

GEOGRAPHIC VARIATION IN LEACH'S STORM-PETREL

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ABSTRACT.—A total of 678 specimens of Leach's Storm-Petrels (*Oceanodroma leucorhoa*) from known nesting localities was examined, and 514 were measured. Rump color, classified on a scale of 1–11 by comparison with a series of reference specimens, varied geographically but was found to be a poor character on which to base taxonomic definitions. Significant differences in five size characters indicated that the presently accepted, but rather confusing, taxonomy should be altered: (1) *O. l. beali*, *O. l. willetti*, and *O. l. chapmani* should be merged into *O. l. leucorhoa*; (2) *O. l. socorroensis* should refer only to the summer breeding population on Guadalupe Island; and (3) the winter breeding Guadalupe population should be recognized as a "new" subspecies, based on physiological, morphological, and vocal characters, with the proposed name *O. l. cheimomnestes*.

The clinal and continuous size variation in this species is related to oceanographic climate, length of migration, mobility during the nesting season, and distances between nesting islands. Why oceanitids frequenting nearshore waters during nesting are darker rumped than those offshore remains an unanswered question, as does the more basic question of why rump color varies geographically in this species. *Received 15 November 1979, accepted 5 July 1980.*

DURING field studies of Leach's Storm-Petrels (*Oceanodroma leucorhoa*) nesting on Southeast Farallon Island, California in 1972 and 1973 (see Ainley et al. 1974, Ainley et al. 1976), several birds were captured that had dark or almost completely dark rumps. The subspecific identity of the Farallon population, which at that time was *O. l. beali*, was thus problematic, because the presence of dark-rumped birds indicated inclusion in *O. l. willetti* (A.O.U. 1957). Not long after the capture of these birds, the A.O.U. (1973) synonymized *O. l. willetti* with *O. l. beali*. This action, following the recommendation of Austin (1952), "solved" the immediate question, but the problem seemed worthy of further pursuit, as Crossin (1974) found it impossible to assign to any of five subspecies most specimens collected away from breeding sites. He thought that most subspecies of *O. leucorhoa* should be synonymized, a recommendation already made by Loomis in 1918. Van Rossem (1942), however, questioned the wisdom of synonymizing all subspecies, and, except for the recent decision on *O. l. willetti*, the A.O.U. (1957, 1973) has followed van Rossem's subspecific definitions. The present study tests Loomis' (1918) and Crossin's (1974) hypothesis that Leach's Storm-Petrel in the eastern North Pacific is a dichromatic species in which the proportions of color phases and mensural characters vary geographically in a cline, rather than there being the series of distinct populations currently recognized. I also compared vocalizations among birds from several localities and tried to reveal those factors that might account for geographic variation in this species.

METHODS

Eight measurements plus a classification of rump color were made on 514 specimens or live individuals separated into 13 samples. The Farallon Island sample included 48 live birds mist-netted on the nights of 29–31 May 1978. All other samples consisted only of study skins. The rump color of an additional 164 skins from Guadalupe Island was classified in order to clarify the relationships of the summer and winter breeding populations there. Only specimens collected on or immediately adjacent to a known breeding locality (i.e. the birds that flew aboard a boat anchored within a few hundred meters of shore) were used for measurement. Besides six standard measurements (Table 2), the shape (roundedness) of the wing tip was assessed by measuring the distance from the tip of primary 10 to the tips of 9 and 7; the greater the

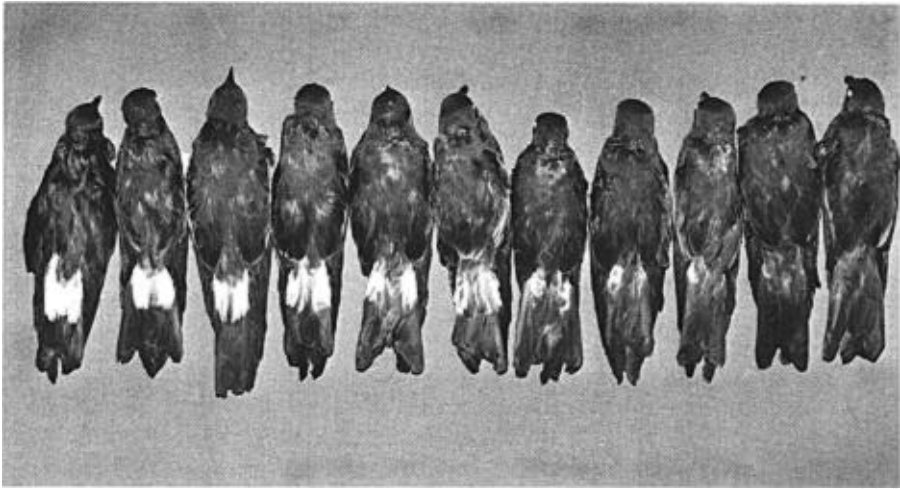


Fig. 1. The series of reference specimens (left to right, 1 to 11) showing color variation in *O. leucorhoa*.

difference in measurement the more pointed the wing. Statistical significance between samples was tested using Duncan's new multiple range test for a one-way classification of variance (Steel and Torrie 1960). Samples were compared at the 1% significance level.

I found, as did Crossin (1974), that female Leach's Storm-Petrels were slightly larger than males but that the difference was not statistically significant without very large sample sizes (over 80 individuals), and it did not vary geographically. I thus combined the two sexes for analysis; within all samples the sexes were represented about equally. This combination allowed me to use unsexed specimens, helped to increase sample sizes, and removed the problem of using incorrectly sexed specimens.

Rump color was classed by comparing specimens with a series of 11 reference skins. Each represented an approximately equal step in a continuum beginning with all upper tail coverts entirely white, except for the feather shafts, which may or may not have been white (class 1), and ending with all upper tail coverts entirely dark or concolorous with the back and tail (class 11). Specimens in the series (Fig. 1), all from the National Museum of Natural History, were as follows: 1 = USNM 201458, 2 = 543662, 3 = 132761, 4 = 545030, 5 = 544507, 6 = 545031, 7 = 543697, 8 = 543694, 9 = 543708, 10 = 543726, 11 = 543659. As for the intensity of a "bluish bloom" on the brown body color, a character that was given great importance in original descriptions of various subspecies and was most recently alluded to by Bourne (*in* Palmer 1962), I agree wholly with Crossin (1974) that it relates to the extent of feather wear and the age of specimens (not the age of the live bird) rather than to geographic variation.

