by Paul Hess

What's Wrong with Vagrants?

A Glaucous-winged Gull in Gloucestershire started it all. The alliterative visitor, a first record for Britain if accepted, recently turned the Frontiers of Field Identification e-mail list ("ID-Frontiers") into an eleven-day symposium on avian vagrants. Things began rather esoterically with comments on the gull's age, molt status, and possibly aberrant plumage. Then the talk turned to opinions about what genetic, environmental, and behavioral factors might send this bird half a world away from where it should be. Soon the discussion became a far-reaching dialectic about the causes and consequences of vagrancy.

The entire conversation is available at the ID-Frontiers archives for 4–14 January 2007 <listserv.arizona.edu/archives/birdwg01.html>. In more than 60 postings, vagrants are characterized variously as birds traveling willingly or unwillingly, purposefully or accidentally, beneficially or disastrously, beyond their usual range. Writers point to extreme weather, genetic flaws, developmental defects, behavioral quirks, facultative decisions, inherent propensities to wander, effects of hybridization, and random chance. Interpretations cover almost every supposed evolutionary basis and outcome imaginable.

Weather conditions are noted, of course, in many occurrences such as a *Katrina*-borne Lesser Frigatebird in Michigan, a Bristle-thighed Curlew fallout on the West Coast, and various species of autumn landbird migrants in the southeastern U.S. windswept northward to Nova Scotia and sometimes all the way to Britain and Ireland.

But vagrancy as an abnormality soon dominates the discussion. There is David DeSante's famous hypothesis of "mirror-image misorientation"—a defective compass pointing small numbers of fall migrants southwestward to the Pacific coast instead of southeastward where normal programming takes their species. There is the likelihood that some vagrants are not merely misoriented but completely disoriented, wandering randomly with no functioning compass at all. More mundanely, there is the possibility that a bird might join a flock of other species by pure chance and follow the flock to a strange destination.

Remarkable cases are described in which a bird revisits a far-out-of-range location year after year: for example, a Golden-crowned Sparrow in consecutive winters at a backyard in New Jersey, a Sky Lark seven winters in a row in California, and an Eared Grebe for a decade in Massachusetts. They may be accidental wanderers the first time, but their subsequent visits are surely not accidents. On a large scale, increasing appearances of Cave Swallows in the Northeast and of western hummingbirds eastward and northward are discussed as newly inherited behaviors.

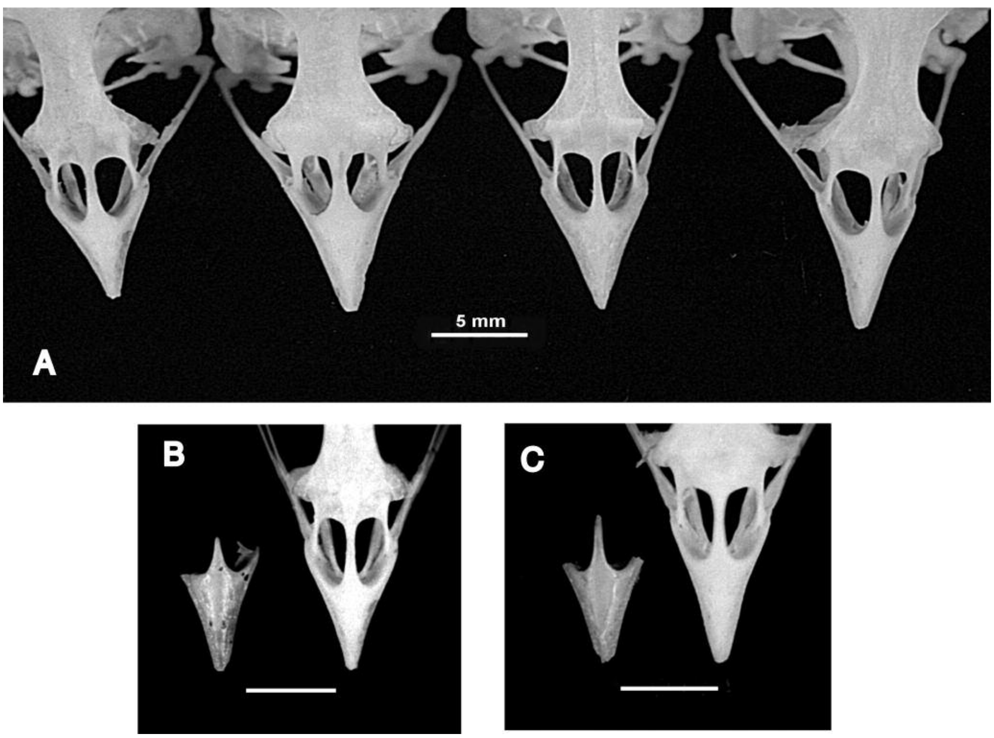
Evolutionary hypotheses and speculations abound. Is vagrancy necessarily bad? Could it be advantageous? Why are some species more prone than others to wander? We read how Joseph Grinnell, writing from a group-selectionist standpoint, viewed vagrants as "pioneers" intentionally seeking new areas to occupy, often sacrificing themselves "in the interests of the species". The neo-Darwinian counter to Grinnell is also advanced, namely, that "vagrancy genes" persist only if they confer fitness on an individual and the individual's offspring, no matter how well the genes happen to serve the species.

