

## THE PHYLOGENETIC SPECIES CONCEPT: CORNUCOPIA FOR LISTERS

by John C. Kricher

Species are real. I know it; you know it; and, most importantly, *they* know it. When was the last time you saw a Tufted Titmouse courtship-feeding his mate, a Northern Cardinal? Sure, both birds have crests, and both come to bird feeders. They're always running into one another as they go about their version of birding, but they never mate. Titmouse sex is between titmice; cardinal sex between cardinals. The result is the gene constellations of titmice and cardinals remain separate: titmice genes don't mix with cardinal genes. And thus, we have two species, two separate gene pools. Each gene pool is a vast array of genes, strings of DNA, that have traveled together through evolutionary time and have coevolved to interact in extremely precise ways. The DNA recipe for Northern Cardinal is quite different from that for Tufted Titmouse. To mix cardinal genes with titmouse genes would be like mixing notes from a Mozart symphony with those of Beethoven. The notes would fail to arrange in any reasonable manner, and the result would be a symphonic monstrosity.

Species are *reproductively isolated* from each other. Genes program each species to recognize others of its kind. Hybrids are rare. When they do occur, hybrids will look and sound different from either parent species, usually causing the hybrid great difficulty in attracting a mate programmed to recognize a different plumage or song. Hybrids are genetic dead ends. It is therefore unsurprising that birds, as well as many other animals, have evolved elaborate courtship displays that function in large part to assure species recognition and thus prevent reproductive wastage. Songs, plumage, and behavior all function as *reproductive isolating mechanisms*.

Some species, such as the Song Sparrow, range very widely, and local populations are genetically differentiated into recognizable races or *subspecies*. When a species is divided into several subspecies, it is *polytypic*. The *National Geographic* field guide is particularly complete in illustrating distinct subspecies. Subspecies are regional populations that have unique genetic identities. But, they are not reproductively isolated from neighboring subspecies, at least not at the moment. Some subspecies may have almost reached the point of *speciation*, but not quite. This last point has been a sore one with many birders, particularly those who place the importance of their life lists next to their love for their children. Listers have taken a real beating of late, because certain populations, once deemed to be full species, hybridize successfully with neighboring populations. Doing so has resulted in lumping what were once designated as separate species into subspecies. Goodbye, Baltimore and

Bullock's orioles. Farewell, Gilded, Red-shafted, and Yellow-shafted flickers. Adios, Myrtle and Audubon's warblers. There are others, as you well know from the erasure marks on your life list. You get the point.

What I have just outlined is called the Biological Species Concept (BSC), championed in large part by Ernst Mayr (1942, 1963). It rests on the presumption that species are reproductively isolated from one another, that they recognize each other and mate accordingly. Spotted Towhees look different from Rufous-sided Towhees, but where they meet, they mate. So they are one species. Black-crested Titmice find Tufted Titmice attractive: one species, not two. Sometimes species don't look distinct to us, but they do to them. The Alder and Willow flycatchers tell us they are two species, not one. So do the Tropical and Couch's kingbirds.

Though the BSC is well entrenched in evolutionary theory, it is not without difficulties. What do we do about Scrub Jays in Florida versus those in California, for instance? The Florida subspecies has a whitish forehead and a cooperative breeding system, making it both morphologically and behaviorally distinct from the western subspecies (Woolfenden 1975). Would a Florida bird mate with a Californian? Who knows? They are separated by a continent and have no opportunity to mate. Their status as subspecies or separate species is not resolvable using the BSC, since the critical criterion, mating, cannot be verified or refuted. A similar situation exists with Marsh Wrens. The western subspecies has a broader song repertoire and distinct brain anatomy from the eastern race (Kroodsma and Canady 1985). Could they or would they mate if an eastern and western individual were together, or are they like the *Empidonax* flycatchers, separate species that merely look alike? When populations do not overlap, all the BSC allows for is an educated guess. Clark's Grebe, newly split from Western Grebe, would in all likelihood still be considered a subspecies were it not for the fact that the ranges of both populations overlap, permitting ornithologists to document whether or not they interbreed. They don't, so they are separate species. Even when ranges overlap, there are difficulties. Black-capped and Carolina chickadees hybridize in a narrow zone in southwestern Missouri but do not hybridize when in contact in many other areas (Robbins et al. 1986). As Judge Wapner would say on *The People's Court*, the "preponderance of the evidence" seems to favor considering the chickadees to be separate species -- for now.

