

Tales from the Cryptic Species

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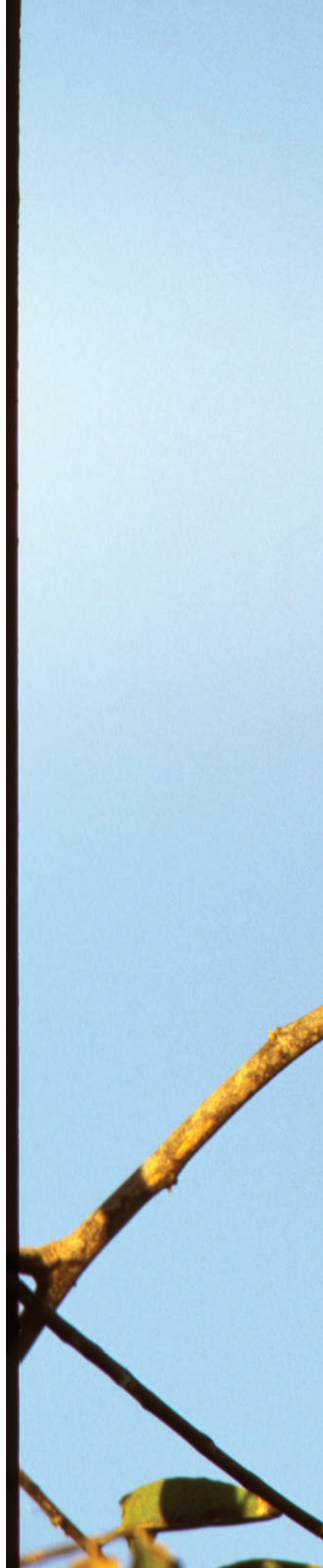
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Now that the AOU publishes its *Check-list* supplements annually in the *Auk*, I think a lot of birders tune in to see which species have been split and which ones have been lumped, partly to determine how they should rearrange their notes and lists. Those of you who were birding in the early 1970s probably recall an awful lot of lumping—for example, all of those different juncos suddenly packaged up into two species, one with dark eyes, one with yellow eyes. Gone were the Myrtle and Audubon's Warblers, and several other species. However, in the past decade or two, things have gone the other way: The splits are coming down the pipeline faster than the lumps, and tongue-twisters such as Pacific-Slope Flycatcher and Saltmarsh Sharp-tailed Sparrow are suddenly on the checklist.

What is going on? Well, there isn't just one answer to this multifaceted matter.

One answer is that there has been a shift in philosophy from a very strict adherence to the Biological Species Concept (BSC). In the past, if any significant amount of hybridization occurred between two species, they were lumped. Now, we have a kinder, gentler BSC: Hybridization is not necessarily a problem, as long as the two species appear to be retaining their integrity (if gene flow is restricted across the hybrid zone, for example).

On the basis of behavioral and ecological differences, the **Great-tailed Grackle** was split from the Boat-tailed Grackle in 1973. Could yet another split be in the offing? Within the species currently recognized as the Great-tailed Grackle, there are significant vocal differences—possibly indicative of distinct species. *Maricopa County, Arizona; December 2005.* © Jim Burns.







Another answer has to do with the realization that there are good species hidden in those museum drawers. They were perhaps never thought of as good species, because they are not all that different as they sit there in the museum collection. These are the “cryptic species”: good species that have not been recognized as such because they just don’t seem that different—to our human eyes. So what has changed? Why are these cryptic species suddenly popping out, left, right, and center? The problem is especially acute, we are learning, south of the U. S. border.

Two things are happening. One is an appreciation of the taxonomic value of vocalizations. The other is the revolution in molecular biology, now being applied with gusto to avian taxonomic studies. I will summarize how these issues have affected the detection of cryptic species, focusing on voice as a tool, and will give some examples of situations where cryptic species may exist.

A classic example of a cryptic species in North America is the case of the “Traill’s Flycatcher”, which we now know as the Alder and Willow Flycatchers. Stein (1963) conducted an extensive study of these birds and came to the conclusion that there was a northern species and a more-southern species. They look quite similar, nearly identical—even in museum trays. But their vocalizations, nesting habitats, distribution, and general biology are different. Birders in places where the two species breed in the same sites, nearly side by side, mutually ignoring each other like good species, may marvel that these two birds were ever considered to be the same thing. But it is one thing to have field experience with these birds and quite another to know them in the museum drawers. So with Stein’s information available for the world to see, the AOU (1973) published the following: “*Empidonax trailli* is divided into two species: *Empidonax traillii* (Audubon), the generally more southern and western bird, of more open country, whose vocalization has been interpreted as ‘fitz-bew’, and *Empidonax alnorum* (Brewster), the generally more-northern bird, of the boreal forest region, whose vocalization has been interpreted as ‘fee-bee-o’.”

