

GEOGRAPHIC VARIATION IN THE EGGS OF CACTUS WRENS IN LOWER CALIFORNIA

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This paper reports a study of the sizes, shapes and colors of the eggs of the Cactus Wrens (*Heleodytes brunneicapillus*) of Lower California. Its purpose is to trace, through analysis of pigmentation and dimensions, some of the heritable geographic variations of these birds.

The eggs of *Heleodytes brunneicapillus* are divisible into four major groups: the Rio Grande, the Colorado Basin, the Western and the Peninsular. (As yet I have been unable to examine material from New Mexico.) The names selected are suggestive of the area from which each comes, although there are irregularities along part of the boundary between the Western and the Colorado Basin groups. The Rio Grande group is confined to the eastern side of the Continental Divide; the other three are represented in Lower California.

The Peninsular group is endemic to Lower California. It consists of all eggs derived from the area from Cape San Lucas north to, approximately, the thirty-first degree of latitude. The western part of the northern boundary of the range can be drawn with fair precision. The line starts slightly north of San Antonio del Mar and skirts the southern slope of Sierra Cresta Blanca. It follows the western foothills of the Sierra San Pedro Mártir as far as that range extends southward. The northeastern boundary runs from the southern tip of the San Pedro Mártirs to the Gulf of California, but little is known of the direction it follows. The probabilities are that the Mesa Alta sets the boundary.

Cactus Wrens within the area assigned to the Peninsular group are isolated from all others of their species. A possible exception occurs in the little known northeastern corner. From just north of San Antonio del Mar until the Tijuana Valley is reached, a matter of a hundred miles, there are no Cactus Wrens. Between Mount San Jacinto, in California, and the lower end of the Sierra San Pedro Mártir there is no place where the birds can cross the Peninsular Range. The waters of the Pacific, together with those of the Gulf, surround the rest of Lower California.

Within the area outlined, however, Cactus Wrens occur continuously. It is true that there are regions, some very large, which are too nearly sterile to support the wrens, but nowhere do these barrens become total barriers. None extends from one coast to the other. There are no mountains or other obstacles that stop interchange; such limitations on the exchange of blood lines as may exist are the intangible barriers of flora and climate, not the physical geography.

The determining factor in assigning eggs from the peninsular part of Lower California to a specific major group is neither their isolation nor their continuity. It is the fact that they are distinguishable, through color and markings, from the eggs of all other groups of Cactus Wrens. I cannot too strongly emphasize that this statement applies only to averages. Individual variations are so great throughout the species that inferences simply are not to be drawn from single specimens. However, certain types do not occur on the Peninsula.

If there were assembled a series of twelve or fifteen representative, run-of-the-mine sets from any one locality, any oologist familiar with these eggs in numbers could tell at a glance whether or not they were laid within the area we are discussing. This is true because nowhere else is there even an approximation of the large percentage of the

light-colored type which is found in the Peninsular area. The egg that is characteristic of the region has a light-brown ground color and is marked with small, faint reddish dots, faintly applied. Not rarely the dotting is so delicate as to seem to be absent. In other localities this type might be found once in six or eight sets; here it is to be expected in four out of every five.

There is another characteristic which distinguishes the Peninsular from the other western groups—a characteristic less convincing only because it is negative. One of the rarer types of Cactus Wren eggs has a pure white background. It may be very lightly spotted, it may be so heavily marked as to appear crusted, or it may be anywhere in between. It is unusual in two respects: in spite of its wide variations it does not blend into the more nearly normal type, and it never has been reported from the Peninsula of Lower California. Yet there are localities, especially in the Colorado Basin, where one set in every eight or ten is of this kind.

Parenthetically, it should be explained that the reason egg colors are not diagnosed statistically is because of two mechanical complications which I, at least, have not been able to overcome. It has not been possible for me to assemble for comparison, at any one time, all the material on which I am working. Also, collectors specialize on the freakish and rarer colorations to an extent that hopelessly distorts averages. It is to be regretted that this is so, for pigmentation is important in geographic variation.

