

# SEABIRD GEOGRAPHIC VARIATION: SIMILARITY AMONG POPULATIONS OF LEACH'S STORM-PETREL

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**ABSTRACT.**—We assessed geographic variation in 13 locality samples of Leach's Storm-Petrel (*Oceanodroma leucorhoa*), 12 from the Pacific coast and 1 from the Atlantic coast of North America. Nine phenetic characters were used with canonical variates analysis to determine similarity among samples. Regression of phenetic distance on geographic distance measured the relation between similarity and interisland distance. We found a clinal pattern of population similarity from the Aleutian Islands in the north to the Farallon Islands in the south. Populations from Los Coronados and San Benitos islands make up a distinct subset when rump color and wing and tail shape indices are included in the analysis, but these populations were part of a dominant clinal trend when only five size characters were used. On Guadalupe Island separate populations breed in summer and winter; these are strongly differentiated from the others and from each other. The North Atlantic sample was aligned closely with that from the Aleutians. The degree of geographic variation was roughly similar to that in certain migratory land birds on the North American continent, but is less than what is found for certain nonmigratory land birds on islands. Our results suggest recognizing four subspecies of Leach's Storm-Petrel in the study area, including two on Guadalupe Island isolated by time of breeding. *Received 7 May 1984, accepted 3 March 1986.*

SEABIRDS often range over wide areas, yet return to specific island sites to reproduce. As a result, the breeding populations of many pelagic species are isolated geographically (King 1974). It is not known if the degree of reproductive isolation and the concomitant potential for divergence of island-breeding seabird populations are any greater than what might be found in land birds. A comparable mainland situation might be a migratory species with populations that nest in isolated habitat "islands." The interrupted breeding distribution of seabirds offers an attractive situation for study of geographic variation. Seabirds, however, have not figured prominently in our understanding of intraspecific evolution; most information on avian geographic variation comes from studies of land birds (e.g. Selander 1971).

In a univariate analysis of geographic variation on breeding populations of Leach's Storm-Petrel (*Oceanodroma leucorhoa*) in the eastern North Pacific and the western North Atlantic oceans, Ainley (1980) found that several characters vary clinally from the Aleutian Islands in the north to the San Benitos Islands off the west coast of Baja California, Mexico. In addition,

the fact that Guadalupe Island supports two morphologically distinct populations, one breeding in summer and the other in winter, led Ainley to describe the winter population as a new race. Bourne and Jehl (1982) criticized some of Ainley's interpretations (see also Ainley 1983 and Jehl and Everett 1985). We reanalyzed the morphological data by combining characters in a multivariate analysis. Information Ainley presented on vocalizations was not considered. We examined the pattern of overall similarity among populations of Leach's Storm-Petrel and the relationship between specific island colonies, aspects of geographic variation that were difficult to assess only through variation in single characters. We also measured the relationship between overall similarity and interisland distance to see if the pattern of geographic variation is a function of geographic distance, as is often the case with land birds.

## METHODS

Eight measurements plus a classification of rump color (RC; 11 gradations from white to dark, with a score of 11 being darkest) were made on 707 specimens or live individuals separated into 13 locality

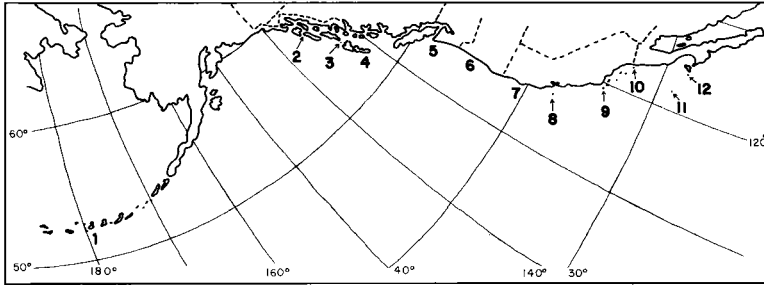


Fig. 1. Sample localities. Individual sites are indicated by numbers and arrows, whereas regional sites (e.g. "Oregon") are indicated by numbers in the approximate location of the mean coordinates weighted by the number of specimens from various sites within the sample: 1, Aleutian Islands; 2, St. Lazaria Island; 3, Forrester Island; 4, British Columbia; 5, Washington; 6, Oregon; 7, northern California; 8, Farallon Islands; (9, San Miguel Island; not used in this analysis, but referred to in the Discussion); 10, Los Coronados Islands; 11, Guadalupe Island; 12, San Benitos Islands.

