THE POTENTIAL IDENTIFICATION AND DISTRIBUTION OF AINLEY'S STORM-PETREL AT SEA BY TIMING OF MOLT

DESMOND E. SIEBURTH, 2644 Hermosa Avenue, Montrose, California 91020; sieburth@stanford.edu

RYAN TERRILL, Moore Laboratory of Zoology, Occidental College, 1600 Campus Road, Los Angeles, California 90041

PETER PYLE, The Institute for Bird Populations, P.O. Box 518, Petaluma, California 94953

ABSTRACT: In 2016, the American Ornithologists' Union split the Leach's Storm-Petrel into three species: Leach's Storm-Petrel (*Hydrobates leucorhous*), Townsend's Storm-Petrel (*H. soccoroensis*), and Ainley's Storm-Petrel (*H. cheimomnestes*). Leach's breeds around the Northern Hemisphere during the boreal summer, while both Townsend's and Ainley's breed on islets off Guadalupe Island, Mexico, the former in summer and the latter in winter. Although morphological differences between Leach's and Ainley's are slight at best, we hypothesized that the difference in breeding schedule may result in a difference between the species in molt schedule, allowing identification of some birds at sea. We examined 528 specimens and hundreds of photographs for molt of primaries, aging each bird by its having juvenile vs. basic flight feathers and the presence of molt clines, and scoring molt by the number of primaries replaced. Using threshold models, we identified ten birds whose timing of molt suggested Ainley's, most occurring off central-to-southern Mexico. In Leach's and/or Townsend's storm-petrels, primaries were being replaced in the second prebasic molt from 21 February (p2) to 15 December (p8) and in the definitive prebasic molt from 24 October (p3) to 22 February (p8). In the smaller sample of Ainley's, these dates were 23 November (p6) to 22 February (p8) and 11 June (p3) to 7 November (p8), respectively. Thus the timing of molt may help identify Ainley's at sea, important for the management of this vulnerable species. Genetic analysis of the specimens may confirm our identifications and the applicability of our technique.

As currently defined by the American Ornithological Society (Chesser et al. 2016), the Leach's Storm-Petrel (*Hydrobates leucorhous*) complex consists of three species: Leach's (*H. leucorhous*), Townsend's (*H. soccoroensis*), and Ainley's (*H. cheimomnestes*) storm-petrels, the last initially described as a subspecies by Ainley (1980). This split was recommended by Howell et al. (2010a) and, at least with respect to birds breeding around Guadalupe Island, Mexico, is supported by genetic evidence (Taylor et al. 2017, Wallace et al. 2017). Leach's Storm-Petrel breeds widely around the Northern Hemisphere, in the eastern Pacific from the Aleutian Islands, Alaska, to San Benito Island, Mexico. As now defined it consists of two subspecies, *H. l. leucorhous*, breeding through most of the range (including the Atlantic Ocean), and *H. l. chapmani*, breeding on the Coronado and San Benito Islands, Mexico (Ainley 1980, Howell et al. 2010a, Howell 2012, Pollet et al. 2021, Clements et al. 2022). The breeding range of both Townsend's and Ainley's storm-petrels is restricted to islets off Guadalupe Island, where the former breeds in summer (May to September) and the latter in winter (October to April). In the Pacific, the pelagic nonbreeding range of the Leach's Storm-Petrel complex extends from the North Pacific Ocean to equatorial latitudes, but the ranges of the component species are not well known (Halpin et al. 2018, Kirwan 2020, Pollet et al. 2021). As far as known, Ainley's Storm-Petrel is morphologically indistinguishable from Leach's Storm-Petrel (Pyle 2008, Howell et al. 2010a, Howell 2012) and has heretofore not been identifiable as specimens or in photographs taken away from the breeding grounds. To our knowledge, no records of Ainley's Storm-Petrel away from Guadalupe Island have been confirmed. The pelagic distribution, ecology, and conservation requirements of this localized and potentially endangered species thus remain completely unknown.

In the definitive prebasic molt of adult Leach's and Townsend's storm-petrels, the primaries are replaced between July and April. In first-year birds undergoing the second prebasic molt they are replaced between May and December (Pyle 2008). The majority of adults and first-year birds molt from October to December (Spear and Ainley 2007). A second prebasic molt earlier than the definitive prebasic molt is common in bird species that do not breed as yearlings, including the Procellariiformes (Pyle 2008:249). Because Ainley's Storm-Petrel breeds in winter, Pyle (2008) and Howell et al. (2010a) hypothesized that it may molt on a schedule seasonally opposite that of Leach's Storm-Petrel, in which case adults should molt primaries between February and November and the second prebasic molt should occur between December and June. These potential species-specific differences in molt timing have yet to be confirmed but could prove useful for identifying birds at sea.

