

by Paul Hess

Molt Migrants' Behavior

For some neotropical migrants, stopover sites during the autumn journey are more than opportunities to rest and feed. They are important places to molt.

Passerines that breed in the interior west of North America may lack adequate food and water during the arid post-breeding period, and many individuals do not linger on the breeding grounds. They migrate to the “Mexican monsoon region” of southern Arizona and northwestern Mexico, where July–September rains bring a burst of fresh vegetation and food resources.

Until recently, studies of molt migration tended to focus on aquatic species—ducks and shorebirds, for example. In the past decade, though, ornithologists have learned that many passerines are molt migrants. These recent studies of molt migration in passerines have emphasized ecology, behavior, evo-

lution, and conservation. In 2005, Sievert Rohwer, Luke K. Butler, and Daniel R. Froehlich interpreted molt migration as an ecological “push” and “pull.” Birds are “pushed” out of the inhospitable breeding grounds and “pulled” into the monsoon region by advantageous conditions there (pp. 87–105 in *Birds of Two Worlds: The Ecology and Evolution of Migration*; Johns Hopkins University Press, Baltimore).

Those authors predicted that more migrant species would be found molting in the Mexican monsoon region than were known in 2005. Indeed, in 2009 after two years of field studies there, Peter Pyle and six coauthors reported nine species of migrants previously undocumented as molting in that area: Yellow-green Vireo, Phainopepla, Nashville Warbler (western populations), Green-tailed Towhee, Chipping Sparrow (western populations), Lark Sparrow, Indigo Bunting, Orchard Oriole, and Streak-backed Oriole (*Condor* 111:583–590).

The Pyle team also studied 11 species previously known to be molt migrants in the monsoon region: Ash-throated Flycatcher, Western Kingbird, “Western” Warbling Vireo, Lucy’s Warbler, Western Tanager, Lark Bunting, Black-headed Grosbeak, Lazuli Bunting, Painted Bunting (south-central population), Bullock’s Oriole, and Lesser Goldfinch.

Indigo Bunting and Orchard Oriole are the only eastern species. Most eastern passerines are reported to molt on the breeding grounds, where environmental conditions typically remain auspicious through the summer. Yellow-green Vireo and Streak-backed Oriole may move to the monsoon region from breeding grounds elsewhere in Mexico.

Cataloguing the species was just the first step for the Pyle team. With conservation in mind, a crucial question is which habitats are most important for molting. To find out, the researchers operated 13 capture stations in southeastern Arizona, central Sonora, and central Sinaloa during the monsoon seasons in 2007 and 2008.

Five “wet” stations had perennial water flow, and eight “dry” stations had ephemeral or no flow. The capture patterns suggest that water is a major factor. During the two years, only 28% of adult migrants captured at the dry sites were molting, whereas 60% captured at the wet sites were molting.

Contrasting weather conditions between the two years provided further evidence. In the relatively dry 2007 season, molting migrants were significantly more concentrated in riparian habitats. During the wetter 2008 season, proportions of migrants molting at wet and dry sites were about equal. Apparently, molt migrants use diverse habitats that become lush in relatively wet years. Native grasslands were used by molting



Some, perhaps most, **Lazuli Buntings** do not linger to molt on their breeding grounds when the habitat becomes arid after the nesting season. The Lazuli Bunting is among a growing list of species known to stop and molt during migration in the more hospitable Mexican monsoon region. *Lane County, Oregon; June 2008. Photo by © Joe Fuhrman.*

granivores in dry years and insectivores in wet years.

Because of this annual variability, Pyle and his colleagues caution that pinpointing optimal areas for conservation may be difficult. Nevertheless, the importance of conserving riparian and native-grassland habitats for molt in the monsoon region is clear.

Mary K. Chambers and four colleagues found similar results in a study of molt migrants' habitat preferences in southeastern Arizona in 2007–2008. Their report, to be published in *Southwestern Naturalist* in 2010, reinforces the importance of those habitats. Among 12 species of molt migrants, native grasslands ranked as the most-preferred molting habitat, with willow and cottonwood riparian sites close behind.

