COMMENTARIES

Variation and Nomenclature of Leach's Storm-Petrels

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In his detailed review of geographic variation in Leach's Storm-Petrel (*Oceanodroma leucorhoa*), Ainley (1980) argues that color characters should be accorded little taxonomic significance. He bases a revised classification, including the description of a new race from Guadalupe Island, México, on vocalizations and breeding seasons. The following points require further discussion.

1. *Coloration.*—Leach's Storm-Petrel shows minor variations in several characters, which result mostly from tendencies of the birds to be slightly smaller and more heavily pigmented in the warmer parts of the range. The several populations overlap in most mensural characters. Variation in color largely involves a bluish bloom on the plumage when it is new and the degree of white marking on the rump. The bloom is soon lost through wear and is hard to assess. The rump color, however, is stable and shows pronounced geographic variation. While it is true that one can construct a graded series of rump patterns (as in Ainley's Fig. 1), it is not accurate to state the patterns change "gradually" (p. 839) from white in the north to black in the south. A certain amount of variation in the color of the rump is found in the northern populations, even in the Atlantic, where one bird photographed (Bourne) on St. Kilda was as dark as Ainley's class 5. Fully dark-rumped birds appear only at Los Coronados, the San Benitos, and Guadalupe Island; a few, whose breeding status is questionable (see below), also occur on the Farallons and on San Miguel Island.

The break in distribution between white- and dark-rumped birds on the west coast is even sharper than Ainley's Fig. 2 shows, as only about 5% of the Los Coronados population shows white on more than one to three feathers and white feathers appear in only about 1% of the birds on the San Benitos (Jehl unpub. data). The somewhat higher incidence of white-rumped birds in museum collections is due in part to selective preservation (Jehl pers. obs.). The break becomes even more impressive when it is realized that the total known population of Leach's Storm-Petrels in the 680-km interval between the Farallons and Los Coronados comprises only several pairs on San Miguel Island ("2+" on Prince Island and "+?" on Castle Rock) and, questionably, several pairs on Santa Barbara Island (Hunt et al. 1980).

The only evidence of a bimodal or polymorphic distribution in rump coloration occurs in the summer-breeding population at Guadalupe. The situation there is complicated by the fact that on Islote Negro most of the population is dark-rumped, whereas at Islote Afuera, only 5.6 km away, more than 90% of the population is white-rumped (Crossin 1974). This situation remains to be studied in detail.

2. *Status and breeding seasons at Guadalupe.*—There is very little evidence that Leach's Storm-Petrel has nested on the main island at Guadalupe. It may have been eradicated by cats early in the century, although birds have been heard there near the north end in summer in recent years. The only known colonies at Guadalupe are on small islets near the south end of the island (Jehl 1972, Crossin 1974, Jehl and Everett MS).

The timing of the breeding season was investigated for over two decades by the late Carl L. Hubbs (1960), who discovered that there were "two separable forms, of similar size, smaller than any of the other subspecies" nesting at different seasons on Islote Negro, as mentioned by Crossin (1974) but not by Ainley. Hubbs considered the slightly larger, white-rumped, winter-breeding population to represent *O. l. kaedingi* (originally described from the vicinity of Guadalupe but usually synonymized with *O. l. socorroensis*) and the smaller, dark-rumped summer birds, *O. l. socorroensis*. Subsequently, Crossin (1974) discovered another small, largely (indeed, sometimes exceptionally) white-rumped, summer-breeding population on Islote Afuera.

Ainley called attention to a possible hiatus in breeding, between 25 April–28 May and from late August through mid-November, as evidenced by the lack of adults in collections. The vast majority of the specimens from Guadalupe were taken by Hubbs and colleagues or by the Pacific Ocean Biological Survey Program (Crossin 1974), however, and these expeditions (summarized in Table 1) were not made at regular intervals through the year, which partly explains the apparent gaps. Further, on some of Hubbs' later trips (1970–1971) little effort was devoted to petrels, and no effort was made to obtain specimen material (Jehl pers. obs.).

The data show that most winter-breeding birds lay late in the year, fledging young by April; most summer breeders begin laying in June and fledge young in October or November. In both cases there may be

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TABLE 1. Annual chronology of Leach's Storm-Petrels breeding at Guadalupe Island.[a]

