by Paul Hess

Foxes and Birds: An Aleutian Saga

Two drastically different ecological categories have divided the Aleutian Islands: fox-free, with seabirds unimaginably abundant; and fox-infested, with once-thriving seabird colonies almost gone. Many species of marine birds have struggled for 250 years as pivotal links in an extraordinary four-step process by which arctic foxes have transformed Aleutian ecosystems from lush grasslands into tundra. Donald A. Croll, John L. Maron, James A. Estes, Eric M. Danner, and G. Vernon Byrd reported this previously-unexplained ecological pathway in 2005 (*Science* 307:1959–1961). Step one was the introduction of arctic foxes to more than 400 islands between the mid-1700s and the mid-1930s for fur-farming. Step two was the foxes' decimation of the islands' birds—easy meals because the birds had never faced native terrestrial predators and, thus, were not adapted to cope with them. Step three was a resulting collapse in the supply of nutrient-rich guano that fertilized the grasses. The final step was a nutrient-deprived plant community able to support little more than tundra vegetation. Croll and his co-authors estimated that the reduced seabird abundance translated to a 98% reduction in annual guano input to the vegetation—a testament to the enormity of the avian decline.

What determines population status of the **Whiskered Auklet** and other bird species that breed on the Aleutians? The presence or absence of introduced arctic foxes is a major factor. And the effects of fox predation have far-reaching ecosystem-level consequences: When seabird populations crash, there is a corresponding loss of nutrient-rich guano, which results in a dramatic conversion of the plant community from lush grasslands to tundra. *Iony Island, Sea of Okhotsk, Russia; June 2005. © Don Doolittle.*

While the authors' purpose was to demonstrate the entire ecological cascade in biogeochemical detail, they also focused new attention on the power of introduced predators to destroy bird populations. How powerful? The investigators found densities of roughly 1,700 seabirds per hectare on fox-free islands but only about 22 per hectare on islands with foxes. A prime example cited in the report is Whiskered Auklet. This little alcid was undoubtedly abundant on its Aleutian breeding islands in the late 1800s, but by 1940 the population was estimated at only a few thousand. Waterfowl, too, have been victims of fox predation. Most famous is the Aleutian subspecies of Canada Goose, now classified as Aleutian Cackling Goose (*Branta hutchinsii leucopareia*). It was thought to be extinct until the discovery of a tiny remnant population on remote Buldir Island in 1962. Five years later, it was officially listed as endangered under the U. S. Endangered Species Preservation Act, and it remained listed under the stronger Endangered Species Act of 1973. Many more species declined severely, especially burrow nesters such as Fork-tailed and Leach's Storm-Petrels, Ancient Murrelet, Cassin's Auklet, and Tufted Puffin, which were easy targets in their burrows. Landbirds were affected as well, including Rock Ptarmigan and possibly Aleutian Song Sparrow (race *maxima*) and other passerines (G. V. Byrd, personal communication).

There is a happy ending for the birds (as well as signs that grasses are returning at some locations). Foxes ate themselves to death on many small islands by extirpating their food supply, but on larger islands where they persisted a turnabout came just in time to save the dwindling prey. It was an eradication effort by the Alaska Maritime National Wildlife Refuge, which encompasses most of the Aleutians. The project began on Amchitka in 1949, and foxes were eliminated from 39 islands by 2005 (S. E. Ebbert, personal communication). Today, these introduced predators remain in the refuge only on Shemya, Tanaga, Kanaga, Atka, and Chuginadak islands. Where foxes were eradicated, bird populations began to recover quickly. By the end of the 20th Century, Whiskered Auklets were estimated to number more than 116,000 on the Aleutians, Jeffrey C. Williams, Byrd, and Nikolai B. Konyukhov reported in

2003 (*Marine Ornithology* 31:175–180). The Aleutian goose, whose winter numbers had plunged to 790 in 1975, rebounded to more than 30,000 by 1999 and was removed from the endangered list in 2001. Today, there are 70,000 (Byrd, personal communication). Other species that have increased substantially in the Aleutians since fox removal include Green-winged Teal, Mallard, Common Eider, Red-breasted Merganser, Red-throated Loon, the ptarmigan, the two storm-petrels, Black Oystercatcher, Parasitic Jaeger, Glaucous-winged Gull, Pigeon Guillemot, and the puffin (Byrd, personal communication). The subtitle of the *Marine Ornithology* paper summarized the 250-year-long saga of destruction and recovery in a few cogent words: "Foxes, Humans, and How to Right a Wrong".

