

by Paul Hess

Great Plains Hybrid Zones

How many pairs of avian taxa interbreed at least occasionally in the Great Plains? James D. Rising counted 11 in a classic review of the phenomenon in 1983 (*Current Ornithology* 1:131–157). Rising also listed three pairs of “ecological counterparts” that are not known to hybridize but whose range limits meet in the Plains. What is it about the region that causes so many mutual range boundaries and hybrid zones to cluster there? In search of an answer, ornithologists have examined various Great Plains zones of introgression—most prominently those of Yellow-shafted and Red-shafted Flickers, Rose-breasted and Black-headed Grosbeaks, Lazuli and Indigo Buntings, and Baltimore and Bullock’s Orioles.

Most investigators have focused on climate, primarily geographic gradients of temperature and precipitation between relatively warm and dry conditions on the western side of the Plains and relatively cool and moist conditions on the eastern side. A general scenario is that different populations of a species became isolated from each other in separate refugia during Pleistocene glacial periods. Next, divergent natural selection adapted one counterpart in the southwest to a warmer, drier climate and the other counterpart in the southeast to a cooler, moister climate. Finally, after the populations moved back into contact as the glaciers receded, they encountered limits of physiological adaptations in the Plains. At those boundaries, some closely related counterparts resumed interbreeding frequently or occasionally, and others did not.

Temperature was the focus of an experiment reported by Rising in 1969 (*Comparative Biochemistry and Physiology* 31:915–925). He demonstrated that the two oriole species differ significantly in tolerance of high temperatures, with Baltimore having a higher metabolic rate under heat stress. Rising suggested that the Baltimore Oriole cannot extend its range westward because it is not adapted physiologically to the hotter conditions suitable for Bullock’s. Precipitation was the variable in a report by William S. Moore and Jeff T. Price in 1993 (*Hybrid Zones and the Evolutionary Process*, R. G. Harrison, ed., pp. 196–225). The authors found a “fairly strong” association between mapped precipitation gradients and the geographic shape and location of the flicker zone of introgression. Moore and Price tentatively suggested that the rain shadow of the Rocky Mountains—arid within the shadow and increasingly moist toward the east—determines the position and width of the flickers’ and other birds’ hybrid zones in the Great Plains.

Nathan G. Swenson recently tried to tease apart the two climatic variables with a statistical method called ecological niche modeling. Niche models seek to identify fundamental ecological requirements that predict the geographic distribution of a species—in this case, which environmental variables most importantly determine the location of Great Plains hybrid zones. The variables in Swenson’s model were precipitation, radiation, elevation, slope, slope aspect (direction relative to the sun), and mean, minimum, and maximum temperatures. He reported in 2006 that, according to his method, mean annual temperature was associated more strongly than precipitation with locations of the grosbeak, bunting, and oriole hybrid zones (*Journal of Evolutionary Biology* 19:717–725). Projecting the picture beyond birds, Swenson suggested that the Great Plains temperature gradients created and maintain an ecological “suture zone”—an area where entire, long-separated biotic communities of animals and plants



The Great Plains region is a hotbed of avian hybridization, producing such spectacular offspring as this **Baltimore Oriole × Bullock’s Oriole**. A recent study linked locations of Great Plains hybrid zones with patterns of temperature rather than precipitation. *Houston, Texas; May 1980. © Barth Schorre / VIREO.*

resumed contact as Pleistocene ice sheets retreated. From that perspective, the orange-shafted flicker in the ABA’s Online Photo Quiz <aba.org/photoquiz/quizzes32.html> is more than a beautiful intergrade. It is a reflection of North American birds’ dynamic evolutionary past.

AOU Check-list Changes

The American Ornithologists’ Union characterizes its 47th Supplement to the *Check-list of North American Birds* in two words: “sweeping changes”. Tringine sandpipers, skuas and jaegers, terns, and cuckoos are involved in a broad array of

taxonomic revisions announced in the Supplement in July 2006 (*Auk* 123:926–936). The changes affect taxa at the family, subfamily, tribe, genus, and species levels. They are based primarily on new data about genetic relationships, sometimes supported by morphological, vocal, and behavioral features—and all are accompanied by extensive rearrangements of checklist sequence.