samples. Samples were collected in the breeding season from the islands shown in Fig. 1 or from areas of ocean immediately adjacent to the islands. The mensural characters were wing length (WL), bill length (BL), bill depth (BD), tarsus length (TR), and tail length (TL). We also calculated depth of tail fork (DF) and distance from the tip of primary 10 to the tips of primaries 9 and 7 [wing shape indices 1 and 2 (WS1 and WS2), respectively]. Measurements from males and females were combined. The rationale for combining sexes and the methods of taking measurements are given by Ainley (1980). Sample sizes differed somewhat from those used in the previous analysis. In the present study sample sizes were as follows (locality code in parentheses): North Atlantic (NATL) 15, Aleutian Islands (ALEU) 47, St. Lazaria Island (SLAZ) 56, Forrester Island (FORI) 31, British Columbia (BCOL) 27, Washington (WASH) 26, Oregon (OREG) 22, northern California (NCAL) 41, Farallon Islands (FARA) 53, Los Coronados Islands (LCOR) 16, San Benitos Islands (SBEN) 62, Guadalupe Island/summer (GUAS) 129, and Guadalupe Island/winter (GUAW) 137.

Data for each character and each sample were screened for coding errors and non-normality by use of the Biomed program BMDP2D (Dixon 1975), which calculates range, standard deviation, mean, and coefficients of skewness and kurtosis, and produces a frequency histogram and other statistics. The multivariate procedures used here require complete data sets. Rather than delete specimens with one or more missing characters, we estimated missing data by linear regression. The entire 13 samples were combined, and then product-moment correlation coefficients and regression statistics were calculated for every pair of characters. When a datum was absent, the character with which it was most highly correlated was used in the appropriate regression formula to estimate its value. All but one character had a very small number

of missing data; for depth of tail fork almost one-quarter of the specimens were missing a measurement. The British Columbia sample was the most seriously affected: we had measurements for this character in only 2 of 27 specimens. As a test of the effect of using estimated values, a canonical variates analysis was performed with depth of tail fork deleted. The results were not appreciably different from those obtained with all nine characters. The use of estimated values therefore was deemed appropriate for depth of tail fork data as well as for all other characters.

We assessed overall similarity by canonical variates analysis (Seal 1966). This was supplemented by calculating Mahalanobis (phenetic) distances between each pair of locality samples (Blackith and Reymont 1971) and connecting those pairs of localities with smallest distances to form a shortest-connection network (Prim 1957). Mahalanobis distances are equivalent to distances in the full-dimensional canonical variates space and the network shows pairs of localities phenetically closest to one another. Geographic distance between sites in nautical miles was based on the mean longitude and latitude (to the nearest minute) of the collecting localities of individual specimens. We excluded the North Atlantic sample from the geographic distance comparisons. In examining the differences between the winter and summer Guadalupe populations, we used a two-group discriminant analysis (Blackith and Reymont 1971).

## RESULTS

*Similarity of samples.*—The canonical variates diagrams for all characters (Fig. 2) indicate one predominant cluster of locality samples from the Aleutians in the north to the Farallons in the south. These samples varied clinally and



TABLE 1. Mahalanobis distances (below diagonal) and geographic distances in nautical miles (above diagonal) between pairs of samples of Leach's Storm-Petrel.

