THE DARK STORM-PETRELS OF THE EASTERN NORTH PACIFIC

SPECIATION, CURRENT STATUS, AND FUTURE PROSPECTS

David Ainley
H.T. Harvey & Associates
3150 Almaden Expressway - Suite 145
San Jose CA 95118
dainley@penguinscience.com

These bleak-looking desert islands are home to huge colonies of dark storm-petrels that probably total millions of birds—Leach's, Black, and Least in decreasing abundance. Leach's nests most commonly on the flatter and lower ground, where birds can dig burrows; Black nests most commonly on the rocky slopes, in crevices and burrows; Least nests most commonly in scree and rock piles around the lower slopes. *San Benito Islands, Baja California, Mexico; 4 July 1999. © Steve N. G. Howell.*

In California one has only to take a small boat a little ways out of Moss Landing or Monterey—row one, even, as Rollo Beck, a giant in marine ornithology, did in the early years of the 20th century—to find oneself immersed in storm-petrels: Ashy, Black, and occasional individuals of several other species. This scenario contrasts greatly with the effort required to see storm-petrels in most other places on the planet. On the North American East Coast where I began my days, storm-petrels are numbered—as they are in most places—among that almost-mythical group of birds which most of us only dream of seeing, and only after a day's trip out of harbor to the deep-water, pelagic habitat they call home. With this image implanted deep in my psyche long ago, there is no way that I can tire of seeing storm-petrels at sea, even having lived on the central California coast now for 30 years and seeing the birds regularly. To me, the excitement of a deep-sea voyage—and I've managed to make a few of these—is generated by the chance to be in the "true" storm-petrel realm, where winds and huge waves remind us of why most humans usually stay close to land.

Among my favorite storm-petrels are the all-dark ones that occur off the West Coast of North America. They are my favorites because there are so many species of them, and I am intrigued about why there should be so many in such a small area of the ocean. In order of ascending body size, they are as follows: Least (13.5–15.0 cm), Ashy (18.5–19.5 cm), the dark populations of Leach's (subspecies *chapmani*, *socorroensis*, and others; 16.5–20.0 cm), Markham's (*Oceanodroma markhami*; 21.5–23.0 cm), and Black (21.5–23.0 cm). Another large species that occurred in this area was the Guadalupe Storm-Petrel (*O. guadalupensis*; 23.0 cm), but it is extinct and had a white rump. (Also present is the all-gray Fork-tailed Storm-Petrel, but it is not all-dark like the others.) The big question, again, is: How can so many storm-petrel species co-exist in the relatively small stretch of ocean from Point Conception (near Santa Barbara) to the Gulf of California? And why so many dark ones?

Besides their all-dark plumages, the common elements in the natural history of these dark storm-petrels, thinking on a broad scale, are as follows: (1) They nest among the rocks of talus slopes on xeric (desert-like) islands, where the soil is non-existent or too crumbly for much burrow excavation (see Ainley 1995, Huntington et al. 1996, Everett and Ainley 2001); and (2) The ocean in the eastern Pacific is deep within a few kilometers of land and richly productive inshore, but with a steep productivity gradient that brings one quickly to unproductive waters just a little farther out to sea (Ainley and Boekelheide 1990). Both of these sets of conditions, I think, have contributed to the impressive storm-petrel speciation that has occurred here. What it comes down to is the following: Dividing up a breeding habitat that does not allow much remodeling—rock crevices—is best accomplished by fitting individuals through the cracks appropriate to their size. (Recall that all storm-petrels nest in subterranean burrows or cavities; and in the temperate and polar regions, in particular, where soil formation is rapid, all storm-petrels are burrowers.)

Moreover, in the eastern Pacific, where there is a definite lack of nesting habitat, there is intense competition among

Tubenoses blown well inland are essentially doomed, with the result that several species appear to have evolved dispersal patterns to prevent them from encountering hurricanes and other powerful storms. For example, **Least Storm-Petrel** movements in late summer and autumn seem to be timed so as to avoid hurricanes. The hurricane-swept individual shown here was unlucky, however, and got swept all the way to Lake Havasu, Arizona, where it probably perished. *September 1997. © Jim Burns.*

seabirds for nesting space (Ainley and Boekelheide 1990). In this region, sea-floor tectonic plates slide beneath the continental plates, in the process gobbling up any islands on which ground-nesting birds might nest free of mammalian predators. To avoid avian predators, small seabirds have taken to nesting in cavities or burrows. Therefore, the fine division of rocky crevices among small, burrowing seabirds has become an important strategy, likely contributing to body-size evolution. In fact, nesting space is so limited in this region, as exemplified by the situation in the Gulf of California, that storm-petrels share precious rock cavities with the likes of tarantulas, Xantus's and Craveri's Murrelets, and fish-eating bats (*Pizonyx vivesi*). Finally, the highly stratified and productive ocean provides a progression of marine communities and foraging habitats. Such stratification would encourage a progression in body and bill size, which in birds is reflected in prey size, resulting in the division of resources available within a storm-petrel's breeding-season foraging range.