21 October 1967. POBS visited Islote Negro, found flying young of summer population, three pairs of winter population by day and 500 visiting by night.
27 October 1957. Islote Negro. Large young of summer population still present; winter population pairing; no eggs.
16 November 1954. Islote Negro. One large downy chick obtained.
23 November 1964. Islote Negro. Fourteen nests of winter race located, most with an egg.
14 December 1957. Islote Negro. Many birds had slightly incubated eggs.
24 January 1970. Islote Negro. Some pairs nesting at all stages from pairs in burrows to chicks up to 10 days old.
30 January 1960. Islote Negro. Many downy young of winter population.
9–14 February 1957. Many white-rumped birds that were distinct from the dark-rumped summer population noted on the three islotes. (Crossin reports that a three-quarters grown chick was taken on I. Afuera).
5 March 1965. Islote Negro. Thirty-six sites checked; one contained an adult with an egg, one an adult, and many sites held downy chicks. A juvenile was collected aboard ship.
4 April 1966. Islote Negro. Only two well-grown young of winter form found in 70 sites.
18–19 April 1970. One adult banded on ship. None found on Islote Negro. One full-grown chick on Gargoyle Rock.
19–20 April 1957. Islote Negro. Some chicks near fledging. Few adults present.
23 April 1963. Islote Negro. Four chicks of winter form in 70 sites.
27 April 1967. Islote Negro. One large chick of winter form.
29 April 1967. POBS found one large chick on Islote Negro.
23 May 1971. Islote Negro. Two birds banded; no eggs. Heard several other birds calling from burrows.
10–15 June 1955. Islote Negro. Dark-rumped birds present with many eggs. White-rumped birds seen on vessel and ashore.
22–28 June 1968. POBS. Islote Negro: 4,000 dark-rumped birds, about 20% with eggs. Islote Afuera: 3,000 birds, 90% with white rumps, with rather more eggs. Variety of birds on vessel, some with brood patches.
29–30 August 1956. Islote Negro and Gargoyle Rock. Many eggs and downy young. Some white-rumped birds on board vessel.

[a] Observations by Carl L. Hubbs (field notes) except where specified as by Pacific Ocean Biogical Survey (Crossin 1974).

some variation and overlap in the times when birds of each population are present. While bimodality is clear, it is not certain that at least some breeding does not occur year-round. Thorough censuses, especially in fall, are needed to confirm whether the peaks represent temporally isolated populations or are part of a continuum.

3. *Vocalizations.*—It appears that northern hemisphere storm-petrels have two main types of vocalizations (Witherby et al. 1940, vol. 4: 30; Palmer 1962), the terminology for which varies (cf. Cramp and Simmons 1977 and Ainley 1980). One is a brief staccatto flight-call of several notes differing in their pattern and lasting about 1.5 s. The second is a prolonged ventriloquial "churr" (the "chattering" call of Ainley), interspersed with pauses, used mainly in the burrow. Ainley shows that the vocalizations of Leach's Storm-Petrels from Guadalupe differ from those at other localities; there are also some differences between summer and winter populations.

The major difference between Guadalupe and other areas appears to be that the phrases are prolonged, with an increase in emphasis on the first note after the longer pause for breath when the bird is churring or chattering and the addition of extra notes to the flight call associated with a change in the notes that are emphasized. The overall pattern is similar in all populations. There may be more variability in the calls of Guadalupe birds than Ainley realized, however. For example, the rate of "churring" is said to be more rapid, averaging 26 notes/s (range 25–27/s) in both summer and winter populations, but the sonagram in Ainley's Fig. 3 shows a rate of approximately 20 calls/s for the winter birds. Further comment is impossible, because the sample sizes of vocalizations are too small for analysis; his descriptions of flight calls are based on 2 winter and 6 summer birds and those of burrow calls on 4 winter and 2 summer. We do not doubt that there are average differences at Guadalupe (or elsewhere), but we consider it premature to use variable vocalizations as characters in support of a formal classification until

those characters can be analyzed as rigorously as traditional mensural characters.

4. *Winter breeding.*—A point stressed by Ainley is that *O. leucorhoa* on Guadalupe is "the only temperate breeding storm-petrel known to nest during the winter" (p. 848). Harcourt's Storm-Petrel (*O. castro*), however, has been reported to have two breeding seasons, June–September and October–January, at Madeira (33°N), which is even farther north than Guadalupe (29°N) (Palmer 1962). Madeira has a Mediterranean climate, with maximum rainfall in the winter, and a variety of birds breed in that area that season (Bannerman 1963–1968). Harris (1969) discussed the breeding of Harcourt's Storm-Petrel at Madeira and was unable to determine whether "there are two seasons a year, one season with some out-of-season nesting, or a less than annual cycle." We agree with Harris that the situation at Madeira is unclear. The same conclusion applies to Guadalupe.