On the basis of specimens and photographs of storm-petrels taken in the Pacific Ocean, we examined whether or not reproductive asynchrony in these species could lead to asynchrony in molt timing and thus aid in field identification and our understanding of the nonbreeding range of Ainley's Storm-Petrel. We used double-hinge threshold models and box-and-whisker plots to assess the timing of the second and definitive prebasic molts and estimated the duration and phenology of the molt of Leach's and Townsend's storm-petrels combined, in order to find phenological outliers that may represent records of Ainley's Storm-Petrel at sea.

METHODS

We examined 528 specimens within the Leach's Storm-Petrel complex housed at the California Academy of Sciences (CAS), San Francisco; the Museum of Vertebrate Zoology (MVZ), University of California, Berkeley; the Natural History Museum of Los Angeles County (LACM), Los Angeles; the San Diego Natural History Museum (SDNHM), San Diego; the Western Foundation of Vertebrate Zoology (WFVZ), Camarillo; and the American Museum of Natural History (AMNH), New York. All specimens were collected in the Pacific Ocean from 57° N south to 4° S; 316 of the specimens were collected on the breeding grounds throughout the complex's range, and the remaining 212 were collected at sea. Specimens were reasonably distributed throughout the year, with all months being represented. We also examined hundreds of photographs of birds of this complex taken at sea south of latitude 40° N in the Pacific that we could locate in the Cornell Lab of Ornithology's Macaulay Library, that were part of the Cascadia Research

Collective's studies off Hawaii (Pyle et al. 2016), or that were provided to us by other photographers (Figure 1).

We categorized the age of each bird as first year or adult by the shape, wear, and condition of the remiges and rectrices. Juvenile and first-year birds, until the second prebasic molt commences, show unmolted juvenile remiges that are uniform in wear, with narrower, more tapered, and more worn outer primaries and rectrices; we include in this category birds undergoing the second prebasic molt on the basis of the unmolted feathers. Older birds ("adults") have broader, more truncated, and relatively fresher outer primaries and rectrices that show a "molt cline" (a gradual freshening of primaries distally and secondaries proximally, except for more worn tertials, along with the outermost secondary fresher than the innermost primary), reflecting protracted sequential feather replacement at sea (Pyle 2008). Molt clines and a contrast between an outermost secondary fresher than innermost primary, due to time elapsed between the replacement of these two feathers,

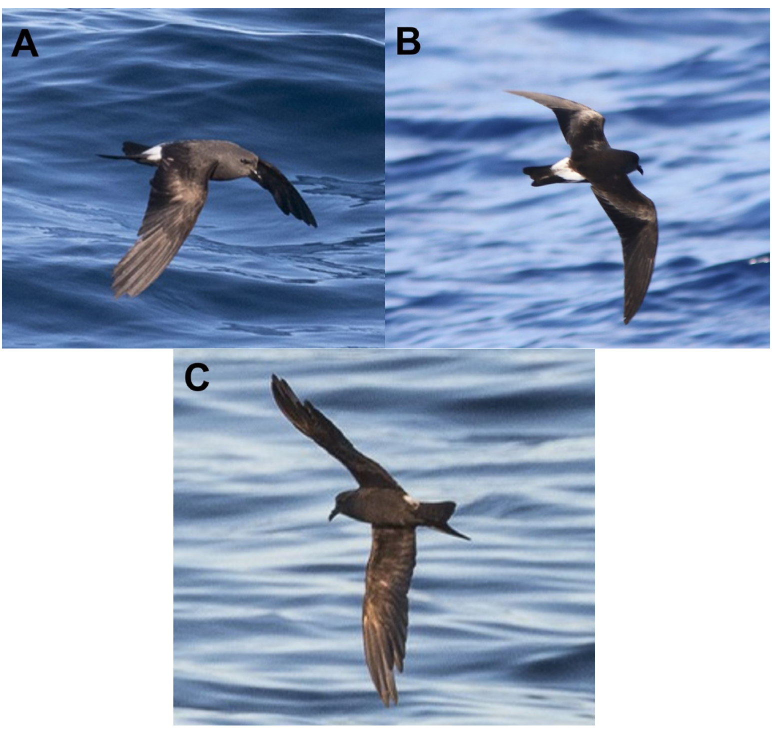

Figure 1. Three storm-petrels photographed off Mexico. A, Adult off Colima, 22 February 2017 (molt score 8). B, First-year bird off Colima, 21 February 2017 (molt score 0). C, First-year bird off Baja California Sur, Mexico, 2 Dec 2015 (ML 21803711). The birds in images A and B were on a molt schedule consistent with Leach's Storm-Petrel, whereas that in image C was not, so it may be an Ainley's Storm-Petrel.