Here's another matter to ponder: During the multiple "ice ages" of the past several million years, sea levels would have been about 120 meters lower than they are now, in this current "interglacial" period. Basically, there was no continental shelf, meaning that all of the shelf-and-slope-species that we know today were all sandwiched in an incredibly narrow zone, with the continental slope just off the shore. The available islands for breeding were the few peaks that we call seamounts today. Talk about competition and ecological bottlenecks! Human observations have come several thousand years too late for us to be able to figure out what was going on. Those must have been exciting times!

Why storm-petrels that frequent close-to-colony waters of low to middle latitudes in the Pacific (i.e., the entire genus *Oceanodroma*) tend to be completely dark is another interesting question. Finding common patterns in seabird plumage patterns leads one to way too many exceptions, and thus for this question I would hazard even fewer suppositions to generate an answer. With regard to the storm-petrels found off the West Coast of North America, no clues jump out at me until someone, some day, conducts a proper genetic study of the North and Central Pacific storm-petrels. Besides the species we are discussing, three other dark storm-petrels (Swinhoe's, Matsudaira's, and Tristam's) occur in the western Pacific and would have to be part of the investigation. In considering all of these dark storm-petrels, it would be essential to know about their "relatedness" or about the "genetic distances"

among them before further contemplating this question. There could well be some surprises, as was found recently in a genetic analysis of the "black-and-white shearwaters" (Austin et al. 2004). Specifically: Among several patterns revealed for the *Puffinus assimilis* / *P. lherminieri* complex (Little and Audubon's Shearwaters), genetic differentiation among and within islands and island-groups was largely inconsistent with current nomenclature and taxonomy for the currently recognized subspecies in this complex.

Distinguishing Among Species

The differences in size among these eastern Pacific all-dark storm-petrels is the basic character needed to tell them apart, the difference being clearly obvious once one has seen all or most of them at least once. But there are exceptions. Markham's and Black are distinctly larger than the others but are very difficult to distinguish on the wing, given their complete overlap in size and the fact that the flight characteristics of storm-petrels of any kind vary greatly with wind speed. Wind speed itself varies radically over the ocean, especially in the eastern Pacific, where wind is what is responsible for the existence of the California Current and all its complex spatial and temporal variation. In calm to light winds, the Markham's Storm-Petrel—a rarity in the California Current region—exhibits slightly shallower wingbeats with slightly longer glides than does the Black. Once wind speed becomes a bit uncomfortable, if you're in a small boat, distinguishing the flight characteristics becomes problematic. The slightly deeper fork of the tail (difficult to see unless close) and the slightly longer buffy bar (relatively easy to distinguish) from the elbow out to the carpal joint (leading edge of wing) separate Markham's from Black. Markham's, which nests in Peru, is extremely rare in the waters off southern Baja California; thus, north of Cabo San Lucas, if you think you've seen a Markham's (not yet on the California or ABA checklists), you have to be sure to have gotten a very good look at the bird. In regard to the amount of gliding in flight, Leach's does a bit less of it than do Black and Markham's, plus Leach's bounces around a bit more; meanwhile, Ashy and Least hardly ever glide, except in high winds (>30 knots). In high winds, storm-petrels don't need to flap at all, unless flying directly into the wind.

Another problem involves distinguishing between Ashy Storm-Petrel and dark individuals of the *socorroensis* ("Socorro Storm-Petrel") race of the Leach's Storm-Petrel, as they are about the same size. The Socorro has characteristic Leach's-like flight and a more

The **Black Storm-Petrel** is the largest of the dark storm-petrels that occur regularly off the U.S. West Coast. What are some of the factors that have led to the diversity of dark storm-petrels in the eastern Pacific (including waters off Mexico)? Habitat heterogeneity—everything from ocean productivity gradients to variation in nest-site availability—appears to have played a critical role. *Monterey Bay, California; 5 September 2004. © Mike Danzenbaker.*

Compared to the other dark storm-petrels of the eastern North Pacific, the **Ashy** (right) is intermediate in size and shape. It is an outlier, however, with regard to various aspects of its phenology: The species exhibits essentially no dispersal at all, and its breeding season is very long. *Monterey Bay, California; 12 September 2004. © Mike Danzenbaker.*