I wonder if this was the first time that a split by the AOU



Despite their similarities in plumage, the **Eastern Meadowlark** (far top) and **Western Meadowlark** (above) exhibit significant vocal and ecological differences, and they have long been recognized as separate species. Variation within the widespread Eastern Meadowlark is considerable, however, and the distinctive southwestern race *liliana* (right), known as “Lilian’s Meadowlark”, may someday be split from the rest of the North American population.

Far Top: Galveston County, Texas; March 2005. © Alan Murphy.

Above: Hansford County, Texas; December 2005. © Greg Lasley.

Right: Cochise County, Arizona; February 2006. © Jim Burns.



so prominently featured the voice of a bird in the published justification. Interestingly, this is the same AOU *Check-list* supplement in which the Yellow-rumped Warbler, Northern Flicker, Northern Oriole, Seaside Sparrow, and Dark-eyed Junco were all created via lumping—the dark days of taxonomy in some birder’s views. But before you buy into this idea of the dark days of taxonomy, consider again the split of the Willow and Alder Flycatchers, signaling, I think, a shift in understanding and a rather radical departure from the criteria that avian taxonomists had been thinking of as important in the determination of species status, e.g., reproductive isolation.

Another split in this *Check-list* supplement was that of the Boat-tailed and Great-tailed Grackles. Here again was a situation involving sympatry, with the breeding ranges of these two overlapping; but the two populations clearly differ in vocalizations, displays, and habitats, even though they are similar in appearance. Vagrant individuals of these species still give us identification nightmares, even though their species status is uncontested. Maybe those weren’t the dark days, but the start of the sunny days?



The two examples noted above—namely, the flycatchers and the grackles—are quite different if we dig a bit deeper. They are both songbirds in the order Passeriformes, but the flycatchers are classified as suboscines, one of the major divisions within the songbirds, while the grackles are oscines. What does this mean? The distinction is an important one, as there are major morphological differences between these two groups. For example, the main vocal structure (the syrinx) is simpler in the suboscines. Suboscines tend to make simpler sounds than do oscines, which is why people keep canaries (which are oscines) and not antbirds (suboscines) in cages.

Also, and crucially important, most suboscines do not learn songs. Alder and Willow flycatchers can be raised in captivity and they will sing entirely normal *fee-bee-o* and *fitz-bew* songs, respectively, without ever hearing versions of these songs (Kroodsma 1984). The songs are effectively hardwired, coded in their genes. Any environmental influence on them is minimal. Thus, suboscines do not have vocal dialects, as oscines do. What this means is the following: If two populations of a suboscine differ in song, then they must also differ in their genes, as songs are hardwired. Further, if you play back the song of Population A to Population B, they will ignore each other. They will not interbreed if they come into contact, so you have two species. Of course, it is always the case in biology that there are exceptions, and some manakins (which are suboscines) may, in fact, learn certain aspects of their songs.



The Red-winged Blackbird exhibits considerable variation throughout its extensive range. Is there just one species in North America, or might there be two or more? *Belknap County, New Hampshire; April 2003.* © Garth McElroy.

Now if you go and look at your field guides of South American birds, you will see that lots of suboscines—flycatchers, antbirds, furnariids, and others—look a lot alike. Some look identical. With this understanding, voice becomes a vital tool for determining species delineations in suboscines. Several years ago, while I was co-leading a tour to northern Argentina with David Stejskal, he played a tape of a species I know well from Chile: the Rufous-banded Miner (*Geositta rufipennis*). But I did not know this bird from Argentina. The song was quite unlike the one I was used to from Chile. Seeing the confusion on my face, David said, “Yup, they sound different here ... Certainly a different species.” Could it be this easy? You just go down to South America, pay attention, record birds, and lo and behold, you suddenly have the information to split species or even describe new species?

