by Paul Hess

Seeing Subspecies in a Genetic Light

What do subspecies have in common with evolutionary reality? Often little or nothing in the case of continental North American and Eurasian birds, according to Robert M. Zink. He surveyed data compiled from his own and others' studies of 41 Nearctic and Palearctic species, which had indicated whether 230 formally recognized subspecies corresponded to distinct evolutionary units based on their mitochondrial DNA (mtDNA). Only seven of the subspecies were distinct, he reported in 2004 (*Proceedings of the Royal Society–Biology* 271:561–564).

Zink pointed to the Cactus Wren as an example. Examining six of its subspecies, he and several colleagues had reported in 2001 that no subspecies showed a monophyletic set of mtDNA sequences—i.e., a genetic pattern evolutionarily distinct from all other subspecies (*Condor* 103:1–10). The only consistency between mtDNA phylogeny and subspecific taxonomy was a collective separation of the six subspecies into two genetic groupings: a continental group throughout the North American range consisting of *couesi*, *guttatus*, and nominate *brunneicapillus*, and a group confined to Baja California consisting of *affinis*, *bryanti*, and *purus*. While the individual subspecies were not genetically distinct from one another, the two groups were reciprocally monophyletic. Interestingly, although Zink did not mention it, the continental group differs from the Baja group not only genetically but also recognizably in the field. In continental populations, dark breast spots coalesce into a large black patch and the flanks are washed with rich cinnamon-buff. In Baja populations, the breast is less densely spotted and the flanks have a pale buffy wash. There are other plumage differences as well.

Recognized subspecies may differ morphologically from other subspecies, yet may not be evolutionarily distinct. For example, Robert M. Zink found that six **Cactus Wren** subspecies form only two genetically distinctive groups. As a general rule, Zink believes that conservation should focus on independent evolutionary units rather than on individual subspecies. *Starr County, Texas; November 2004. © Brian E. Small.*

Zink's point in the 2004 report was that conservation action should focus upon historically independent units representing evolutionary history, not necessarily upon named subspecies that may reflect trivial morphological differences. He granted that many species show geographical variations in morphology that might be local adaptations important to the survival of the species. But these variations, he said, can change rapidly, while genetically distinct taxa often take tens of thousands of years to evolve. Applied to the Cactus Wren, his view is that the continental and the Baja populations merit conservation attention at the group level but that the individual subspecies do not. (The severely declining *sandiegensis* subspecies, an ecologically separate population inhabiting southern California's coastal sage-scrub, was not examined.)

Subspecies fare somewhat better in an analysis by Albert B. Phillimore and Ian P. F. Owens published in 2006 (*Proceedings of the Royal Society–Biology* 273:1049–1053). The authors used data on 259 subspecies of 67 species, which included not only Nearctic and Palearctic birds but also continental and island taxa in Africa, Australia, Indo-Malaysia, the Neotropics, and Oceania. Zink had predicted that more islandic and tropical subspecies would correspond to evolutionary units than those of temperate zones. The Phillimore-Owens results support this view: 36% of their survey's subspecies are evolutionarily distinct, compared to 3% in Zink's survey. The proportion is greatest at 57% of subspecies in island-dwelling taxa, where isolation typically produces more differentiation, but even in their continental sample 29% of subspecies are distinct.

Why do substantially fewer subspecies in continental Nearctic and Palearctic regions coincide with genetic distinctiveness than do subspecies in other biogeographical realms? Phillimore and Owens suggest that perhaps North American and Eurasian subspecies have had less time to differentiate genetically during the post-glacial period. Unlike Zink, they believe that low levels of evolutionary divergence should not rule out subspecies as targets for conservation around the world—especially in cases where phenotypic divergence is considerable or where molecular data are not available.