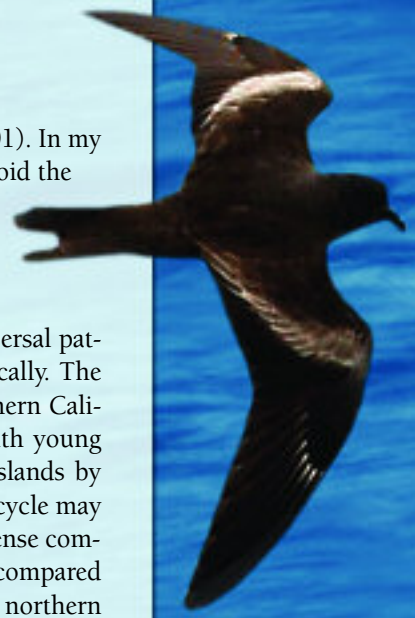
robust carpal bar—the best characters for separation from Ashy. The Socorro also has a more-deeply-forked tail.

Movements

Among the dark storm-petrels of the eastern North Pacific, the dark Leach's is the most divergent ecologically. Like the white-rumped individuals, these dark birds are found in the relatively unproductive waters that lie in the outer or western portions of the California Current (or beyond), except, of course, when they are commuting between those waters and their nesting islands, all of which occur close to (indeed, within sight of) mainland shores. However, most of that commuting is done in the late evening or by dark, as these birds don't arrive at nesting colonies until several hours after sunset (Ainley et al. 1974). Thus, without night-vision goggles, seeing a dark Leach's near to shore would be unusual. This pattern is quite unlike what is seen with the other dark storm-petrels, which forage within a few hours of the nesting colonies and can be found cavorting in the air above nest sites within an hour of sundown. In contrast, light-rumped Leach's tend to occur even farther offshore than do the dark individuals (Howell and Webb 1995). Leach's Storm-Petrels (including Socorro and Chapman's) off Mexico migrate in autumn to equatorial waters; thus, they would be mostly absent from California waters during the late autumn into the winter (Huntington et al. 1996). The other dark storm-petrels can be found year-round in California and Baja California waters, although an unknown proportion of the Black Storm-Petrel population disperses south to mix with Markham's Storm-Petrels in the Gulf of Panama and northern South America, thus making matters more difficult for observers there (Everett and Ainley 2001).

Above: On this **dark Leach's Storm-Petrel**, note the relatively shallow tail fork, compared to Black and Ashy Storm-Petrels. *Isla San Benito Oeste, Baja California, Mexico; 3 July 1999. © Steve N. G. Howell.*
Below: In this comparison of **Least** (left), **dark Leach's** (middle), and **Black** (right) Storm-Petrels, note that Black, and to a lesser extent Leach's, can show whitish bases to the primary shafts. *Isla San Benito Oeste, Baja California, Mexico; 3 July 1999. © Steve N. G. Howell.*

Black and Least Storm-Petrels vacate the waters of the Gulf of California and southern Baja California during the autumn and winter. Some move north and others move south. This is a pattern shared by Black-vented Shearwaters and Craveri's Murrelets, whose



Although not yet recorded from the ABA Area, the large **Markham's Storm-Petrel** should be looked for off the U.S. West Coast. To distinguish this species from the similar Black Storm-Petrel, note the Markham's shallower wing-beats, longer glides, more-deeply-forked tail (a minor mark), and slightly longer upperwing bar. *Eastern tropical Pacific Ocean; October 2003. © Hadoram Shirihai.*

breeding range overlaps that of these two storm-petrels (Everett and Ainley 2001). In my opinion, these four species have opted for this dispersal strategy in order to avoid the hurricanes that commonly move through the waters of the Gulf and vicinity, during the late summer and autumn. Otherwise, all would suffer the fate of the stragglers brought by hurricanes to places like the Salton Sea, well inland from the ocean.

Alone in this group of storm-petrels is the Ashy, at least in terms of its dispersal patterns (Ainley 1995). In fact, it does not really disperse at all, except very locally. The Ashy Storm-Petrel is endemic to the waters stretching from southern to northern California. Moreover, the Ashy population has an extended breeding season, with young birds fledging from late summer to late winter; pre-breeding visitation of islands by adults often begins in February. Their sedentary nature and lengthy breeding cycle may have to do with the even-greater paucity of islands—combined with more-intense competition for nesting space—in the northern portion of the California Current compared to the more-southern reaches of the current. Ashy Storm-Petrels nest in the northern Channel Islands north to the Farallon Islands, with some tiny populations nesting on various offshore rocks in between.