Kleptoparasitism—stealing food—has been documented in a number of bird species, including the **Roseate Tern**. Does crime pay for Roseates? Yes—kleptoparasitic Roseate Terns in Connecticut fledge 50% more young than do non-kleptoparasitic parents. *Seavey Island, New Hampshire; 3 July 2003.* *© Garth McElroy.*

Piracy Profits Roseate Terns

When we think of avian piracy, rapacious attacks by frigatebirds, skuas, and jaegers come first to mind. But Roseate Terns? Indeed, small numbers of these exquisitely buoyant fliers are habitual kleptoparasites—food robbers. The practice brings a big payoff in parental success. Piratic parents fledge significantly more chicks than "honest" parents. David A. Shealer, Jeffrey A. Spendelow, Jeff S. Hatfield, and Ian C. T. Nisbet reported the finding in 2005 (*Behavioral Ecology* 16:371–376) after a 10-year study at a colony on Falkner Island, Connecticut, where 100–180 pairs of Roseate Terns and 3,300–4,400 pairs of Common Terns nested.

The authors observed only 10 Roseate Terns regularly stealing fish from other terns of both species to feed their own chicks. The vast majority made no attempts at theft—perhaps a surprising fact, considering that kleptoparasitism was associated with superior growth rates in chicks and consistently higher breeding productivity by their parents. Roseate Terns have two chicks, and the study assessed growth performance of the first and the second hatchlings separately by three measures: body mass on the third day after hatching, growth rate during the next nine days when chicks grew most rapidly, and average mass of chicks at fledging. Growth was an important predictor of survival. Both the first and the second chicks from nests with a parental pirate grew larger and faster than the chicks from nests with no parasitic parent. Over the 10-year period, an average of 1.2 young birds fledged from nests with a thieving parent, compared to an average of only 0.8 from nests with no parasitic parent. The difference primarily reflected survival of second hatchlings.

The reason for the better growth was clear. Shealer and Spendelow had shown in 2002 that kleptoparasites delivered 2–13 fish per hour to their young, but no "honest" parents sustained a rate of more than 1.2 fish per hour (*Waterbirds* 25:436–441). Thieves chose from among four methods. Most often, a tern patrolled over the island until it spotted a bird returning to the colony with a fish in its bill, and then swooped down to snatch the fish. Sometimes a pirate scanned from an elevated perch and made a brief flying lunge to grab fish from a returning bird that passed it closely. Sometimes the robber stood between chicks and a parent that had landed with a fish; when the parent attempted to feed the chicks, the thief lunged to grab the food. The fourth tactic was strikingly sly. A female would repeatedly beg and adopt a submissive posture toward a male (not her mate) that was bringing in a fish for his young. Such female behavior typically invites courtship feeding and copulation. Using the tactic for theft instead, the female would allow the stranger to mount her, and then suddenly she would reach up, grab the fish from the startled male, and fly off to feed her chicks.

Shealer and his three coauthors wondered why only three to five percent of Roseate Terns were habitual robbers, despite the apparent substantial increase in productivity enabled by piracy. The behavior did not appear to be

inherited; none of 29 chicks reared by kleptoparasitic parents was known to be parasitic. Nor was any phenotypic character evident that might have predisposed certain individuals to be thieves. Whatever the basis, for at least a few Roseate Terns, crime does seem to pay.

Another Wren for *Troglodytes*?

The House Wren receives the longest taxonomic notes of any species in the current (1998) edition of the American Ornithologists' Union *Check-list*. Besides nomenclatorial issues involving its specific name, *aedon*, the notes discuss five unresolved "groups" under the House Wren's taxonomic umbrella, each group possibly warranting species status. The AOU says tersely, "Species limits within this complex are not well understood"—a statement that usually attracts birders' attention because it could imply splits in the future. An issue less significant in a birding context, but notable from the viewpoint of classification, is that the House Wren's genus, *Troglodytes*, has unsettled limits as well.

For instance, should Winter Wren remain in *Troglodytes*? No, it should not, said Nathan H. Rice, A. Townsend Peterson, and Griselda Escalona-Segura in 1999. After a phylogenetic analysis based on mitochondrial DNA sequences in 10 *Troglodytes* species, they suggested that Winter Wren be separated into a genus of its own (*Condor* 101:446–451). A different revision proposed by Sergei V. Drovetski and seven coauthors in 2004 would split Winter Wren into as many as six species, including one in eastern and one in western North America (*Proceedings of the Royal Society of London–B* 271:545–551). Based on the Drovetski team's phylogenetic analysis, Pierre-André Crochet asserted in 2005 that the western North American populations "certainly deserve species status" (*Birding World* 18:2).

The Winter Wren proposals will undoubtedly require extensive discussion by the AOU, but another, simpler change proposed for *Troglodytes* in 2005 may have a chance of swifter acceptance. Juan E. Martínez Gómez, Brian R. Barber, and Peterson recommended that Socorro Wren (*Thryomanes sissonii*) be moved from its current place in the Bewick's Wren genus to the House Wren genus (*Auk* 122:50–56). Socorro Wren, endemic to Socorro Island, off the tip of Baja California, has been a sort of taxonomic waif, shuttled from genus to genus for almost a century and a half since it was first described. Most taxonomists have linked it to Bewick's Wren. In fact, Ernst Mayr and Lester L. Short went so far as to suggest in *Species Taxa of North American Birds* (1970) that these two wrens might be conspecific. Steve N. G. Howell and Sophie Webb expressed the opposite view forcefully in *A Guide to the Birds of Mexico and Northern Central America* (1995): "Traditionally placed in the genus *Thryomanes*, this species is quite obviously a House Wren in its manners, song, plumage, etc."