Recordings of Leach's Storm-Petrel vocalizations were made by R. L. DeLong, Pacific Ocean Biological Survey Program (POBSP), at the Coronado and San Benito islands in May 1967 and at Guadalupe Island in June and October 1967, using a Uher Report-L 4000 tape recorder and microphone. I recorded vocalizations at the Farallon Islands in May 1975, using a Sony TC-800B recorder and an Altec microphone. Sonagrams of Flight Calls and burrow Chatters were made at the Museum of Vertebrate Zoology, Berkeley, using the wide audio band on a Kay Instrument Company Sonagraph.

Populations at Guadalupe Island.—Two populations of *O. leucorhoa* breed at different seasons on Guadalupe Island, but information about them, summarized by Crossin (1974), is fragmentary. I considered specimens collected on or near the island from October through April to be from the winter population and those collected from May through September to be from the summer population. This was deduced by comparing the proportions of color morphs from month to month (Table 1), a procedure suggested by Crossin's discovery that these proportions seemed to differ between the two populations. A clear separation became obvious (Fig. 2): the colors of summer birds were spread between classes 1–11 but concentrated bimodally between 2–3 and 7–10. Supporting this separation were the facts that (1) the only September specimens in the 10 collections searched were recently fledged (collection dates were within the last few days of that month); and (2) observations of fledglings by other persons, summarized by Crossin, also occurred late in September with occasional dates as late as early November. It appears that the peak of fledging of summer chicks occurs in very late September and early October. Extrapolating

TABLE 1. The number of individuals of each color morph in samples of *O. leucorhoa* collected at Guadalupe Island.

Months	Color morphs ^a											Total specimens
	1	2	3	4	5	6	7	8	9	10	11	
October		3	6	12	10	6	1	1				39
November			1	3	5	7	1					17
December	1	4	4	10	8	3						31
January		2	2	4	4	4	1					17
February	1		1	3	2	3	2	1				13
March	1	(1)	(1)	2	2	1	1					9
April		1		(1)	1	1						4
May	1	8						1	1			11
June	2	12	12	2	2	2	7	11	15	7	2	74
July		7	1	2	1			2	1			14
August	1	5				1	6	9	9	3	1	35
September	(1)	(1)		(1)								3
Total												267

^a Numbers in parentheses are fledglings.

from information on breeding phenology at the Farallons (Ainley et al. 1974), egg laying of the summer breeding population of Guadalupe should occur from late May to the end of June. Crossin (1974: 174) surmised the egg-laying peak to be late in the third week of June 1968, when the POBSP made a visit to Guadalupe. As for the winter population, information given by Crossin (1974: 174), plus the dates of three fledging specimens I inspected, suggested that most chicks fledge from early March to mid-April. The latest April specimen was recently fledged and the other three April specimens (adults) were at a stage of molt or showed a degree of feather wear that, judging from information on molt in *O. leucorhoa* at the Farallons (Ainley et al. 1976), clearly placed them in the winter breeding population. Again using the Farallon data, egg laying in the summer population of Guadalupe should occur from mid-November through December. Crossin reported no eggs present during a POBSP survey on 21 October 1967.

The second type of information that supported my division of breeding populations is the fact that no adult specimens of *O. leucorhoa* have been collected (or at least were among the 267 specimens I examined) at Guadalupe during the periods 25 April–28 May and 31 August through mid-October. This is consistent with the supposition that May and October mark the initial month of the summer and winter breeding seasons, respectively. During those months adults would make sporadic visits at night to court and prepare nest sites and would not remain during the day. The few adults from the previous breeding seasons still providing for late chicks would visit only for a few hours at night, and probably not every night, to feed their chicks (which would be near to fledging). Thus, persons intent on collecting storm-petrels, and who would probably undertake the hazardous trip ashore only during daylight, would be unlikely to find petrels. Hence, fewer specimens are available from the initial months of breeding seasons. On the other hand, I do not know how many collectors visited Guadalupe during those periods; the POBSP, however, found only six storm-petrels during the day on their October visit.

RESULTS

Rump color variation.—The proportions of rump color classes gradually changed with decreasing latitude, the Guadalupe samples excepted (Fig. 2). From the Aleutians to Sitka (St. Lazaria Is.), as well as in the North Atlantic, classes ranged from 1 to 4, and 2 and 3 were dominant. From Forrester Island, Alaska south to northern California, color classes ranged from 1 to 5; initially 2 and 3 prevailed, but with decreasing latitude 4 and 5 increased and class 2 decreased. This shift toward darker rumps continued, with much larger steps, from the Farallons to the San Benitos. Only two skins from San Miguel Island were available, but four birds mist-netted and released in 1976–77 were “white-rumped” (S. Speich pers. comm.), i.e. among classes 2–7. As for Guadalupe Island, the distribution of classes differed between the two samples (winter vs. summer, see Methods) and showed no relationship to

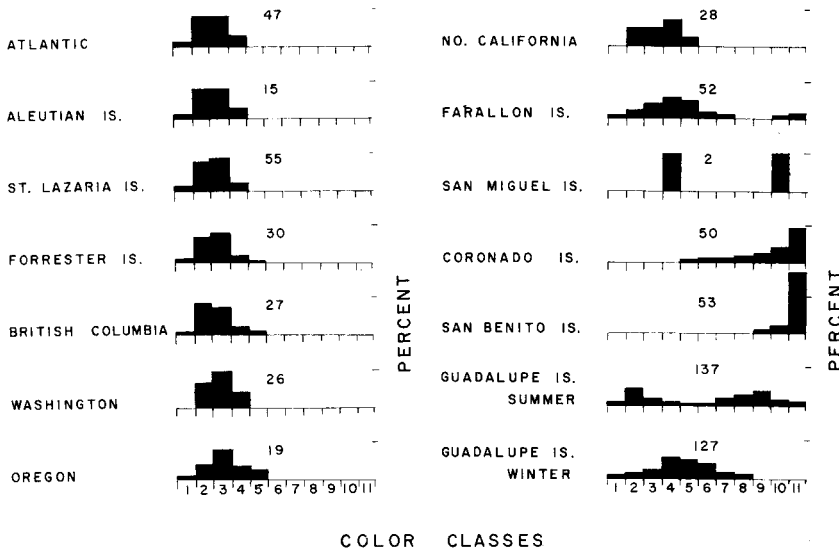


Fig. 2. The proportion of color classes in samples of *O. leucorhoa*.

the clinal change evident in the other Pacific samples. The Guadalupe winter and Farallon samples were very similar except that only the latter contained the very darkest rump classes. The pattern in the Guadalupe summer sample resembled none of the others.