	NATL	ALEU	SLAZ	FORI	BCOL	WASH	OREG	NCAL	FARA	LCOR	SBEN	GUAW	GUAS
North Atlantic	—												
Aleutian Is.	1.16	—											
St. Lazaria Is.	1.83	1.58	—	1,623	1,791	2,110	2,220	2,354	2,538	2,978	3,251	3,083	3,083
Forrester Is.	2.41	2.14	1.16	151	335	672	834	1,074	1,298	1,722	1,950	1,934	1,934
British Columbia	2.92	2.43	1.53	—	—	521	692	923	1,147	1,571	1,799	1,783	1,783
Washington	3.35	2.92	1.69	1.64	—	337	508	739	963	1,387	1,615	1,599	1,599
Oregon	2.73	2.11	1.35	1.22	1.82	—	171	402	626	1,050	1,278	1,262	1,262
Northern California	2.96	2.46	1.46	1.36	0.73	1.56	—	231	455	879	1,107	1,091	1,091
Farallon Is.	2.75	2.51	1.74	1.39	0.92	1.48	1.06	—	224	648	876	860	860
Los Coronados Is.	5.38	5.17	4.87	4.65	4.38	2.12	1.59	1.43	—	424	652	636	636
San Benito Is.	6.23	5.98	5.56	5.36	4.99	5.41	5.08	4.63	3.60	—	286	212	212
Guadalupe/winter	4.58	3.87	3.42	3.35	2.48	2.97	2.38	2.55	4.24	1.17	—	177	177
Guadalupe/summer	6.73	6.11	5.44	5.22	4.24	4.76	4.48	4.09	4.32	4.24	4.63	—	0
												2.87	—

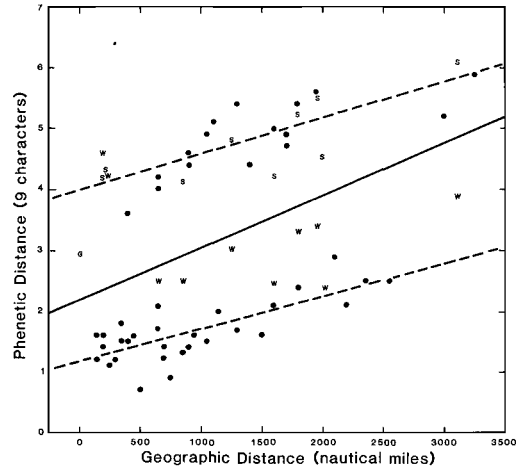


Fig. 4. Regressions of Mahalanobis distances between locality samples against geographic distances (nautical miles) for all characters in the phenetic distance measure. The regression statistics for the solid line are:  $Y = 2.17 + 0.00083X$ , coefficient of determination (CD) = 0.20. Regression statistics for the upper, out-group subset are  $Y = 3.99 + 0.00059X$ , CD = 0.67, and for the lower, in-group subset are  $Y = 1.16 + 0.00054X$ , CD = 0.58. Plotted, but not included in any of the subset regression statistics, are locality pairs involving Guadalupe/winter (W), Guadalupe/summer (S), and the relation between Guadalupe/winter and Guadalupe/summer (G).

geographically would be relatively far apart phenetically. A strong relationship between phenetic distance and geographic distance indicates smoothly clinal variation, while a weak relationship indicates an absence of geographic variation or a disjunct pattern relative to geographic position.

The relationship between the nine-character morphological similarity measure and geographic distance was assessed by plotting Mahalanobis distance against geographic distance for each locality pair (Table 1, Fig. 4). The North Atlantic sample was excluded because of the extreme geographic distance from all other samples. The regression of phenetic distance on geographic distance was significant ( $P < 0.01$ ), but only 20% of the variation in phenetic distance was explained. The residual variation did not appear as a random scattering of points. Instead, two distinct patterns were apparent. To understand the patterns we grouped certain localities into sets. Set I contained the following samples: Aleutian Islands, St. Lazaria Is-