Washington, Oregon, and California had an unprecedented fallout of **Bristle-thighed Curlew** migrants in 1998. These birds' abnormal occurrence is among many examples cited in an extensive discussion of avian vagrancy on the "ID-Frontiers" e-mail list. *Marin County, California; May 1988. © Larry Sansone.*

Finally, the commentaries come full circle in a principle that vagrants' tendencies are not likely governed by genes alone but by complex genetic and environmental interactions called "norms of reaction". If the term is unfamiliar, it guarantees—as does the complete dialogue—that the next time we thrill at a vagrant from far away, we will have a lot to ponder after our high-fives are finished and our adrenalin settles back down.

Fossil Birds in Kansas

Northern Mockingbird, *Zonotrichia* sparrows, Dark-eyed Junco, McCown's Longspur, Lapland Longspur, Chestnut-collared Longspur, and Western Meadowlark are on the Meade County list in Kansas. They were there in the Pliocene epoch nearly five million years ago, too—as apparently was Sprague's Pipit, now a regular transient through the state but with no Meade County record (Chuck Otte, Kansas Bird Records Committee secretary, personal communication).



Subtle differences mark bills of four modern longspurs (A, left to right): Chestnut-collared, McCown's, Smith's, and Lapland. Fragments of ancient fossil bills found in Kansas are identified as Chestnut-collared (B) and Lapland (C) in a study by Steven D. Emslie. © *American Ornithologists' Union.*

Evidence of the ancient presence of those species comes in 2007 from a small box of fossils that sat uncatalogued at the University of Michigan since they were collected six decades ago from early Pliocene deposits in the county. Among the fragments are dozens of premaxillae, which Steven D. Emslie confidently or tentatively classifies as the earliest record of each taxon (*Auk* 124:85–95). The premaxilla is a bone that forms the upper edge and tip of the upper mandible.

To identify the fossils, Emslie compares twelve morphological features of their bills with those of living species. His degree of confidence varies. The mockingbird and the junco compare well with their modern counterparts, and the three longspurs are distinguishable by the size and shape of their premaxilla. Emslie is less certain about the pipit but says the specimens are more similar to Sprague's than to five other pipit species. He is also tentative about Western Meadowlark; the fossils compare well but may represent a small form whose taxonomic status cannot be determined without further samples. Interestingly, the single *Zonotrichia* bill does not precisely match any living member of the genus. Emslie ventures that it may represent an undescribed species.