Photos by Amy McAndrews (A, B) and Ken Chamberlain (C) is proving a consistent method for assessing the ages of storm-petrels because of their protracted molt during the nonbreeding season (Pyle 2008). These characters, along with the shapes of the primaries and rectrices, allowed us to categorize the ages of both specimens and birds in photographs with a high degree of confidence. Nevertheless, assessing the level of wear can be difficult in adults because of damage to the remiges while nesting birds are entering and exiting their burrows.

We examined each specimen and photograph for active molt in the primaries, which are replaced sequentially from the innermost (p1) to the outermost (p10). We gave each specimen and photographed bird a molt score of p0 to p10 based on the number of primaries it had replaced or dropped. Following DeSante et al. (2019), we gave each specimen a wear score from 0 to 5, with 0 indicating extremely fresh outer primaries and 5 indicating extremely worn primaries. Although we identified some specimens as Townsend's Storm-Petrel from information on their labels and from measurements (Pyle 2008), for this analysis we pooled Leach's and Townsend's, as some specimens and many photographed birds were not distinguished with certainty. We identified breeding adults collected at Guadalupe Island from October to February or fresh juveniles collected from January to April as Ainley's Storm-Petrels.

In order to search for outliers in the timing of storm-petrel molt, we used a circular data-distribution approach for presence and absence of molt, and a double-hinge threshold model (Fong et al. 2017, Terrill et al. 2021) fit to molt-timing data. Because the annual cycle of birds can be best represented as a repeated circle, we used the package "circular" (Agostinelli and Lund 2017) in R version 3.6.1 (R Core Team 2019) for presence/absence data of molt and to search for outliers. First, we used a Rayleigh test (Wilkie 1983) for circular uniformity to test whether the seasonal distributions of molting and nonmolting birds were nonrandom. We then applied Watson's two-sample test of homogeneity (Mardia 1969) to determine whether the phenological distributions of molting and nonmolting birds differed significantly. Finally, we measured the circular mean and constructed a box-and-whiskers plot adapted from Tukey (1977) for circular data (Buttarazzi et al. 2018) to search for statistical outliers. We constructed these plots for both summer-breeding species (Leach's and Townsend's) lumped together. To estimate the onset and duration of molt, we excluded the outliers and fit a double-hinge threshold model with 1000 bootstrap replicates by using the package "chngpt" (Fong et al. 2017) in R (R Core Team 2019). We used the bootstrapping to generate 95% confidence intervals for adult Leach's Storm-Petrels (excluding potential Ainley's) on the basis of birds in active molt or with extreme wear scores (feathers either very fresh or very worn). By the same procedure we built a separate model for the potential Ainley's Storm-Petrels.

RESULTS

Among the 528 specimens analyzed, we categorized 442 as adults or birds undergoing the definitive prebasic molt (outermost primary basic) when collected, 86 as first-year birds or birds undergoing the second prebasic molt (outermost primary juvenile). Of the 528, we considered the 73 collected at

Guadalupe from 7 December to 11 February to be Ainley's Storm-Petrels, none of which were in molt. Of the remaining 455 specimens, 33 of 369 adults and 18 of 86 first-year birds were in active molt. Among the hundreds of storm-petrels we examined through photographs, we identified 39 undergoing molt. Of these, we categorized 8 as first-year and 7 as adults; we could not categorize the remaining 24 because of the photo's poor quality or angle.

Among specimens initially identified as Leach's or Townsend's Storm-Petrel, Rayleigh's test for circular uniformity confirmed that both molt (t = 0.55, p = 0.0002) and lack of molt (t = 0.43, $p < 0.001$) are seasonal. Watson's two-sample test of homogeneity confirmed that in adults these seasons are significantly different (t = 0.93, $p < 0.001$), with molt taking place primarily in late winter (Figure 2). Among first-year birds, however, the sample was too small for this test to distinguish the temporal distributions of molt and lack of molt (t = 1.5, $p > 0.1$).