The first step in gaining an understanding of the Peninsular group of wrens is a realization that the color of the egg has been determined hereditarily. The alternative is to believe that the tint and the markings on the shell have been brought about by external influences. If that were so, one wonders what those influences could be. Certainly not food. Examine a large series of Elegant Tern eggs or a series of murre eggs. Among them one will find an almost infinite variety of colors, markings and composition. Except as between two eggs laid by the same female, each is readily recognizable. Yet in any colony there has been but one diet for all terns, but one diet for all murrets.

In an aviary, with a number of species feeding from but one tray, the eggs of unrelated birds show no tendency to develop resemblances. Captivity of parent does not affect markings in any manner that can be detected by oologists. Indeed, if pigmentation were influenced by anything in the environment, climate, altitude, soil, or plant associations, we collectors long ago would have discovered that fact. Our weakness is avarice for brilliantly marked eggs, but in our search for them we find only accumulating indication that the one general factor responsible for pattern is heredity.

If we accept egg colors as a manifestation of heredity, which surely we must, then we have recognized, in addition to the Peninsular group of eggs, a group of birds physically different in their egg-producing mechanism from any other group. The question of whether or not the differences in egg-producing machinery have been paralleled by other differences, either adaptive or accidental, is in a way extraneous to this study. Nevertheless it is quite in order to note that it would be astonishingly out of keeping with our experiences in the practical workings of evolution should any group of birds differ from its neighbors in one inherited fundamental respect and yet be identical with them in all others.

The segregation of the Peninsular group by the method here used might seem more convincing if its eggs were all of the characteristic type and if that type were found nowhere else. It is not the incomplete differentiation that obscures the analysis, however. It is the fact that the colors have not been expressed in mathematical terms. Could that have been done and had we a table showing precise values and frequencies of occurrence of each, the *t*-test for the significance between two means could be applied.

The Peninsular group of eggs is itself divisible, through comparative measurements, into subgroups. I have compiled a table of measurements of all eggs of the group to which I have had access; they are fairly representative of about half the geographic range. Of the four subgroups disclosed, three have been described and given scientific names and, since there seems to be no doubt of the validity of the various subspecies thus designated, I naturally have followed accepted nomenclature. The designation Punta Prieta is intended merely to suggest the geographical center of the fourth subgroup.

	Sets	Eggs	Cc. ¹	Axes	Ratio of axes
<i>H. b. affinis</i>	12	32	3.58	24.50 × 17.20	1.42
<i>H. b. purus</i>	36	72	3.37	24.04 × 16.84	1.43
Punta Prieta	5	11	3.92	25.40 × 17.68	1.44
<i>H. b. bryanti</i>	54	152	3.59	24.73 × 17.14	1.44

¹ Cubic contents, in cubic centimeters, are approximated from the only two measurements made, those of the major and the minor axes. The formula used is based on $\pi ab^2 \div 6$. However, since an egg is not a perfect geometrical figure, it has been found that the actual size is less than the calculated size. Because egg shapes are widely variable, no fixed percentage of correction is applicable. Tests seem to show that if the egg is assumed to be 94.4 per cent of $\pi ab^2 \div 6$, the figure that has been adopted throughout this paper, the error rarely will be greater than one per cent. In any event, for comparative purposes this error may be disregarded *in toto*.

Of the 36 sets of *H. b. purus*, two, of 3.52 and 3.47 cc., respectively, came from San Ignacio Lagoon on the Pacific Ocean. Eight are from the vicinity of Santa Rosalia, from the narrow strip between the shores of the Gulf and the almost perpendicular eastern side of the peninsular mountains. These averaged 3.31 cc. The remaining 26 sets, averaging 3.38 cc., were collected on the cooler western slopes, at altitudes of from 1200 to 1800 feet. From this and other evidence we know that the belt of small eggs extends all the way across the Peninsula and, by so doing, definitely isolates the birds of San Quintín from those of the Cape region.

