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Further Notes on Variation in Leach's Storm-Petrel¹

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Bourne and Jehl (1982; = B & J) disagree with my taxonomic treatment of *Oceanodroma leucorhoa* (Ainley 1980) at the southern end of the species' range in the eastern North Pacific, particularly my merging of *O. l. chapmani* with *O. l. leucorhoa* and my separation of populations at Guadalupe Island. In regard to *O. l. chapmani*, they attempt to substantiate its validity as a subspecies. They give two reasons for recognizing a sharper distinction between it and more northerly populations than my data indicate. First, they claim their data on ratios of color morphs on Los Coronados and San Benitos (p. 793) are closer to the truth than the patterns in the 103 specimens available in museums (i.e. my Fig. 2, 1980). Their unpublished data cannot be assessed, but, in general, they still help to illustrate the point that I emphasized, namely, that whitest morphs predominate in the north and darkest ones in the south, while those in between are mixed. The situation is thus akin to that of *Fulmarus glacialis* and *Puffinus pacificus* of the Pacific region, where similar color variation has not been given taxonomic significance; B & J should explain why color variation should be treated differently in Leach's Storm-Petrels.

Even if color were a useful character, their second point (p. 796), that 90% of all dark birds in the eastern North Pacific breed on the San Benitos and Coronados, which would therefore validate *O. l. chapmani* as a subspecies, is pertinent only after they first merge *O. l. willetti* (Los Coronados) with *O. l. chapmani*. This is contrary to Austin (1952), to the A.O.U. (1957), and even to Bourne's earlier opinion (*in* Palmer 1962) and thus requires much more support with data than they offered. Furthermore, in their com-

parison of population sizes they do not point out that storm-petrel populations in the Channel Islands have not been well studied and that on islands except San Benitos, and especially on Guadalupe, Los Coronados, and the Channel Islands, populations have been drastically reduced and forced onto adjacent rocks and islets by the introduction of exotic mammals to main islands (e.g. R. L. DeLong and R. S. Crossin, "Status of seabirds on Islas Guadalupe, Natividad, Cedros, San Benitos, and Los Coronados," unpubl. MS, Pacific Ocean Biol. Surv. Progr., Smithsonian Inst.). Thus, most dark-rumped birds do *presently* nest on San Benitos, but, if we applied B & J's 90% rule in regard to color as the only basis for recognizing *O. l. chapmani*, then the subspecies could be invalidated if cats and goats were introduced someday to the San Benitos and the storm-petrel population there was reduced in size as a result!

Finally, they ask that the dark birds found among breeding populations in the Channel Islands and the Farallon Islands be ignored, because these birds were supposedly visiting from the south (p. 795). This is special pleading. Even if these birds were established immigrants from the San Benitos, such an unusually high rate of interchange between islands (6% of the Farallon population would thus have to be derived from San Benitos) would be evidence that we are dealing essentially with only one population. A much higher degree of philopatry, however, is characteristic of storm-petrels and most other species of pelagic seabirds. Many of the dark birds caught on the Farallon Islands have incubation patches during the appropriate season and at least two, which were banded and released, were recaptured there in the same and in subsequent years (PRBO unpubl. data). These facts reduce even more the slim likelihood that these birds were visitors breeding on islands more than 800 km away.

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TABLE 1. The percentage of color morphs (after Ainley 1980) among specimens collected at four Guadalupe Island localities; based on inspection of 239 specimens and not including those where collecting locality was specified only as "Guadalupe Island."

Population	Color morphs											n
	1	2	3	4	5	6	7	8	9	10	11	
ISLOTE AFUERA = ZAPATO												
<i>O. l. cheimomnestes</i>				61	13	13	13					8
<i>O. l. socorroensis</i>		38	21	12	4	4	8	4	6			24
ISLOTE NEGRO												
<i>O. l. cheimomnestes</i>	1	7	16	30	26	19	1					74
<i>O. l. socorroensis</i>			4				14	28	39	7	7	28
GARGOYLE ROCK												
<i>O. l. cheimomnestes</i>				25		25	25	25				4
<i>O. l. socorroensis</i>							22	33	33		11	9
MAIN ISLAND, NORTHEAST ANCHORAGE^a												
<i>O. l. cheimomnestes</i>		11	14	25	27	18	2	2				44
<i>O. l. socorroensis</i>	4	19	14	2	4	2	8	14	19	12		48

^a These birds flew aboard anchored vessels at night.