Except for Guadalupe, where samples obviously differ from one another and from all others, Loomis' (1918) proposal appears more or less correct, i.e. that Leach's Storm-Petrels in the eastern North Pacific are a single polychromatic population in which the proportion of dark phase (i.e. dark-rumped) individuals increases with decreasing latitude. Thus, although rump color was central in the original descriptions of several subspecies of Leach's Storm-Petrel, it should be accorded little more taxonomic significance than in other procellariiformes showing similar color variation, for example the Northern Fulmar (*Fulmarus glacialis*, Palmer 1962: 142–143), Wedge-tailed Shearwater (*Puffinus pacificus*, Murphy 1951), and White-throated Storm-Petrel (*Nesofregatta albigularis*, Crossin 1974). This is especially so because every possible gradation between totally white- and totally dark-rumped individuals occurs. Furthermore, excluding Guadalupe samples, the continual shift in proportions of color variants indicates that some factor selecting for dark rumps comes gradually to bear on populations, or conversely the factor selecting for white rumps lessens, rather than there being distinct, all-inclusive differences from one population to another. The fact that Guadalupe populations depart markedly from the pattern shown in adjacent coastal populations may help to explain the color variation.

Size variation.—Average measurements of all characters were largest in the Aleutian Island and Atlantic samples (Table 2). In the latter, the tail fork was deeper than in many but not all Pacific samples. Within the coastal Pacific samples (Guadalupe not included), measurements changed gradually with decreasing latitude, but first a decrease occurred through several samples, followed by an increase. For example, the culmen was largest in the Aleutian (52°–59°N) and St. Lazaria (57°) samples, decreased to Forrester Island (55°), remained at about that level to northern

California, and then increased to a level shared by the Farallon to San Benito samples. The same general pattern was apparent in all other characters, except tarsus length and wing shape. Tarsus length gradually and consistently declined with decreasing latitude, with the exception of the Coronados' sample, where it was inconsistently large. Wing shape showed little in the way of gradual change; rather, samples separated into two groups, birds with pointed wing tips (Atlantic and Aleutians to northern California) and birds with round wing tips (Farallon to San Benito). Within the latter samples, roundedness increased with decreasing latitude. Size characters in the Guadalupe samples were consistently smaller than in almost all others. The summer breeding birds were, in turn, always smaller than the winter birds. The summer birds had the roundest wings of all samples; wing shape in winter birds was similar to the Farallon sample.

Significant differences in the five most reliable mensural characters are summarized in Table 3; due to large CV's, depth of tail fork and wing shape are excluded. From the Aleutians to northern California, and to a lesser degree to the San Benitos, the decreasing number of significant comparisons as one moves from left to right in the table indicates that samples are more easily separated as the actual geographic distance between sample sites increases. In most cases birds from adjacent colonies or nearby regions cannot be separated. There are, in addition, several unsampled nesting sites between the Aleutians and St. Lazaria (Sitka) and at least one between the Farallons and Coronados (San Miguel Island). Quinlan (pers. comm.) recently measured birds from the Prince William Sound area and found measurements to be intermediate between Aleutian and Sitka samples. This demonstrates further the clinal nature of geographic variation in this species. Is it possible then to distinguish any of the samples from the others?

Samples from St. Lazaria, Coronados, San Benitos, and Guadalupe (both seasons) are distinguishable at the 1% level from at least one other sample by at least one of five "reliable" characters (Table 3). It would be folly, however, to propose six subspecies, because placing an individual into one of the four presently recognized is virtually impossible (Austin 1952, Crossin 1974)! Here is a good example of why taxonomy at or below the species level in clinally varying populations is not the same problem in seabirds as it is in most landbirds. Seabirds are highly philopatric, and, because their breeding localities are islands (which, naturally, are disjunct), gene flow is very much disrupted and fragmented. When environmental factors vary slightly from one island to another, slight morphological differences between samples result. Often, as in the present species, these differences are recognizable only when the breeding locality of a specimen is known. The problem in Leach's Storm-Petrels is aggravated by the extensive range in latitude and environment of nesting islands (see Discussion). Such a range is shown in few other seabirds (another example is *Puffinus puffinus*). The resulting slight average differences in morphology between samples, which led to the description of an array of subspecies, no doubt underlies the taxonomic difficulties I am trying to overcome in this study.

Within Table 3, three groupings of samples emerge. The first, and largest, includes all samples except those from Guadalupe Island. Each sample is either similar in all respects to at least one other sample (e.g. Aleutian and eastern Atlantic samples) or is distinguishable from other samples only by virtue of one character (e.g. San Benito sample). In cases similar to the latter, while one character might on the average be different from another sample in the group, never does it differ consistently from *all*

TABLE 2. Measurements (mm) of Leach's Storm-Petrels; values given are $\bar{x} \pm SD$, the range, and the coefficient of variation. Also shown are average sea surface temperatures (National Marine Fisheries Service 1971).

Sample and temperature during egg laying	n	Wing length	Culmen chord	Bill depth	Tail length	Depth tail fork	Tarsus length	Difference in primary lengths ^a	
								10 vs. 9	10 vs. 7
North Atlantic 5.0°C	47	157.2 ± 3.9 146-164 2.5	16.0 ± 0.5 14.7-17.0 3.1	5.9 ± 0.3 5.5-6.4 4.8	79.7 ± 3.4 72.4-86.5 4.2	17.7 ± 2.7 12.7-22.5 15.2	24.1 ± 0.6 23.1-25.5 2.5	-11.0 ± 1.8 -6.6 to -14.5 16.4	-0.2 ± 2.6 -6.7 to +5.7 129
Aleutian Islands 6.0°C	15	155.3 ± 3.5 148-159 2.2	15.7 ± 0.6 15.3-16.5 3.8	5.7 ± 0.2 5.4-6.2 3.4	78.3 ± 3.4 76.0-84.4 4.2	16.0 ± 2.6 11.1-19.4 16.5	24.0 ± 0.7 23.1-25.6 2.9	-10.6 ± 2.0 -6.8 to -14.2 18.7	-0.6 ± 2.5 -4.3 to +5.3 414
St. Lazaria Island 9.5°C	55	151.5 ± 4.1 142-163 2.7	15.6 ± 0.5 14.4-16.6 3.1	5.8 ± 0.3 5.4-6.6 4.6	76.6 ± 4.4 71.5-84.3 4.4	17.6 ± 3.0 13.0-24.9 17.0	23.6 ± 0.7 22.3-24.8 2.9	-10.7 ± 2.1 -7.2 to -16.0 20.1	-0.4 ± 2.4 -6.7 to +5.1 605
Forrester Island 10.1°C	30	151.7 ± 3.4 146-157 2.2	15.3 ± 0.4 14.3-16.0 2.8	5.6 ± 0.3 5.2-6.1 5.1	76.8 ± 3.4 74.0-82.3 4.5	19.0 ± 3.2 12.2-25.6 17.0	23.5 ± 0.7 22.4-25.2 3.1	-10.7 ± 1.5 -6.6 to -12.6 13.8	-0.5 ± 2.1 -3.2 to +3.5 424
British Columbia 10.0°C	27	149.9 ± 3.8 142-159 2.5	15.3 ± 0.4 13.9-16.2 2.6	5.6 ± 0.3 5.0-6.0 5.0	74.9 ± 3.0 69.0-81.8 4.0		23.0 ± 1.1 20.3-24.5 4.8	-9.0 ± 2.2 -5.0 to -13.5 23.8	-0.5 ± 2.8 -3.0 to +5.8 186
Washington 12.9°C	26	147.6 ± 4.1 142-156 2.8	15.2 ± 0.5 14.3-16.0 3.1	5.6 ± 0.2 5.2-6.0 4.2	75.2 ± 2.2 71.4-80.3 3.0	18.4 ± 3.0 14.0-21.5 16.5	23.1 ± 0.6 22.5-24.1 2.4	-10.9 ± 1.7 -8.1 to -14.1 15.6	-0.7 ± 2.8 -7.2 to +2.4 393
Oregon 12.5°C	22	149.7 ± 3.7 144-155 2.4	15.3 ± 0.4 14.6-16.0 2.5	5.5 ± 0.2 5.1-5.8 3.9	75.8 ± 3.3 68.7-81.3 4.3	16.6 ± 2.3 12.3-22.0 13.9	23.1 ± 0.5 22.1-24.1 2.2	-9.2 ± 1.3 -8.2 to -10.6 14.1	-0.6 ± 2.0 -3.8 to +4.6 341