In total, through our statistics and from examining the timing of molt in our sample, we identified eight specimens and two photographs of birds that were undergoing molt coinciding with the hypothesized schedule of Ainley's Storm-Petrel. These comprised five adults and five birds undergoing the second prebasic molt (Table 1, Figure 3). However, there were many outliers in the sample of adult storm-petrels not in molt, so we do not propose potential Ainley's Storm-Petrels among them, as the outliers have represented first-year birds that we had mis-categorized as adults.

When the molting adults of potential Ainley's Storm-Petrels were modeled, the double-hinge threshold model rejected a flat slope (p = 0.049) and recovered an initiation date for molt of the primaries of 12 May (95% CI: 20 March–2 July; Figure 3A). Dates of these adults' molt of primaries ranged from 11 June (p3) to 5 October (p9). The threshold model for adult Leach's Storm-Petrels in molt also rejected a flat slope (p = 0.002) and recovered an initiation date for molt of the primaries of 7 December (95% CI: 16 November–17 January). With respect to potential first-year Ainley's, the threshold

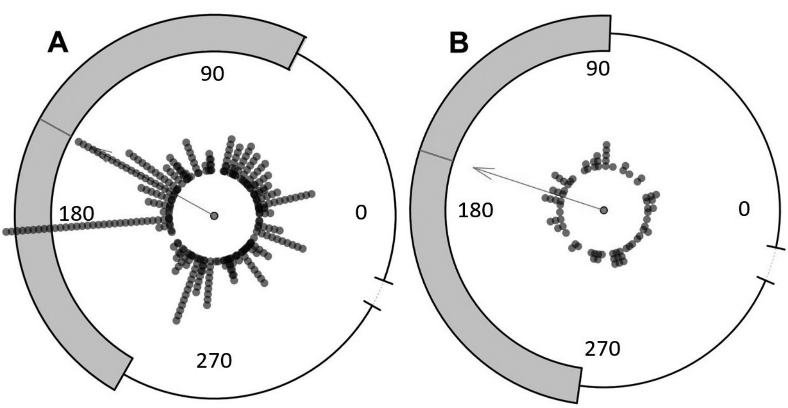

Figure 2. Timing of molt in Leach's and Townsend's Storm-petrels. A, adults; B, first-year birds. Each gray circle represents one individual at any stage of replacement of the primaries. 0, 1 January. Blue arrows and lines represent the mean dates of molt.