Recently some ornithologists have challenged the BSC, advocating its replacement with something they call the Phylogenetic Species Concept (PSC). The PSC, it is argued, would eliminate the subjectivity evident in attempting to use the BSC when populations don't overlap in range. It would also be a major windfall for listers. The PSC was strongly advocated by Cracraft (1983) and is detailed by McKittrick and Zink, the lead paper of the February 1988 *Condor*.

The PSC defines a species as "the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent." Notice that any reference to reproductive isolation is missing. Notice also that the "diagnosis" of species status is entirely up to the taxonomist, not the organisms themselves. It makes no difference who breeds with whom. A species is what the taxonomist says it is, based on observing any anatomical, behavioral, vocal, or other genetic characteristic that is held in common by lineage. Sharpen your pencils, listers; the Bullock's is back! Ditto the juncos and flickers. Western Fox Sparrows are now a species distinct from Eastern Fox Sparrows. Pay attention to those *nelsoni* Sharp-tailed Sparrows, or should I say "Nelson's Sparrow?" The Green-winged Teal and Common Teal are separate again. And oh joy, oh rapture! Think of all those new species of Canada Goose created just by the stroke of a taxonomist's pen.

You are not dreaming. The PSC folk really do advocate making a species out of virtually any population that has genetic identity. This would, of course, include just about all of the subspecies and maybe then some. The advantage of the PSC, so say its advocates, is that it defines *lineages* which are presumed to be the most recent and therefore the most significant evolutionary entities. The evolutionary picture is thus clarified rather than muddled as PSC advocates claim it often is with the BSC. One hypothetical example, given by McKittrick and Zink, supposes that a population of Trumpeter Swan is discovered to have one extra hooklet on a barb of the seventh primary. (I realize that this would present a significant field problem -- it's their example, not mine.) Rather than dismiss the additional hooklet as trivial, McKittrick and Zink argue that such a character may reflect most recent evolutionary history, the "cutting edge" of evolution. Good enough to call these Trumpeters a new species? Why not? McKittrick and Zink recognize that some genetic characters, such as hooklet number, may vary even within a localized population, presenting a problem in judging whether or not the population should be awarded species status. Their solution: call these populations "potential incipient phylogenetic species" (PIPS)! I can well imagine the birding elite studying blurred slides as they one-up each other on PIPS identifications.

What of reproductive isolation as a species delineator? The PSC recognizes reproductive isolation as a primitive character, not sufficiently precise to utilize in species definition. The one characteristic that, in fact, does actually separate gene pools is summarily dumped.

The PSC is not without its own problems. Many populations vary gradually from north to south, for instance. Where does the taxonomist draw the lines to separate *gradual* variation? Some variation is not genetic. Red-winged Blackbirds are considerably larger in Colorado than in Florida. Should this body size difference confer species status on each population? No way, since

transplant studies have shown that the offspring from Florida red-winged eggs, hatched and raised in Colorado, grow to the size of typical Colorado birds and vice versa (James 1983). The geographic differences are *environmentally induced*, not genetic, and thus insufficient for species designation. It would be like saying fat birds are a different species from thin birds. Notice, however, that without the careful transplant studies, a PSC taxonomist might well have decided to confer species status on these Red-wing populations.

The PSC is a response to frustration by taxonomists. People who like to put up predawn mist nets and collect the dead birds at dusk have no way of knowing about reproductive isolation. They have only specimens. Classifying such specimens as to species status is greatly facilitated by the PSC. The subspecies category is eliminated (though PIPS sounds suspiciously like subspecies reincarnated), and we generate a neatsy keen list of "good" species. Bravo.

I believe the PSC to be far less useful than the BSC. It focuses on traits rather than process. It is artificially static because by reducing species to merely a population with any distinct genetic trait, it loses the dynamism evident in the realization that speciation is often gradual and often incomplete, because such is the nature of the evolutionary process. The BSC, for all its shortcomings, focuses on process, on characteristics of real biological significance, such as behavior, ecology, and biogeography. I believe we have learned much more about evolution from applying the BSC than we would now know had we always used the PSC.

One final point. Consider how the PSC would apply to what you see in the mirror each day. The last time I rode the T there were at least four species in the bus with me. There was *Homo caucasiensis* along with two caucasiensis PIPS, irishensis and italianensis. Then there was *Homo negroensis*, *Homo asianensis*, and *Homo hispaniensis*. You can't have it both ways. If you're going to split the birds, you gotta split the folks too. Human racial variation is genetic: Thus, races ought to be given species status under the rules of PSC. By applying PSC to humans, its real ludicrousness is apparent. Humans are one gene pool, one species. It is worth recognizing that races (subspecies) and species are two different things. To apply the PSC to humans would set back social enlightenment two hundred years. It would also mask biological reality. Neither is a good thing.

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