by Paul Hess

California × Gambel's Quail Hybridization

In an oft-quoted image from 1990, Richard G. Harrison called hybrid zones "windows on the evolutionary process". One such window is a narrow strip of mountain and desert country in southern California, primarily in Riverside County, where the ranges of California Quail and Gambel's Quail overlap and the two species regularly interbreed. Jennifer M. Gee has studied this zone near Palm Desert since 1997, along a 20-kilometer transect from the California Quail's side in the west, through the strip of hybridization, to the Gambel's side in the east. Recently, in a sample of 435 quails from the area, she analyzed genetic traits at seven polymorphic microsatellite loci (which are short, highly variable DNA sequences useful for determining levels of genetic differentiation and patterns of hybridization between closely related species) and physical traits in seven aspects of plumage and size (weight, tarsus and topknot length, and flank, belly, cap, and forehead color). To characterize the ecology of the zone, she profiled patterns in rainfall, temperature, and vegetation. Gee's combined analysis of the biological and environmental factors, which she reported in 2004 (*Evolution* 58:1108–1121), produced strikingly concordant patterns. Abrupt clines in the birds' genetic and morphological features coincided with sharp gradients in climate and vegetational structure.

California and Gambel's Quails hybridize where their ranges overlap, with the mixed progeny exhibiting considerable variation. A morphological gradient from west to east in the hybrid zone corresponds to a gradient of environmental factors. Note that the birds shown here are not museum specimens but live captures released after they were photographed. *Top row: males. Bottom row: females. Column 1: California Quail. Columns 2–4: hybrids. Column 5: Gambel's Quail. © Jennifer M. Gee.*

West to east across the hybrid zone, transitions from California Quail traits to Gambel's Quail traits corresponded to decreasing average rainfall, to increasing average temperature, and to a trend from larger areas of trees and shrubs to larger areas of open ground. Fluctuations in rainfall because of El Niño during the 1997–2001 study period were correlated with differences in the proportions of California Quails and Gambel's Quails present within the zone: more California individuals in wetter years and more Gambel's in drier years. These changes suggested that rainfall is the most important factor governing the location of the hybrid zone and perhaps the range limits of the two species in that area. It was already known, Gee noted, that as a general rule the California Quail occupies relatively moist habitats and that the Gambel's Quail is more suited physiologically to arid habitats.

The author related her findings to broad concepts of adaptation, natural selection, hybrid fitness, and potential evolutionary consequences for species that interbreed in narrow zones. Too little is known for firm predictions about these closely related quail species' evolutionary future. "The present study serves as a foundation for directing future studies in this previously undescribed system of natural hybridization," Gee wrote. She is continuing her own research because many more aspects of the system await discovery, and many basic questions await answers. Seldom, if ever, is a hybrid zone's "window" completely clear.

Meanwhile, Gee has answered a special question for *Birding* readers: What does a California × Gambel's hybrid look like? The only illustration widely available is in *Pheasants, Partridges, and Grouse* by Steve Madge and Phil McGowan (Princeton University Press, 2002). See their Plate 58 for what Gee considers the most-easily-recognized combination of characters marking a hybrid male, namely, the scaled flanks of California around the black belly-patch of Gambel's. Various combinations of the two species' cap and forehead colors also occur. Plumage coloration is less distinctive in hybrid females; differences in size between the species—particularly weight, tarsus, length, and topknot length—are more important, she said. Hybrid combinations of these measurements would obviously be difficult to judge in the field. In both sexes, Gee added, "Hybrids range from looking very much like one parental species to looking much like the other. The traits are not always equally expressed in their intermediate nature. The most easily mistaken hybrids are those that are quite Gambel's-like. Often they have just a bit of scaling on the edges of the belly near the flank, whereas the rest of the breast and belly is solid." Try identifying hybrids at many places in Riverside County where they have been spotted, such as San Gorgonio Pass, White Water, Deep Canyon, and throughout the western edge of Anza-Borrego Desert State Park.

Migration Counts in Massachusetts

Do counts of migrants reliably reflect changes in birds' populations? More particularly, can numbers of passerines mist-netted along migratory routes serve as valid gauges of species' population trends? These questions have bedeviled ornithologists for decades, because observed patterns in migrant captures can be influenced by factors unrelated to population levels. Changes in vegetation, food availability, or other ecological requirements may affect a banding station's attractiveness as a stopover site. Species may change their migratory behavior in route, speed, or timing because of climatic or other environmental conditions. Sampling procedures can be inconsistent over time. Moreover, even if a trend in mist-net captures actually does represent a population pattern, is the change range-wide or perhaps only in some undefined region of the distribution of the species? Researchers have worked diligently for decades to tease meaningful information from the uncertainties. Trevor L. Lloyd-Evans and Jonathan L. Atwood expressed the problem bluntly in 2004 (*Wilson Bulletin* 116:1–16): "[M]onitoring changes in breeding populations through counts of migrants obtained by mist-net captures is risky business."