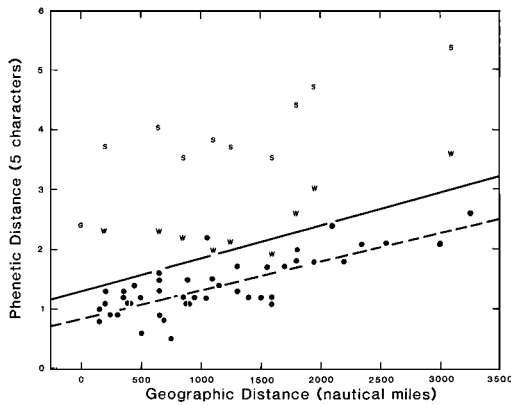


Fig. 5. Regression of Mahalanobis distances between locality samples against geographic distances for the reduced set of five characters in the phenetic distance measure (solid line) ( $Y = 1.31 + 0.00056X$ ,  $CD = 0.18$ ). The subset regression (dashed line) excludes pairs involving Guadalupe/summer and Guadalupe/winter (S, W, and G) ( $Y = 0.87 + 0.00047X$ ,  $CD = 0.60$ ).

land, Forrester Island, British Columbia, Washington, Oregon, northern California, and the Farallon Islands—all northern samples that appeared closely related on the canonical variates diagrams. Set II consisted of three samples: Los Coronados, San Benitos, and Guadalupe/summer. Guadalupe/winter will be discussed separately.

What we call "out-group" comparisons are represented by dots that tend to be on the upper part of Fig. 4 and are pairs of samples in which one sample is from Set I and the other from Set II (e.g. the pair Aleutians-Los Coronados). A separate pattern exists on the lower part of the graph for pairs of locality samples within Set I or II. We call these "in-group" comparisons. For example, the pairs Aleutians-St. Lazaria and Los Coronados-San Benitos are in-group comparisons. Sets I and II were derived by inspection of the plots; they are not otherwise statistically derived. These sets, however, match the sets identified in the all-character canonical variates plot (Fig. 2), indicating concordance between the two types of analyses. Regression lines were fitted for in-group and out-group comparisons (dashed lines in Fig. 4) with the result that more of the variation in phenetic distance is explained by geographic distance than if the samples were

combined: 67% in the out-group and 58% in the in-group set.

The subset regression lines excluded Guadalupe/winter. There was some question about placement of locality pairs that included Guadalupe/winter. Clearly, Guadalupe/winter comparisons seemed distinct, but fell closer to the in-group set. This coincides with the fact that Guadalupe/winter was closer to the other samples in the canonical variates plots.

The second comparison of Mahalanobis distance and geographic distance was with the reduced set of five mensural characters (Fig. 5). For all locality samples a statistically significant relationship existed ( $P < 0.01$ ), but only 18% of the variation in phenetic distance was explained by geographic distance. Again, a subset was suggested that excluded only those pairwise comparisons that involved Guadalupe/winter and Guadalupe/summer. There was a stronger relationship between phenetic and interisland distance for all locality pairs other than those that involved Guadalupe/winter and Guadalupe/summer. For the subset without Guadalupe comparisons (dashed line), 60% of the variation in phenetic distance was explained by geographic distance. Again, the results agree with the canonical variates analysis.

*Similarity between two Guadalupe Island samples.*—Ainley (1980, 1983) described differences between two samples on Guadalupe Island, one with a summer and the other with a winter egg-laying period. The collecting sites for the specimens in these two samples are given in Appendix 2. Ainley described the winter breeding population as a new subspecies, *O. leucorhoa cheimomnestes*, but this was questioned by Bourne and Jehl (1982). The history and complicated status of Leach's Storm-Petrel on Guadalupe has been summarized by Jehl and Everett (1985).

Before comparing summer and winter breeding populations, we determined whether each of those samples was morphologically homogeneous. Some information suggests that the summer population was not. Crossin (1974) reported that summer nesters on Isote Negro were dark rumped, while 90% of those on Isote Afuera were white rumped (see also Jehl and Everett 1985). Since the introduction of cats on the main island, the rocks and islets ("islotos") nearby have been the major nesting sites for this and many other seabird species. Jehl (pers.

