by Paul Hess

"Lilian's" Meadowlark

Ornithologist Harry C. Oberholser was intrigued by meadowlarks collected in 1929 near Arizona's Huachuca Mountains, because their size, structure, and plumage differed from those of the Western Meadowlark and from known variations of Eastern Meadowlark. In 1930 he described the specimens as a new Eastern Meadowlark subspecies and named it *lilianae* to honor Lilian Baldwin, who had donated the collection (*Scientific Publications of the Cleveland Museum of Natural History* 1:83–124).

We now know it as "Lilian's" Meadowlark, of desert grasslands in the southwestern U.S. and northern Mexico, where it is distinguishable from Western Meadowlark with careful study by eye and ear. In identification guides, *lilianae* received little attention and no illustration until the *National Geographic Field Guide to the Birds of North America* in 1983. Kevin J. Zimmer offered tips in *Birding* (August 1984, pp. 155–156) and in his books *The Western Bird Watcher* (Prentice-Hall 1985) and *Birding in the American West* (Cornell University Press 2000). Alvaro Jaramillo and Peter Burke provide the most complete guidance in *New World Blackbirds* (Princeton University Press 1999).

Extensive scientific studies of "Lilian's" had already been published. Wesley E. Lanyon separated it morphologically, vocally, and ecologically from the Western Meadowlark in 1962 (*Auk* 79:183–207), and his details contributed to distinguishing *lilianae* from other Eastern Meadowlarks. Analyzing 30–35 morphological characters statistically, Sievert Rohwer demonstrated in 1976 that *lilianae* and the widespread Eastern nominate subspecies *magna* differ as much from each other as either differs from the Western Meadowlark (*Occasional Papers, University of Kansas Museum of Natural History* 44:1–14). Rohwer suggested that further investigation might show *lilianae* and *magna* to be incapable of interbreeding—that is, to be two biological species.

Genetic analysis was the next logical step, but it was a long time in coming. In an oral presentation at the 21st International Ornithological Congress in Vienna in 1994, Jon C. Barlow, W. Bruce McGillivray, and Tom Dickinson mentioned genetic research supporting species status for *lilianae*. An abstract was made available in that year (*Journal für Ornithologie* 135:28), but no details about the findings have been published.

At last, a large-scale genetic report by F. Keith Barker, Arion J. Vandergon, and Scott M. Lanyon arrived in 2008 (*Auk* 125:869–879). They examined two mitochondrial DNA (mtDNA) genes and one nuclear locus in 14 Eastern Meadowlark subspecies throughout the North American, Central American, and South American range.

The results indicate a long history of evolutionary divergence between *lilianae* and all except one other Eastern Meadowlark subspecies, *auropectoralis* of central and southwestern Mexico. Barker and his colleagues propose recognition of *lilianae* and *auropectoralis* together as a species. By convention, it would be named *lilianae* because that subspecies was described first.

A recent genetic study indicates a long history of evolutionary divergence between **"Lilian's" Meadowlark** and all but one other Eastern Meadowlark subspecies. The authors propose recognition of "Lilian's" as a species. *Presidio County, Texas; September 2005. © Greg Lasley–VIREO.*

Two of the Barker team's other findings within the Eastern Meadowlark complex are notable. First, the Cuban subspecies *hippocrepis* differs significantly from all continental populations in cytochrome-*b* gene sequences. The authors do not yet suggest species status, but they call for more study. Second, other than *lilianae* and *hippocrepis*, major genetic diversity is remarkably limited for a species that breeds from Quebec to Brazil. A relatively minor difference in mtDNA between the North American taxa (including Mexico) and the Central and South American taxa is well short of species-level.

The prospect of official species status for "Lilian's" has an obvious implication for birders: Look carefully at meadowlarks in the southwestern U.S. and northwestern Mexico. Listen carefully, too. Nathan Pieplow compares "Lilian's" and other meadowlarks' vocalizations in June 2009 postings on his blog <Earbirding.com>.

Birds' Winter Distributions

When we think of large-scale changes in bird distribution, range expansions and contractions often come first to mind. National Audubon Society researchers have documented an entirely different set of patterns in North America. Major range *shifts* have occurred in birds' areas of greatest winter abundance during the past 40 years, some northward, some southward, and others inland from coasts.

In a highly publicized "Birds and Climate Technical Report" in February 2009 <birdsandclimate.audubon.org>, Daniel K. Niven, Gregory S. Butcher, and G. Thomas Bancroft tracked the biogeography of 305 species in Audubon Christmas Bird Count (CBC) data throughout the lower 48 states, southern Alaska, and southern Canada. The results show many conspicuous latitudinal shifts in birds' centers of abundance between the winters of 1966–1967 and 2005–2006. Among all 305 species, 58% shifted north, 26% shifted south, and the others made no statistically significant shift. Of those that shifted northward, the average distance was 99 miles.