TABLE 2. Continued.

Sample and temperature during egg laying	n	Wing length	Culmen chord	Bill depth	Tail length	Depth tail fork	Tarsus length	Difference in primary lengths ^a	
								10 vs. 9	10 vs. 7
Northern California 12.3°C	36	150.2 ± 3.5 144-158 2.4	15.2 ± 0.5 13.8-16.0 3.0	5.7 ± 0.2 5.4-6.1 4.3	74.8 ± 2.6 69.0-79.8 3.5	16.9 ± 1.3 15.2-19.1 7.5	22.9 ± 0.6 21.2-24.1 2.7	-10.5 ± 1.7 -8.4 to -13.5 16.4	-0.5 ± 3.0 -4.9 to +6.0 446
Farallon Islands 11.8°C	54	150.7 ± 3.3 142-158 2.2	15.6 ± 0.4 14.5-16.5 2.8	5.7 ± 0.3 5.1-6.4 5.3	77.4 ± 2.8 73.6-84.8 3.6	18.1 ± 1.9 14.2-23.5 10.5	22.8 ± 0.5 21.7-23.8 2.2	-9.9 ± 1.6 -7.9 to -14.5 15.8	-0.2 ± 2.1 -4.3 to +5.4 106
San Miguel Island 16.0°C	2	146 ± 0.0	15.2 ± 0.4 14.9-15.5 2.8	5.3 ± 0.1 5.2-5.4 2.7	80.4 ± 5.7 76.4-84.4 7.0	20.5 ± 7.6 15.1-25.9 37.2	22.2 ± 0.2 22.1-22.4 1.0	-10.1 ± 2.6 -12.0 to -8.3 25.9	-0.1 ± 3.4 -2.5 to +2.3 394
Coronado Islands 18.5°C	50	152.7 ± 2.9 146-159 1.9	15.5 ± 0.5 14.7-16.8 3.0	5.6 ± 0.2 5.1-6.0 4.4	76.2 ± 3.3 71.3-83.6 4.4	19.6 ± 2.3 13.3-24.5 13.2	22.6 ± 0.6 21.1-23.8 2.7	-9.4 ± 1.3 -12.0 to -7.1 14.3	+1.1 ± 2.2 -3.8 to +4.7 198
San Benito Islands 16.8°C	53	150.2 ± 3.0 143-155 2.0	15.4 ± 0.5 13.6-16.1 3.1	5.7 ± 0.3 4.9-6.2 4.8	75.7 ± 2.7 68.4-82.2 3.6	18.8 ± 2.5 13.4-23.6 13.3	22.3 ± 0.9 19.4-24.4 3.9	-8.9 ± 1.5 -11.5 to -6.3 17.2	+1.1 ± 2.3 -2.9 to +8.3 211
Guadalupe Island summer 17.4°C	50	144.6 ± 3.3 139-152 2.3	14.3 ± 0.5 13.5-15.7 3.7	5.2 ± 0.2 4.7-5.7 4.2	71.8 ± 2.6 65.6-77.0 3.7	15.0 ± 2.1 11.0-18.1 13.8	20.7 ± 0.7 19.3-23.1 3.6	-8.4 ± 1.6 -11.1 to -5.4 19.0	+1.2 ± 2.5 -4.9 to +6.4 206
Guadalupe Island winter 15.7°C	50	146.4 ± 3.3 140-154 2.3	14.9 ± 0.5 13.5-16.1 3.6	5.3 ± 0.3 4.6-6.1 6.4	75.8 ± 2.8 69.4-80.7 3.7	16.1 ± 2.3 11.8-23.0 14.4	22.1 ± 0.5 20.8-23.3 2.3	-9.8 ± 1.4 -14.1 to -7.8 14.7	-0.6 ± 2.0 -5.3 to +3.4 326

^a The signs of the mean and range indicate whether the tip of the 10th primary falls short of (-) or exceeds (+) the tip of the other (9th or 7th).

TABLE 3. Number of reliable mensural characters (bill depth and culmen, wing, tarsus, and tail length) distinct ($P < 0.01$) when each sample is compared against all others using Duncan's new multiple range test.

	North Atlantic	Aleutian Is.	St. Lazaria I.	Forrester I.	British Columbia	Washington	Oregon	No. California	Farallon Is.	Coronado Is.	San Benito Is.	Guadalupe I., Summer	Guadalupe I., Winter
North Atlantic	—												
Aleutian Islands	0 ^a	—											
St. Lazaria Island	4	1	—										
Forrester Island	5	0	1	—									
British Columbia	5	3	2	0	—								
Washington	5	4	4	1	0	—							
Oregon	5	2	1	0	0	0	—						
Northern California	5	4	2	1	0	0	1	—					
Farallon Islands	5	2	1	1	2	3	1	2	—				
Coronado Islands	5	1	2	1	1	1	1	2	0	—			
San Benito Islands	5	3	1	1	1	1	2	1	1	1	—		
Guadalupe Island, Summer	5	5	5	5	5	5	5	5	5	5	4	—	
Guadalupe Island, Winter	5	5	4	4	4	3	4	4	5	4	4	3	—

^a Significant at $P < 0.05$.

samples. The Guadalupe samples, however, are easily distinguishable. They differ from each other and from all other samples on the basis of at least three, and often more, characters. Van Rossem (1942), Austin (1952), and Crossin (1974) all agreed that Guadalupe *O. leucorhoa* are distinct, but as first surmised by Crossin and shown here, the winter and summer populations are far more different morphologically from one another than are samples from the Aleutians to San Benitos.