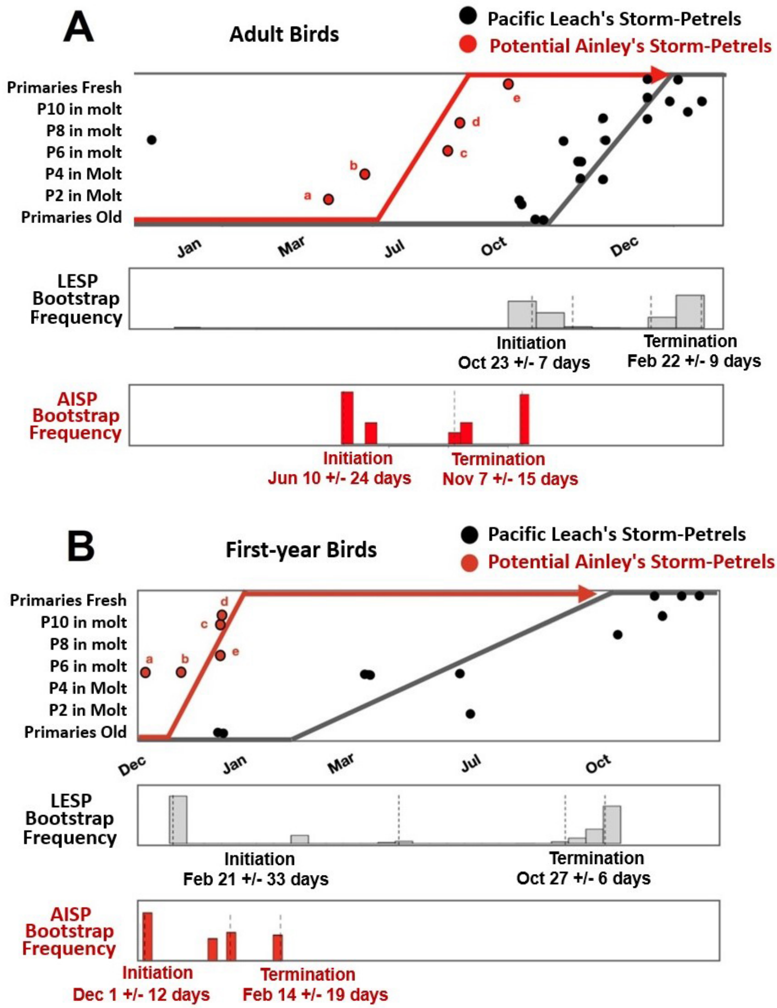

Figure 3. Threshold model fit to Leach's (black circles, model fit in gray line) and potential Ainley's (red, judged from outlier analysis) storm-petrels, with initiation and termination dates, as well as 95% confidence intervals generated from bootstrap replicates. Bootstrap histograms are shown beneath each plot. A, Threshold model fit to adult Leach's and potential adult Ainley's storm-petrels. B, Threshold model fit to first-year Leach's and potential first-year Ainley's storm-petrels.

model recovered an initiation date for molt of the primaries of 1 December (95% CI: 23 November–22 February [p8]; Figure 3B). The dates of these younger birds' primary molt ranged from 2 December (p6) to 15 February (p8). The threshold model for molt of the primaries in first-year Leach's Storm Petrels recovered an initiation date of 12 May (95% CI: 20 March–2 July).

Table 1 Ten Potential Ainley's Storm-Petrels Identified away from Guadalupe Island

Age and specimen or photo number[a]	Key to location plotted in Figure 5	Location	Date	Molt score	Wear score
Adult					
CAS 484	A	4.333° S, 93.5° W	11 Jun 1906	3	4
LACM 107383	B	0° N, 100° W	3 Jul 1988	5	2
MVZ 123467	C	45° N, 145° W	12 Sep 1950	6	4
LACM 20081	D	600 miles W of San Pedro, CA	22 Sep 1941	7	4
CAS 465	E	14.467° N, 107° W	5 Oct 1906	9	3
First year					
SDNHM 39176	F	13° N, 112° W	6 Jan 1975	6	4
SDNHM 39801	G	1° N, 127° W	19 Jan 1976	7	3
AMNH 528635	H	5.5° N, 102° W	17 Jan 1901	8	4
ML 21803711	I	24.930° N, 115.775° W	2 Dec 2015	6	4
2S8A8702-03[b]	J	95 miles WSW of Cabo San Lucas, Baja California Sur	13 Feb 2017	7	3

[a]See acknowledgments for definition of abbreviations for museums and photo archives.
[b]Photo courtesy Amy McAndrews and Jorge Montejo.

Because Watson's two-test sample was unable to distinguish the distributions of molting and nonmolting first-year birds, these birds may include some Ainley's, but no such identification is supported by our statistical analysis. In addition, because the sample of potential Ainley's is so small, the date ranges of our samples may not reflect the true or complete temporal distribution of the species' molt.

The patterns inferred from wear scores were not as definitive as those inferred from molt scores. We attribute this to wear being more difficult than molt to score consistently, and to wear varying with different degrees of solar exposure at different latitudes and with the birds' behaviors. For example, nesting adults can show flight feathers significantly more worn than do older nonbreeding birds, due to entering and exiting nest burrows.

After we identified these potential Ainley's Storm-Petrels, Pyle compared three of the specimens (CAS 465, 484, and MVZ 123467) with specimens of Leach's Storm-Petrels to see if there were any detectable differences in plumage (Figure 4). The potential Ainley's Storm-Petrels appeared darker and glossier-headed than Leach's Storm-Petrels collected at the same time of year and may also have differed in this way from with Leach's collected at the same stage of molt and wear (essentially six months offset). This difference could prove useful for identification at sea, especially in spring and summer, when Ainley's Storm-Petrels should be fresher and Leach's Storm-Petrels are more worn.

DISCUSSION

The timing of events in birds' life cycles is important to both breeding and adults' survival (Holmgren and Hedenström 1995, Cotton 2003, Borgmann et al. 2013). The topic of timing has received attention from the standpoint of