Among broad ecological categories, 64% of landbirds shifted north and 18% south, 52% of waterbirds shifted north and 35% south, and 45% of strictly coastal species shifted north and 39% south. Among landbirds of different habitats, 70% of woodland species shifted north and 11% south, 67% of shrubland species shifted north and 18% south, and 61% of generalist species shifted north and 27% south. Grassland birds were an exception to the northward tendency, with nearly equal frequencies of 38% northward and 35% southward.

Beyond those general classes, the 177 species that shifted northward defy categorizing. For example, they include year-round residents (Pileated Woodpecker), regular migrants (Fox Sparrow), and irruptive species (Purple Finch). Some use feeders regularly (American Goldfinch), and others rarely or never do (Common Yellowthroat). There are raptors (Red-tailed Hawk), wetland/aquatic species (Ring-billed Gull), obligate insectivores (Golden-crowned Kinglet), and conifer specialists (Pine Siskin). Further analysis of the immense database might elicit patterns from behavioral and dietary groups.

Birds that shifted southward vary greatly as well. These include Merlin, Short-eared Owl, Red-headed Woodpecker, and Yellow-headed Blackbird. Those that did not shift are also diverse, such as Horned Lark, Yellow-rumped Warbler, and Brewer's Blackbird.

Niven, Butcher, and Bancroft make clear that many factors not yet analyzed are contributing to the changes, but they suggest that these birds' great diversity in habitat-use, behavior, and diet indicates involvement by some factor of continental magnitude, particularly in the preponderance of shifts northward. The factor they consider most likely to be responsible comes as a question in the technical report's subtitle: "a response to warmer winter temperatures?"

The authors offer four lines of evidence as support for an involvement of warming climate in northward shifts during the 40 years. (1) Annual variation in latitudinal centers of abundance is correlated with annual variation in November/December temperatures, just before and during the CBC period. (2) Regional rates of population change shown in CBC data for the lower 48 states are correlated with rates of temperature change, independent of latitude. (3) Larger shifts in bird distribution inland than in coastal areas are correlated with higher winter temperature increases inland. The abundance of many species has shifted inland from coasts, just as it has northward. (4) Different patterns of movement among birds centered in northern and southern regions of North America are generally consistent with predictions based on a hypothesis of climate-change effects. An initial draft of the technical report is available on the "Birds and Climate Change" website. Niven tells *Birding* that a final version is being prepared for publication.

According to a National Audubon Society analysis, the **Purple Finch's** center of greatest winter abundance shifted by a continent-wide average of 433 miles northward between the winters of 1966–1967 and 2005–2006. *Kern County, California; January 2005. © Brian E. Small.*

Icterids' Colors and Songs

Why, in so many bird species, are males brightly colored and tuneful, whereas females are duller and less inclined to sing? Since *On the Origin of Species* in 1859, Darwin's concept of sexual selection has struck most biologists as logical: "I can see no good reason to doubt that female birds, by selecting, during thousands of generations, the most melodious or beautiful males, according to their standard of beauty, might produce a marked effect."

That process has been confirmed experimentally many times, but judging by two recent papers, males are not the only objects of selection in the family Icteridae (meadowlarks, blackbirds, grackles, cowbirds, orioles, caciques, and oropendolas). Evidently, in many icterid species, females also have changed in plumage coloration and in rates of vocalization. In both studies, those conclusions emerged from a complex analytical method known as "reconstruction of ancestral character states." The approach traces a trait's (or "character's") evolutionary past back through the avian "family tree" to infer how the trait may have changed or remained stable as taxa diverged and multiplied from shared ancestors.

Deep in their evolutionary past, **Baltimore Oriole** females evidently looked quite different from this familiar one. New research suggests that females of various oriole species were originally as brightly colored as males but gradually lost their similarity. *Galveston County, Texas; April 2006. © Brian E. Small.*

Christopher M. Hofmann, Thomas W. Cronin, and Kevin E. Omland recently analyzed the evolution of sexual dichromatism—differences in male and female coloration—in 43 oriole species and subspecies. Orioles are particularly appropriate for analysis because their evolutionary relationships are well-known and their diversity from monochromatism to dichromatism is extreme. For example, males and females are colored virtually alike in Altamira and Audubon's, but the sexes are strongly dichromatic in Baltimore and Bullock's.

Results reported by Hofmann and his coauthors in 2008 (*Auk* 125:778–789) depart from Darwin's classic view of sexual dimorphism in which sexual selection drives increasingly elaborate male colors, whereas natural selection favors dull or cryptic females. In many oriole species, ancestral females were as bright, or nearly so, as males. Gradually, females' similarity to males was lost in species such as Hooded, Baltimore, and Bullock's Orioles as the females became less and less elaborate.

Meanwhile, J. Jordan Price, Scott M. Lanyon, and Omland were using the same method to analyze females' rates of song in 65 icterid taxa, orioles, and others. Their results, published in 2009, suggest losses of female song in nearly all icterid species that breed in the north and south temperate zones (*Proceedings of the Royal Society–B* 276: 1971–1980).