It's not quite that easy, but nearly so. Since my epiphany with Dave, I have been following up on Dave's suggestion and have recorded or gathered recordings of Rufous-banded Miners. I discovered that one song type is found from central Bolivia to central Argentina, always east of the continental divide. The other song type is found in Chile, and in the high Andes of central Argentina south to the Patagonian Andes. Along one road in Mendoza, Argentina, I found that the “Argentine type” is found up to approximately 2,000 meters in dry valleys, while the “Chilean type” is found above 2,500 meters in Alpine habitats, and crosses into Chile. Even though these two populations are nearly identical visually, the fact that they are very different vocally, that they use different habitats, and that they nearly come into contact clearly suggests that there are two species here. Another cryptic species has come into view. Now I just have to finish the analysis and publish all of this. That's the part that isn't so easy.

This issue of learned vs. hardwired songs is important not only in the passerines, but also in the non-passerines. There are some non-passerines that clearly learn songs, like parrots of course, but also hummingbirds, surprisingly. Conversely, there are other groups in which the evidence suggests that there is no vocal learning, as with the shorebirds. For example, Least Sandpipers from various parts of their extensive range sound pretty much the same, with no clear vocal dialects (Miller 1986). In another study I have been involved with, I have been comparing voices of the Southern Lapwing



The **Rufous-banded Miner** is a Neotropical ovenbird (Furnariidae) that is widespread in the southern Andes. Vocally there are two groups, one in Chile and Patagonia and the other from central Argentina to Bolivia. While members of these two groups look nearly identical, they evidently belong to two separate species. This individual, showing the eponymous rufous band on the wings, is of the Chilean population. *Farellones, Chile; 26 January 2004. © Alvaro Jaramillo.*

(*Vanellus chilensis*), a gorgeous and common plover from South America. The different subspecies of this bird are similar, although they differ in shape, size, and some aspects of coloration. It turns out that there are large, long-winged and short-legged, bright-plumaged birds from Chile and Patagonia, which have one vocal type. From central Argentina north through the Amazon Basin to Trinidad and Colombia, there is a smaller, long-legged, short-winged, and duller-plumaged bird that has another voice. In this case, there is a narrow zone where there are intermediates. Despite some mixing, perhaps with our newer ideas about biological species we are really dealing with two species here. More work is needed.

Continuing with shorebirds, the American and Pacific Golden-Plovers are an example of two very similar species that were separated partly because of consistent differences in vocalizations. Could other shorebird splits be in the offing? The Willet is a good one to think about. The eastern and western populations of this species are geographically isolated while breeding, so it is difficult to test if the two would interbreed. However, keeping in mind that vocalizations are of importance in delimiting species in this group (think of yellowlegs and dowitchers), it is reasonable to propose that maybe there are two species of Willets, as the two differ consistently in voice, breeding habitat, size, and some aspects of plumage. In playback experiments of Western Willet song (the *pill-will-willet* vocalization) to Eastern Willets, it was found that Easterns respond much less to the songs of Western birds than to those of Eastern birds (Douglas 1998). The author notes that “it is possible that song discrimination between the races results in reproductive isolation.” In other words, a cryptic species alert. Although they are not all that vocal, the Snowy/Kentish Plover complex could probably be nicely addressed using vocalizations as a tool. I am not a betting man, but I bet there are more than two species involved here.

What about seabirds? Here is another one of these groups in which voice appears to be hardwired and to be important in pair formation. Perhaps if we had good vocal data on both Herald Petrels of the Pacific Ocean and Atlantic “Trinidad Petrels”, we would not have uncertainties as to how many species are involved. Leach's Storm-Petrels have vocalizations that are not all that different between the North Pacific and North Atlantic populations. There is some geographic variation in size and plumage, with Mexican populations sometimes being dark-rumped. However, the most intriguing issue is that vocalizations in the Leach's Storm-Petrel do not differ much overall, until you get down to Guadalupe Island in Mexico. There, vo-

calizations change abruptly from those farther north. To make things especially confusing, two different populations breed on this one island (Ainley 1980). One population (*socorroensis*) breeds in summer; it is small and polymorphic although usually dark-rumped. The other population (*cheimomnestes*) breeds in winter. These birds are larger and typically white-rumped. Not only do these birds differ vocally from other Leach's Storm-Petrels, but they differ somewhat from each other. There appear to be at least two species of Leach's Storm-Petrels, maybe three. The vocal study of seabirds will surely help to clear up many taxonomic issues in the future.