Hybrid Zone Diversity

Hybrid zones come in many shapes and sizes: small, disjunct points of contact; continental-scale bands thousands of miles long that vary in width, direction, and habitats; narrow, well-defined belts that extend for short distances; and large, amorphous regions where the extent of interbreeding differs greatly from place to place.

Some zones move; others appear to be stable. Some are linked to extrinsic environmental gradients; others seem unrelated to ecological features. Some are maintained by intrinsic barriers to gene flow; others persist despite extensive gene exchange. Hybridization may be regular and frequent, or irregular and rare. Interbreeding may affect hybrids' reproduction and survival adversely, or it may not obviously be harmful. Hybridizing taxa may be closely related phylogenetically, or deeply divergent. All of those parameters have important evolutionary implications.

One such factor is the reproductive fitness of mixed pairs and their hybrid offspring vs. that of pure pairs and their descendants. Two studies published in 2009 examine zones that contrast interestingly in this respect. D. T. Tyler Flockhart and Karen L. Wiebe report on the "Yellow-shafted" Flicker × "Red-shafted" Flicker zone in central British Columbia (*Auk* 126:351–358). Raeann D. Mettler and Garth M. Spellman focus on the Black-headed Grosbeak × Rose-breasted Grosbeak zone in southern South Dakota (*Molecular Ecology* 18:3256–3267).

Flockhart and Wiebe compared reproductive performance of "red," "yellow," and hybrid "orange-shafted" phenotypes in an area where mixed pairs and hybrids are numerous. (Their proportion in the flicker population was not determined.) In 865 breeding attempts monitored during nine years, egg-laying date, clutch size, hatching success, and fledging success did not differ according to the phenotype of either the male or



"Red-shafted" and "Yellow-shafted" Northern Flicker subspecies hybridize with no negative consequences for reproduction, according to a recent study. This individual has the red malar and gray face of "Red-shafted," the red nuchal crescent of "Yellow-shafted," and an intermediately orangish tail. Victoria, British Columbia; March 2010. Photo by © Tim Zurowski.

the female parent. Breeding behavior was compatible among all three phenotypes, with no negative influence on reproductive output. Additionally, observations and experiments showed no differences among the phenotypes in ability to defend territory in aggressive encounters.

This equality in breeding success and competitive capability indicates that interbreeding has no negative consequences on reproduction or survival and suggests that there is no barrier to gene flow between the taxa. Extensive intergradation is why the American Ornithologists' Union merged the Red-shafted, Yellow-shafted, and Gilded flickers as a single species in 1973. (Gilded Flicker was reclassified as a species in 1995 on grounds that its interbreeding with other Northern Flicker taxa is "extremely limited.")

The grosbeak study indicates consequences at the other extreme. Mettler and Spellman inferred a reduction in hybrid fitness from the small proportion of hybrids found in the grosbeak zone, rather than by measuring reproductive factors

directly. Of 129 males collected along a hybrid-zone transect in 2007, only 19 had plumage characters indicating hybrids.

Analysis of a species-specific mitochondrial DNA fragment and four independent nuclear DNA markers returned a similar result: very few grosbeak intergrades. Morphological and molecular patterns were concordant in a sharp “cline”—the transition between the two species’ characters across the contact zone—which implies a strong barrier to gene flow.

The zones’ contrasts embody Richard G. Harrison’s often-quoted metaphor from 1990 (*Oxford Surveys in Evolutionary Biology* 7:69–128): “Hybrid zones are windows on evolutionary process, but each window opens on a different landscape.”

American Kestrel Trends

What is happening to the American Kestrel? Migration counts, North American Breeding Bird Surveys, Christmas Bird Counts, and nest-box projects suggest widespread long-term declines, especially in the northeast and parts of the west. Long-term trends at hawkwatch sites in some regions have been stable or upward, although declines have begun to appear at these sites during the past decade.

David M. Bird of McGill University organized a symposium on the subject at a 2007 meeting of the Raptor Research Foundation and Hawk Migration Association of North America. As an outgrowth, the December 2009 *Journal of Raptor Research* (13:261–383) is devoted to kestrel studies. Two articles examine migration and nest-box trends.

