

by Paul Hess

First-year Migrants May Need Experience

Inheritance or experience? Genetic programming or practical learning? Various studies show that both inherited and learned information helps birds to migrate to the right place in fall and to return to the right place in spring. Immature birds apparently use an innate compass that may not always allow them to deviate from “hard-wired” direc-



White-crowned Sparrow migrants' navigational ability apparently improves with age. When transported across the continent and released, adults adjusted their route appropriately toward the normal wintering grounds, whereas first-year birds could not do so. *Salton Sea, California; February 2001. © Kevin T. Karlson.*

tions, even if deviation would be advantageous. In contrast, adults appear to have a more sophisticated navigational map drawn from experience, which importantly augments their inherited programming. This evidence typically comes from researchers who transport migrants far from the usual route, and then infer performance from banding returns.

The classic example is Dutch scientist A. C. Perdeck's immense project in the 1950s. He famously banded 11,000 European Starlings during their southwesterly fall migrations through western Europe, transported them from The Netherlands to Switzerland, and released them there. Band recoveries of 58 adults later in the season indicated that they were navigating northwestward back toward their normal wintering grounds in France and southern England. In contrast, 171 banded immature birds had resumed the pre-

sumably innate southwesterly bearing, and many ended up in Iberia far south of the usual winter range. His report in 1958 suggests that adults improve their inherent navigational map based on experience, but that first-year birds' directional behavior has not progressed beyond an inherited rudimentary compass (*Ardea* 46:1–37).

Fifty years later, Kasper Thorup and six coauthors have added a radio-tracking dimension to similar research using White-crowned Sparrows. Results they report in 2007 are a near-perfect analogy to Perdeck's findings, except that long-distance, non-social, nocturnal migrants are studied rather than short-distance, social, diurnal migrants (*Proceedings of the National Academy of Sciences* 104:18115–18119). Fifteen adult and 15 first-year southbound migrants of the *gambelii* subspecies were captured at a fall stopover site in Washington state and transported to New Jersey, where each was fitted with a tiny radio transmitter. The birds' initial movements near the release site were monitored by ground crews, but after flying away from the immediate area (usually at night) they were tracked individually by aircraft for distances as far as 122 kilometers.

Adults and immatures rapidly demonstrated a conspicuous behavioral difference. On average, adults flew west-southwest toward the usual wintering grounds of their subspecies in the southwestern U.S. and northwestern Mexico. Even with no previous experience in eastern North America, adult *gambelii* apparently have a navigational map that spans the continent, informing them which direction to travel. In contrast, first-year birds on average flew southward in their population's usual migratory direction, which from New Jersey would take them—like Perdeck's starlings—far away from their normal winter range.

Observing actual migratory movements of individual birds is an improvement over interpreting random banding recoveries, but Thorup and his colleagues stress that short-distance tracking is not enough. Ultimately needed, they say, is a method to track small passerines over long distances for long time periods—a global satellite-based system of the kind now limited to use with large birds. Martin Wikelski at Princeton University has started an international collaboration called the ICARUS (International Cooperation for Animal Research Using Space) initiative to encourage development of this advanced technology. He is the chief author of a spirited commentary in 2007 explaining the need for the system (*Journal of Experimental Biology* 210:181–186). It is available on the initiative's website <www.icarusinitiative.org>.

Western Warbler Hybrid Zones

Knowledge of Townsend's Warbler × Hermit Warbler hybridization came slowly during the past century, and discoveries continue. The story began in 1913 when Stanley Jewett collected an "off-colored male Hermit Warbler" in Oregon. It lay in his collection for 30 years until he discovered another one in Washington and decided to investigate. Finally, in 1944, he reported that these and two museum specimens he studied were hybrids. Jewett described variations, but his tiny sample suggested a frequent plumage combination: a Hermit's head and a Townsend's body (*Condor* 46:23–24).

Four decades passed until Michael L. Morrison and John William Hardy analyzed hybrids' plumage and songs, and estimated frequencies of hybridization (*Murrelet* 64:65–72). Few birders knew of that 1983 article, and identifying hybrids largely remained a mystery. Help arrived that year when the *National Geographic Society Field Guide to the Birds of North America* provided the first widely available illustration of a hybrid. Further aid came in 1998 with *A Field Guide to Warblers of North America* by Jon Dunn and Kimball Garrett, which has five paintings, a photograph, and a discussion of hybrid varieties including some with a Townsend's-type head. A photographic gallery by Thomas Eckert in *Birding* (August 2001, pp. 342–350) depicts a dozen hybrid variations.