Blackcaps Reveal Evolution in Action

Europe's Blackcap (*Sylvia atricapilla*) has taught us much about migration since the 1950s when German ornithologist E. G. Franz Sauer discovered that this endearing warbler could navigate by the stars. The Blackcap's most recent revelation is a novel pattern of migratory behavior evolving so rapidly that people can watch the progress year by year in their gardens. Stuart Bearhop and eight coauthors suggested in 2005 that the observers might be witnessing incipient speciation as well (*Science* 310:502–504).

In the 1960s a few wintering Blackcaps began to appear at feeders in southern England and Ireland, where the species had been strictly a summer resident. These were not local birds that had failed to migrate. Bands proved that they had come northwestward from breeding grounds in Germany and Austria instead of taking the traditional route southwestward to Iberia. By the 1980s several thousand Blackcaps were being reported annually in winter in the British Isles.

A change in migratory behavior by the **Blackcap**, an Old World warbler, is a dramatic example of rapid evolution. More and more Blackcaps from central Europe fly northwestward to winter in Britain instead of southwestward to the traditional winter range in Iberia. This novel, inherited trait could lead eventually to speciation. *Rivières-le-Bois, Haute-Marne, France; 6 August 2003. © B. Gadsby.*

Experimenting with captive-bred and wild birds, Peter Berthold and the late Andreas J. Helbig and colleagues demonstrated that the migratory behavior was guided by a genetically programmed map, which was being inherited (e.g., Berthold 1988, *Journal of Evolutionary Biology* 1:195–209; Helbig 1991, *Behavioral Ecology and Sociobiology* 28:9–12; Berthold et al. 1992, *Nature* 360:668–670). The growing population of Blackcaps traveling northwestward indicated that selection favored the new behavior as adaptive. Did the easier access to winter food at increasingly numerous British and Irish feeders and the shorter migration distance than from Iberia improve the energy available for breeding? Did the earlier onset of increasing daylight at higher latitudes advance the birds' migratory urge and send them back to the breeding grounds sooner than their counterparts wintering in the south? Did earlier arrival enable them to occupy the best nesting territories and thus to produce the most offspring? Helbig proposed those advantages in 1996 (*Journal of Experimental Biology* 199:49–55) but lamented, "Unfortunately, no markers for birds of different winter origin are yet available that would allow us to test this hypothesis."

In their report in *Science*, Bearhop and his coauthors announced that they had found ideal markers: stable hydrogen isotopes recently synthesized in Blackcaps' new claw tips. Isotopic ratios vary geographically, reflecting the amount of rainfall absorbed by plants and passed up the food web. The isotopic "signature" shows where tissues were grown—in this case, whether a breeding Blackcap in central Europe had wintered in Britain or in Iberia. These isotopes produced the long-awaited evidence. Blackcaps were 2.5 times more likely to pair with individuals that had wintered in the same region. Males from Britain and Ireland tended to arrive on the central European breeding grounds and pair earlier than those coming from southern Europe. Females in these pairs were more likely to have a successful breeding attempt and to produce larger clutches than females arriving later. Selection evidently continues to favor the behavior. Nearly 20,000 Blackcaps were reported in Britain on 28–29 January 2006 during the annual "Big Garden Birdwatch" sponsored by the Royal Society for the Protection of Birds (Mark Eaton, RSPB research biologist, personal communication).

Bearhop's team pointed to one potential result of assortative mating in which males and females pair primarily within their own subpopulation. Differential timing could lead to reproductive isolation between the earlier and the later arrivals—and ultimately to their division into two sympatric species. The concept of sympatric speciation—i.e., divergence of populations within the same geographic range, not separated by any physical barrier—was dismissed by evolutionary biologists through much of the 20th century but has lately gained support. Elizabeth Pennisi reviewed recent evidence among various taxa, including birds, in an article in 2006 (*Science* 311:1372–1374). Speciation is not the only possible outcome, but the evolution of a major shift in migratory behavior in less than half a century is remarkable in itself. The Blackcap research was prominent among studies that led the journal *Science* to proclaim "evolution in action" as the scientific Breakthrough of the Year in 2005.