Christopher J. Farmer and Jeff P. Smith provide the first continent-wide analysis of autumn counts at 20 hawkwatch sites in the east, the west, and along the Gulf of Mexico. Steep long-term declines have occurred at three Atlantic coastal and two western sites.

The coastal downtrends ranged from 3.1–4.5% per year at Lighthouse Point, Connecticut, and Montclair and Cape May Point, New Jersey, from the mid-1970s to 2004. The decline at each site totaled more than 50% during the 30-year period. Another eastern hawkwatch showed a smaller decline: 1.7% per year at Hawk Mountain, Pennsylvania, in 1966–2004.

Declines in the west were 7.9% per year at Bonney Butte, Oregon, in 1994–2005 and 3.6% per year at Wellsville Mountains, Utah, in 1987–2004.

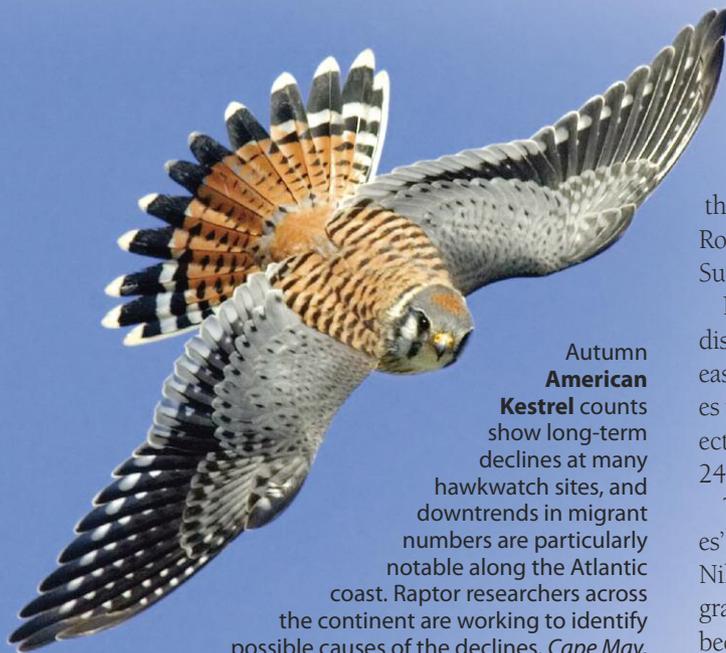
Two sites showed *upward* long-term trends for American Kestrel: 3.2% per year at Hawk Ridge, Minnesota, in 1974–2004, and 3.4% per year at Goshute Mountains, Nevada, in 1983–2005. However, Farmer and Smith report shorter-term declines even at those locations within the past ten years. Migration counts have been stable at 14 other sites in Quebec, Ontario, Pennsylvania, Washington, Montana, Idaho, New Mexico, Arizona, and on the Gulf coast of Texas, Florida, and Mexico. During the past decade, there were no upward trends at any of the 20 sites.

Farmer and Smith suggest that the Atlantic coastal declines may involve effects of increasingly dense human populations, and that more-recent western declines may reflect drought, predation by larger raptors, and pesticide poisoning.

The authors see no evidence that migratory “short-stopping” is a factor in the hawkwatch trends. Christmas Bird Counts to the north do not show the expected increases if kestrels were wintering northward. Nor are there signs of a distributional shift, such as described for the Rough-legged Hawk by Edward R. Pandolfino and Kimberly Suedkamp Wells in 2009 (*Western Birds* 40:210–224).

Meanwhile, John A. Smallwood and 13 coauthors report disturbing trends at eight nest-box projects in Canada and the eastern U.S. Since peak years in proportions of available boxes in which kestrels bred, the occupancy rates in all eight projects decreased an average of 3% per year during the past 15–24 years.

The authors saw no evidence of problems in the nest boxes’ vicinity, such as lack of nest cavities, habitat change, West Nile Virus, and predation by Cooper’s Hawks. Mortality in migration could not be a factor in the southern nesters’ decline, because they are nonmigratory. Smallwood and his colleagues believe major problems lie beyond the study sites—perhaps



Autumn American Kestrel counts show long-term declines at many hawkwatch sites, and downtrends in migrant numbers are particularly notable along the Atlantic coast. Raptor researchers across the continent are working to identify possible causes of the declines. *Cape May, New Jersey; September 2004. Photo by © Jim Zipp.*

habitat loss and degradation on a regional scale.