5. *The Guadalupe Storm-Petrel.*—Ainley (p. 851) speculates on the possibility of interactions, including competition for nest sites, between Leach's and the larger, extinct, Guadalupe Storm-Petrel (*Oceanodroma macrodactyla*). However, there is no evidence for, and much against, the idea that *macrodactyla* and *leucorhoa* "bred sympatrically and temporally." Ainley's discussion seems based on the assumption that *macrodactyla* bred at low elevations and in summer. In fact, it bred in burrows in the soil in forested areas atop the main island, which rises to 1,200 m (Bent 1922), and nested early in the year, probably starting to lay in mid-February. This is a month or two later than the winter-breeding population of *leucorhoa* and much earlier than the summer-nesting form (Bent 1922, Jehl and Everett MS), which, on Guadalupe, normally nests in rock crevices on talus slopes only slightly above the sea.

In any case, it is very unlikely that nesting sites were ever a limiting factor for either species on that large, rugged, volcanic island. While A. W. Anthony (*in* Bent 1922), a veteran explorer and collector at Guadalupe, did write that *leucorhoa* used the same burrows as *macrodactyla* but "after they [*macrodactyla*] are through breeding," a complete review of the literature shows that this tale originated with Kaeding (1905) and has been repeated uncritically ever since (Jehl and Everett MS).

It should be emphasized that the Guadalupe Storm-Petrel was never seen alive anywhere except at its nesting burrows or, questionably, at sea at the very base of the island (Jehl and Everett MS). While speculation on its feeding habits, ecology (see also discussion under *O. melania* in Palmer 1962), and competitive interactions may be of heuristic value, this is not an adequate basis for classification.

6. *Visiting between colonies.*—Ainley's paper was stimulated by the occurrence of several dark-rumped birds on the Farallons (p. 837), and he implied that the Farallon population is polymorphic in rump color. However, the provenance of these dark-rumped birds, as well as those reported from San Miguel Island, is far from established. Banding studies in Europe (notably results summarized annually for the British scheme) have shown that hydrobatids may visit colonies up to 1,100 km apart and participate in communal displays there.

Whether or not wandering during the breeding season is an important component of dispersal in other storm-petrels is unknown, but the phenomenon is sufficient to account for the occasional appearance of dark-rumped birds on the Farallons or San Miguel, or of birds from any of the southern North American populations at Guadalupe. As evidence, we note that a Galápagos Storm-Petrel (*O. tethys*) has also been found in a crevice on Guadalupe, 4,800 km from the nearest known nesting locality (Huey 1952).

Systematic Considerations

In his revision of Leach's Storm-Petrel, Ainley attempted to emphasize the "evolutionary pressures that account for geographic variation in these populations, an important goal in modern systematics" (p. 845). This is laudable, but his discussion of selection pressures (p. 849–852) is so speculative that it cannot be used as a basis for interpreting or reconstructing phylogenies. He then uses breeding season and vocalizations as characters.

The recognition of "physiological races" of birds based upon their annual cycle was first proposed for the Starling (*Sturnus vulgaris*) by Bullough (1942), who also suggested the use of vocalizations. The idea was received enthusiastically at first as part of the "new systematics" but was eventually discarded because it failed to provide a means of telling populations apart (Witherby 1943). This decision was reinforced by the observation that "physiological races" had emerged among descendants of a handful of Starlings introduced into North America (Bullough 1945) and the discovery that variations in vocalization can be learned and so may not have a genetic basis (Thorpe 1958). These do not seem helpful taxonomic criteria.

Ainley's conclusion is that all of the various populations of Leach's Storm-Petrel, excepting those on Guadalupe, should be merged into one race, *O. l. leucorhoa*. He justifies this position by noting that his scheme "lessens the problems of assigning specimens collected or individuals encountered at sea to appropriate populations, a difficulty inherent in the presently accepted scheme (Austin 1952, Crossin 1974)." While it is true that all birds cannot be identified under the present classification, Ainley's alternative fails to improve the situation. By this massive merging of races he has merely obviated the problem of identification, except in the case of birds from Guadalupe, which remain equally indistinguishable individually either at sea or in the hand.

If Ainley's classification were adopted, it would result in a situation in which very similar extremes of variation usually would be treated as separate species [Leach's Storm-Petrel (*O. leucorhoa*) and Swinhoe's Storm-Petrel (*O. monorhis*)] on the west side of the Pacific but would be both combined in the nominate race of *O. leucorhoa* on the east side! An investigation of the situation in the west Pacific, especially of the voice of *O. monorhis*, seems overdue.

The facts of morphological variation, which had already been established by Austin (1952), are not in dispute: the birds are progressively smaller and darker as one moves from north to south and as temperatures in breeding areas increase, a trend that is predicted by zoogeographical rules; there is a local interruption in this cline in the area of cool upwelling water off the coast of California; at the southern end of the range the rump is entirely dark in *O. l. chapmani* in Baja California and in *O. (l.?) monorhis* in Japan, but it is variably white in part of the Guadalupe Island population.

