CORRELATION OF VARIATION IN THE WRENTIT WITH ENVIRONMENTAL GRADIENTS

By DARL E. BOWERS

Correlations between environment and animal size or color have long aroused the interest of biologists and have stimulated the formulations of ecogeographical rules and the evaluation of the validity of these principles in many different animals. The questions that arose concerning the mechanisms governing correspondence between environment and the animal led to early, unsuccessful experiments to establish direct effects of humidity, temperature, and color of surroundings (Beebe, 1907; Ogle, 1934; Sumner, 1934; and many others) on captive animals raised under artificially controlled conditions. The geographical principle concerned with high levels of melanism found in vertebrates inhabiting humid regions, namely Gloger's rule, has been described in general terms many times. However, there is a paucity of evidence causally relating humidity and other environmental factors with color expression. It is even stated in a recent paper (Hamilton, 1958:336) that the adaptive significance of increase in pigment deposition with increases in environmental humidity is unknown.

The work of Sumner (1932) on *Peromyscus maniculatus* and *Peromyscus polionotus* indicates clearly that differences of pelage color in these mammals are under genetic control. Similar genetic analyses of wild species and races of birds have not been made in so far as I know, but there seems to be no reason to suppose that similar results would not be obtained in birds, and the genetic control of variation of a species such as the Wrentit (*Chamaea fasciata*) is therefore assumed.

The best evidence for adaptive value of presumably genetic factors of coloration is indirect in birds and comes from field investigations of the larks in which it has been found by Meinertzhagen (1951) and Bates (1936), especially for *Ammomanes deserti* of Asia, that the plumage coloration of various races of this species agree very closely with soil colors on which the races exist when the environments otherwise are similar. Thus dark birds are found on dark soils and light birds on light sandy soils. Behle (1942) has described the same close association between plumage colors and soil colors in the Horned Larks (*Eremophila alpestris*) of western North America. Both these birds are prey species for several predatory birds, and since they are open-ground dwellers, the need for concealing coloration, in this case correspondence with local soil color, is evident.

In the races of the Wrentit in northwestern California, there is variation of plumage color that presents a rather consistent clinal pattern. The darkest birds, ascribable to the race *Chamaea fasciata rufula*, exist in the coastal humid belt from San Francisco Bay northward. The lightest birds of the race *C. f. henshawi* occur from the southern tip of the Vaca Mountains in Solano County northward and northwestward. In between the two, the race *C. f. intermedia* is found (see Grinnell and Miller, 1944). This race has been thus named because the coloration of the breast and belly regions is somewhere between that of the other two. The aim of the present work is not to review the rather artificial racial entities but to consider precise correlations in a series of populations which grade sharply in color from the coast interiorward.

After collecting 267 specimens in fresh fall plumage, I noticed that there were also variations in several dimensions of the Wrentits. In addition to a study of the color variation, then, an analysis of some of the body parts was undertaken.

The geographic area of California under consideration, as shown in figure 1, consists of all of Marin, Sonoma, and Napa counties and the adjoining parts of Solano, Yolo, and Lake counties. Wrentits are inhabitants of chaparral and scrubby vegetation bordering forested areas. They are extremely sedentary, nonmigratory birds with an average breeding territory size, according to Erickson (1938), of about eight-tenths of an acre. The species ranges throughout the large growths of brush that cover much of the coast and inner coast ranges of the area of investigation. Densities vary and aggregations of Wrentits brought together at localized food sources may be found in the autumn. The sedentary mode of existence means that transmission of genetic characteristics between