Convergent Plumage in Two Woodpeckers

Downy Woodpecker and Hairy Woodpecker are so similar in plumage that they might seem to be sister species, each other's closest taxonomic relative. Surprisingly, they are not. Based on genetic analyses of the genus *Picoides*, Amy C. Weibel and William S. Moore reported in 2002 that the two do not share a recent ancestor (*Molecular Phylogenetics and Evolution* 22:65–75, 22:247–257). Instead, they belong in distantly related phylogenetic clades—groups of species that evolved separately from a shared ancestor far in the past. Weibel and Moore developed their phylogeny by analyzing two mitochondrial genes, cytochrome oxidase I and cytochrome *b*, and a nuclear intron gene (introns are portions of the genome that do not code for proteins). The research uncovered many evolutionary relationships that conflict with previous *Picoides* phylogenies based only on plumage characters. Downy is in a clade of small woodpeckers composed of Ladder-backed, Nuttall's, and Lesser Spotted (*P. minor* of Eurasia). Hairy is in a clade of larger species composed of Strickland's (here referring to Arizona Woodpecker), Red-cockaded, and White-headed.

Hairy Woodpecker and Downy Woodpecker are extremely similar in plumage, but a genetic study shows that the two species are not close taxonomic relatives. Authors of the study suggest that the similarities result from evolutionary convergence. *Kern County, California; January 2005. © Brian E. Small.*

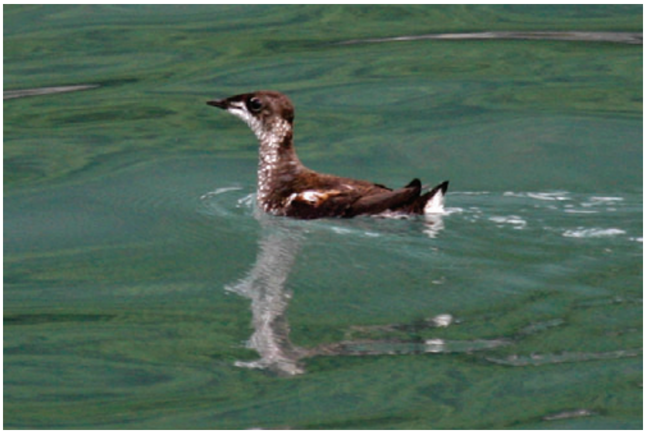
The discrepancy between plumage similarities and genetic differences led Weibel and Moore to suspect that some resemblances in Downy and Hairy plumage are not homologies (representing shared ancestry), but rather are homoplasies (arising independently by parallel or convergent evolution). They tested the hypothesis by assessing a variety of ancestral and derived plumage character states in the context of their previous phylogenetic framework. The study spanned twenty *Picoides* species in seven clades, but the authors emphasized Downy and Hairy relationships in reporting the results in 2005 (*Condor* 107:797–809). The test began with a two-part premise: Homologous characters would be congruent among all species in a clade, whereas characters incongruent with those of the other species in a clade would likely be independently derived.

Among thirteen adult and six juvenal plumage colors and patterns, Weibel and Moore identified four adult features that are similar in Downy and Hairy but are incongruent with features of the other species within their respective clades. Downy and Hairy both have unstreaked crowns, but Downy is the only such species in its clade. Downy and many Hairy populations have a solid white back, but each is the only such species in its clade. Downy and Hairy both have a full supercilium, but Hairy is the only such species in its clade. Downy and Hairy have an unbarred mantle (here defined as back plus scapulars), but Downy is the only such species in its clade. The disparities indicated to the authors that these plumage characters represent multiple independent evolutionary modifications.