TABLE 2. Discriminant analysis between Guadalupe Island summer- and winter-breeding populations of Leach's Storm-Petrel.

Character	Discriminant weights	
	Nine characters	Five characters
Wing length	0.241	0.152
Bill length	-2.309	-1.906
Bill depth	1.832	1.985
Tarsus length	-2.195	-2.165
Tail length	-0.749	-0.503
Depth of tail fork	0.318	—
Wing index 1	0.138	—
Wing index 2	0.159	—
Rump color	0.601	—
Mean, summer	-80.497	-76.063
Mean, winter	-88.420	-81.716
SD	3.825	3.541
Middle value	-84.398	-78.829
F-value (df) <sup>a</sup>	56.716 (9, 256)***	73.971 (5, 260)***

<sup>a</sup> \*\*\* =  $P < 0.001$ .

comm.) stated that the differences in rump color were between those found on I. Negro and on I. Afuera and I. Zapato combined. Therefore, using single-variate analysis of variance we compared the 27 birds from I. Negro with 19 combined from I. Afuera and I. Zapato. Only rump color showed a significant difference ( $P < 0.05$ ). We concluded that for the morphological comparison between summer and winter populations on Guadalupe, it was relatively safe to combine the birds from islots Negro, Afuera, Zapato and other sites into a single "summer breeding" sample.

We analyzed multivariate differences between summer and winter samples by discriminant function analysis. The analysis was repeated, once with all nine characters and once with only the five mensural variables (Table 2). In both cases the differences between summer and winter breeders were highly significant ( $P < 0.001$ ).

The discriminant weights (Table 2) maximized the between-group difference relative to that within groups and could be used to separate the two samples. The discriminant analysis was specific for the Guadalupe samples; it could not be used to classify specimens from outside that area. Character values for each of the Guadalupe Island specimens were multiplied by the appropriate discriminant weight and the resulting products summed so that a single discriminant score was obtained for each specimen. If the sum was less negative than the

middle value, the specimen was classified with the summer population, but if the sum was more negative, it was classified with the winter population, regardless of the specimen's origin. The purpose was to see whether summer and winter breeding birds were classified correctly. With all characters in the discriminant function, 94.6% of summer birds and 90.5% of winter birds were correctly classified (Table 3). With only the five mensural characters, 87.6% of summer birds and 89.8% of winter birds were classified correctly. Overall, there was only a small amount of phenetic overlap between the two populations when measured multivariately.

#### DISCUSSION

In overall similarity of breeding-season samples, Leach's Storm-Petrel varies clinally from the Aleutian Islands south through the Farallon Islands. Geographic variation in this region is gradual. Northern birds tended to have the longest wings, largest bills, and longest tarsi, while southern ones were the smallest in these characters. Ainley (1980) believed this trend may be relative to an approximately north-to-south increase in sea surface temperature during the egg-laying period.

In the canonical variates analysis of all nine characters, the Los Coronados and San Benitos populations formed a distinct phenetic subset. In the analysis using only wing length, bill

TABLE 3. Results of discriminant classification analysis of Guadalupe Island summer- and winter-breeding populations of Leach's Storm-Petrel.

	Classified as summer	Classified as winter
Nine characters		
Collected in summer	122 (94.6%)	7 (5.4%)
Collected in winter	13 (9.5%)	124 (90.5%)
Five characters		
Collected in summer	113 (87.6%)	16 (12.4%)
Collected in winter	14 (10.2%)	123 (89.8%)

length, bill depth, tarsus length, and tail length, these two populations aligned closely with the clinal pattern existing among populations to the north. The distinguishing characters for the Los Coronados and San Benitos birds were a darker rump, slightly more rounded wing, and slightly deeper notch to the tail fork.