Reconstruction of ancestral character states can also trace the evolution of female song or any other non-morphological trait; the only requirement is that the trait have a genetic component. The reconstruction by Price, Lanyon, and Omland indicates that these females' tropical ancestors sang at the same rate as males did, but the use of song diminished in association with evolutionary shifts of the species from tropical to temperate breeding ranges.

Further, the analysis suggests that decreases in female song occurred multiple times, happening independently in different periods and in different icterid groups. Currently, only two temperate-breeding icterids reportedly have frequent female song: Bullock's Oriole in the north and Golden-winged Cacique (*Cacicus chrysopterus*) in southern South America. At the same time, female song rates differ from male rates in only a few tropical cowbirds, grackles, caciques, and oropendolas.

What selective factors might lead to female loss of coloration and song? Price suggests in a separate report in 2009 that mating, nesting, and migratory behavior could have roles in the loss of song (*Behavioral Ecology* 20:967–977). In a paper soon to be published in the journal *Evolution*, several authors including Hofmann associate the evolution of sexual dichromatism with the evolution of migration. The patterns seem clear, but the processes are elusive.

Aimophila and *Pipilo*

Sparrows in the genus *Aimophila*—Rufous-winged, Cassin's, Bachman's, Botteri's, Rufous-crowned, and Five-striped on the ABA *Checklist*—are diverse in morphology, behavior, and ecology. These and eight other *Aimophila* species in Mexico, Central America, and South America offer a classic case history of taxonomic uncertainty.

In *The Birds of North and Middle America* (1901), Robert Ridgway divided *Aimophila* into five groups of species based on coloration, size, and physical structure. He doubted that all five belonged together: "I am far from satisfied with the limits which are here assigned [to] the genus *Aimophila*, but [I] have not been able, after repeated and tedious efforts, to devise any improvement."

Half a century later, many ornithologists remained dissatisfied. Robert W. Storer concluded in 1955 that *Aimophila* "is not a natural assemblage" (*Condor* 57:193–201). Larry L. Wolf suggested in 1977 that some members of the genus "may well be related to different genera" (*Ornithological Monographs* No. 23). After extensive analyses, neither author could confidently recommend new taxonomy based on *Aimophila* biology then known.

Finally, Jeffrey M. DaCosta, Garth M. Spellman, Patricia Escalante, and John Klicka added a molecular approach in 2009 (*Journal of Avian Biology* 40:206–216). They evaluated evolutionary relationships by independent analyses of variation within each of two complete mitochondrial DNA genes across all current members of *Aimophila* and *Pipilo* (the towhees), plus 33 additional species representing 17 other genera in the family Emberizidae. These authors recommend dividing current *Aimophila* species into four genera:

- *Peucaea*. Rufous-winged, Cassin's, Bachman's, and Botteri's Sparrows are assigned to this genus, which resurrects a century-old name. Others placed in *Peucaea* are the Mexican and Central American Stripe-headed (*A. ruficauda*) and the endemic Mexican Black-chested (*A. humeralis*), Bridled (*A. mysticalis*), and Cinnamon-tailed/Sumichrast's (*A. sumichrasti*) Sparrows.
- *Aimophila*. Only Rufous-crowned Sparrow remains here, as do Mexican endemics Oaxaca (*A. notosticta*) and Rusty (*A. rufescens*) Sparrows. Surprisingly, these three are more closely related to towhees than to the other current *Aimophila* species.
- *Amphispiza*. Five-striped Sparrow, distantly related to *Aimophila* species, rejoins Black-throated Sparrow in this genus, where it was placed in the American Ornithologists' Union *Check-list* from 1983 until 1997. (Sage Sparrow, another *Amphispiza*, was not evaluated.)
- *Rhynchospiza*. Tumbes Sparrow (*A. stolzmanni*) and Stripe-capped Sparrow (*A. strigiceps*) of South America are placed in a genus that revives a long-dormant name.

Botteri's Sparrow is one of 14 species in the genus *Aimophila*. Authors of a recent analysis of evolutionary relationships among current *Aimophila* sparrows suggest that these species should be separated into four genera. *Pima County, Arizona; July 2007. © Brian E. Small.*

The DaCosta team also examined the towhee genus *Pipilo*, traditionally viewed as a "rufous-sided" group composed of Green-tailed, Spotted, Eastern, and Collared (*P. ocai* of Mexico) and a "brown" group composed of Canyon, California, Abert's, and White-throated (*P. albicollis* of Mexico). The new molecular analysis supports those groupings.

It may come as a surprise that, genetically, these two groups are not close relatives. The "rufous-sided" are most closely related to neotropical brush-finches of the genus *Atlapetes*. The "brown" are most closely related to Middle American ground-sparrows of the genus *Melozone*.

DaCosta and his colleagues recommend that *Pipilo* retain only "rufous-sided" species and that "brown" species be moved to a resurrected genus, *Pyrgisoma*. As in *Aimophila*, newly uncovered genetic relationships in *Pipilo* give taxonomists much to ponder.