxonomic conventions. It is also important to note that although not entirely driven by taxonomic questions, some of the detailed evolutionary research between closely related avian taxa is motivated by knowledge gaps identified by taxonomic committees. It's not entirely clear whether this would change if Gill's (2014) proposal were adopted, but with an a priori assumption of reproductive isolation, it could be argued that researchers might be less inclined toward such investigations.

More generally, Gill (2014) suggested that the time and effort put into careful examination of reproductive isolation between divergent groups by nomenclature committees might be better spent elsewhere. Indeed, there are undoubtedly deep genetic divisions within currently recognized species that warrant straightforward taxonomic splits. However, I would argue that committees should continue to strive toward coupling the best knowledge of reproductive isolation with the identification of avian species. And unless the current taxonomic philosophy emphasizing the biological species concept is changed, it would be a mistake to make a priori presumptions about isolating barriers without additional evidence.

Avian taxonomy has already been through a major paradigm shift with the application of the biological species concept (Haffer 1997). Many would suggest that prior to this shift, species-level designations were being applied too freely. Others would submit that following the application of this species concept, the burden of proof in delimiting species is too stringent. Both of these arguments have merit. I argue that we do not need another wholesale ideological shift in avian taxonomy. Moreover, until a more compelling argument is made for altering the status quo, it seems prudent for nomenclature committees to continue to use the best available evidence to make informed decisions about the extent of reproductive isolation between putative avian species.

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