Guadalupe Island supports two populations of *O. leucorhoa*, one that breeds in winter and the other in summer. Birds from both populations were distinct morphologically from other populations in the eastern North Pacific and North Atlantic, a distinction that occurs because the Guadalupe birds are smaller in almost all mensural characters. The two populations were also distinct from one another; the summer breeding birds were smaller on average in all size characters except tarsus length. Of the two, the winter population was more similar to the others in this study, which suggests that the winter population was derived more recently. The summer population probably diverged relatively early in the evolution of Leach's Storm-Petrel in this region.

The North Atlantic Ocean breeding population was separated from others in this study by a relatively great geographic distance. It was quite similar to the Aleutian Islands population, however, and seemed to be a northward continuation of the phenetic trend seen for the Pacific populations. The evolutionary derivation of the North Atlantic population is not clear. Similarities with the Aleutians population may be due to a comparatively recent evolutionary divergence from North Pacific stock, or to natural selection by factors that are similar in both regions.

The comparison of phenetic and geographic distance supports a relatively continuous geo-

graphic variation among populations from the Aleutians south to the Farallons. Geographic and phenetic distance are correlated for these populations. The phenetic-geographic continuum is disrupted when more southern populations are considered. With all characters included in the measure of phenetic distance, populations from Los Coronados, San Benitos, and Guadalupe islands fall outside the primary phenetic-geographic distance pattern. This suggests divergence from the selection or gene-flow regime of the more northern populations. When the five mensural characters with lowest coefficients of variation are used, the Los Coronados and San Benitos populations join the primary pattern. Only the two Guadalupe populations are excluded from the main phenetic-geographic trend. The Guadalupe populations are phenetically shifted and not just the end point of a geographic continuum. In the region between the Aleutians and the Farallons, populations may be responding to natural selection due to environmental factors that vary broadly, such as marine climate, and there may be gene flow among populations. Our evidence suggests, however, that different selection factors and reduced gene flow exist for the Los Coronados-San Benitos assemblage, the Guadalupe/summer population, and the Guadalupe/winter population. The large number of recent storm-petrel species (5) in this southern region, compared with the north (2), further indicates a difference in selection factors.

The clinal trend may be explained by Bergmann's ecogeographic rule, namely that endotherms in colder climates are larger than members of the same species in warmer regions (Mayr 1963; see also James 1970). The Los Coronados and San Benitos populations are similar to one another, differing from the others primarily in rump color. It is not clear what selection factors would account for a preponderance of dark-rumped birds in this region (including three other species). Perhaps rump color is related to individual recognition or is selectively neutral. Whatever the explanation, it must consider the fact that predominantly white-rumped and dark-rumped individuals nest separately on the islets off Guadalupe Island during the summer breeding period. If the five mensural characters reflect overall body size, however, then the Los Coronados and San Benitos populations fit into a clinal trend that

may conform to Bergmann's rule. The two Guadalupe populations also correlate weakly with the rule. We say "weakly" because individuals in both populations are smaller than the others in this study but the populations are not the southernmost. The water is cooler here, however, than for the more southern populations closer to the Baja California coast. In accordance with the temperature relationship, summer birds are on average smaller than winter birds; although they breed at the same latitude, summer birds reproduce at the warmest time of year. On the other hand, the North Atlantic population was very similar to the northernmost Pacific population, even though the two are separated by a great distance. Other factors such as migration distance and climate during the nonbreeding season (e.g. Fretwell 1972) may affect body size and proportions, but we have at present no information on the contribution of these factors.

In general, populations typically intergrade along geographic or ecologic chains. Phenetic and genetic variation among intergrading populations may be smoothly clinal or may form more abrupt step clines (Mayr 1963, Endler 1977, Wright 1978). Endler (1977) and others have argued that the effect of gene flow can be small and that to have much effect selection must be weak and mean gene-flow distance large. Depending on the selection gradient, geographic differentiation can be strong even though gene flow may exist among populations. Clines may be shifted by the presence of a partial barrier or a reduction in population size. Certainly, with populations breeding on islands there are barriers to dispersal. This is true if the populations are philopatric seabirds or land birds restricted by reduced over-water dispersal. Also, island populations are prone to founder effects when new island sites are established by very small numbers of colonizers. The preponderance of dark-rumped individuals on Los Coronados and San Benitos islands, and in subpopulations at Guadalupe (see Ainley 1983), may be due to a founder effect. Similarly, if the few individuals reported to be breeding near San Miguel Island (Fig. 1) in the northern Channel Islands group (Hunt et al. 1980) represent the beginning of colonization in that area, the resulting population could carry distinguishing traits of the founders. (The San Miguel Island population may not be a new

population; it could be dying out or it could simply never have been well established.)