I made the distinction earlier between the oscines and sub-oscines, and left the oscine grackles hanging there, so let's now return to them. Grackles, like other icterids, learn their songs. Even so, song is incredibly important in mate recognition and pair formation. If you play a Great-tailed Grackle song to a Boat-tailed Grackle, the song will be ignored. Vocalizations are taxonomically useful, even in birds that learn songs, but larger-scale patterns have to be looked at in these situations. The

Eastern and Western Meadowlarks can learn each other's songs, but it is interesting that some of their call notes appear to be largely hardwired (Lanyon 1957). The two species hybridize rarely and are often found breeding side by side in parts of the Midwest: They are good species. Both the learned and hardwired components of their vocalizations aid in species recognition.

In general, with those species that learn songs, one would expect dialects to evolve due to errors in learning. And since birds learn the dialect from others in the breeding population, birds will then sound more like neighbors than like breeders from more distant regions. Sometimes, in populations that show geographic variation in vocalizations, there is a large break somewhere that divides two or more clearly different vocal groups which are found over a large portion of the range of the species—a "macro-geographic" pattern of vocal difference. These large-scale differences in vocalizations suggest that the populations have been separate for some time, allowing for differences to accumulate, with gene flow between the populations restricted or completely cut off. These are prime conditions for cryptic species.

Indeed, *within* the Great-tailed Grackle, this appears to be the



Despite its superficial drabness, the **Winter Wren** is amazingly diverse. There are 41 subspecies worldwide, including 12 in North America. Shown here is an individual of the race *alascensis*. The 12 North American subspecies fall into three major groupings, and several authorities have proposed that multiple species may be involved. *Pribilof Islands, Alaska; July 2005.* © Bob Steele.

case. Those of you living in Texas listening to those Great-tailed Grackles with their branch-cracking sounds and sharp rising whistles may not recognize the rather different songs given by Great-taileds in West Mexico and Arizona. The eastern song continues south at least to Belize, while the western song is restricted largely to the lowlands west of the central Mexican plateau. Could there be different species? Maybe, but more research is needed, particularly since the two populations may be intergrading in the western U. S., with both having recently moved into areas from which they were previously absent.

There are many examples from North America of macro-geographic variation in vocalizations. The Red-winged Blackbird exhibits vocal variation throughout its range, and the situation is especially interesting in California. There, some Red-winged Blackbirds lack the yellow border to the epaulets, and they have certain vocalizations that are heard nowhere else in North America. How about every Seattle birder's nightmare? No, not the hybrid gulls or the rain, but the crows. Where does the Northwestern Crow start and the American Crow end? Does the Northwestern Crow exist? Here is another example of a cryptic species, best tackled with vocal or genetic data or, even better, with both types of data.

I have been collecting recordings of crows and have yet to analyze the matter seriously, but my hunch, based on what I have

heard and recorded thus far, is that there are two vocally similar, but diagnosable entities in the West. Rather than a Northwestern Crow, there may be a Western Crow ("Pacific-Slope Crow"?). What I mean is that the birds west of the Sierras in California and west of the Cascades farther north are consistently hoarser and deeper in tone than those from the rest of the continent. So perhaps the entity we know as the Northwestern Crow is actually the smaller, more northern extreme of a western population found as far south as northernmost Baja California Norte, Mexico. There may be hope, Seattle birders!

I won't go too much into molecular work, other than to say that it often reveals surprising patterns of relationships between populations that were not known or that were unclear previously. A good example is the work of Omland et al. (2000), which showed that boreal and Rocky Mountain ravens are genetically similar to Common Ravens from the Old World, but distinctive from a different group that occurs in California. Interestingly, the sister taxon of the California population is the Chihuahuan Raven. There appears to be a region where the two Common Raven populations hybridize, but this matter needs more study. In the end, it is possible that a cryptic species of raven will be split. Surprisingly, no one had really noted any great morphological differences between California Common Ravens and the rest, other than their smaller size. Vocally, however, California

ravens appear to be different from boreal ravens, both in the frequency and structure of their calls. Those birders who are keyed in to voice might eventually have noted a macro-geographic pattern of vocalizations. But in this case, we were beaten to the punch by the genetic data.

It would be interesting to see a similar study on the Nashville Warbler complex. The two major population-groups of this species are well-isolated, in contrast to any other North American warbler currently classified as a single species. The western population (also known as the Calaveras Warbler) wags its tail, and it has songs and calls that are consistently different from those of its eastern counterpart. Interestingly, the tail wagging and vocalizations of the Calaveras Warbler are similar to those of the Virginia's Warbler. A hypothesis worth testing is that "Calaveras Warbler" is actually more closely related to Virginia's Warbler and that plumage resemblance to Nashville Warbler is ancestral.