Movement patterns of storm-petrels in the eastern North Pacific are affected by large-scale ecological phenomena. Global warming needs to be taken seriously, of course, as it is causing major problems for Earth's ecosystems, but one sidelight has been the greater northward post-breeding dispersal of Black and Least Storm-Petrels as California Current waters have warmed (Ainley et al. 1995, Ainley and Divoky 2001). Not long ago, Black Storm-Petrels were found in large numbers as far north as Monterey Bay only during El Niño events (every 4 or 5 years); Least Storm-Petrels occurred that far north only during the most-intense El Niño years, e.g., 1957, 1983, 1997 (Ainley 1976, Ainley et al. 1995; personal observation). During El Niño events, waters become warm and unproductive—more so in the southern California Current than in the north. Because of El Niño, not only do seabirds forego breeding, but they also disperse more widely, perhaps in search of food. However, over a longer time span—during the past decade—Black Storm-Petrels have increased their frequency of visitation to Monterey Bay and farther north and now do so pretty much yearly in the autumn (NCCOS 2003). This changing pattern is related to increasing temperatures of the California Current, exacerbated by the warm phase (1976–1998) of the Pacific Decadal Oscillation, or PDO. The PDO, which is driven by variation in the strength and position of the Aleutian Low Pressure System, shifted to its cold phase around 2000 (Schwing et al. 2002). Except for the fact of global warming, with colder waters we should expect to be seeing *fewer* Black and Least Storm-Petrels as far north as Monterey Bay. It is too soon to know for sure whether this is the case, as a few Blacks have continued to visit in the north.

What Does the Future Hold?

The story of the Guadalupe Storm-Petrel really says a great deal about the factors that may or may not conspire to insure the continued existence of a diverse group of storm-petrels in the eastern North Pacific. Mainly, it has to do with the introduction of exotic species to the very few islands that occur in the California Current region. Because of the introduction of goats and cats to Guadalupe Island during the

late 1800s, the Guadalupe Storm-Petrel was driven to extinction in the early part of the 20th century (Everett and Anderson 1991). The goats destroyed the protective vegetation, and the cats ate the storm-petrels, which were even more exposed in their nesting habitat. The Guadalupe Storm-Petrel was confined to breeding on the main island, where it nested in burrows and was excluded, I suspect, from the offshore islets by the scarcity of large nesting cavities. The offshore islets are where the smaller storm-petrels today can be found nesting. The cats likely wiped out any smaller storm-petrels nesting on the main island as well, but the cats didn't make it to the offshore islets.

Mammals were introduced both purposely and inadvertently by sailors and fishermen to many other islands along the California and Baja California coasts. It is likely that storm-petrel and other seabird populations were affected, but without pre-introduction surveys, it is impossible to know the level of impact. In the past decade, active measures have been undertaken to remove exotic mammals from various islands (McChesney and Tershy 1998). An example is the removal of rats from Anacapa Island, in the Channel Islands, during the past few years. Depending on whether storm-petrels respond by re-colonizing the island, we may have the means by which to gauge the level of the former impact in a sort of reverse scenario. For example, when European hares (*Oryctolagus cuniculus*) were removed from the Farallon Islands in 1974, the population of burrow-inhabiting Rhinoceros Auklets, which use cavities of about the same size that the hare does, grew dramatically (Ainley and Boekelheide 1990). The supposition that the hares were having an impact was proved by their removal.

Exotic species destructive to island ecosystems of the California Current region are not just animals. Ashy Storm-Petrel populations on the Farallon Islands may be suffering from the grasses and other plants brought to the island in the feed of stock animals. Not being forceful burrowers, the storm-petrels may have difficulty penetrating the surface to reach the crevices in the rocky talus, owing to the mat of grasses and the soil it is generating. The bigger crevices are occupied by the larger, more aggressive, cavity-nesting alcids, which hold sway over all but the very slimmest of cracks.

Although not perhaps the most scenic setting on the planet, this south-facing talus slope of Lighthouse Hill on Southeast Farallon Island is critical to the Ashy Storm-Petrel. In fact, ca. 10% of the world's population nests within the view shown here. © *David Ainley.*

Research Priorities

Other than the genetic study proposed above (pp. 60–61), prioritizing research is difficult, as storm-petrels are sensitive to human activities and handling. Popula-

tion monitoring, through carefully conducted mist-netting efforts or by at-sea surveys (Clarke et al. 2003), would be a worthwhile activity, especially after predator or exotic plant removal from islands. A far greater priority, in terms of management, is removal of predators and exotic plants.

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