It would be interesting to compare geographic variation in an oceanic species with that of land birds in a similar geographic setting. Unfortunately, no land birds have the same breeding distribution as Leach's Storm-Petrel. Comparisons can be made, however, with species of migratory land birds that return to the same area to breed each year. For instance, Power (1970) examined geographic variation in the Red-winged Blackbird (*Agelaius phoeniceus*) in central North America, and Barlow and Power (1970) studied the Red-eyed Vireo (*Vireo olivaceus*) and the Philadelphia Vireo (*V. philadelphicus*) in a transect across Canada. The degree of differentiation found for the Red-winged Blackbird and Red-eyed Vireo in the areas studied was roughly similar to that found for Leach's Storm-Petrel in the area from the Aleutians to the Farallons, and including the Los Coronados and San Benitos islands when only the five-character subset is used. On the other hand, for certain nonmigratory populations of land birds on islands, geographic differentiation seems to be much greater than for seabirds on islands or land birds on a continent. Power (1979), for example, demonstrated the effect of isolation on a resident land-bird species by comparing geographic variation among island and mainland populations of the House Finch (*Carpodacus mexicanus*). The extent of differentiation over the range of Leach's Storm-Petrel from the Aleutians to the Farallons is about what is found for the House Finch over the much smaller area of the California Islands from San Miguel in the north to Los Coronados in the south.

San Benitos and Guadalupe islands emerge as influential in the evolution of Leach's Storm-Petrel, as they have for many land birds (Power 1980). For example, the San Benitos populations of the House Finch and Rock Wren (*Salpinctes obsoletus*) are differentiated and tend to be phenetically intermediate between populations on Guadalupe and those on the other California Islands. For Leach's Storm-Petrel, the San Benitos population, along with that from Los Coronados, is distinct from the others, although it is not phenetically intermediate. The uniqueness of the avifauna of Guadalupe Island has been recognized for over a century (Ridgway 1876). The Leach's Storm-Petrel pop-



ulations from that island are strongly differentiated, as are the resident land birds. The interesting fact about the storm-petrel is that two differentiated populations are seemingly separated not by geographic isolation but by the temporal aspects of their breeding schedules.

*Comments on taxonomy.*—The subspecific taxonomy of *Oceanodroma leucorhoa* is confusing and has been debated recently (Ainley 1980, 1983; Bourne and Jehl 1982; Jehl and Everett 1985; see also A.O.U. 1957, Hubbs 1960, Palmer 1962). There appears to be a phenetic break between the Aleutians-to-Farallons and the Los Coronados-San Benitos assemblages. Evidence exists that breeding may take place on the California Channel Islands, which are geographically between these two assemblages, but the populations are small and what role they may have in the phenetic picture is not clear. Hunt et al. (1980) reported occurrences of Leach's Storm-Petrel in the Channel Islands region. In 1976 and 1977 they captured six individuals on Prince Island; one bird had a well-developed brood patch. A specimen in the National Museum of Natural History taken on 14 May 1968 from Castle Rock was the first known breeding record from the area; it was taken from a rock crevice and had a brood patch. (Prince Island and Castle Rock are both adjacent to San Miguel Island.) Hunt's group also captured Leach's Storm-Petrels off Santa Barbara Island for the first time in 1978 and reported that the species may breed there in small numbers. Clearly, there is not a significant breeding population in the Channel Islands, and the phenetic position of the presumed Channel Islands breeders remains problematical.