B & J also objected to my taxonomic treatment of populations on Guadalupe Island. Though mensural data showed that the summer and winter breeding populations are easily separable from each other and from mainland populations, they argue against my subspecific separation on other grounds. First, they claim (pp. 793-794, 796) that data are insufficient to describe the patterns of color variation at Guadalupe. Thus, they again infer, without supporting data, that color is the key to classifying this species! In response to this claim, I present the existing verifiable data, which I had originally considered as peripheral to the problem, for the first time in Table 1. The situation is indeed complex and interesting, but it is not as confusing as B & J imply. In *O. l. cheimomnestes*, the distribution of color morphs is essentially the same at all four sample localities: representation of morphs 1-8, with 56% of birds at 4 and 5. In *O. l. socorroensis*, the situation is much different. At Islole Negro and Gargoyle Rock, morphs 3 and 7-11 are represented, with 67% at 8 and 9, the dark end of the scale. There is much overlap at Islole Afuera, where morphs 2-10 are represented, but, in contrast, 61% are at 2-4, near the white end of the scale. These islets are only a few kilometers apart at the south end of Guadalupe Island. Among the specimens that flew aboard ships anchored several kilometers away at the north end of the main island adjacent to an area where breeding is suspected (DeLong and Crossin, *op. cit.*; B & J, p. 793), the pattern is as follows: morphs 1-10 are represented, with 33% of birds at 2 and 3 and 33% at 8 and 9. Because this pattern is a composite of other summer localities, these birds probably came from all the various islets as well, perhaps, as the main island, and, therefore, the sample is of no further use here. In any case, variation in color is cer-

tainly more complex in the summer than in the winter population. The lack of differences in measurements (e.g. note the small standard deviations in Table 2 of Ainley 1980) that are consistent

TABLE 2. The total number of visits by ornithologists to Guadalupe Island by month, divided according to whether eggs, downy chicks, or large chicks/fledglings were encountered; data are summarized from Bourne and Jehl (1982) except for those referenced in footnotes a-d.

Month	Total visits	Breeding evidence found		
		Eggs	Downy chicks	Large chicks/fledglings
June	2	2		
July	2 ^a			
August	1	1	1	
September	1			1 ^b
October	2			2
November	3	1		2 ^c
December	1	1		
January	2	1	2	
February	1 ^d	1	1	
March	1	1		1
April	6			6
May	1 ^e			

^a Adult specimens collected in July 1922 and 1937; no indication of breeding status.

^b Fledgling collected, September 1929; specimen data.

^c Includes a partly downy fledgling that flew aboard ship anchored near shore, 12 November (year?): DeLong and Crossin MS (see text).

^d Three adults collected with eggs, one with downy young, February 1957; specimen data.

^e One visit in May 1971; no evidence of egg laying, although adults found in burrows and two banded.

with the bimodality in color among subunits of the summer population makes further differentiation among the summer breeders difficult. This closest of looks at the Guadalupe data brings us little nearer to understanding the environmental basis for color variation in this species (see Crossin 1974, Ainley 1980), but it gives us another variable with which to deal, and certainly an interesting one at that. Variation in color over small distances on one island is also manifested among the Southern Giant Petrels (*Macronectes giganteus*) breeding on Macquarie Island, and similarly its causes are unexplained. Shaughnessy (1971 and other papers), who studied the phenomenon in detail, noted that the high degree of philopatry exhibited by this (and other) petrel(s), which reduces gene flow drastically even over small distances, is probably involved.

Second, in regard to Guadalupe, B & J try to show that there are not two distinctive breeding seasons (pp. 793–794) or that the situation is unclear (pp. 795–796). Hubbs (1960), Crossin (1974), and I, however, all agree that two distinctive egg-laying periods exist, although “breeding seasons” do overlap, i.e. the last near-to-fledging chicks of one population are present during initial egg laying of the next population. To support their position, B & J reveal their only verifiable new data, a chronological list of paraphrased field notes from Carl L. Hubbs and data from Crossin (1974). To increase the clarity of these data, I summarized them along with some additional observations. The result (Table 2) shows that in 23 visits to Guadalupe Island by ornithologists intent on collecting or studying the storm-petrels, large chicks and fledglings have been encountered only during two periods: March to April and September to early November. The large downy chick reported on 16 November 1964 (B & J, Table 1) would probably have come from an egg laid in mid- to late August. In addition, no eggs or small downy chicks have been detected in the periods April to May or late September to October. Almost two-thirds (14) of the visits were made during the periods when no eggs were found. Because the incubation period for this species is a minimum of 42 days, many of the eggs reported in August and March were probably laid the previous month, or earlier, and the egg-laying periods are no doubt even shorter than Table 2 superficially indicates. The summer breeding season is therefore almost identical in timing, duration, and synchrony to that of *O. l. leucorhoa* on the Farallons (Ainley et al. 1974), whereas the winter season is drawn out at least one month longer and nesting is apparently less synchronous. Other evidence supports the existence of two distinct egg-laying seasons: few adults have been found, and none on eggs, during day-time visits by ornithologists in April or in September–October (see Ainley 1980: 839, for details). Furthermore, only a few Leach’s Storm-Petrels, in sharp contrast to another Pacific species, *O. homochroa*, overlap molt

with prebreeding or the final weeks of breeding activities; the time required for molt plus that needed for breeding and migration precludes less-than-annual breeding in *O. leucorhoa* (Ainley et al. 1976). Thus, thanks to B & J, we have amassed respectable evidence for and have developed an even better understanding of the separate egg-laying periods of the two seasonal Guadalupe populations.