Variation in vocalizations.—No studies have critically analyzed the behavioral significance of vocalizations in storm-petrels. In my experience with five species, two important calls, and the two that are perhaps the most frequently used, are Chattering and the Flight Call. The first is given only in the burrow, usually when both members of the pair are present, and often they duet. The message (cf. Smith 1977) in the call must have to do with association. The second, the Flight Call, is usually given as a bird flies about in the colony, especially when it passes over its burrow in a repeating circle. It is also given from the burrow, especially when a flying bird calls nearby. These and other contexts suggest this call to be the storm-petrel *song*, in the classical sense of territory and self-declaration.

Tape recordings of Chattering in *O. leucorhoa* were available from five populations. Some qualities of the calls are compared in Table 4, and sonagrams are presented in Fig. 3; sonagrams of calls from North Atlantic *O. leucorhoa* are presented in Hall-Craggs and Sellar (1976). When Chattering, a storm-petrel utters a rapid series of chirps or clicks, ranging from about 0 to 2 kHz, and then produces a long wheeze as it takes a breath. Series of chatters and wheezes may go on continuously for many minutes. In the Atlantic and coastal Pacific samples, the frequency of chatters is 15–23/s ($\bar{x} = 19.6$), and a breath lasting about 0.4 s is taken every 2–4 s. When the bird is taking a breath, the wheeze is as loud as the chatters. All chatter notes are approximately the same sound except that the first one after a breath is a bit stronger than the others. In the two Guadalupe populations, the

TABLE 4. Characteristics of burrow Chattering in different Leach's Storm-Petrel populations.

Population	Calls/ individual	Chatters/s ^a	Time between breath onsets (s)	Breath duration (s)	Breath note audible ^b	Note at start vs. others
Iceland ^c	4+/4+	15-22	3.1-4.8	0.4-0.6	Yes	Slight emphasis, same quality
Farallon Islands	12/5	17-21 (18)	1.0-3.0	0.2-0.4	Yes	Slight emphasis, same quality
San Benitos Islands	7/3	22-23 (22)	3.3-3.9	0.40	Yes	Slight emphasis, same quality
Guadalupe, summer	4/2	26-27 (26)	5.1	0.6	Barely	Strong emphasis, different note
Guadalupe, winter	9/4	25-27 (26)	4.3-4.6	0.6-0.8	Barely	Strong emphasis, different note

^a The range and mean number of chatters/s are given.

^b To human ears.

^c From Hall-Craggs and Sellar 1976.

frequency of chatters is more rapid, ranging 25-27/s ($\bar{x} = 26.0$), and a breath is taken every 4-5 s. The wheeze at inhalation is barely audible and lasts about 0.6 s. The first note after inhalation is distinctly different from the chatters that follow and is much louder. Chattering in the two Guadalupe populations is similar, and it differs from that in the other samples.

Tape recordings of the Flight Call in *O. leucorhoa* were analyzed for six populations (Table 5 and Fig. 4). In all cases the length of the call was about equal and notes ranged from 0.5 to about 3.5 kHz. The quality of notes was also similar, except for the Guadalupe winter birds, whose notes were raspy and much less "melodious." Other major differences arose in the total number of notes in a call and the location of the accent or emphasis. In North Atlantic and Pacific coastal populations, calls consisted of 9-12 notes (usually 11) with accents placed on 3 notes, 1 at the start and 2 in the middle. The call of Guadalupe summer birds was much different. There were many more notes (11-20 but usually 17), and emphasis was placed on only 1 note about two-thirds through the sequence. In the winter birds, not only were notes more numerous and very raspy, but emphasis was placed on 4 notes, 1 at the start and 3 at the end.

Systematic revision.—The results indicate that the taxonomy of *O. leucorhoa* should be reorganized. The revision proposed below 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). The proposed revision emphasizes the evolutionary pressures that account for geographic variation in these populations, an important goal in modern systematics (Selander 1971).

Oceanodroma leucorhoa leucorhoa Vieillot:
ocean near Picardy, France.

This population breeds in the North Atlantic and in the North Pacific from the Aleutian Islands northeast to southeast Alaska and south on coastal islands to Islas San Benitos, Mexico (and probably southwest from the Aleutians to southern Japan

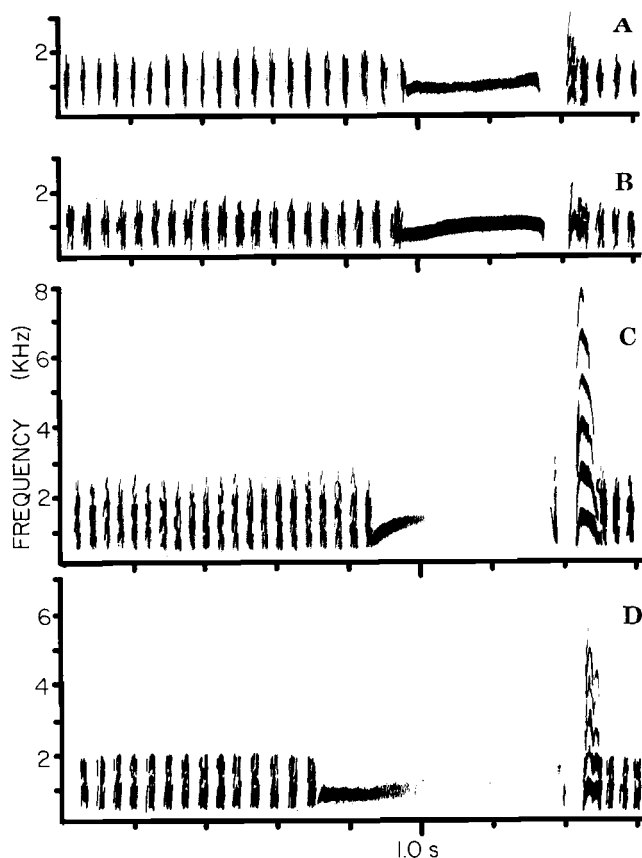


Fig. 3. Sonograms of Chattering in *O. leucorhoa* nesting at the Farallon Islands (A); San Benito Islands (B); and Guadalupe Island, summer (C) and winter (D).

TABLE 5. Characteristics of Flight Calls in different Leach's Storm-Petrel populations.