Martínez Gómez and his colleagues unequivocally expressed the latter view after analyzing 516 base pairs of mtDNA sequences in the Socorro Wren and 14 other wren taxa. Every analytical test of the genetic data pointed to the same conclusion: Socorro Wren is not closely related to Bewick's Wren. On the contrary, it is nested phylogenetically within *Troglodytes* and is very closely related to three taxa in this genus that are considered by some ornithologists to be separate species: Northern House Wren (*T. aedon*), the widespread form in North America; Brown-throated Wren (*T. brunneicollis*) in southeastern Arizona and montane Mexico, and Southern House Wren (*T. musculus*) from Mexico through Central and South America. The AOU comments in its current *Check-list* that, *contra* Mayr and Short, the Socorro Wren "may be better placed in *Troglodytes* … but no analysis has been published." Perhaps this new analysis will prompt the genus-to-genus transfer.

The wren genus *Troglodytes* is taxonomically unresolved. For example, both of the widespread species in North America—the Winter and House Wrens—may involve multiple species. There is also the matter of the **Socorro Wren**, currently placed with the Bewick's Wren in *Thryomanes* but apparently more closely related to the House Wren in *Troglodytes*. *Isla Socorro, Mexico; date unknown. © A. M. Sada / VIREO.*

Weather Effects on Productivity

We all know that weather influences birds' breeding productivity, but few examples are so dramatic as a collapse in nesting success among four passerine species in San Diego County, California, in 2002. Wrentit, Spotted Towhee, California Towhee, and Rufous-crowned Sparrow had a near-total nesting failure in the driest year there in 150 years. Meanwhile, halfway across the continent in 2002, Yellow Warblers at the Delta Marsh in southern Manitoba were emerging from a decade of fluctuations in annual productivity corresponding to climatic effects of the El Niño / Southern Oscillation (ENSO). Two papers reporting those cases in 2005 were linked by a similar concern. The authors noted that some models of global climate change predict more frequent and more extreme climatic fluctuations. If so, will breeding success in the good years be sufficient to outweigh failure in the poor ones?

In California, Douglas T. Bolger, Michael A. Patten, and David C. Bostock compared the failure in 2002 with productivity in 2001 when rainfall was about average (*Oecologia* 142:398–406). Samples of each species ranged from 30 to 47 pairs in each year. The year-to-year contrast could scarcely have been greater. In 2001, 88.4 percent of observed pairs attempted at least one clutch, 47.7 percent of the nests fledged young, and productivity averaged 2.4 fledglings per pair among all four species. In parched 2002, only 6.7 percent of pairs even attempted a clutch, only 1.8 percent of pairs fledged young, and the average output was a meager 0.07 fledglings per pair. Rufous-crowned Sparrow data for 2002 were combined with productivity and rainfall data from the same sites in 1997–1999. The number of fledglings was strongly correlated with annual variation in rainfall. What was the connection for all of those species? Evidently, food. During the disastrously dry 2002 breeding season, the birds' vital resources of grasshoppers, beetles, caterpillars, and craneflies were much lower than in 2001. Bolger and his coauthors said bluntly, "Any change in climate that would increase the frequency of extreme dry conditions would likely endanger populations of these species."

In Manitoba, Daniel F. Mazerolle, Kevin W. Dufour, Keith A. Hobson, and Heidi E. den Haan found Yellow Warbler productivity in 1992–2001 to be associated with local climatic conditions resulting from ENSO patterns (*Journal of Avian Biology* 36:155–163). During El Niño periods, winters and springs in the Canadian prairies are warmer and drier than average—conditions seemingly beneficial for breeding. But productivity in those years, as indicated by capture rates of hatching-year birds, was relatively low. Conversely, during La Niña periods at the other ENSO extreme, the weather is colder and wetter—conditions seemingly less than optimal. Yet production of young in those years was relatively greater. Why the paradox? Potentially, food. Warmer-than-average springs during El Niño periods cause earlier hatches of arthropods. When that happens, the peak abundance of food could be out of synchrony with the period of greatest need for feeding young, the authors speculated. Another speculation was that harmful environmental effects related to El Niño in the warblers' winter range might lead to poorer body condition in spring and, consequently, to lower reproductive success. The researchers' eight-year sample of banded Yellow Warblers did not support the latter explanation. Whatever the reason, Mazerolle and his coworkers concluded that more-frequent El Niños resulting from global climate change "could negatively affect populations of Yellow Warblers and other Neotropical migrants breeding in this region."

Productivity, measured as fledglings per breeding pair, crashed for **California Towhee** and other southern California passerines in 2002. The reason: severe drought. Several climate change models predict an increasing frequency of extreme weather events and fluctuations, with possible deleterious effects on long-term population health in many bird species. *San Diego County, California; February 1999. © Brian E. Small.*