Before attempting to interpret the table it must be made clear that the analysis of dimensions deals only with averages. The value of averages depends in part on the number of specimens totalled and in part on the percentage of divergence. In the case of Cactus Wrens I like to have 25 sets and 100 eggs with which to establish the value for a station. Even with half these numbers, however, if the birds are relatively homogeneous within the area and if the sampling has been representative, more data seldom are productive of material changes in average values.

The differentiation of subgroups presupposes that the size of an egg is determined by the heredity of the mother. This tenet, as the *sine qua non* of this investigation, should be held to the strictest proof. Space, however, permits no more than a sketch of the sustaining evidence.

To a limited extent the size of an egg is a matter of chance or else is determined by non-hereditary factors of which we have no definite knowledge. If this were not so, all the eggs of any one set would be identical. But eggs within a set do vary. To analyze the differences I have chosen the 54 sets of *bryanti*, having more of them than of any other subgroup, and have compared lengths, the most variable dimension. In the 16 sets of two the difference between the eggs averages .7219 mm.; in the 32 sets of three, .5767 mm.; in the 6 sets of four, .5886 mm.; in the 54 sets as a whole, .5953 mm. The smaller figure in the larger sets is due to the fact that the latter normally contain at least two eggs which are virtually identical.

When the 152 eggs under consideration are subjected to the method known as the analysis of variance, by which the variance within and between clutches is compared as an indication of homogeneity, we find that there is less than one chance in ten thou-

sand that individual egg variation, as exemplified by the differences within the sets, could account for the differences between sets.

Similarly, average sizes show definite individualities in the subgroups. For instance, if we apply the *t*-test for the significance between two means to the 54 sets of *bryanti* and the 36 sets of *purus*, the significance *P* is .006 and the coefficient of divergence 5.64 per cent. As between *purus* and the 5 Punta Prieta sets the significance *P* is .0002 and the coefficient of divergence 13.78 per cent. This establishes these differences as reliable and not due to chance or error in sampling, in spite of wide fluctuation and frequent overlapping. There is proof that the averages of eggs from certain areas are unlike eggs from other areas. That this is not due directly to food or environment will be shown. This process of elimination is offered as proof that the variances are due, directly, to heredity. Mr. Laurence M. Klauber worked out with and for me much of the statistical mathematics. I am greatly indebted to him and to his specialized knowledge.

The best evidence that egg sizes are not governed wholly by food or similar outside influences is given us by commercial poultrymen. Here there have been found no effective means, except selective breeding, of obtaining the large eggs that are desired.

There is no place better than San Ignacio in which to illustrate that the character of the country the wrens inhabit has no direct bearing on the size of their eggs. The environs of that pueblo are the most nearly barren of any area which supports an appreciable number of these wrens. Both the Cape Region and the canyons about El Rosario are so much more fertile that the difference is apparent to any casual traveller. Less obvious is the important fact that the total food supply in the central area shows relatively little difference between the laying and the non-laying months. This impoverished condition is disclosed by the comparative number of eggs in individual sets. Three's are quite common with *affinis* and with *bryanti*; they are virtually unknown in *purus*, except that, in 1930, when there was an almost unprecedented rainfall in San Ignacio, we did take several three's and even one four. The number of eggs in a set, of course, within the limitations of heredity, is an expression of the divergence between the maximum and minimum food supplies of any region. Here it is indicative of the barrenness of San Ignacio.

If sterility of environment would explain small Cactus Wren eggs anywhere, it would do so in central Lower California. That it does not is shown by conditions at the northern extreme of the Pacific range of the species. There is a subgroup which inhabits what is probably the most fertile part of the entire habitat of *brunneicapillus*. The area in question includes the Ventura, Simi and San Fernando valleys in southern California. It skirts the foothills of the San Bernardino Mountains and continues through Azusa at least to the eastern boundary of Los Angeles County. To date I have measured 209 eggs from this section. Their averages, 23.76 x 16.77 and 3.30 cc., are smaller than any from Lower California.

