

by Paul Hess

“Deep” Avian Relationships

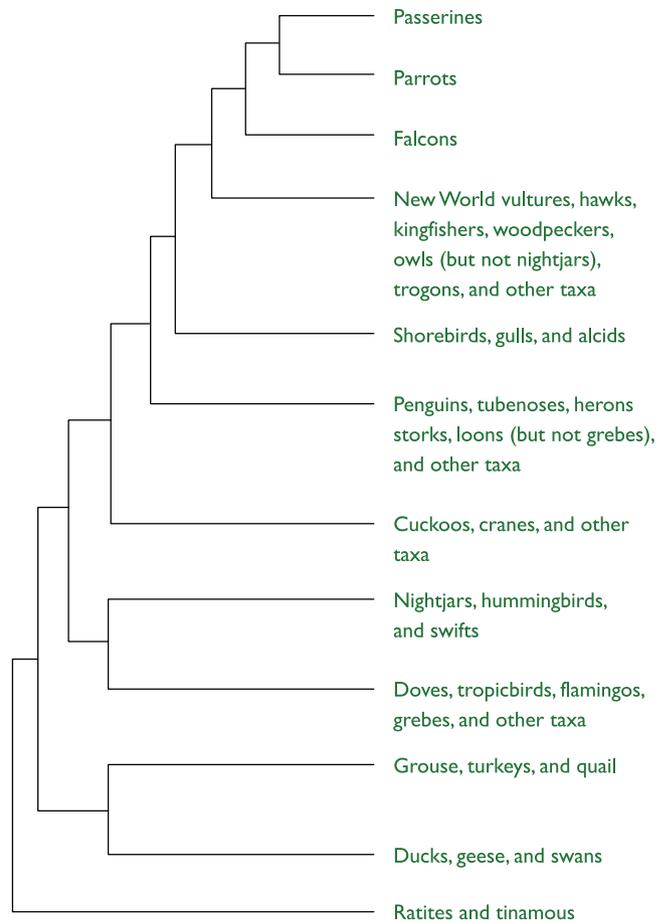
We are accustomed to seeing taxonomic arrangements shuffled, reshuffled, and then shuffled again as knowledge of avian evolutionary history is refined. Rarely are rearrangements so dramatic, though, as those proposed in a far-reaching genetic study published in 2008 by researchers in a project named “Early Bird.” Particularly newsworthy is a finding that falcons are more closely related genetically to songbirds than they are to other raptors, but Shannon J. Hackett and 17 coauthors report results that challenge many other current classifications as well (*Science* 320:1763–1768).

The term describing the team’s approach is “phylogenomic,” which refers to analysis and interpretation of the avian family tree from nuclear DNA sequences examined in multiple chromosomes (15 in this study) rather than limited to single genes. The results provide what the authors call “a robust phylogeny from a genome-wide signal.” Although the conclusions are based on DNA samples from 169 avian species, the authors’ focus is not directly on the individual species. Instead, they are primarily concerned with “deep” phylogeny—historically early branching at the taxonomic rank of orders.

Evolutionary divergence at any level can be viewed in terms of *clades*, groups of taxa whose members are descendants of a single shared ancestor. Genetic relationships among clades range from distant relatives, representing earlier divergence, to *sister taxa*, representing two groups more closely related to each other than to any other group. Large-scale phylogenomic analysis based on nuclear DNA is particularly suited to resolving deep relationships among major clades.

This study confirms a long-established basal division of ratites and tinamous from all other birds. At the next branching level, the analysis supports a recently recognized separation of a clade consisting of waterfowl and gallinaeous birds from all other bird species. Thenceforth, some results are surprising, to say the least:

- Parrots and passerines are sister taxa, whereas they have been distantly separated in virtually every previous taxonomic scheme.
- Even more unexpectedly, falcons are sister to the parrot-passerine clade and are related distantly to other diurnal raptors.
- Diurnal hummingbirds and swifts evolved from nocturnal and crepuscular nightjars. The hummingbird/swift clade is deeply nested within a larger clade that also includes frogmouths, potoos, and nightjars.