The more northerly populations are strong migrants, reaching most of the warmer seas of the world. Bourne and Dixon (1973) plotted part of the winter range. In the eastern Pacific the southern populations are more sedentary (Crossin 1974), but in the western Pacific there is a sharp transition in Japan to a strongly migratory dark population, *monorhis*, which reaches the Indian Ocean (Bailey et al. 1968).

The main novel development is the discovery by Hubbs (1960), further documented by Crossin (1974), that some birds of intermediate character breed in the winter on Guadalupe Island, in addition to the locally variable endemic race, *socorroensis*, which breeds in the summer and in which strong average differences in rump color occur in colonies on two closely adjacent islets. Other differences between the summer and winter populations are not marked. Ainley also showed that Guadalupe Island birds of both populations have vocalizations that differ somewhat from those found in other Atlantic and Pacific colonies, although the calls may be more variable and less diagnostic than he realized.

It cannot be fully decided how this situation should be handled taxonomically until we know more about the distribution of morphs, the duration of the breeding season(s), and the significance of variations in vocalization. At present, we suggest that it can be dealt with adequately by small modifications in the classification proposed by Austin (1952), without the need for introducing additional names.

O. l. chapmani is usually restricted to a population of about 50,000 almost uniformly dark-rumped birds (Crossin 1974) nesting on the San Benito Islands. This should be expanded to include the only other important predominantly dark-rumped population of about 200 birds nesting on Los Coronados (Jehl unpubl. data), formerly known as *O. l. willetti* and recently combined with *beali*. The merging of *chapmani* and *willetti*, originally proposed by Hubbs (1960), is supported by Ainley's data, which show that these birds are similar in size, proportions, and rounded wingtips. This merging would achieve Ainley's goal of permitting the identification, both in the hand and at sea, of over 90% of the dark-rumped members of the species in the eastern Pacific, excluding only one population of approximately 4,000 birds nesting in summer on Islote Negro, Guadalupe (Crossin 1974). Dark-rumped birds appear to have a limited migration and range in winter as far south as 11°30'N, off southern Nicaragua (Jehl pers. obs.).

The taxonomy of the Guadalupe populations cannot be satisfactorily resolved until they have been studied in greater detail. The original description of *socorroensis* emphasizes that it had some white on the rump (Townsend 1890). Hubbs (in manuscript) considered formally naming the dark-rumped birds of Islote Negro as early as 1956 but later (1960) decided that they were probably inseparable from other summer-breeders, i.e. *socorroensis*.

The slightly larger, white-rumped, winter-breeding birds named *cheimomnestes* by Ainley might represent a secondary invasion of Guadalupe, from near-shore island populations, that have developed distinct vocalizations either by imitation or by hybridizing with the original form, or they might represent the winter-breeding segment of the original population that has developed minor differences in size and color. In any event, inasmuch as the winter breeders are intermediate between the coastal populations and the summer-breeding *socorroensis* and as they are inseparable except by previous knowledge of their geographic origin, breeding season, or vocalizations, we find no justification for naming them as a new subspecies. For the present time, they may be lumped with the variable form currently known as *O. l. beali*, an action that would indicate the occurrence of variation among Guadalupe birds, as suggested by Hubbs (1960).

Meanwhile, Ainley's observations emphasize the need for more investigation of many aspects of the biology of Leach's and other storm-petrels, especially the other dark-rumped derivative of Leach's Storm-Petrel, Swinhoe's Storm-Petrel in Japan. Should further study reveal that the sympatric populations of Leach's Storm-Petrel breeding on Guadalupe Island are reproductively isolated, the next development would not be to recognize an additional race, but to treat one as a distinct species, "The Other Guadalupe Petrel."

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The Condor Case: a Rallying Cry!

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The plight of the California Condor (*Gymnogyps californianus*) has generated a great deal of debate in the popular and technical literature. Questions about safeguards have been raised in the National Audubon Society and government-funded Condor Programs, and, more recently (Pitelka 1981, Auk 98: 634), there has been controversy about decisions that designate priorities of species to be saved. The essential question is whether we try to save the Condor or some other species that has a higher probability of surviving. This is an important question in a time of limited funding and reduced government emphasis on environmental programs.

I agree with much of Pitelka's concern about decisions regarding which species should be saved and how they should be studied. Accordingly, I believe that three points may need careful consideration: (1) the danger of attaching a "seems doomed anyway" label to species without supporting scientific evidence; (2) the need for a rallying cry to motivate people "innocent still of what man is doing" or to educate properly those "philosophically opposed to the notion that man is doing anything wrong"; and (3) the eventual disposition of the "large-scale investment" being made.

As a more environmentally aware people, we have been preoccupied with many species that have been on the brink of extinction. There are presently 752 species listed by the federal government as endangered or threatened (Endangered Species Technical

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