What selective advantage might drive convergent evolution of nearly identical characters? In 1969 Martin L. Cody noted that such resemblances typically involve sympatric species whose ecological requirements overlap. He proposed interspecific territoriality as the selective force—the advantage being mutual recognition of the other species as a direct competitor for resources, which should be excluded aggressively from one's territory (*Condor* 71:222–239). Cody did not discuss Downy and Hairy Woodpeckers, but the striking parallels between east-to-west plumage variation in both species strongly support his hypothesis of mutual recognition. Both are brightly patterned black-and-white in eastern populations, and both trend similarly toward a drabber appearance, with less white, in Pacific Coastal populations. Varying in common, they would recognize each other throughout their extensive, shared range. Weibel and Moore agreed with Cody's territorial concept, and they suggested that the limiting resources for Downy and Hairy are trees suitable for nest cavities. They emphasized, however, that field studies will be required to substantiate territoriality as the explanation. Whatever selective factors were the cause, the authors are confident that convergent evolution was the effect.

Marbled Murrelet in Dietary Trouble

The Marbled Murrelet was listed in 1992 as threatened in Washington, Oregon, and California, and preserving its old-growth-forest breeding habitat has since been the highest priority. Food has received scant attention, however, as a possible factor in the little alcid's severe decline. "[I]t is difficult to imagine that overfishing may currently affect Marbled Murrelet prey resources in the Pacific Northwest," the U.S. Fish & Wildlife Service recovery plan said in 1997. A recent study makes it much easier to imagine. Benjamin H. Becker and Steven R. Beissinger reported in 2006 that murrelets' food resources in the Monterey Bay area are substantially less nutritious than they were a century ago (*Conservation Biology* 20:470–479). An energy-deficient diet may be one reason why Marbled Murrelets' breeding productivity has collapsed in central California.



Poor-quality food could be partly responsible for a recent decline in **Marbled Murrelet** breeding success in central California. Stable isotopes in feathers indicate that murrelets' diet a century ago had more nutritional value than the diet today. *Seward, Alaska; 12 June 2005. © George Armistead.*

To evaluate the birds' diet, Becker and Beissinger compared ratios of stable carbon and nitrogen isotopes in feathers from specimens collected in 1895–1911 and from living birds in 1998–2002. Stable-isotope signatures in the feathers reflect the trophic level—and, thus, the energy value—of prey eaten while the birds were molting into new plumage. Pointedly, the two sampling periods came before and after overfishing greatly reduced populations of sardines, anchovies, and squid. Those food resources, the isotopes show, were primary components of murrelets' high-trophic, high-energy diet a century ago. Today, according to the isotopes, murrelets feed mainly at lower levels of the food web on less-nutritious krill, sandlance, and young rockfish.

The energy obtained from a single sardine requires about 80 krill or 3.5 rockfish—a fateful equation because more energy spent foraging for low-quality prey means less energy available to produce young. Egg production is energetically costly for a murrelet, because its single egg weighs one-fourth of its body mass. Studies have indicated that 50–90 percent of murrelets fail to breed each year in central California, perhaps because they cannot find enough high-energy food. Becker and Beissinger recommended establishing marine reserves protected from fishing to increase the abundance of high-quality prey.

Meanwhile, protecting extensive old-growth forest from logging remains essential. Martin G. Raphael reported in the same issue of *Conservation Biology* (20:297–305) that the Northwest Forest Plan, a system of large reserves on federal lands, has achieved its short-term objective. When the Plan was adopted in 1994, Washington, Oregon, and California had 1.6 million hectares of breeding habitat highly suitable for murrelets. Half of that area was on federal lands, and only 2 percent of the protected habitat was lost during the past 10 years (primarily because of fire). In contrast, logging destroyed 12 percent of the remaining habitat on nonfederal lands during the same period.

Now loggers have petitioned the government to de-list the Marbled Murrelet as threatened in the three northwestern states, contending that these birds are not biologically distinct from populations estimated at 800,000–900,000 in British Columbia and Alaska. Even with threatened-species protection, the small U. S. population of 22,000 will still face habitat losses on nonfederal lands, nest depredation (primarily by jays, crows, and ravens), oil spills, death in gill nets, and poor-quality foraging habitat at sea. Without that protection? Raphael's conclusion was forcefully terse: "Time will tell."