This partial cladogram (an evolutionary “family tree”) shows selected highlights from a recent analysis of relationships among major avian taxa. The complete cladogram appears on p. 1765 of the 27 June 2008 issue of the journal *Science*. *Figure by Kei Sochi.*

- A large waterbird clade includes penguins, tubenoses, boobies, pelicans, cormorants, herons, ibises, storks, and loons—but this clade does not include grebes, flamingos, tropicbirds, shorebirds, gulls, and alcids.
- Shorebirds, gulls, and alcids form a separate group, which appears to be the sister taxon of a huge clade of landbirds that includes New World vultures, hawks, falcons, parrots, kingfishers, woodpeckers, owls, trogons, and all passerines. But the latter clade does not include three other landbird groups—pigeons/doves, cuckoos, and nightjars/swifts/hummingbirds—all of which appear to be rather distantly related to one another and even more distantly separated from the major landbird grouping. In fact, cuckoos may be most closely related to rails and cranes.

- Several other interesting relationships emerge: Grebes and flamingos are sister taxa in a clade distantly separated from loons (a sister relationship recognized by the American Ornithologists' Union Committee on Classification and Nomenclature in 2008, but which the committee still links closely to the loons). New World vultures and hawks are sister taxa, and they are only distantly related to storks (a relationship recognized provisionally by the committee in 2007, reversing its previous decision that had allied vultures and storks). Woodpeckers are placed within a large clade that includes todies, motmots, and kingfishers.

The authors consider most of their conclusions to be strongly supported by consistent results found with multiple analytical methods, but they report that some relationships suggested by their data remain uncertain. For example, the compositions and exact placements of the shorebird/gull/alcid clade and of a clade of rails, cranes, and allies depend largely on the presence of only one gene; further study will be required to determine the validity of those clades.

Collecting DNA sequences for the study took more than five years, funded by the National Science Foundation's "Assembling the Tree-of-Life" research program. Yet more sequence data will be required to answer the remaining questions, and the authors hope their results will stimulate further work.

Black Swift Nests

Clinging to a rope ladder on a cliff 90 feet above the California surf near Santa Cruz, A.G. Vrooman was looking for cormorants' eggs one morning when he accidentally found the first known nest and egg of a Black Swift in North America. His announcement in 1901 (*Auk* 18:394–395) brought no celebration. Few, if any, ornithologists believed him; surely, the egg was a storm-petrel's. In 1915, after more nests were documented in California, the respected naturalist William Leon Dawson apologized on behalf of the nonbelievers (*Condor* 17:8–12): "It seemed incredible, and the writer was among those who indulged in cheap witticisms at the expense of this newest aspirant to oölogical honors."

The first nest of this North American subspecies (*borealis*) to be found farther inland than California was in Alberta in 1919. Not until 1949 was breeding confirmed as far east as Colorado when Owen A. Knorr and A.

Lang Baily discovered a nesting colony at 10,000 feet in the San Juan Mountains (*Auk* 67:516). Next, in a ten-year marathon of mountaineering, Knorr located approximately 80 nests at 27 sites in the state. Reporting the results in 1961 (*Wilson Bulletin* 73:155–170), he listed five ecological features as apparent requirements for Black Swift nesting microhabitat: presence of falling water, inaccessibility to terrestrial predators, a "commanding position" above surrounding terrain, extensive or complete protection from the sun's rays, and an unobstructed flyway to and from the nest.

After a survey even more extensive than Knorr's monumental effort, Richard G. Levad and four coauthors both supported and refined those conclusions in 2008 (*Wilson Journal of Ornithology* 120:331–338). More than 100 field workers directed by Rocky Mountain Bird Observatory and U.S. Forest Service personnel confirmed nesting at 96 sites in Colorado and three sites in New Mexico from 1998 to 2005. Most were in Colorado's San Juan Mountains, Rocky Mountain National Park, and White River Plateau. Seventy of the sites were previously unknown, though their locations extend only slightly the distribution documented by Knorr.