Finally, B & J disparage my taxonomic treatment by considering that vocalizations, and particularly my analysis of them, are not useful in supporting the definition of subspecies in *O. leucorhoa* (pp. 794–795). The tapes recorded the calls of many individuals, but only a few calls were separate enough from others to allow analysis by sonograph. Whereas I had proposed that at least four measurable characteristics of the species’ song (i.e. “Flight Call”) and five characteristics of another vocalization (the “Chatter” or “Churr”) are distinguishable between Guadalupe and other populations, they mention only one characteristic as being too variable for taxonomic use (the number of notes per second in the “Chatter”). Although chatter rate is perhaps not as taxonomically useful as I had thought, this does not mean that vocalizations are not taxonomically significant or even that other characteristics of the “Chatter” are not useful. Even B & J later tell us (p. 796) that a study of *O. (l.) monorhis* in the western Pacific should include work “especially on the voice.” The vocal differences between Guadalupe and other populations are especially obvious in the species’ song, so much so that, on first hearing tapes of the Guadalupe birds, I believed them to have been recorded or played at the wrong speed or to be of some other species. R. L. DeLong was similarly incredulous when he collected some of the singing individuals after recording them. One can listen to commercially available recordings of this species’ song (most recorded in Maine or the Maritime Provinces) and then easily recognize the species at any of its breeding islands in the Atlantic or eastern Pacific, except at Guadalupe Island.

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What Systematic Method Will Ornithology Adopt?—A Reply to Olson (1982)

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The question posed by the title of this response—What Systematic Method will Ornithology Adopt?—is at the heart of the differences between Olson (1982) and myself (1981a) and is far more significant for ornithology than any contention about the relationships of a particular group. In his scientific papers, including his critique (1982) of my paper, Olson has exhibited an apparent disinterest in discussions about systematic theory and methodology, preferring instead to believe that a persistent pursuit of new "facts" or data will eventually give rise to statements or conclusions of greater generality. In contrast, I have suggested that a major problem in systematic ornithology has been the lack of an effective comparative method: all observations ("facts") are theory-laden and make sense only within the context of some organizing principle, be it a theory, hypothesis, or a specific comparative method. Without question, the systematic community at large is increasingly adopting phylogenetic systematics (cladistics) as its method of choice.

In my paper, virtually all the commentary on the papers of Olson and his colleagues focused on their inadequacies in phylogenetic argumentation; other ornithologists have raised similar criticisms of that work (Clark 1981, Raikow 1981). Olson's only response to cladistics is to cite Mayr (1981) in support of the proposition that not everyone is willing to accept the same methodology, but an appeal to authority does not substitute for a cogently reasoned rationale of one's own scientific methods. In fact, one searches in vain through Olson's papers for a statement describing and rationalizing a comparative method of any kind.

A major purpose of my paper was to delineate in detail—for the first time in the ornithological literature—the importance of pursuing cladistic classifica-

tions in place of the "eclectic" approach that has been our tradition. In his critique, Olson fails to state why cladistic classification is not a desirable goal for ornithology. Such a classification promotes the recognition of natural groups, i.e. those postulated to represent strictly monophyletic taxa. If Olson agrees with this goal, then it is difficult to understand why he did not exhibit some charity toward my paper instead of the sustained invective he directed at it. If he does not agree with this goal, then perhaps he can apprise ornithologists why we should instead be classifying unrelated groups together.

Philosophical matters aside, Olson promotes two major arguments, both strawmen and without validity. His first claim is that my arrangement of orders into "divisions" was the most important focus of my paper; he then proceeds to point out the dicey nature of those groups. It is clear, however, that I viewed (1981a: 685–686) the category of division as *the most tentative* of all systematic groupings—that is why I did not formally name those hypothesized taxa, even when several referees strongly recommended that I do so. Olson's second line of argumentation was to choose a liberal number of my admissions of uncertainty and display them as if they constituted the entire content of my paper. Without belaboring the point, I call the reader's attention to p. 685 of my paper where I state, unequivocally, that there are still many uncertainties in our knowledge and that these will be openly admitted. The paper was titled "*Toward a phylogenetic classification . . .*" intentionally, and I made no claim that I could provide supporting data for each taxonomic group. If a reader wishes to criticize my efforts on the grounds of prematurity, all well and good, but surely that same criticism must then be applied to all previous classifications and, because knowledge is always uncertain, to all those that will follow.

Another major purpose of my paper was to hypothesize natural groups for the higher taxa *within orders* to the extent that present knowledge permits. A comparison between the classic papers of Mayr

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