Population	Calls/ individual	Duration (s)	Total notes ^a	Number emphasis notes	Emphasis notes
Iceland ^b	1/1	1.3	10	3	1, 4, and 5
Farallon Islands	9/3	1.2-1.3	10-12 (10.7)	3	1, 4, and 5 or 1, 5, and 6
Coronados Islands	2/1	1.3	12	3	1, 5, and 6
San Benitos Islands	16/7	1.2-1.5	9-12 (10.7)	2-3	1, 4, and 5 or 1, 5, and 6 or 1 and 6
Guadalupe Island, summer	8/6	1.2-1.6	11-20 (16.8)	1	7 16 11 15 12 13
Guadalupe Island, winter	4/2	1.4	14	4	1 12 14

^a The range and mean number of notes are given.

^b From Hall-Craggs and Sellar 1976.

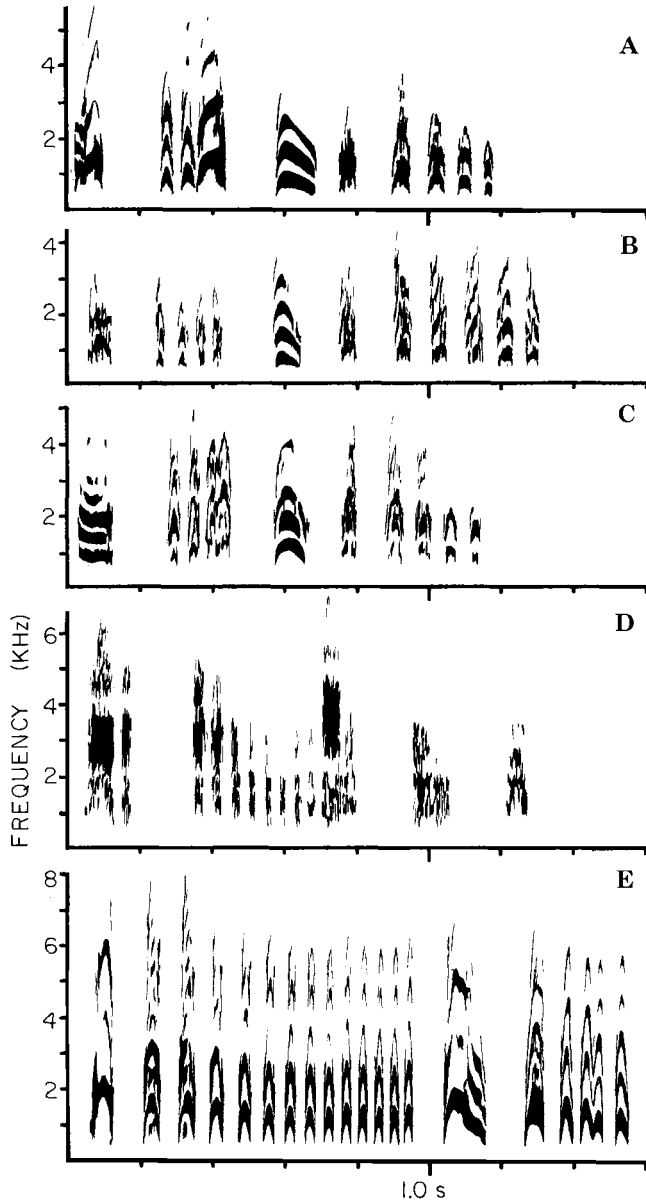


Fig. 4. Sonograms of Flight Calls in *O. leucorhoa* nesting at the Farallon Islands (A); Coronado Islands (B); San Benito Islands (C); and Guadalupe Island, summer (D) and winter (E).

and Korea). Individuals nesting on North Atlantic islands winter and molt in the equatorial Atlantic. Individuals nesting on Pacific islands do likewise in the equatorial Pacific, with dark-rumped birds wintering at the eastern portion of this region (Crossin 1974, Ainley pers. obs.).

Size varies continuously and clinally from the Atlantic and Aleutian islands south to the San Benitos. The largest individuals, those from the Aleutians and North Atlantic, have white rumps. South of the Aleutians, rump coloration darkens at first

very gradually but accelerates rapidly with decreasing latitude beginning at the Farallons; most birds at the southern extreme of the population's range have entirely dark rumps. Much the same trend apparently occurs with decreasing latitude in the western Pacific (Austin 1952), but further study is required. The Flight Call, or song, is virtually the same throughout the range in the Atlantic and the northern and eastern Pacific, as is the Chattering vocalization.

This grouping thus synonymizes *O. l. beali* Emerson (type locality Sitka, Alaska) and *O. l. chapmani* Berlepsch (type locality San Benito Is., Baja California) under *O. l. leucorhoa* and supports the recent incorporation of *O. l. willetti* van Rossem (type locality Coronados Is., Baja California) into *O. l. beali* (*O. l. leucorhoa*).

Oceanodroma leucorhoa socorroensis Townsend: ocean near Socorro Is., Mexico (Synonym: *O. l. kaedingi* Anthony).

This population breeds on islets off Guadalupe Island, Mexico, and perhaps formerly on the main island itself, during the summer (from May into October). Birds winter and molt in the equatorial Pacific, primarily in the eastern portion of that region (Crossin 1974). Individuals are smaller in all measurements than in any other population. Rump color indicates all variations with two distinct peaks, one at the white and the other at the dark end of the scale. The song of *O. l. socorroensis* is similar to but clearly distinct from that of all other subspecies. Another call, Chattering, is similar in this and the following subspecies but is different from that in the others.

***Oceanodroma leucorhoa cheimomnestes* subsp. nov.**

Type: Adult male; USNM 305762, among the earliest collected specimens I inspected; Guadalupe Island, Mexico; 2 March 1911; collected by P. I. Osburn.

Subspecific characters: Similar in color variation to *O. l. leucorhoa* in central California (Farallon Islands), except that individuals have at least some white in feathers at either side of the rump, i.e. totally dark individuals are lacking. Most measurements smaller than in all other populations except *O. l. socorroensis*; in particular, wing and tarsus length separate individuals from northern and bill measurements from southern *O. l. leucorhoa*. Differs morphologically from *O. l. socorroensis* by having a distinctly longer bill, tail, and tarsus and more pointed wings. The song is distinct from that in all other populations, and the Chatter vocalization is similar only to *O. l. socorroensis*. The only temperate breeding storm-petrel known to nest during the winter.

Measurements of type: wing 142; culmen 14.8; bill at base 5.4; tarsus 22.3; tail 71.0; depth of tail fork 15.2; color class 4.