Bird keynoted the *Journal* issue with a call for further research to “ascertain beyond any doubt whether the species is declining, the causes behind it, and more important, what we can do about it.”

Golden-fronted Woodpecker

Study the Golden-fronted Woodpecker illustrations in *A Guide to the Birds of Mexico and Northern Central America* by Steve N. G. Howell and Sophie Webb. Two words summarize what the paintings depict: “complex variation.”

Subspecies differ in bewildering combinations of features, including wide vs. narrow barring on the upperparts, barred vs. plain tail, separation vs. connection between red crown patch and gold nape, red vs. gold nasal tufts, duskiness of the underparts, and relative size of the bill.

Howell and Webb caution that the features also combine variably in intermediate populations. No wonder the Golden-fronted Woodpecker’s taxonomic history has been a patchwork of conflicting views.

The great ornithologist Robert Ridgway classified it as a single species in 1881 (*Proceedings of the U.S. National Museum* 4:93–119), and then he separated it into four species in his *Manual of North American Birds* in 1887 and *Birds of North and Middle America* in 1914. Taxonomic opinions have been divided ever since.

Morphological studies culminated in an extremely detailed monograph by Robert K. Selander and Donald R. Giller in 1963 (*Bulletin of the American Museum of Natural History* 124:213–274). The authors examined Golden-fronted Woodpecker specimens from 34 sampling areas spanning the range in Texas, Mexico, and Central America. They quantitatively analyzed 12 categories of nape color, eight categories of frontal region color, 12 categories of belly color, and seven categories of dorsal tail pattern. Their conclusion was that all populations intergrade at zones of contact and represent a single species—which is how the American Ornithologists’ Union (AOU) currently classifies the Golden-fronted Woodpecker.

Now, as with so many avian studies, genetic analysis adds a new chapter. Based on distinctions in maternally inherited mitochondrial DNA (mtDNA), Erick A. García-Trejo and three coauthors suggested in 2009 (*Condor* 111:442–452) that the Golden-fronted Woodpecker comprises two evolutionary lineages that should be treated as separate species:

- A “northern” group ranging from Texas and southern Oklahoma south through the Mexican Plateau to Zacatecas and Jalisco. It would retain the current species’ name *Melanerpes aurifrons*.

- A “tropical” group ranging from southern San Luis Potosí and northeastern Querétaro south along the Atlantic slope of Mexico to Honduras and along the Pacific coast from easternmost Oaxaca and Chiapas to north-central Nicaragua. By nomenclatorial priority as the oldest-named in its subspecies group, it would be *M. santacruz*. In fact, in 1896 Ridgway classified it as the “Santa Cruz’s Woodpecker (*M. santa-cruzi*)” in the second edition of *A Manual of North American Birds*.

For their overall phylogenetic analysis, the García-Trejo team compared portions of three mtDNA genes in 89 individuals of 11 *Melanerpes* species. These broader comparisons include the Red-bellied Woodpecker, and here the authors report another notable result: In the three mtDNA sequences, the “northern” Golden-fronted group is even more closely related to the Red-bellied Woodpecker than to the “tropical” Golden-fronted group.

As of this writing, the AOU’s Committee on Classification and Nomenclature of North and Middle American Birds has not received a formal proposal for dividing the Golden-fronted Woodpecker into two species.

(A taxonomic note: In their guide, Howell and Webb place the Golden-fronted Woodpecker in the genus *Centurus*. The AOU merged *Centurus* into the genus *Melanerpes* in 1976, and virtually all other current field guides use *Melanerpes*.)



Authors of a recent genetic study suggest that the **Golden-fronted Woodpecker** should be divided into two species. This individual in Central America would be included in a new “tropical” species, *Melanerpes santacruz*, separate from a “northern” species in the southern U.S. and northern Mexico. *Tikal National Park, Guatemala; March 2001. Photo by © Rick Bowers.*