His paleontological view contrasts with many genetic analyses that emphasize North American passerine diversification much more recently during the late Pleistocene glacial-interglacial epoch, less than 250,000 years ago. These studies judge ages of taxa by using a "molecular clock" based on estimated rates of divergence in mitochondrial DNA (mtDNA). Emslie's fossils show that some of the species existed for one million to three million years longer than their mtDNA clocks indicate. He cites two studies that do point to passerine radiation as long ago as the Pliocene. John Klicka and Robert M. Zink reported molecular characteristics in 1997 corresponding to divergence of the longspurs more than four million years ago (*Science* 277:1666–1669). Irby J. Lovette and Eldredge Bermingham offered mtDNA evidence in 1999 suggesting origin of 24 *Dendroica* warbler species in the early Pliocene or perhaps even earlier, in the late Miocene (*Proceedings of the Royal Society of London–Biology* 266:1629–1636).

Four-million-year-old stasis in passerine morphology seems remarkable for an avian order conventionally characterized as highly susceptible to rapid evolutionary change at the species level and below. Yet, in some taxa, even an ecologically critical feature such as bill structure has persisted through the wrenching environmental dynamics of the Ice Age. Emslie does not doubt that the late Pleistocene glacial/interglacial cycles led to additional diversity, but he urges ornithologists to pay more attention to passerine origins much, much longer ago.

Storm-Petrels' Voices

Is the Band-rumped Storm-Petrel actually two, three, or more species? Could some of its populations be geographically sympatric—share the same breeding grounds, even the same nesting burrows—yet remain reproductively isolated from one another? Studies of colonies in the Azores and the Galapagos Islands raise those intriguing possibilities.

Luis R. Monteiro and Robert W. Furness reported in 1998 that each of two Azorean islets has a "cool-season" and a "hot-season" breeding population, which nest in the same colony but out of phase by four to five months (*Philosophical Transactions of the Royal Society of London* 353:945–953). These seasonal groups are distinct in up to nine morphological characters, with no interchange of individuals observed between the groups. Monteiro and Furness suggested that each temporally segregated population may warrant recognition as a species, pending research on genetics and vocalizations.

Genetic evidence came in 1998 from Vicki L. Friesen, Vinay Lodha, Monteiro, and Furness (*Ostrich* 69:400–401). Birds breeding in separate seasons on the same islet in the Azores differ distinctly in mitochondrial DNA (mtDNA) control region sequence, and variations in nuclear microsatellite loci support the mtDNA findings. In contrast, birds breeding in the same season on different islets are genetically similar despite their geographic separation.

Mark Bolton offers vocal evidence in 2007 (*Ibis* 149:255–263). The two seasonal populations' calls differ significantly in acoustical structure; moreover, hot-season storm-petrels show no significant behavioral response to calls of cool-season birds. For burrow-nesting birds active at night in a colony, vocalizations are critical to breeding behavior, including pair formation and mate recognition. Bolton suggests that the lack of response could represent a pre-mating reproductive barrier between the two sympatric populations and, thus, maintain them as distinct species.

In the Galapagos, Andrea L. Smith and Friesen describe distinctions analogous to those in the Azores (*Molecular Ecology* 16:1593–1603). Wet-season and dry-season breeding populations display low yet significant differentiation in mtDNA, in five morphological variables, and in one male vocalization. Smith and Friesen consider these seasonal groups to be in early stages of divergence, not sufficiently differentiated for status as separate species.

How closely are Atlantic and Pacific populations related? Bolton's research demonstrates that hot-season breeders in the Azores do not react to calls of corresponding dry-season breeders in the Galapagos—perhaps indicating that these two groups are not only geographically distant but also biologically distinct. Indeed, Friesen, Theresa M. Burg, and Karen D. McCoy report in 2007 that Atlantic and Pacific populations differ significantly in mtDNA (*Molecular Ecology* 16:1765–1785). Friesen and her colleagues recommend further study of genetic, geographic, and behavioral factors for a fuller understanding of how the populations are related.

Band-rumped Storm-Petrel populations in the Azores may breed sympatrically and yet remain reproductively isolated from one another by nesting in separate seasons. The same phenomenon of temporal isolation evidently occurs in the Galapagos. *St. Helena, Atlantic Ocean; April 2006. © Mike Danzenbaker.*

From a North American birder's viewpoint, Band-rumped Storm-Petrels' vocal distinctions are perhaps esoteric because the birds call only at breeding colonies in the nesting season. They are silent during nonbreeding travels when North American observers encounter them off the southeastern Atlantic coast and in the Gulf of Mexico. In the eastern Pacific, this species rarely if ever ventures up the coast as far as the United States. The California Bird Records Committee accepted one sight report off San Diego in 1970, but later rescinded it because of misgivings about the identification.