Lloyd-Evans and Atwood analyzed 32 years of data and looked for changes in passerine numbers banded during spring and fall migrations at the Manomet Center for Conservation Sciences in coastal Massachusetts. Comparing mean capture-rates during 1970–1985 with rates during 1986–2001, they found a striking overall pattern. Of 87 species listed, 54 declined significantly between the two sampling periods in one or both seasons, and only five increased significantly. The declines included 20 warbler species, led by Tennessee (down 95%), Cape May (down 93%), and Bay-breasted (down 86%). The only warbler significantly increasing was Black-throated Blue (up 42%). Other severe decreases were shown by Eastern Kingbird, Brown Thrasher, Scarlet Tanager, Eastern Towhee, Field Sparrow, Rose-breasted Grosbeak, and Purple Finch—all down by more than 70 percent.

Seeking to validate the Manomet trends, Lloyd-Evans and Atwood compared them with trends shown in the North American Breeding Bird Survey (BBS). There was no way to know which breeding populations the migrants represented, so the authors chose three BBS physiographic regions in the Northeast as the most appropriate areas for comparison. The results were decidedly mixed. For 33 species whose BBS data were considered statistically adequate, Manomet's trends were positively correlated with BBS trends within northern New England in both seasons, within southern New England only in fall, and within a spruce-hardwoods region located mainly in the Maritime Provinces in neither season. Inconsistent results appeared at the individual-species level as well. On the one hand, the migration counts did reflect the extreme declines in species such as Tennessee Warbler, Cape May Warbler, and Bay-breasted Warbler, whose populations exploded during spruce budworm outbreaks in the late 1970s and have plummeted since then. The migration counts also reflected well-known dramatic increases of Tufted Titmouse, Carolina Wren, and Northern Cardinal in New England during recent decades. On the other hand, Yellow-bellied Flycatcher, Red-eyed Vireo, Gray Catbird, Yellow-rumped Warbler, and Ovenbird showed significant increases in BBS counts but significant decreases in Manomet captures. Furthermore, of 16 species with increasing trends in the BBS, only one (Northern Cardinal) increased in the Manomet data.

In the manner of many investigators before them, Lloyd-Evans and Atwood admitted that they could not explain the inconsistencies between migration-count and BBS data. Nevertheless, the authors noted that many species' declines at Manomet coincided with BBS declines and that the decreases far outnumbered the increases. A tenfold preponderance of 54 species declining and only five increasing in the last three decades at Manomet, whatever the comparison with BBS trends, is surely a basis for concern.

It is tempting to extrapolate the results of any given avian trend analysis to broader spatial and temporal scales. But is it valid to do so? A recent study of population data from Massachusetts highlights the need for caution in such an approach. For example, **Yellow-rumped Warbler** captures have declined at a coastal banding station in Massachusetts, but Breeding Bird Survey data have indicated an increase within the warbler's eastern spruce-hardwoods nesting region. *Wellfleet Bay Audubon Sanctuary, Massachusetts; October 2004. © Eric Smith.*

Golden-cheeked Warbler Haven

Tanks, bombs, artillery, and large-scale troop maneuvers are obviously not the most favorable environments for breeding birds, but military bases are not bereft of ecological value. These installations are often "oases of habitat" amid fragmented and developed landscapes, as Chris Eberly emphasized in the October 2002 issue of *Birding* ("Defending the steppingstones of migration", pp. 450–458). Eberly, Partners in Flight

Fort Hood is an active Department of Defense Installation in Texas. It is also a stronghold for the endangered **Golden-cheeked Warbler**. Indeed, Fort Hood populations of the warbler increased substantially during the 1990s, thanks to a proactive, integrated management plan at the base. Recovery of this endangered species will require continued successes at Fort Hood, coupled with population increases elsewhere in the Golden-cheeked Warbler's range. *Kerr, Texas; April 2002. © Mike Danzenbaker.*

Program Manager for the U.S. Department of Defense, explained how training grounds and air bases can be havens for endangered and threatened species. Among his examples was the Golden-cheeked Warbler at Fort Hood, Texas, where an estimated 4,500 pairs constitute the largest known breeding population under a single management authority. This species nests exclusively in mature oak-juniper woodlands in central Texas—specialized habitat that has been destroyed at an alarming rate by urban development and agricultural conversion. Since the Golden-cheeked Warbler was listed as federally endangered in 1990, the Department of the Army has provided management for its population (as well as for the endangered Black-capped Vireo) at Fort Hood.