Another difficulty lies in establishing the extent of reproductive isolation between the two populations breeding on Guadalupe Island. Bourne and Jehl (1983) wrote, "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 variation in vocalizations." Our results suggest a tentative subspecific taxonomic arrangement for *Oceanodroma leucorhoa* within the study area. The subspecies and breeding localities are as follows:

*O. l. leucorhoa*: North Atlantic Ocean and eastern North Pacific Ocean from the Aleutians south to the Farallon Islands.

*O. l. chapmani*: San Benitos and Los Coronados islands.

*O. l. socorroensis*: Guadalupe Island, summer breeding.

*O. l. cheimomnestes*: Guadalupe Island, winter breeding.

Bourne and Jehl (1983) stated that "inasmuch as the winter breeders *cheimomnestes* 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." Our multivariate results show that the phenetic distinction relative to other populations in the eastern Pacific region we studied is sufficient to warrant named designation.

#### ACKNOWLEDGMENTS

We acknowledge the persons and institutions who made specimens available: L. C. Binford (California Academy of Sciences), R. W. Campbell (Victoria Provincial Museum), N. K. Johnson and V. M. Dziadosz (Museum of Vertebrate Zoology), S. L. Olson and R. L. Zusi (U.S. National Museum of Natural History), K. C. Parkes and J. Loughlin (Carnegie Museum of Natural History), R. A. Paynter (Museum of Comparative Zoology), A. M. Rea (San Diego Museum of Natural History), R. W. Schreiber (Los Angeles County Museum), L. L. Short and J. Farrand (American Museum of Natural History), and D. E. Willard (Field Museum of Natural History). J. R. Jehl, Jr., and R. G. Strauch, Jr., reviewed an earlier draft of the paper. This is contribution No. 240 of the Point Reyes Bird Observatory.

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APPENDIX 1. Means of characters by locality. Samples have had missing data estimated, not skipped, in calculating means. See Methods for explanation of character (columns) and locality (rows) codes.

	WL	BL	BD	TR	TL	DF	WS1	WS2	RC
ALEU	155.3	15.69	5.73	24.01	78.24	16.17	-10.59	-0.57	2.63
NATL	157.2	16.03	5.93	24.13	79.87	17.84	-10.98	-0.19	2.51
SLAZ	151.6	15.61	5.82	23.55	76.58	17.31	-10.58	-0.41	2.47
FORI	151.6	15.33	5.63	23.49	76.96	18.92	-10.63	-0.65	2.71
BCOL	150.0	15.30	5.55	22.90	74.94	16.49	-8.86	1.51	2.67
WASH	147.6	15.12	5.62	23.14	75.53	18.39	-10.74	-1.57	2.65
OREG	149.8	15.35	5.50	23.20	75.55	16.57	-9.28	0.64	2.89
NCAL	150.1	15.19	5.63	22.90	74.74	16.86	-10.03	-0.04	3.41
FARA	150.7	15.57	5.76	22.78	77.48	17.90	-9.89	-0.15	4.32
LCOR	152.5	15.51	5.61	22.54	76.50	18.67	-9.37	0.81	9.72
SBEN	150.1	15.32	5.67	22.33	75.74	18.52	-8.83	1.36	10.81
GUAS	144.0	14.27	5.09	20.76	71.33	14.64	-8.38	1.34	6.15
GUAW	146.4	14.94	5.18	22.07	75.48	15.21	-9.24	0.20	4.44

APPENDIX 2. Collecting localities for samples from Guadalupe Island, as recorded on specimen labels.

Locality	No. summer breeders	No. winter breeders
Islote Negro	27	74
Islote Zapato	16	—
Islote Afuera	3	5
Melpomene Cove	—	31
NE Anchorage	31	14
Guadalupe Is.	11	3
Gargoyle Rock	10	3
East side	18	2
Lava Pinnacle	2	—
Outer Guadalupe Is.	8	—
Elephant Beach	3	—
Yellow or Ship Pt.	—	1
Barrack's Cove	—	1
South end	—	3