Data & Discoveries in the World of Birds

A 2020 Birder's Guide to Avian Species Concepts

In the second chapter of *On the Origin of Species*, Charles Darwin distilled the trouble with "species" in the following line: "No one definition has as yet satisfied all naturalists; yet every naturalist knows vaguely what he means when he speaks of a species."

Like so much of what Darwin wrote, this line is as lucid now as it was in 1859. There's often no need to overthink what a species is. The moment you step outside, you see living things differ from one another. We know an American Robin and a House Sparrow, for example, are different the instant we see them. We also know an American Crow is different from a Common Grackle. With a little training, we even know an American Crow is different from a Common Raven—no need for sophisticated genetic analyses, mating experiments, or philosophical gymnastics.

The trouble is, nature doesn't always make it easy for us. For every case of easy identification, there are challenging edge cases to boot. Take the Golden-winged and Blue-winged warblers, whose outward appearances are radically different, yet whose genomic divergence is 0.03%—a far cry from the 1.24% separating humans from chimpanzees. Should they be considered the same species? Or take the *Scytalopus* tapaculos of the Neotropics, whose appearances are virtually indistinguishable. Their whole genomes have not been sequenced, but their mitochondrial DNA has; compare their mitochondrial divergence of as much as 12.0% to the 8.9% separating humans and chimps. Is that genetic divergence more compelling than their identical appearances?

This is where *species concepts* come in. Their purpose is to make sense of a range of cases, to bring clarity to the question of how "kinds" of organisms, both the striking and the cryptic, can be recognized, discussed, and studied.

An Incomplete History of Species Concepts

Taxonomy, like language more generally, serves a critical function: It supplies a vocabulary for describing the world around us. But unlike language in the normative sense, taxonomy is scientific; it uses evidence to create a system of terms that are as stable, universal, and *real* as possible.

A stable, evidence-based taxonomy is all well and good—it's why high school biology students learn the name Linnaeus. But then there's Darwin. His work revealed a kind of evolution that's not just part of life's history; it's an ongoing process. Continual change puts strain on a system of static labels, a strain that biologists have been grappling with ever since.

An array of *Anas* ducks—two-way hybrids and possibly even three-way hybrids—are flying over the Rio Grande, at a spot where Mallards, Mottled Ducks, and Mexican Ducks are breeders. All three duck species show deep genomic divergence and evidence of reproductive isolation. That's why earlier this summer, the American Ornithological Society elevated the Mexican Duck to full-species status. Scenes like this, where all birds have mixed ancestry, are not necessarily an impediment to recognizing populations as separate species. *Starr County, Texas. Photo by © Alex Lamoreaux.*

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This bird represents the first-known putative hybrid between a Chestnut-sided Warbler and a Golden-winged x Blue-winged warbler hybrid. A hybrid like this one—transcending not only species lines, but also genus lines—proves that interbreeding happens in unexpected and complex ways. Birds like this remind us of the challenge to establish "species concepts"—and to define "species." *Blair County, Pennsylvania. Photo by © Lowell Burkett.*

The most prominent attempt to reconcile static taxonomy with dynamic evolution is the Biological Species Concept (BSC), coined during the "Modern Evolutionary Synthesis" period by Harvard ornithologist Ernst Mayr. In his 1942 book *Systematics and the Origin of Species*, Mayr gave species a simple, intuitive definition: "Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups."

The operative words here are *interbreeding* and *reproductively isolated*. The BSC is built on the view that interbreeding blurs the line between two species, blending their respective gene pools. For species to be valid (or "good"), something must prevent or protect them from such blending. Biologists refer to these protections as "reproductive isolating barriers," because that's exactly what they are: They isolate organisms and keep them from reproducing with each other. Isolating barriers can be anything from genomes that physically can't combine during fertilization to specialization on different habitats.

While the BSC has proved remarkably enduring, it is not without its critics, who focus predominantly on the *interbreeding* part of the definition. If a lack of interbreeding is the top criterion for species status, then how do you test for it in species that never encounter each other? Take the American Dipper and the White-throated Dipper of Europe. These species never occur in the same place, and thus never have the opportunity to interbreed. How do we tell whether they *would* interbreed? And what if they still have the *ability* to mate and produce fertile offspring? If that were the case, Mayr's BSC would declare them one species.

Understandably, this strict no-interbreeding requirement has troubled many biologists. On the one hand, the BSC is ill-equipped to assess *species limits* in geographically isolated populations. On the other hand, the strictest possible interpretation of the BSC would require species lumping upon any sign of interbreeding—even if the parents are very different. So interbreeding alone may be the wrong criterion.

