

The Howard & Moore Complete Checklist of the Birds of the World: framework for species delimitation

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INTRODUCTION

The core of any taxonomic checklist comprises species-level delimitations. These should be made as consistent as possible among different taxa, within a single checklist but also between checklists and major taxonomic groups, and thus follow a common framework. This concise text explains the guidelines for species delimitation applied in the process of gradually updating the *Howard & Moore Complete Checklist of the Birds of the World* (4th Edition) as it evolves into an online list with continuous updating. This text is not aimed at providing a comprehensive review on different species concepts and species delimitation procedures, but instead explains the basis used in the Howard & Moore Checklist for assessing species rank of valid taxa. It is not an entirely new or original approach, as it draws its foundations from previous publications on speciation, species concepts or guidelines for taxonomic decisions and has previously been employed in other groups of animals (e.g., Speybroeck *et al.*, 2020).

BACKGROUND

Most biologists would probably agree that variation in nature is generally not continuous; however, there may be no single optimal way to divide this discontinuity into different species (*cf.* Sangster, 2018). Species can generally be considered as separately evolving metapopulation lineages or distinct branches in a phylogenetic tree (De Queiroz, 2007). However, while it is clear that all species are distinct evolutionary lineages, it does not follow that all such lineages can be considered to be species (*cf.* Hillis, 2019, 2020). This is because speciation, the evolution of reproductive isolation between distinct evolutionary lineages allowing them to ultimately coexist in the same location (Mayr, 1942), is a continuous process. Speciation can be considered as achieved with the attainment of complete reproductive isolation between two evolutionary lineages (e.g., Coyne & Orr, 2004), although it has to be acknowledged that it is neither a deterministic, nor necessarily is speciation an irreversible process before complete reproductive incompatibility is achieved. Moreover, speciation does not need to be completed for lineages to be ranked as species, because diverging lineages may attain enough reproductive isolation to maintain distinct gene pools without complete geographical isolation while still possessing the ability to produce viable hybrid offspring or hybrid populations.

Any framework or guiding principles for species delimitation should be approached by making the distinction between the species concept, i.e., a theoretical framework describing

what species are, and the species criteria used to delimit species in practice (Mayden, 1997; *cf.* Sangster, 2018).

SPECIES CONCEPT AND SPECIES DELIMITATION CRITERIA

The *Howard & Moore Complete Checklist of the Birds of the World* (5th Edition) aims to recognize as species those lineages that have acquired substantial reproductive isolation in accordance with the biological species concept (Mayr, 1942). Reproductive isolation is thus considered as the most important criterion for species delimitation as it is the prerequisite for evolutionary lineages to maintain their integrity through space and time (*cf.* Helbig *et al.*, 2002). The first major difficulty with that criterion is that reproductive isolation is measurable only when lineages are in direct contact, e.g., in sympatry or parapatry. As speciation in birds usually proceeds through an initial phase in allopatry (Phillimore *et al.*, 2008; Price, 2008), many closely related, but geographically separated lineages cannot directly be assessed for species status using the reproductive isolation criterion. The second major difficulty with the criterion of reproductive isolation is that, even though hybridization is generally rare on an individual level (Mayr, 2014; Justyn *et al.*, 2020), mating between different species has been documented for a large number of widely recognized bird species often accompanied by gene flow across species boundaries (Grant & Grant, 1992; Mallet, 2005; McCarthy, 2006; Price, 2008; Rheindt & Edwards, 2011). This indicates that even though strong reproductive isolation can evolve in birds on short time scales of 1–2 million years or much less (Weir & Price, 2011), its completion can take much longer (Price & Bouvier, 2002) and postzygotic compatibility may remain in place for a long time between lineages that are isolated by prezygotic mechanisms. Proponents of the biological species concept have argued that some level of hybridization and gene flow between evolutionary lineages should not preclude their treatment as species-level taxa, unless it leads to a complete merging of their gene pools and consequently the loss of their distinctness (Coyne & Orr, 2004). Consequently, for the Howard & Moore Checklist, speciation does not need to have reached complete reproductive isolation for lineages to be ranked as species. Instead, we regard as species distinct evolutionary lineages that exhibit enough reproductive isolation to coexist durably in sympatry or parapatry or that have evolved a degree of distinctness in allopatry that would make coexistence in sympatry or parapatry likely. Taxa connected through populations of admixed origin (such as hybrid zones) are treated as valid species if barriers against interspecific gene flow exist and are strong enough to ensure persistence of their distinct gene pools over evolutionary time scales (e.g., maintenance of a narrow hybrid zone).

CRITERIA FOR RANKING TAXA AS SPECIES

The Howard & Moore Checklist applies the following species criteria to assess the status of evolutionary lineages under the biological species concept by focusing on reproductive isolation as defining the criteria.

In the simplest case, evolutionary lineages coexist in sympatry and show complete reproductive isolation, i.e., reproduction occurs only within a group and not among groups and are thus considered different species. Besides direct observation of reproductive behaviour, e.g., of mate choice or offspring parental identity, proxies such as genetic, morphological, vocal, behavioural, and ecological differentiation may be used to indirectly assess reproductive isolation among such sympatric lineages. In more difficult cases, where (i) reproductive isolation cannot be assessed directly, i.e., in allopatric lineages, or (ii) where

reproductive isolation is incomplete, i.e., hybridizing lineages in sympatry or parapatry, the status is assessed as follows:

i) In the case of allopatric lineages, multiple lines of evidence are taken into account to assess the potential for the existence of reproductive isolation in a hypothetical scenario when the two lineages in question would meet in parapatry or sympatry. As a proxy for the potential existence of reproductive isolation, we evaluate their degree of divergence compared to closely related taxa that are demonstrated to be valid species. Data on the genotype and the phenotype, such as physiology, morphology, vocalization, behaviour as well as ecology are considered in an integrative way – taking into account all available evidence without requiring evidence to be available for every type of data (Sangster, 2018). Species rank is assigned when evolutionary lineages with strict allopatric distributions differ using various proxies at similar levels to those exhibited by closely related pairs of taxa that are reproductively isolated and unambiguously assigned to species rank, as proposed by Helbig *et al.*, (2002). However, as reproductive isolation can evolve largely independently of divergence in phenotype, ecology or genotype (Stankowski & Ravinet, 2021) and intrinsic postzygotic barriers can evolve in morphologically cryptic lineages that additionally do neither differ obviously in sexual signalling nor in ecology (Pulido-Santacruz *et al.*, 2018; Cronemberger *et al.*, 2020), we do not apply any form of scoring of character differences between evolutionary lineages for establishing species limits based on predefined thresholds (Tobias *et al.*, 2010; Donegan, 2018). Such a scoring approach may overlook substantial cryptic diversity given the relative and highly variable nature of the speciation process across lineages, and moreover, despite what is advocated by its proponents, it often suffers from low reproducibility (Rheindt & Ng, 2021). Instead, we assess multiple lines of available evidence taking into account time of divergence as well as lineage-specific characters that vary between well-established species of the same lineage and/or are involved in reproductive isolation in that specific lineage.

ii) In the case of evolutionary lineages distributed in parapatry or sympatry that do not show complete reproductive isolation, we apply the following criteria to identify species rank. For sympatric lineages, the circumstances of gene flow should suggest they will not lead to the complete merging of their gene pools and the loss of their distinctness (Coyne & Orr, 2004). Lineages that exhibit a parapatric distribution with a hybrid zone as the result of secondary contact are considered species when sufficient barriers to gene flow away from the hybrid zone prevent the complete merging of the two distinct gene pools by taking into account that selection against introgression often varies across the genome and parts might be merged. Such barriers to introgression may include assortative mating, i.e., preferential mating within species, or reduced fitness of hybrids or admixed genotypes compared to parental lineages in the hybrid zone or in their respective ranges. Examples of potential proxies of such barriers include estimates of gene flow across hybrid zones from multilocus genetic data based on many independently evolving genetic markers, or especially from neutral alleles (Westram *et al.*, 2022); linkage disequilibrium of multiple unlinked genetic regions differentiated between lineages (Poelstra *et al.*, 2014; Toews *et al.*, 2016); bi- or multimodal trait or genotype distributions in hybrid zones (Gay *et al.*, 2008); or patterns of mate choice in contact zones (Brambilla *et al.*, 2008). Such proxies are considered again in an integrative way, considering all available evidence without requiring evidence to be available for each proxy (Sangster, 2018), to evaluate whether gene pools of parapatric lineages are likely to remain distinct.

Species should generally be monophyletic, unless there is evidence for rapid (peripatric) or hybrid speciation (Hermansen *et al.*, 2011; Elgvin *et al.*, 2017) or the prevalence of ‘combinatorial mechanisms’ – the reassembly of old genetic variants into novel combinations

(Marques *et al.*, 2019) – during the speciation process that could leave some taxa to become paraphyletic. As a consequence, we also use phylogenetic relationships (branching patterns in addition to divergence) to assess species limits whenever information on reproductive isolation is missing (unstudied contact zones or allopatric lineages). However, phylogenetic hypotheses should preferably not be evaluated on the basis of single non-recombining units such as mtDNA (so-called gene trees), as phylogenetic reconstruction based on or dominated by such types of data (i.e., mtDNA combined with a few uninformative nuclear data) do not necessarily represent the true history of lineages (the so-called species tree). Stochastic processes resulting in incomplete lineage sorting, introgression (e.g., Edwards, 2009; Edwards & Bensch, 2009; Toews & Brelsford, 2012) including retention of haplotypes resulting from ancient introgression of an extinct species (Hogner *et al.*, 2012; Zhang *et al.*, 2019), or non-neutral evolution (Pavlova *et al.*, 2013; Fossoy *et al.*, 2016), can generate discordance between gene trees and the species tree. We thus caution against drawing taxonomic conclusions solely based on phylogenetic hypotheses stemming from mtDNA. Nonetheless, phylogenetic analyses and estimates on divergence times from single-marker studies are important supporting information for delimitation of lineages supported by multiple lines of evidence, and these can be compared to those between other closely related lineages unambiguously assigned to species rank.

CONCLUDING REMARK

By applying a biological species concept and focusing on the defining criteria of reproduction isolation as the cornerstone of the speciation process, we apply a prospective approach (*cf.* Sangster, 2018). Species delimitation decisions are thus made on the basis of present-day or potential future processes or interactions among lineages. To evaluate whether lineages are likely to fuse in the future, our approach relies on integrating multiple lines of evidence by evaluating all present data. Consequently, species delimitation decisions concern hypotheses that need to be documented and reevaluated when new evidence becomes available.

One common criticism to the use of the biological species concept as a basis for species delimitation is the subjectivity involved on where to cut the speciation continuum for ranking taxa connected by hybrid zones and for ranking allopatric taxa. We fully acknowledge this difficulty but wish to point out that the use of other delimitation criteria under alternative species concepts come with the same level of subjectivity. For example, defining species as “separately evolving metapopulation lineages” under a unified species concept (de Queiroz, 2007) requires in our opinion a similar amount of subjectivity to assess how much “separation” is enough to grant species rank. However, the use of the the isolation version of the biological species concept presents the advantage of having a clear definition of what speciation is: the evolution of reproductive isolation.

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