Friesen and her colleagues are doing the sort of work David Ainley recommended in urging genetic studies of the Pacific Ocean's dark storm-petrels (*Birding*, January/February 2005, pp. 58–65). "There could well be some surprises...," he wrote. Perhaps the surprises emerging from those band-rumped birds in the Galapagos might spur someone toward research with dark species as well.

Shorebird Populations

Estimating shorebird populations is not a confidence-builder either for those who make the estimates or for those who read the results. Example: Solitary Sandpiper. The Canadian and the U.S. Shorebird Conservation Plans published in 2000–2001 estimate its North American population conservatively as 25,000 in the absence of reliable data. When we notice that this is only half the estimated Hudsonian Godwit population, we suspect something is amiss. No one suspects it more than the researchers who originally suggested the number. They rate the confidence level of the Solitary Sandpiper estimate as "poor"—with poor defined as "based on an educated guess".

An immense data-gathering project has revised the numbers for 75 shorebird taxa in North America, culminating in 2006 with an update by R. I. Guy Morrison and seven coauthors (*Wader Study Group Bulletin* 111:67–85). The new estimates are increases for 24 taxa, decreases for 15, and unchanged for 36.

The authors emphasize that increases more likely reflect better survey coverage and former underestimates than actual population growth. Dramatic examples are Solitary Sandpiper from 25,000 to 150,000, White-rumped Sandpiper from 400,000 to 1,120,000, and Stilt Sandpiper from 200,000 to 820,000.

In contrast, greatly decreased estimates are thought to reflect real declines: Red Knot populations in the Atlantic Flyway from 170,000 to 30,100, Semipalmated Sandpiper from 3,500,000 to 2,000,000, and Short-billed Dowitcher from 320,000 to 153,000.

Morrison and his colleagues lament that accuracy remains low for many species. The U.S. Plan originally rated confidence as "poor" or "low" for 62.5 percent of estimates, and the new study improves that proportion only to 57 percent. The Plan's editors, Stephen Brown, Catherine Hickey, Brian Harrington, and Robert Gill, expressed a "compelling and urgent" need for better monitoring of shorebird numbers. Morrison's team echoes the call with a comment that obtaining more accurate data is expensive and challenging, but that "increased efforts need to be made."

New data on North American shorebirds point to much higher population sizes than previously estimated for some species but to much lower sizes than previous estimates for others. **White-rumped Sandpiper** numbers are now thought to be three times as numerous as old, less comprehensive, data indicated. *Ashtabula County, Ohio; May 2006. © Matthew Studebaker.*

One recent effort is a survey in the Arctic National Wildlife Refuge conducted by Manomet Center for Conservation Sciences and the U.S. Fish & Wildlife Service. The site is 674,000 hectares on the coastal plain where Congress ordered evaluations of fish and wildlife resources—and of potential oil and gas reserves. It is a shorebird paradise. Brown and six coauthors report in 2007 that fourteen species were confirmed breeding there (*Condor* 109:1–14). Six of them are classified as species of high-priority conservation concern: American Golden-Plover, Whimbrel, Ruddy Turnstone, Western Sandpiper, Dunlin, and Buff-breasted Sandpiper. The others are Semipalmated Plover, Semipalmated Sandpiper, Baird's Sandpiper, Pectoral Sandpiper, Stilt Sandpiper, Long-billed Dowitcher, Red-necked Phalarope, and Red Phalarope.

The authors estimate that 230,000 shorebirds were present. In fact, this area only half the size of Connecticut hosts 13 percent of the continent's total estimated population of Pectoral Sandpipers, 8 percent of American Golden-Plovers, and 5 percent of Ruddy Turnstones. Highest densities of breeding species are in wetlands along the coast—unfortunately, the locations most likely to be targeted for oil and gas development. Brown and his coauthors urge consideration of these habitats' importance when decisions about petroleum development are made.