The strongest contender with the BSC—of the 30+ species concepts out there!—is the Phylogenetic Species Concept (PSC). The PSC has multiple, more abstruse definitions. But they all boil down to species occupying distinct branches on the tree of life—ones which contain no smaller sub-branches. On each branch, members of the species are identified by diagnostic

genetic and morphological differences that are not shared with any other species.

To put it simply: If a population doesn't freely mix genes with any other such population, it's a *biological species*; if it occupies its own distinct branch on the tree of life, it's a *phylogenetic species*. Often, these two definitions overlap almost perfectly. Most "good" biological species are "good" phylogenetic species, and vice versa.

Now for the fun part.

Splitting and Lumping, Inflation and Inertia ■ Phylogenetic species and biological species *don't* always overlap. Discordance between the two has fueled considerable theoretical development, and, more recently, disagreements between the two concepts have affected conservation. The BSC vs. PSC debate is as intense as ever.

On the PSC side, where more splitting is the order of the day, a 2016 study by American Museum of Natural History ornithologist George F. Barrowclough and colleagues found a striking result. Using a PSC-like species concept on genetic data, they estimated there are about 2.4 species-level taxa for every recognized species in our current taxonomy (*PLoS ONE* 11 [11]: e0166307; tinyurl.com/Barrowclough-18000-birds). After analyzing a separate morphological database, they recommend that ornithologists split the approximately 10,000 bird species currently recognized into more than 18,000! Barrowclough and his team argue these species represent worthy targets of conservation and study. A 2018 paper by Peter A. Hosner of the Smithsonian Institution, along with six colleagues, drew similar conclusions in the Philippines: From 19 currently recognized species, they found 40 species using a PSC-like concept (*Conservation Genetics* 19 [5]: 1153–1168; tinyurl.com/Hosner-Philippine-diversity). These new species importantly included endemics worthy of conservation. Barrowclough and Hosner and other thinkers have sounded the alarm on persistent lumping or "inertia" in our taxonomy, arguing that the BSC-driven status quo fails to recognize real, important diversity.

For practical reasons, many conservation-minded scientists take the opposite stance. Exorbitant splitting or "inflation," they argue, would render conservation of species impossible. In 2004, Nick J. B. Isaac, now at the U. K. Centre for Ecology & Hydrology, partnered with two colleagues to review the effects of splitting on conservation. The team concluded that conservationists must "avoid unrealistic expectations of species lists," citing the unreliability of taxonomy in times of upheaval (*Trends in Ecology & Evolution* 19 [9]: 464–469; tinyurl.com/Isaac-taxon-inflation). And just last year, David W. G. Stanton and eight others threw their hands up entirely, arguing that we shouldn't use species lists for conservation at all. Instead, measures of genetic diversity and adaptive potential ought to guide conservation. Taxonomy, in its current state of flux, is, in this view, too unruly (*Conservation Genetics* 20 [1]: 101–113; tinyurl.com/Stanton-conservation-grist).

Many others stand somewhere between—or outside—the fray. In 2007, Smithsonian Institution herpetologist Kevin de Queiroz proposed that most scientists agree on what a species is: a group of populations sharing a unique evolutionary trajectory. After naming this idea the "unified species concept," de Queiroz declares all other considerations "secondary criteria" for identifying species with different lines of evidence (*Systematic Biology* 56 [6]: 879–886; tinyurl.com/de-Queiroz-unified-species). George Sangster, at Stockholm University, followed up on de Queiroz's view. In 2013, Sangster published a review of literature from between 1950 and 2009, finding that the most popular species concepts among ornithologists are in fact closest to the PSC. If this is the case, the "debate" is overblown (*Biological Reviews* 89 [1]: 199–214; tinyurl.com/Sangster-avian-taxonomy). And quite recently, Ashley T. Simkins of BirdLife International and three colleagues assessed the impact of about a thousand splits on the

If you were to sequence the genome of this Common Raven from central coastal California, you would likely find the ghostly evidence of another divergent raven species. That other species appears to have been reproductively isolated. But after Pleistocene Epoch glaciers receded from the region, that raven was no longer reproductively isolated. Genomic evidence suggests that these two ravens then fused—a fascinating example of "reverse speciation." *San Mateo County, California. Photo by © Alvaro Jaramillo.*

IUCN Red List for birds. Their findings were surprising: Newly split species have been, on average, *less* threatened than the previously unrevised species. These new splits also tended to be distributed in locations that are already conservation priorities, such as Java and the Philippines (*Animal Conservation* 2019; tinyurl.com/Simkins-taxon-revision). If this result is accurate, then splitting should not negatively affect conservation.