A notable split redivides Blue Grouse into Dusky Grouse (*Dendragapus obscurus*) of the Rocky Mountain regions and Sooty Grouse (*D. fuliginosus*) of the coast ranges, Cascades, and Sierra Nevada. [See “Blue Grouse Split”, pp. 34–35.] But the Supplement’s most remarkable aspect is the wide reach of its revisions, a process the AOU assures us will intensify: “Changes of classification of entire genera, tribes, subfamilies, and even families will become more frequent as DNA evidence continues to provide new or confirm old concepts of relationships.”

The following is a summary of the AOU’s decisions in the 47th Supplement that affect the ABA Checklist. By stipulation, AOU classifications and nomenclature are adopted by the ABA. The Supplement and the updated AOU list are available online <aou.org/checklist/index.php3>.

New records for the ABA Area

- Cape Verde Shearwater (*Calonectris edwardsii*), newly split from Cory’s Shearwater: one off Hatteras Inlet, North Carolina, on 15 August 2004.
- Black-bellied Storm-Petrel (*Fregatta tropica*): one off Oregon Inlet, North Carolina, on 31 May 2004.
- Social Flycatcher (*Myiozetetes similis*): one in Hidalgo County, Texas, 7–14 January 2004.
- Black-headed Nightingale-Thrush (*Catharus mexicanus*): one in Hidalgo County Texas, 28 May – 29 October 2004.

Revisions at the family level

- The skua and jaeger subfamily Stercorariinae is elevated to family status as Stercorariidae, and this entire family is moved to a new place in the checklist sequence between Black Skimmer and the family Alcidae. DNA sequence data indicate that skuas and jaegers are more closely related to alcids than to gulls and terns.
- In the family Cuculidae, the New World Cuckoo subfamily Coccyzinae is merged into the Old World Cuckoo subfamily Cuculinae, based on a genetic analysis. The checklist sequence of cuckoo species is rearranged.

Changes in genera

- Gray Hawk becomes *Buteo nitidus*, moved from its former genus *Asturina*.

- Among Tringine sandpipers, Willet becomes *Tringa semipalmata*, moved from its former genus *Catoptrophorus*. Wandering Tattler becomes *T. incana* and Gray-tailed Tattler becomes *T. brevipes*, moved from their former genus *Heteroscelus*. Meanwhile, the checklist sequence is rearranged for the first 15 sandpipers in the family Scolopacidae—that is, all of the species before Upland Sandpiper.
- Nine North American tern species formerly classified in the genus *Sterna* are placed in different genera: Sooty Tern (*Onychoprion fuscatus*), Bridled Tern (*O. anaethetus*), Aleutian Tern (*O. aleuticus*), Least Tern (*Sternula antillarum*), Gull-billed Tern (*Gelochelidon nilotica*),



Nine tern species formerly classified in the genus *Sterna* are placed in new genera by the American Ornithologists’ Union. A male **Least Tern**, one of the reclassified species, offers a fish to his mate as part of their copulation ritual. *Welles, Maine; June 2005.*
© Bob Steele.

Caspian Tern (*Hydroprogne caspia*), Royal Tern (*Thalasseus maximus*), Sandwich Tern (*T. sandvicensis*), and Elegant Tern (*T. elegans*). The entire checklist sequence of noddy and tern species is rearranged.

New species

Two casual visitors to Alaska are classified as species after splits from taxa outside the AOU/ABA Area. These replace other species on the list and are not additions:

- Oriental Cuckoo is reclassified as *Cuculus optatus* and retains its English name. It was formerly considered conspecific with Himalayan Cuckoo (*C. saturatus*).
- Taiga Flycatcher (*Ficedula albicilla*) replaces Red-breasted Flycatcher (*F. parva*). It was formerly considered a subspecies of *parva*.