Judging from a report by Angela D. Anders and Donald C. Dearborn in 2004 (*Southwestern Naturalist* 49:39–47), the warbler has fared well at the Fort since the management program began. Surveys from 1992 to 2001 showed a significant increase in numbers. In fact, the mean count of Golden-cheeked Warblers at survey points almost doubled during the 10-year period, despite fires sparked by military ordnance in 1996 that destroyed 15 percent of the Fort's mature oak-juniper forest. A primary goal of the management plan was to mitigate potential damage to the habitat by direct military activities. From 1991 through 1999, all Golden-cheeked Warbler breeding habitat was protected from such disturbance during the breeding season. Since 2000, a less-restrictive plan has continued to limit operations in "core" areas of relatively large blocks of habitat but has lifted restrictions in "non-core" areas of smaller, more-isolated habitat patches. Nevertheless, the Golden-cheeked Warbler population at the Fort continued to grow through 2001. Management efforts also have included Brown-headed Cowbird control, because the warbler is highly susceptible to brood parasitism by the cowbird. The authors' data showed no signs of parasitism at 83 nests and 349 monitored territories in 2000 and 2001—a welcome indication that at least part of the population increase might have involved greater productivity of young.

Although they call the long-term trend "potentially encouraging", Anders and Dearborn caution that it might not signal an increase in the Golden-cheeked Warbler's overall numbers or productivity. Instead, it may reflect little more than increased immigration of warblers into the Fort from other areas where their habitat has disappeared under development pressure. Immigration could have concealed decreases in pairing success, production of young, or survival that were being caused by military activities in undetected ways. Studies are in progress to evaluate those factors. For whatever reasons, the Golden-cheeked Warbler population at Fort Hood seems to be in better condition than populations in other parts of the range, but the authors emphasize that environmental management at the Fort alone cannot guarantee the warbler's future. Rather, they predict that "the persistence of viable populations at other sites will be necessary for recovery of this species."

A Fresh Look at Blue Birds

The blue of a bluebird is the blue of the sky, correct? We learned that long ago. Olin Sewall Pettingill, Jr., put it plainly in his textbook *Ornithology in Laboratory and Field*: "Blue color results from a scattered reflection of blue light—the same phenomenon that causes the blue of the sky..." Even the brand-new *Birdwatcher's Companion to North American Birdlife* explains, "The romantically inclined will be pleased to learn that the blue of bird feathers owes its existence to the same phenomenon that makes the sky blue...” Well, recent research has turned this century-old optical dogma on its head, and we suddenly face romantic disappointment. Correctly enough, we have known that birds’ blue colors do not arise from pigment but rather are produced by an interplay of light upon extremely small structures. The surprise is that this effect evidently does *not* arise from the same process that turns the sky blue.

Richard O. Prum, Rodolfo Torres, Scott Williamson, and Jan Dyck reported the finding for feathers in 1998 (*Nature* 396:28–29) and 1999 (*Proceedings of the Royal Society of London–B* 266:13–22). Then Prum and Torres extended the result to blue skin in 2003 and 2004 (*Journal of Experimental Biology* 206:2409–2429 for birds; 207:2157–2172 for mammals). The basis of the sky’s blue was described in detail as long ago as 1869 by Irish physicist John Tyndall and later refined by British physicist Lord Rayleigh. In the sky, randomly distributed molecules of gas and other atmospheric particles scatter light waves at the blue end of the color spectrum. By a different process, fairly regularly distributed microscopic forms—air cavities in the keratin of feather barbs, or collagen fibers in the skin and the outer covering of the bill—produce structural blues in birds and mammals. Prum and his colleagues determined that these nanostructures are too closely spaced to create sky-style scattering. Rather, the color is produced by constructive interference, a process in which separate light waves travel in phase and reinforce one another at a certain wavelength—in this case, blue. Brilliant iridescent colors arise from the same general process, Prum said. “The amazing thing is that the size of the tiny air cavities in the feathers has to be exactly right to create the right color. If the air bubbles are different in size by, say, five millionths of an inch, the result is an entirely different hue.”

The bright blue bill of the adult male **Ruddy Duck** in breeding plumage is unmistakable. What is the source of blue coloration in birds? It is not an actual pigment, as birders have long known. But neither is it caused by the scattering of light at blue wavelengths, as has been commonly thought. Instead, blue coloration—in feathers and bare parts alike—is caused by a process called constructive interference. *Kern County, California; April 2004. © Bob Steele.*

For their plumage studies, the authors analyzed feathers that produce blue in a Plum-throated Cotinga (*Cotinga maynana*), blue and green in a Peach-faced Lovebird (*Agapornis roseicollis*), light blue in a mutant Budgerigar (*Melopsittacus undulatus*), and violet-purple in a Gouldian Finch (*Poephila guttata*). During their more-recent study, they identified structurally-colored violet, blue, or green in the skin, bill, legs, or feet in more than 250 bird species spanning 129 avian genera, 50 families, and 16 orders around the world. Prum and Torres analyzed structural tissues in 32 of those species, including the legs and feet of a Blue-footed Booby, the breeding-season bill of a Ruddy Duck, and the facial skin of a Wild Turkey—all still stunning, even if science tells us that we should no longer link them romantically to the sky.