Levad and his colleagues developed a statistical model to predict the ecological probability of a potential nest site's occupancy. In a sample of 291 potential sites, the model identifies six habitat characteristics that correctly predict occupancy for 95% of the sample. Five correspond to Knorr's list. The sixth, for these birds of the southern Rocky



Black Swift nest sites in the southern Rockies share a predictable suite of microhabitat features, which are described after a survey of nearly 300 potential sites in Colorado and New Mexico. *Ouray County, Colorado; July 2004.* © Bill Schmoker.

Mountains, is availability of moss for nest-building.

Black Swifts show remarkable long-term fidelity to a successful nesting site: 23 of 24 sites Knorr had found were

still active a half-century later. Such fidelity may reflect a dependence on specialized habitat features. Clearly, for example, safety from predators is paramount for a species with a low reproductive rate (one egg per year), a long incubation period (23–30 days), and an extended nestling period (44–50 days). Less clear is an advantage of continuously cool, damp, and dark nest sites. Levad and his coauthors speculate that these conditions may slow nestlings' metabolism, permitting adults to leave them unattended for many hours during wide-ranging foraging flights.

The statistical model suggests that most of the region's highest-quality Black Swift nesting habitat is already occupied and, thus, may limit the population. Urging continued high-priority efforts to locate and protect suitable habitat, the authors comment, "The U.S. Forest Service clearly carries the greatest conservation responsibility for this species in the southern Rocky Mountains." That is because 73% of the occupied sites found in Colorado and two of the three in New Mexico are on national forest lands.

Yellow Warbler Life History

From arctic Alaska south to central Peru, the Yellow Warbler has the largest latitudinal breeding range of any wood-warbler. The breeding ecology of its far-flung populations should reflect adaptations to a great diversity of environmental conditions. Indeed, such adaptations differ significantly between tropical and temperate-zone populations of this warbler, according to research published in 2008 by Javier Salgado-Ortiz, Peter P. Marra, T. Scott Sillett, and Raleigh J. Robertson (*Auk* 125:402–410).

Taxonomically, the American Ornithologists' Union divides the species into three groups: migratory Yellow Warbler (*aestiva*) breeding in North America, resident Golden Warbler (*petechia*) of southernmost Florida and the Caribbean, and resident Mangrove Warbler (*erithachorides*) of coastal Middle America and northern South America and the Galapagos Islands. The authors studied the *bryanti* subspecies of Mangrove Warbler at the Celestún Biosphere Reserve on Mexico's Yucatan Peninsula.

In three years of field work, they obtained a detailed picture of *bryanti* "life history"—the term for interacting traits involving reproduction and survival that are usually considered to be evolutionary and ecological adaptations. Next, they compared these findings with corresponding data published for other tropical resident birds and for northern Yellow Warblers.

Salgado-Ortiz and his colleagues report that many traits of *bryanti* Yellow Warblers are more similar to those of oth-

er tropical resident species than to migratory *aestiva* Yellow Warblers. Relative to *aestiva*, the birds at Celestún have significantly larger territories, lower population densities, longer breeding seasons, smaller clutch sizes, longer incubation and nestling periods, lower rates of nesting success, more frequent re-nestings, and a higher probability of annual adult survival.

The most striking contrast is in nest success from incubation through fledging. Young were fledged at only 26% of 284 active *bryanti* nests, whereas success ranged from 42% to 95% in nine Yellow Warbler populations studied in North America. By far, the primary reason for nest failure at Celestún was depredation: 64% of failures were caused by predators (mainly Green Jays). Another 8.5% of failures were caused by Bronzed Cowbird nest parasitism, and the rest by infertility, weather, and other factors. To maintain



"Mangrove" Warbler, a tropical subspecies group in the Yellow Warbler complex, includes one population with a life history more similar to other tropical resident birds than to migratory northern birds of its own species. *Soto La Marina, Tamaulipas, Mexico; May 2007.* © Greg Lasley.

stability of the tropical population, compensating factors are obviously essential—such as the multiple re-nestings and higher annual adult survival rates (thus, greater lifetime productivity) recorded at the study site.