Not affecting the ABA Checklist

- African Collared-Dove (*Streptopelia roseogrisea*) replaces Ringed Turtle-Dove (*S. “risoria”*) because the latter is

considered merely a domesticated form of *roseogrisea*. The ABA Checklist Committee does not regard these birds as having a self-sustaining wild population anywhere in North America. For that reason and for its questionable status as a separate species, “*risoria*” was removed from the ABA Checklist in 1992.

- Socorro Wren (*Troglodytes sissonii*), a Socorro Island endemic, is moved from the Bewick’s Wren genus *Thryomanes* to the House Wren / Winter Wren genus *Troglodytes*.
- Barbados Bullfinch (*Loxigilla barbadensis*) is split from populations of Lesser Antillean Bullfinch (*Loxigilla noctis*) on other islands in the Lesser Antilles.



Blue Grouse officially became two species in 2006, **Dusky Grouse** of the Rocky Mountains and Sooty Grouse of far-western mountain ranges. The American Ornithologists’ Union split them based on genetic, morphological, and behavioral differences. *Grand Teton National Park, Wyoming; June 2000. © Brian E. Small.*

- The family Dendrocolaptidae (woodcreepers) is merged into the family Furnariidae (Central and South American ovenbirds).

Blue Grouse Split

Ornithologists have known for more than a century that “Dusky Grouse” populations in the Rocky Mountains and “Sooty Grouse” populations in the far-western mountains differ in many morphological, vocal, and behavioral characters. Male Dusky’s vocal sac is red; Sooty’s is yellow. Male Dusky typically sings five extremely soft, low-frequency hoots from the ground; Sooty typically sings six much-louder, higher-frequency hoots from high in a tree. Adult

Dusky’s tail is rather square, and typically has 20 rectrices with truncated tips; Sooty’s tail is rounded, and typically has 18 rectrices with graduated tips. Dusky chicks are grayish-brown above with a whitish supercilium and underparts; Sooty chicks are reddish-brown above with a yellowish supercilium and underparts.

Yet from 1873, when Robert Ridgway described the Sooty as a western “variety” of the Dusky, they were classified as a single species, *Dendragapus obscurus*, for six decades. Eventually, in 1931 the American Ornithologists’ Union separated Sooty as *D. fuliginosus*, referring to extensive morphological, vocal, and behavioral differences that Allan Brooks had emphasized in 1926 (*Auk* 43:281–287). The split lasted only until 1944 when the AOU controversially reunited the two, citing no primary research. Joseph Grinnell, who never shrank from voicing exasperation, reacted quickly. Within a year, he and coauthor Alden H. Miller inserted a gruff footnote in *The Distribution of the Birds of California*: “We think it incorrect to merge *D. fuliginosus* with *D. obscurus* in accord with a freely exercised vogue for joining [into] one species related geographically complementary forms. There are some very trenchant structural and behavioristic differences between these types of grouse and thus far no proved intergradation.”

There the matter rested for six more decades until George F. Barrowclough, Jeff G. Groth, Lisa A. Mertz, and R. J. Gutiérrez added genetic divergence to that trenchant list. Analyzing complete control region sequences of mitochondrial DNA in 147 Blue Grouse individuals from 14 localities throughout the range, the authors found a major genetic and phylogeographic division between two sets of populations—a division that corresponds closely to the traditional Dusky and Sooty groups. Evidence of interbreeding came from several small areas where Sooty and Dusky populations meet in British Columbia and Washington, but the estimated gene flow was too low to forestall further genetic differentiation. Combined with morphological and behavioral distinctions, the genetic evidence led the authors to propose species status for both groups in 2004 (*Molecular Ecology* 13:1911–1922). The AOU’s re-split of the Blue Grouse [see “AOU Check-list Changes”, pp. 32–34] is based largely on the Barrowclough team’s findings.