How do we reconcile inflation and inertia? What does it take to know if a split or a lump is really "worth it" and not susceptible to being undone a decade or two later? To answer these questions, we must return to those twin components of the venerable BSC: interbreeding and reproductive isolation.

The "How" of Species ■ For many students of this topic, the now-classic 2004 text *Speciation*, authored by the University of Chicago's Jerry Coyne and the University of Rochester's H. Allen Orr, frames the conversation about species concepts. In the text's first chapter, after endorsing a less strict version of the BSC, Coyne and Orr offer the following assessment:

> *We feel that it is less important to worry about the species status than to recognize that the process of speciation involves acquiring reproductive barriers, and that this process yields intermediate stages when species status is more or less irresolvable.*

This statement sheds light on why classification can be so challenging. Species are of course still evolving. Sometimes, they aren't quite there yet—and based on the process of speciation, *that's to be expected*. It may be that the interesting question isn't: "What is the species status of this complex?" Instead, the more fruitful question may be: "How have these populations come about?"

Genome sequencing has revealed that interbreeding is surprisingly widespread—a persistent echo from criticisms of the BSC. This means the bird documented on p. 15—a hybrid between a Chestnut-sided Warbler (genus *Setophaga*) and a Golden-winged x Blue-winged warbler hybrid (genus *Vermivora*)—shouldn't flabbergast us. Birds probably don't lose the *ability* to reproduce as rapidly as Mayr believed. Regular hybrids between the recently split Mexican Duck and Mallard are not outliers, either. Recent, genome-wide evidence demonstrates that the two remain deeply independent of one another.

Do these cases mean Mayr was wrong? Does interbreeding present no risk of blending species back together? In 2008, Patrik Nosil, then at the University of British Columbia, addressed this question in the *Biological Journal of the Linnean Society* (95 [1]: 26–46; tinyurl.com/Nosil-on-Ernst-Mayr). Nosil amassed evidence showing that two populations, on their way to complete reproductive isolation, need not be geographically separate and incapable of interbreeding, as Mayr emphasized. Instead, populations can speciate *despite interbreeding* if they are subject to different selective pressures.

Nevertheless, there has to be some amount of interbreeding across species lines that's simply too much. In the June 2018 issue of *Birding* (pp. 30–31), this column covered "speciation reversal" in a California species of raven. After Pleistocene Epoch glaciers retreated northward some 22,000 years ago, too few isolating barriers were in place to prevent uninhibited interbreeding. As a result, this California raven, once an independent lineage, fused with the Common Raven.

The question has shifted. It's no longer enough to ask: "Do they or don't they interbreed?" The question is now more nuanced: "Do they interbreed minimally enough to maintain separation?" As Nosil and others have argued, to understand whether some amount of interbreeding risks speciation reversal, we need to expand our conception of isolation mechanisms. It's the progress of speciation, considering multiple isolation mechanisms, that matters for classification. This dynamic interpretation of evolution may be the most lasting endowment of Mayr's BSC.

As birders, we might think of potential isolating barriers like boxes on a checklist. To check each box, the barriers they represent must be studied. Today's ornithologists are doing precisely that. In each year's crop of American Ornithological Society *Check-list* proposals, you'll see one "box" to check in the form of measures of genetic divergence, which signify the history of reproductive isolation between two taxa. You'll see studies that quantify interbreeding, another "box." If that interbreeding is limited, as in the case of a narrow hybrid zone, that's another "box" to check. You may also see studies documenting differences in songs, in mating preferences, and in social dynamics—more "boxes." Ecological differentiation, wherein each species uses different resources and tolerates different conditions, is yet another "box" checked by many studies. Taken together, these factors confirm isolating barriers and signify progress in speciation.

Want to see these considerations in play? Look—or, rather, listen—no further than Nate Swick and Nick Block on the Apr. 15, 2020, episode of the American Birding Podcast (aba.org/2020-splits-and-lumps-with-nick-block). You'll hear them discuss isolating barriers and the progress of speciation for some of the most likely splits, including the now-accepted split between the Mallard and the Mexican Duck.

Finally, here's where birders come in. For birds, perhaps more than any other group, birders, citizen scientists, and students push speciation studies forward with their observations. So biologists have a head start because knowledge already exists about the organisms in question. Isolating barriers aren't obscure mysteries visible only to scientists. They can be inferred from everyday observations, as many intriguing differences between species may have played a role in their speciation. By doing what we birders do—finding birds, making careful observations, and accurately reporting those observations—we ensure fertile ground for much more progress on the frontiers of speciation science. Best of all, we remind ourselves that the question of species, far more than being grounds for intellectual conflict, encompasses the history of life on Earth and the many paths it took toward the splendid diversity we see today.