North American wrens present an-



As though the challenge of separating Chihuahuan Raven from **Common Raven** weren't bad enough, it now turns out there may be two species of the latter in North America. The distinctions fall mainly along genetic and vocal lines—two divisions that modern ornithologists are increasingly emphasizing. This individual is of the California population, showing a short bill and long nasal bristles, features typically associated with Chihuahuan rather than Common Raven. *Half Moon Bay, California; 11 October 2005. © Alvaro Jaramilla.*

No “species” elicits greater fear and trembling in American birders than the entity currently known as the **Red Crossbill**. Eight or nine apparently valid species roam about the conifer forests of North America, distinguished by fine details of feeding ecology, call notes, and morphology. *Connecticut; February 2004. © Jim Zipp.*

other interesting problem for the student of macro-geographic variation in vocalizations. In the wrens, complexity of vocalizations is due not only to the structure of a specific song, but also to the overall repertoire size. Some species of birds sing one or two song types and that’s it, while others have a full bag of tricks—as in the wrens. Marsh Wrens in the East have 30–60 song types in their repertoire while those in the West have 100–200. In addition, western Marsh Wrens use harsher sounds in their songs, and they begin their songs with *click* or *chuck* notes, instead of the short introductory *bzz* of eastern Marsh Wren (Kroodsma and Verner 1997). The division between eastern and western populations is in the Great Plains, and at least in Saskatchewan both types occur in the same marshes. Preliminary evidence suggests that the two populations mate assortatively (western males with western females, eastern males with eastern females) in Saskatchewan, although mixed pairs are sometimes observed (Kroodsma and Verner 1997). Even so, there is good evidence for recognition of two Marsh Wren species.

You probably know the beautiful song of the Winter Wren, but do you know the 66 songs of an Oregon Winter Wren (Kroodsma 1980)? Yes, western Winter Wrens have a much greater repertoire size than do their eastern and boreal counterparts. An eastern Winter Wren may sing only one to three song types, and European and Asian Winter Wrens sing four to seven song types (Hejl et al. 2002). In addition, call notes of eastern and western Winter Wrens differ markedly and are field identifiable; presumably, call notes are not learned and therefore imply a period of isolation and genetic differences between these populations. Hejl et al. (2002) note that “at least two species might exist in North America and another across Eurasia.” I surmise the “at least” part implies that more information is needed to understand where the Alaskan island populations fit in.



I have left the biggest headache for last. The Red Crossbill is a well-known nomadic species that follows rich conifer crops. For a long time ornithologists had realized that there are different bill size classes, and they named subspecies based largely on overall size and bill size. The distribution of these subspecies sometimes overlaps when the cone crop is really good, which was puzzling. Then Groth (1993) found that Red Crossbills of different sizes have different flight call types and songs. He described eight different types, and suggested that they were different cryptic species. Since some of these types differ only slightly in average bill size and in their short call notes, the only way to identify them in the field would be to record them and



make a sonogram.

What needs to be clarified is whether the call types are indeed integral to pair formation, and whether differences in calls are enough to restrict gene flow among the various types. Crossbills, like other cardueline finches, learn their flight calls (Mundinger 1979). Within North America, White-winged Crossbills do not exhibit macro-geographic complexity in call type, but Pine Grosbeaks and Evening Grosbeaks do (Adkisson 1981, Hahn et al. 2001, Sewall et al. 2004). Adkisson (1981) showed that Rocky Mountain and Canadian Shield Pine Grosbeaks do not respond to each other’s calls, but they do respond to playbacks of their own population’s calls.

More surprises are almost certainly in the offing. The ravens were a complete surprise, and the description of the Gunnison Sage-Grouse (the first *nova avis* in North America in more than a century) was just incredible. It wasn’t a split, but a brand-new species that appeared out of nowhere. Distinctive populations of the Spruce and Blue Grouses are worthy of study, the Brown-throated Wren may make a new appearance in the future, and there are interesting macro-geographic patterns in vocalizations of White-breasted Nuthatch, Warbling Vireo, Spotted Towhee, and Western Scrub-Jay, to name a few.

Now if you are interested in Neotropical birds, you could spend an entire lifetime publishing new splits of cryptic

species of suboscines, and those are only the ones we know about! The key is to keep your mind open, and start to think that looks aren't everything. Vocalization, habitats, and biology are all important aspects to be conscious of when studying geographic variation in birds. And the next time you grab your binoculars and go birding, take a mike and a recorder too!

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