The 1990s brought a burst of research by Sievert Rohwer, Chris Wood, Scott Pearson, and colleagues. They studied plumage and molt in the parental species as a basis for studying hybrids' appearance. They mapped three hybrid zones in Washington's Olympic Mountains, the Washington Cascades, and the Oregon Cascades. They learned that the parental species and hybrids compete for the same territories and sing the same song; that male Townsend's are more aggressive and more successful in maintaining territories; that female Hermits will accept Townsend's as mates if male Hermits are not available; and that Townsend's average the largest clutch size. This dominance drives the Townsend's breeding range slowly southward at the Hermit's expense.

Rohwer and Paul R. Martin report in 2007 that the three zones differ greatly in hybrid frequency (*Auk* 124: 1347–1358). Judged by plumage, 60.4% of males collected

in the Olympic zone, 43.3% in the Washington Cascades, and 27.8% in the Oregon Cascades are hybrids. Why are the proportions different? The authors find no environmental, behavioral, or genetic factors that might be responsible. Rather, they believe the frequencies depend upon how many Townsend's are dispersing into each zone and how long the two species have been in contact.

Their hypothesis is that the Olympic Peninsula and Washington Cascades are old zones where hybridization has occurred for thousands of years and, thus, where relatively high hybrid frequency is expected. Genetic analyses show that more Townsend's Warblers disperse into the Washington Cascades zone from Rocky Mountain populations than into the relatively isolated Olympic zone. A continual influx of pure Townsend's would dilute this zone's proportion of hybrids.

The Oregon Cascades may also receive Townsend's dispersing westward from the Rockies, but this corridor across the Blue and Ochoco Mountains was created or greatly ex-



Frequencies of **Townsend's Warbler × Hermit Warbler** hybridization differ greatly among three localities in Washington and Oregon, according to new findings. This hybrid shows a classic combination of Hermit's yellow face and Townsend's yellow breast. *Cascade Mountains, Washington; May 2004.* © Thomas Eckert.

panded by fire control and forest management practices within the past century. Thus, the Oregon zone may have originated only after forest composition enabled dispersal of enough Townsend's to create this third area of contact. The diverse hybrid-zone dynamics are sure to stimulate further research for a long time to come.

See WebExtra <aba.org/birding/v40n3p35w1.pdf> for an annotated list of references.



Grebe–Flamingo Relationships

Loons and grebes have been linked tightly together in many familiar taxonomic arrangements, but recent molecular and morphological analyses question that link. Many researchers now believe that grebes are most closely related to flamingos.

The Taxonomic Subcommittee of the British Ornithologists' Union Records Committee finds the evidence convincing and recommends moving the grebes away from the loons to a position next to flamingos in the British List. George Sangster, J. Martin Collinson, Alan G. Knox, David T. Parkin, and Lars Svensson propose this in the subcommittee's report in 2007 (*Ibis* 149:853–857).

The revision would place the Order Podicipediformes (grebes) immediately after the Order Phoenicopteriformes (flamingos). This pair of sister taxa would be inserted in the British List between Ciconiiformes (bitterns, herons, and allies) and Accipitriformes (in British taxonomy, diurnal raptors except falcons). The subcommittee cites seven