Figure 4. Potential Ainley's Storm-Petrel (CAS 484, collected 11 June 1906, left in each image) in comparison with presumed Leach's Storm-Petrels. A, Comparison with two Leach's Storm-Petrels collected at the same time of year, CAS 482 collected 11 June 1906 (middle) and CAS 87883 collected 15 June 1958 (right). B, Comparison with Leach's Storm-Petrels collected at the same stage of molt, CAS 478 collected 19 November 1906 (middle) and CAS 477 collected 19 November 1906 (right). All storm-petrels were categorized as adults. CAS 484 and 477 were molting p3, CAS 478 was molting p4, and CAS 482 and 87883 were not molting primaries. Note how the potential Ainley's Storm-Petrel appears much darker and fresher than the Leach's Storm-Petrels at the same time of year (A) but only slightly darker when compared to Leach's Storm-Petrels at the same stage of molt (B). A glossier head and darker (fresher) plumage in from May to October and paler (more worn) plumage from November to April may indicate Ainley's Storm-Petrel at sea.

life-history evolution (Martin 2004), including the potential consequences of phenological mismatches induced by climate change (Reed et al. 2013, Bowers et al. 2016). Differences in the timing of molt may aid in the identifications of species and populations of birds otherwise difficult to distinguish in the field (Pyle 2008, Howell et al. 2010b, Howell 2012), but no studies have formally analyzed molt-timing data. Here, we confirm the concept that molt timing may be useful in identifying some birds in the field; however, we caution that Ainley's Storm-Petrels at sea may ultimately need to be identified through an independent method, such as genetic sequencing or isotopic or other analysis of feathers grown at natal sites. Although the schedules of prebasic molt of most bird species, including the Procellariiformes, are reasonably well defined, the timing, location, and extent (but not sequence) of molt are rather plastic (Pyle 2013), so exceptions or outliers might be expected in the Leach's Storm-Petrel complex. Leach's broad breeding distribution in the eastern Pacific from Alaska to the San Benito Islands leads to significant variation in the timing of breeding, likely causing variation in the timing of molt. For example, fledging in British Columbia is nearly two months later

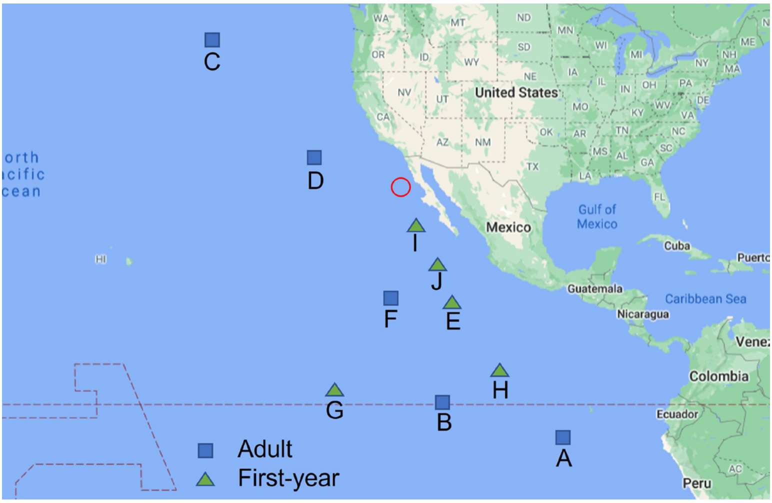

Figure 5. Distribution of the ten potential Ainley's Storm-Petrels identified away from Guadalupe Island (circled in red). Eight of these birds were collected or photographed well south of Guadalupe Island, of which four were collected near the equator.

than fledging in central California (Pollet et al. 2021). The somewhat recent discovery of Leach's-Storm Petrels breeding in the Southern Hemisphere (Underhill et al. 2002) could only exacerbate this problem.

Ainley's Storm-Petrel is listed as vulnerable with an estimated population of fewer than 10,000 individuals, and invasive species pose a serious threat to it (Kirwan 2020). To develop conservation strategies that will ensure the species' continued survival, knowledge of its distribution at sea is essential. Our results show that Ainley's Storm-Petrel may disperse south after the breeding season, as eight of the ten potential Ainley's we identified were found south of Guadalupe Island, perhaps indicating the species' primary nonbreeding range (Figure 5). On the other hand, the birds collected off Oregon on 12 September and off California on 22 September may indicate a broader nonbreeding distribution, or they could represent Leach's Storm-Petrels that had molted on an atypical schedule. These two birds were collected more than 200 nautical miles offshore and are therefore outside of areas considered by state records committees. Medrano et al. (2022) used tracking devices to follow foraging adult Ainley's Storm-Petrels during the breeding season, finding that they ranged south to the San Benito Islands and north to the ocean off southern California. Similar tracking of Ainley's during the nonbreeding season would provide a substantially clearer understanding of the species' pelagic distribution, including periods of molt. We also encourage observers to document and report any storm-petrels of the Leach's complex in molt.

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