The authors discuss the tropical and temperate warblers' contrasting features in the context of a multitude of life-history hypotheses. For example, lower population densities, larger territories, and smaller clutch sizes are thought by some biologists to reflect lower food availability. Perhaps

migratory populations' larger clutch sizes have evolved to produce more young in compensation for higher mortality during migration.

But the validity of almost every life-history hypothesis has raised questions and spawned quarrels for 60 years. There are good reasons for uncertainty. Reviewing the contentious life-history literature in 2000 (*Condor* 102:3–8), Robert E. Ricklefs remarked, "In contemplating the diversity of life histories, we are studying an immensely complex phenomenon."

Salgado-Ortiz and his coauthors believe that the contrasting Yellow Warbler life histories are influenced both by local limiting factors and by costs associated with migration. They suggest that further research comparing life histories within other taxa along latitudinal gradients will help to sort out how life-history traits evolve.

Staring at Starlings

It stands to reason that an incubating gull considers a human walking directly toward the nest as a more serious threat than a human walking tangentially past. That expectation was supported by a study of Herring Gulls and Great Black-backed Gulls described by Joanna Burger and Michael Gochfeld in 1981 (*Journal of Comparative and Physiological Psychology* 95:676–684). Plausible, too, is that a bird might be more uneasy about a human face with two eyes staring directly toward it than about the same face turned in the opposite direction. Robert R. Hampton experimentally confirmed that response by House Sparrows in 1994 (*Behaviour* 130:41–51).

Evidently, European Starlings can assess the potential danger of a human "predator" by using a more subtle cue: the exact direction in which a person's eyes are aimed while the person is facing the bird. Julia Carter, Nicholas J. Lyons, Hannah L. Cole, and Arthur R. Goldsmith reported this result in 2008 after a series of experiments with starlings in an outdoor aviary (*Proceedings of the Royal Society-B* 275:1709–1715). A human "predator" sitting just outside the aviary confronted the birds, testing their responses to three increasingly subtle hints about the possibility of predation: the position of the predator's head and body, the presence or absence of the predator's eyes, and the direction of the predator's "eye-gaze." The authors interpret the birds' reactions by differences in feeding behavior. Less attention to the food suggests greater attention to the predator, which was judged as indicating a bird's perception of higher risk.

In the first experiment, starlings took significantly longer to go near a food source, ate more slowly, and ate less food if the predator's head faced the food source than if it faced



Experiments indicate that **European Starlings** can assess the potential threat of a predator by paying attention to a very subtle cue: the exact direction of the predator's gaze. *Boulder County, Colorado; March 2006. © Bill Schmoker.*

the opposite direction. In the second experiment, starlings responded with reduced feeding activity if the predator's eyes were visible than if the eyes were covered. In the last experiment, the predator's head remained facing the food source, moving only its eyes. The starlings perceived greater risk when the eyes gazed directly toward the food than when the gaze was angled away. To the authors' knowledge, this third experiment is the first explicit demonstration of a bird responding appropriately to a subtle change in the direction of eye-gaze as a cue of predation risk.

Carter and her colleagues offer several hypotheses about what mental process might enable birds to infer a predator's intention from the direction of eye-gaze. Perhaps starlings are innately able to judge that a predator looking directly at them may intend to chase them. Perhaps the tested starlings learned to associate their capture with humans who looked directly at them. Perhaps the geometric pattern of eyes gazing straight toward a starling is more likely to attract and hold its attention than eyes averted at an angle. Other studies have shown that "eyespot" are a strong stimulus in various predator-prey contexts. Whatever the reason, an approaching predator might have better success by not looking directly at a starling.

Bill Schmoker, whose photographs appear frequently in *Birding*, says starlings are "pretty cagey" and "out in the open don't usually cooperate." Could an averted gaze allow closer approach without stressing the bird? Maybe, but Schmoker comments, "The problem with photography is that at some point, you've got to point the lens right at the bird—perhaps the equivalent of a big staring eye." Judging by the Carter team's results, a binocular's two big staring eyes might be even more unsettling.