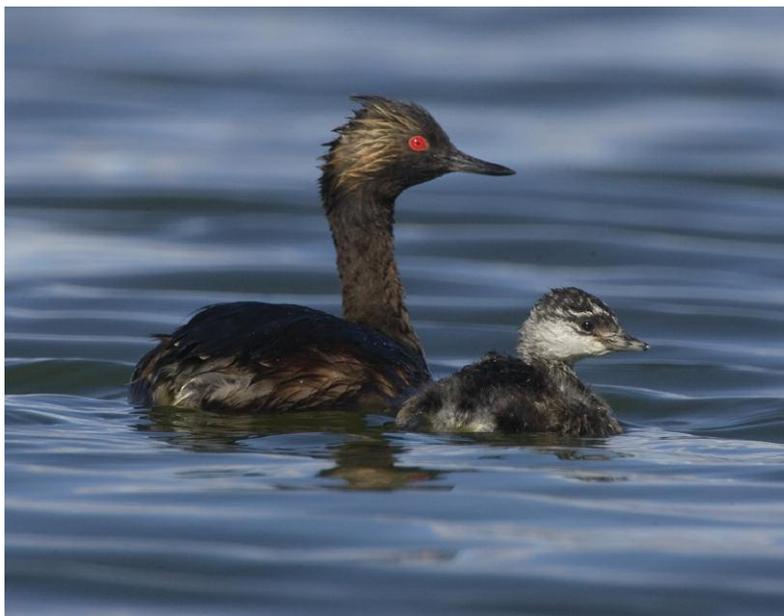
ed, Marcel van Tuinen and three colleagues report in 2001 that DNA sequencing and hybridization consistently unite flamingos with grebes (*Proceedings of the Royal Society of London-B* 268:1345–1350). The authors consider this finding unexpected for two groups of species that otherwise show no resemblance. They offer a twofold interpretation: 1. The close relationship has been overlooked because grebes' and flamingos' exceptional morphological adaptation to different aquatic niches has obscured their evolutionary history; 2. The distant relationship of loons and grebes has been obscured because these groups' similar structure represents independent, convergent adaptations for catching fish by foot-propelled diving.

Ironically, new morphological evidence arises from the types of characters that long led researchers to an opposite conclusion that grebes and loons are closely allied: bone characteristics. After analyzing 148 osteological and soft tissue characters, Gerald Mayr and Julia Clarke concluded in 2003 that grebes and flamingos are a sister-group (*Cladistics* 19:527–553). Mayr followed with a report in 2004 that 70 morphological characters highly support grebe-flamingo monophyly—i.e., that the two groups are the only descendants of a single shared ancestor (*Zoological Journal of the Linnean Society* 140:157–169).

That conclusion has not gone unchallenged. In a letter in 2006 (*Auk* 123:1183–1184) Robert W. Storer complained that Mayr's analysis is “far off the mark” with “inaccurate representations of skeletal characters that lead the reader to suppose the skeletons of grebes and flamingos are more similar than is the case.” Mayr responded in the following year with examples that “many of [Storer's] claims are incorrect” (*Auk* 124:1446–1447).

After analyzing 150 avian taxa using 2,954 morphological characters, Bradley C. Livezey and Richard L. Zusi asserted in 2007 that loons and grebes are indeed sister-groups (*Zoological Journal of the Linnean Society* 149:1–95). Unimpressed, the British subcommittee points out that the Livezey-Zusi paper contains several taxonomic hypotheses that are not supported by highly congruent results of other studies.

The American Ornithologists' Union Committee on Classification and Nomenclature (the “Check-list committee”) is considering recognition of the presumed grebe-flamingo relationship, Chairman Richard C. Banks tells *Birding*. If it is approved, the change will be published in the AOU *Check-list* supplement in July 2008.



These **Eared Grebes** look nothing like flamingos, but looks can be deceiving. Recent research indicates that grebes have a close evolutionary relationship with flamingos, shown by genetic characters and by bone and tissue features. Kern County, California; August 2006. © Bob Steele.

publications pointing to a very close evolutionary relationship between grebes and flamingos on molecular and morphological grounds.

Molecular evidence comes from phylogenetic studies based on DNA–DNA hybridization, mitochondrial DNA sequences, and nuclear DNA sequences. In one reference cit-

Widespread Impact of West Nile Virus

Which of the following have been victimized widely by West Nile Virus? American Crow, Blue Jay, Black-capped and Carolina Chickadees, Tufted Titmouse, House Wren, American Robin, Eastern Bluebird. All of them, according to a report by Shannon L. LaDeau, A. Marm Kilpatrick, and Peter P. Marra in 2007 (*Nature* 447:710–713).