The story has an unexpected twist. Barrowclough and his colleagues discovered a prominent genetic division between northern and southern Dusky Grouse populations in Colorado, which does not closely match the geographic distribution and plumage differences of currently recognized subspecies in that region. The southern population occurs from southern Colorado south through the rest of

the range in New Mexico. The authors surmise that interbreeding between these two populations has been limited for tens of thousands of years by fragmentation of their high-elevation habitat in Colorado. Evidently, that period has not been long enough to create phenotypic differences between the genetically distinct populations. (Dusky/Sooty divergence is estimated at hundreds of thousands of years ago.) The report does not hint at the prospect of another split. For now, this finding is simply a taxonomic surprise requiring further study.

Rusty Blackbird Decline

No birder today could describe a Rusty Blackbird migration as did the Rev. J. Hibbert Langille in his book *Our Birds in Their Haunts* (1884). Langille saw them “trooping by in immense numbers” at New York’s Tonawanda Swamp on 1 May 1880: “The sombre wave, thus constantly rolling on, must have carried hundreds of thousands over this highway in a day.” Contrast that with a lament by Russell Greenberg, director of the Smithsonian Migratory Bird Center, on the Center’s website in 2003: “Now, most of us consider it special to see a Rusty Blackbird anywhere. The Rusty Blackbird is a species in deep, deep trouble.”

Here is the trouble: Rusty Blackbird numbers have declined 97% on the North American Breeding Bird Survey and 85% on the Audubon Christmas Bird Count since 1966. After analyzing historical accounts of previous abundance, Greenberg and Sam Droege suggested in 1999 that the downtrend began at least a century ago (*Conservation Biology* 13:553–559). The trend has accelerated in recent decades. Prime suspects include loss and degradation of wetland habitats essential for the species on its boreal forest breeding grounds in Canada and the northern United States as well as on its wintering grounds in the Southeast. Toxic chemicals at breeding and wintering locations, competition with other icterids in winter flocks, and blackbird-control programs in the Southeast could also be involved. No one knows which factors are most significant.

In 2004 Partners in Flight rated the Rusty Blackbird as a species of high-priority concern in the North American Landbird Conservation Plan. The Plan emphasized population monitoring as the crucial, immediate need. Without knowing particular locations, habitats, and environmental conditions where blackbirds are disappearing fastest, direct causes of the decline cannot be identified. To close the information gap, a twelve-member consortium of government, academic, and private interests, named the Interna-

tional Rusty Blackbird Technical Group, was organized in 2005 under the Smithsonian’s auspices. The monitoring challenge is especially formidable in the far north, where the species breeds in remote swamps, bogs, and sloughs. Inaccessibility has prevented not only population research but also quantitative studies of the blackbird’s basic ecology and natural history.

The group quickly began to investigate breeding habitat requirements; to collect samples for stable-isotope, genetic, and toxic-chemical analysis; to establish sites for in-depth ecological research; to assess winter habitat use and potential competition with other blackbird species; and to study individuals’ winter movements by radio-tracking them. The ultimate goal is a set of solid scientific recommendations to wildlife and land-management agencies for revers-



No one is certain how to prioritize conservation measures for the **Rusty Blackbird**, one of North America’s most severely declining avian species. A new coalition of experts is working to identify the most crucial environmental problems. *Virginia; date unknown.* © Arthur Morris / VIREO.

ing the decline. A detailed report of the activities, an extensive species account, and Greenberg’s dramatic essay, “The Troubled Blackbird of the Bog”, can be consulted online <nationalzoo.si.edu/ConservationAndScience/MigratoryBirds/Research/Rusty_Blackbird>.

A footnote: Six widespread regions in the Fall Migration 2005 issue of *North American Birds* (Vol. 60, No. 1, 2006) reported Rusty Blackbird numbers that were unusually high by recent years’ standards. For example, a flock of 5,000 appeared in Wisconsin. Hundreds migrated past Point Pelee, Ontario, almost daily in November. Was this merely one exceptional nesting season? A sign of things to come? Greenberg interpreted it this way (personal communication): “I think given a 30-year downward trend in most indicators, we need to wait to put a single year in context.”