Specimens examined: AMNH 131326, 131324, and USNM 305763, collected 2 March 1911, plus many specimens, all collected more recently, in USNM, AMNH, MVZ, LACM, SDNHM, and one at CAS (28152); AMNH 131317, a male, collected in the "vicinity of Guadalupe Island" on 5 March 1911 is identifiable as *O. l. leucorhoa*.

Remarks: Crossin (1974), who suspected the distinctiveness of this population, proposed that the name *O. l. kaedingi* Anthony be reinstated for it. This name had earlier been synonymized under *O. l. socorroensis* (van Rossem 1942, A.O.U. 1957). The type of *kaedingi* (Carnegie Museum 22219) and a large series of paratypes, all

collected at sea north of Guadalupe on 25 July 1897, are from the summer population, as is the type of *socorroensis* (USNM 117497; wing 140, culmen 14.0, bill at base 5.0, tarsus 19.6, tail 70.0, depth of fork 12.5). Because *socorroensis* was described before *kaedingi*, its name takes priority for Guadalupe's summer population, leaving the winter population unnamed.

Three other oceanic birds also exhibit temporally distinct breeding populations: *Pterodroma mollis* in Madeira (Bourne 1957), *Macronectes (giganteus and halli)* on Macquarie Island and other subantarctic islands (Bourne and Warham 1966), and *O. castro* in the Galapagos (Harris 1969). The last shows no morphological or behavioral differences between populations, and thus there is no reason to consider separate taxonomic status. The two populations of *P. mollis* are distinct in several regards, but, as they never meet, Bourne (1957) maintained their subspecific status. The two temporal populations of *Macronectes*, however, nest side by side without interbreeding on Macquarie, their breeding being a few weeks out of synchrony, and they exhibit minor morphological and behavioral differences as well. Bourne and Warham (1966) recommended that they be recognized as distinct but sibling species. On Guadalupe, the two populations of *O. leucorhoa* are morphologically and behaviorally distinct, but, as they do not meet one another, their situation is somewhat similar to that of *P. mollis*. For consistency then, separate subspecific status is appropriate. On the other hand, for the sake of argument, so different are their songs that, if they met, it is questionable that interbreeding would occur. Much more work is needed on vocalizations in *O. leucorhoa*.

Etymology: from the Greek, *cheimon*, winter, and *mnestes*, suitor, a masculine noun; *cheimomnestes* refers to the winter breeding season of the population.

DISCUSSION

Factors known to affect geographic variation in landbirds were reviewed by Selander (1971), and I attempt here to relate some of them to Leach's Storm-Petrels. Tarsus and wing length have been used as measures of body size, and, using such information with air temperatures, tests of Bergmann's ecogeographic rule have been made. A comparison of tarsus and wing length of storm-petrel samples to ocean temperature in the vicinity of nesting areas (Table 2) indicates agreement with Bergmann's rule in the eastern North Pacific. Given the rather general nature of the data for ocean temperature, (i.e. a 1-month average for 1971 taken from a large-scale isotherm map) and the fact that at least one other factor strongly affects wing length (through wing shape, see below), it is understandable that correlation between wing length and temperature is not quite significant ($r = 0.5765$, $P > 0.05$). If two rather divergent samples, Coronados and San Benitos, are disregarded because their very rounded wing tips (see below) probably have affected wing length, then a very significant negative correlation exists ($r = -0.7901$, $P < 0.01$). At Guadalupe, where the two breeding populations experience different temperatures, their respective tarsus and wing lengths are in agreement with the expected response to temperature.

Why *O. leucorhoa* should be slightly larger in the western North Atlantic than in the northern North Pacific is not obvious from a comparison of the available sea-surface temperature data. Average August temperatures are the same for both regions (Sverdrup et al. 1942: chart IV). On the other hand, temperatures are much colder in the western North Atlantic area earlier in the year (Sverdrup et al. 1942:

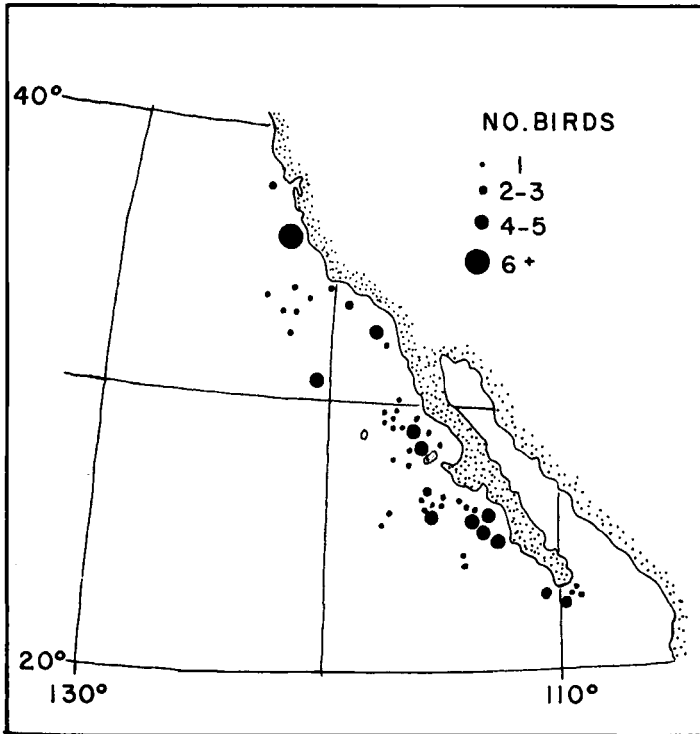


Fig. 5. The localities of dark storm-petrels (all species) seen or collected (summarized from reports in Crossin 1974).

chart III). It is likely that storm-petrels in the Atlantic *begin* nesting under colder conditions than they do in the Aleutians. Climate is also generally more severe in the Atlantic than the Pacific (see Briggs 1974) and, on these grounds, the larger size of North Atlantic *O. leucorhoa* is explainable.

Another morphological characteristic that varied geographically was wing shape. It has been demonstrated that some terrestrial long distance migrants have longer or more pointed wings than the shorter distance migrants (see review in Dorst 1962). This could also be so in Leach's Storm-Petrels, although the trend may be confounded somewhat by differences in foraging distances during breeding, which for some populations could involve hundreds of kilometers (see below). Terrestrial migrants rarely forage so widely! The major wintering area for Pacific *O. leucorhoa* is the equatorial Pacific (Crossin 1974, Ainley pers. obs.). More northerly breeding individuals would have longer distances to travel between wintering and summering areas, and having longer, more pointed wings would assist them during migration.