In contrast to the coastal valleys, the Mojave Desert is inhospitable. In fertility it might be considered as a mean between them and El Rosario. I have measured 209 eggs from Palmdale and Victorville through to Wickenburg, in Arizona. The averages are 24.62 x 17.15 mm. and 3.58 cc., virtually the same as the figures for *bryanti*. Bordering the San Fernando subgroup on the south, in apparently the same type of associations and with no recognizable line of demarcation, lies a subgroup whose eggs are the largest of the entire Western group.

Such contradictions as have been cited could be multiplied indefinitely, for there simply is no pattern—no pattern, that is, that connects the nature of the country inhabited with the size of the egg. The largest eggs I have are from Punta Prieta, the

smallest from Guaymas. It seems to me that the probability is strong that if a female from either of those regions were transplanted to the other, the size of her eggs would not be affected. If they would not be, then the control must be heredity.

The hypothesis that egg colors and sizes are indices of inheritance clarifies an important portion of the history of the Peninsular group of wrens. We have the picture of a one-time single group of eggs of distinctive mass coloration, a group which eventually split into smaller units identifiable by measurements. This picture is logically and, I believe, technically correct.

There is evidence to support the belief that not only in Cactus Wrens but also in birds in general egg colors and markings have come down through the ages with less alteration than have many other physical qualities. With the few exceptions of protective coloration, egg tints do not enter into the struggle for survival.

The Western group is composed of the darkest eggs of any of the Cactus Wrens. The territory it occupies is the western watershed of southern California from the Tijuana Valley to the northern limit of the range of the species. A subgroup extends southward from north-central San Diego County to the Tijuana Valley, and that subgroup, in turn, is broken down into three divisions. One centers around Escondido, one around the bay region of San Diego and the other, in Lower California, apparently is confined to a small area east of Rodriguez Dam.

Eggs from the Colorado Basin, except for some confusion at the western end of San Geronio Pass, are more brilliantly colored and have a far greater percentage of sets with white backgrounds than those from either the Pacific or Gulf of Mexico watersheds. One of the subgroups extends southward from the international line in a gradually narrowing triangle between the Cocopah Mountains and the Colorado River bed. The birds breed freely both in the heavy riparian growths of the Delta and the cholla associations above the ancient shore line.

Undoubtedly the subgroup that occurs on the eastern slopes of the mountains in San Diego County also extends into Lower California—there is no break in the continuity of the country; but I have been unable to examine any specimens from that area. In any event, eggs of the western end of the Colorado Basin groups are to be found in Lower California in an area that is small indeed when compared to the one covered by these groups in the United States and on the Mexican mainland. The analysis of the eggs from either of the northern corners of Lower California belongs more properly to a specific discussion of each group as a whole.

When distinguishable groups of birds are separated by geographical isolation, a satisfactory picture is to be had. Pressure from within against fixed borders might be expected to spread the differentiations evenly throughout the subgroups. In the Peninsular group of Cactus Wrens there are, however, no geographical barriers, in fact, no barriers of any kind that are readily discernible. Virtually the only factor I have been able to discover is that, as one goes south, plant development and the breeding season of the wrens come progressively later in the season. That does not help much in telling us why there is more than one race of Cactus Wrens on the Peninsula, or why the hereditary types do not diffuse back and forth from San Antonio del Mar to San Jose del Cabo to produce a single homogeneous species.

This paper, admittedly, is but one step of an investigation into why there are several subgroups within each of the three groups of Cactus Wrens under discussion. Tabulations of measurements of eggs both from north and east of the Peninsula will prove helpful, as will correlation of the information we already have with an accurate revision of the taxonomy of *brunneicapillus*.

Cuyamaca Club, San Diego, California, July 1, 1945.