The authors designed a predictive model to test whether the virus (WNV) has caused significant population declines in a broad taxonomic variety of species. Predicted impacts were based on published laboratory experiments that assessed the susceptibility of a species to WNV infection. These predictions were then tested against 26 years of trend data from 228 U.S. Fish & Wildlife Service Breeding Bird Survey routes across the continent. WNV impact is indicated by a sudden population decline that began when and where the virus was known to arrive. Following are the findings on a continental scale:

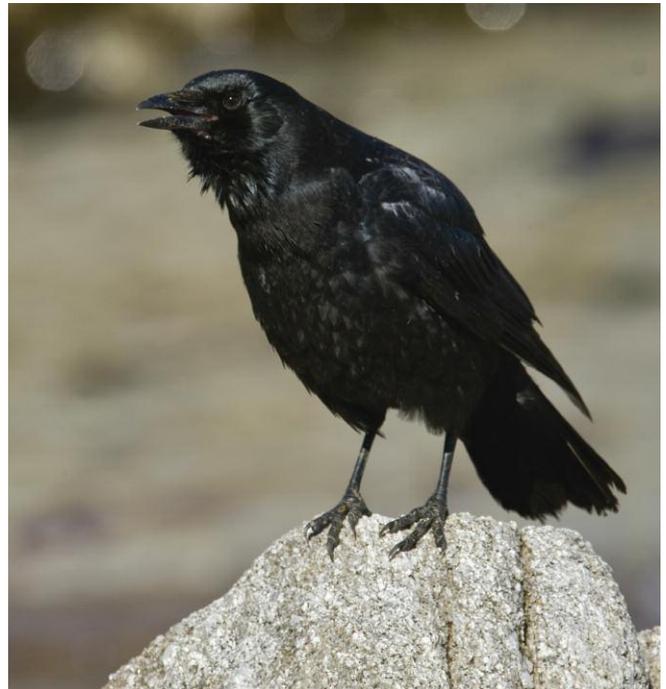
- High impact was predicted for American Crow, Fish Crow, Blue Jay, and Tufted Titmouse. Populations of all but Fish Crow declined sharply.
- Moderate impact was predicted for chickadee (Black-capped and Carolina combined), House Wren, American Robin, Northern Cardinal, Song Sparrow, and Common Grackle. The robin, wren, and chickadee declined. The cardinal, sparrow, and grackle did not.
- Low impact was predicted for Mourning Dove, Downy Woodpecker, Wood Thrush, Gray Catbird, and Northern Mockingbird. Correspondingly, their populations did not decline.

The study includes five additional species whose susceptibility to WNV has not been determined and, thus, *a priori* predictions could not be made: White-breasted Nuthatch, Eastern Bluebird, Eastern Towhee, Chipping Sparrow, and Baltimore Oriole. Among those, only the Eastern Bluebird—a classic conservation success story during the past quarter-century—decreased suddenly and severely after the arrival of the virus. The authors suggest that this unexpected bluebird decline could indicate that other species that have not been evaluated for susceptibility may also be affected.

There are exceptions on a regional level. For example, Common Grackles declined significantly in Maryland after the virus emerged there, but they remained at expected abundances in other regions. Oppositely, Eastern Bluebirds continued their long-term trend upward in Illinois, but decreased throughout the Northeast, Maryland, and Virginia.

Varying regional impacts on a species may reflect regional differences in the intensity of viral transmission, a topic LaDeau and her coauthors view as important for future studies.

Kilpatrick, LaDeau, and Marra describe another aspect of WNV in a review and commentary in 2007 (*Auk* 124: 1121–1136). It is “host competence,” the probability a



Some species are more susceptible than others to West Nile Virus infection, and a new study finds population trends corresponding to known degrees of susceptibility. **American Crow**, a highly susceptible species, has declined severely. *Monterey County, California; October 2006.* © Bob Steele.

mosquito will become infected when it bites a bird that hosts the virus. In effect, this is the probability that the mosquito will pass along WNV when it bites another creature. The most competent species—i.e., those most important to the pathogen life cycle—are, in order: Blue Jay, Western Scrub-Jay, American Crow, Common Grackle, House Finch, House Sparrow, Ring-billed Gull, Black-billed Magpie, American Robin, and Eastern Screech-Owl. Next on the list, unfortunately, is Greater Sage-Grouse. Its sudden decline in some populations is “an alarming demonstration of the possible effect of WNV on an already threatened species,” the authors say. They call for much more research to prevent and cope with the virus—not only for threatened species but also for entire ecological communities, and not only in North America but throughout the Western Hemisphere.