If and when rump color variation can be explained, the following points will probably have to be considered. (1) Three other entirely dark oceanitids nest sympatrically with those of Leach's "populations" that include dark individuals but not with those that have only light individuals; these species are the Black Storm-Petrel (*O. melania*), Ashy Storm-Petrel (*O. homochroa*) and Least Storm-Petrel (*Halocyp-tena microsoma*). (2) All dark-rumped forms, including dark-rumped Leach's, occur only near the coast during summer (Fig. 5). (3) Dark oceanitids winter nearer the

coast and white-rumped *Oceanodroma* winter in the central Pacific. (4) Dark-rumped individuals breed at Guadalupe during summer (and not during winter) when other dark oceanitids are also breeding. (5) The samples having a large percentage of dark forms have rounder wing tips than the birds from predominantly white-rumped samples. The first three of these five "coincidences" were also noted by Crossin (1974). Some factor(s), then, is (are): (1) selecting for dark-rump coloration in storm-petrels nesting during the summer from the Farallons to the San Benitos, including Guadalupe Island; (2) selecting more strongly for this factor with decreasing latitude; (3) selecting less strongly for it during winter; and (4) selecting for it in populations that are less mobile or short-ranging. Consistent with these is the fact that the white-rumped winter Guadalupe population has more pointed wings than the more dark-rumped summer one.

It is also interesting that another white-rumped storm-petrel, *O. macrodactyla*, until recently bred at Guadalupe during the summer. If like other white-rumped forms it fed at great distances from the nesting site, its presence offshore may have made it more opportune for some *O. leucorhoa* to feed close by. This would be added selection pressure for lessened mobility in the latter. *Oceanodroma macrodactyla* may have had another effect on *O. leucorhoa* as well: its large size probably favored the small size of *O. l. socorroensis*, with which it bred sympatrically and temporally, in that a limited number of rock crevices are available for nesting. The latter would nest in the small ones, and *O. macrodactyla* would take the larger.

It is not clear why dark rumps would be selected for in less mobile, coastal storm-petrels (including *O. markhami* and *O. tristrami* in Peru and Hawaii, respectively). Of all the dark forms, only the Ashy Storm-Petrel has been studied intensively (Ainley et al. 1974), and an explanation of the color phenomenon and all its correlates probably awaits studies of other dark, coastal storm-petrels. Crossin (1974) felt dark coloration made storm-petrels less visible to predators, especially the large gulls (*Larus*), which mostly occur near the coast. To me, white-rumped storm-petrels are not more visible than dark ones, and I would think that predators would find this true as well. Furthermore, while frequenting offshore waters might reduce contact with gulls, it increases contact with jaegers (particularly during winter), which are also potential predators. A relationship to predation pressures is thus not obvious. Selander (1971) reviewed several studies that related color to humidity, with darker-colored individuals occurring under more humid conditions. By remaining near the coast in California and Baja California (as does *O. markhami* in Peru, also), storm-petrels would encounter significantly more fog and overcast skies than those that frequent more offshore waters; this might also be true of *O. tristrami* in that it would maintain closer contact with the cloud forest conditions of the Hawaiian Islands. Along the Pacific coast of North America on the other hand, dark storm-petrels, *O. leucorhoa* or other species, nest only at sites within the Californian and Sonoran biogeographical provinces; in South America *O. markhami* nests in the very similar Pacific Desert province (see Urdvary 1978; Fig. 6). The summer climate of these regions includes much fog and no rain; *O. l. cheimomnestes*, which lacks completely dark individuals, nests during the rainy season. Hence, there seems to be a correlation between storm-petrel color and biotic provinces, but the relationship is not clear, because based on studies of other birds (Selander 1971), the darker birds should occur in the wetter conditions.

Geographic variation in *O. leucorhoa* has probably been affected by the amount

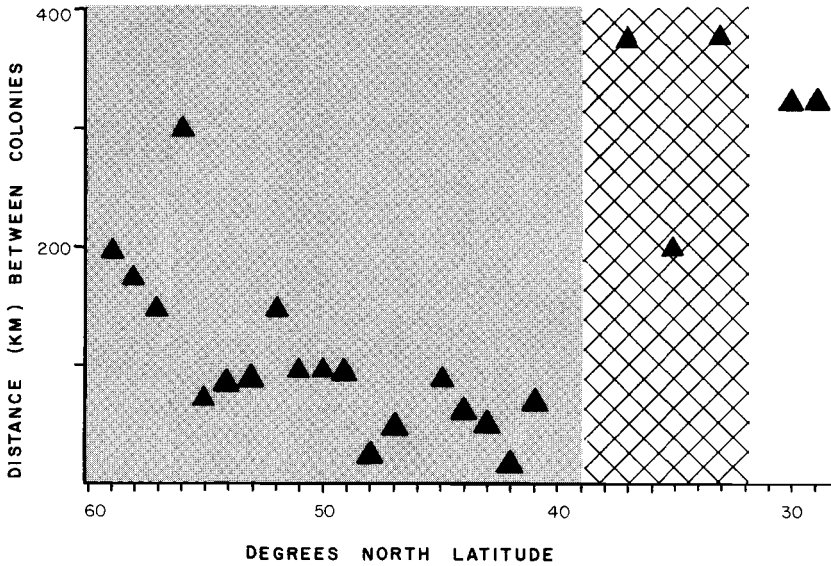


Fig. 6. Mean distance (km) between breeding localities by latitude (data from Drent and Guiguet 1961, Sowls et al. 1979, Varoujean 1979) and the relationship of breeding latitudes to biogeographical provinces: shading, the Aleutian, Sitkan, and Oregonian rain forests; cross-hatching, the Californian coastal scrub; and white area, the Sonoran desert (see Udvardy 1978).

of interbreeding among storm-petrels from adjacent islands as a function of inter-island distance. Morphological characters differed much more among birds from one nesting site to another in the southern region, where adjacent colonies were separated by greater distances than in the northern region. Average distances between colonies by latitude are graphed in Fig. 6, where it should be noted that north of British Columbia many additional but yet unknown nesting sites probably exist (Sowls et al. 1979). It is perhaps not surprising that most of the subspecies of *O. leucorhoa* named at one time or another nest at single islands or island groups in the south, where one would expect lessened interchange among individuals from different colonies.

ACKNOWLEDGMENTS

I wish to thank the individuals and donors whose memberships in and contributions to the Point Reyes Bird Observatory ensure the continued existence of the Farallon research station. There this study began. I wish also to acknowledge the help of persons and institutions who made specimens and other information available to me: 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), D. E. Willard (Field Museum of Natural History). S. M. Speich offered his unpublished information. M. I. Cristy (Museum of Vertebrate Zoology) prepared the sonagrams and instructed me in their interpretation. S. L. Olson offered much encouragement and sorely needed advice; G. E. Watson and W. L. Hoffman provided helpful comments on the MS. This is contribution 128 of the Point Reyes Bird Observatory.

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