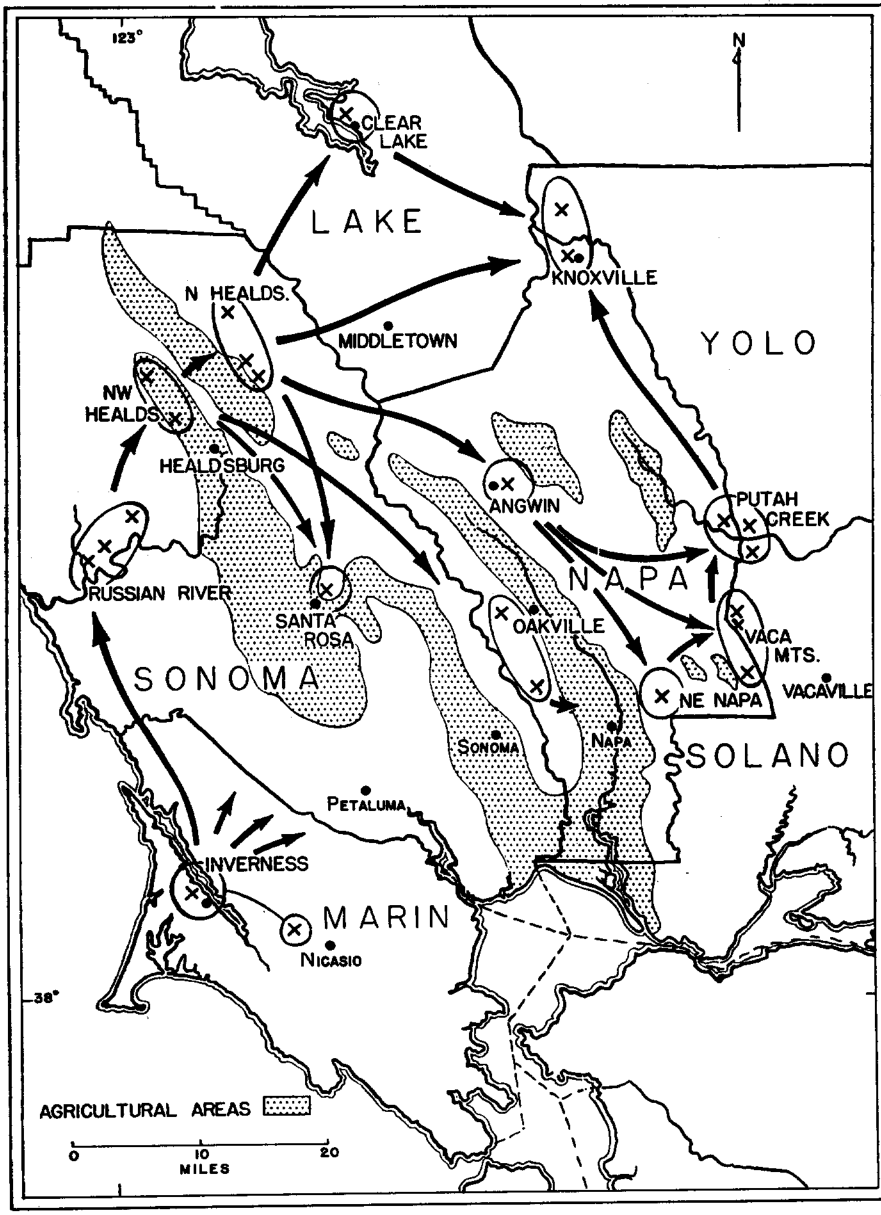

Fig. 1. Map of the area of investigation showing collecting localities (encircled) and color trends. Arrows point toward lighter colors.

populations is relatively slow, thus favoring establishment of clines. The lack of good habitat for the Wrentits in parts of the area studied has produced partial isolation of some populations.

I would like to acknowledge the assistance with plant identifications given by Dr. Helen Sharsmith and her associates in the University of California Herbarium under the direction of Dr. Herbert L. Mason. Dr. Mason also offered constructive criticism of the original manuscript. Dr. Frank A. Pitelka has kindly given assistance and valuable criticism concerning concepts and presentation of data. Dr. Robert T. Orr of the California Academy of Sciences generously made available to me the specimens in the collection there. Thanks are here expressed to my fellow graduate students who aided in the collection and preservation of specimens. To Dr. Alden H. Miller I owe a debt of thanks for his aid in the procurement of equipment and resources and for his critical assistance in evaluation of evidence and for guidance throughout the study and during the preparation of this manuscript.

ANALYSIS OF VARIATION

The specimens used for mensural characters were those collected by me in the autumn of 1951, 1952, and 1953, plus those skins in the California Academy of Sciences in San Francisco and those in the Museum of Vertebrate Zoology at the University of California, a total of 425. Color determinations and comparisons were made only from the 267 skins recently taken by me and obtained at the time of year when plumage is least worn, that is, when the feathers have just been renewed in the autumn after postjuvenal and postbreeding molts.

SEXUAL VARIATION

The females average smaller than the males in the four body dimensions of wing, tail, tarsus, and bill; they are also lighter in weight. The degree of difference between the arithmetic means for males and females varies from sample to sample. The back and breast coloration of new fall-taken specimens shows no significant difference between the sexes either in birds of the year or in adults. The color data for the sexes therefore have been combined.

SEASONAL VARIATION

Since there is but one molt period in the course of the year, once wing or tail feathers are free of basal sheaths, barring tip breakage, they are considered to represent their full lengths. As expected, birds collected in the spring and summer showed a higher incidence of broken feather tips than birds taken in the fall. Rectrices and remiges that had obviously been broken were not measured, but unobservable wear may have reduced some of the feather lengths. To analyze this influence, the data for the males of a relatively large sample of 73 birds from Marin County was broken down into two six-month periods for comparison. Measurements of birds taken from September through February were grouped, and those from March through August were handled similarly. September birds have largely completed their molt and hence have the newest plumage. The spring months are represented by birds carrying out breeding activities and these presumably would have the most shortened feathers due to wear. Such treatment shows that at least for this group of birds from Marin County there is no significant variation from one half of the year to the other.

Tarsal length is assumed to be constant the year around and throughout the life of the bird from the time it reaches its full size in the summer and fall of its first year.

Bill length is perhaps a more complexly variable attribute than tarsal length or feather length since the horny bill is growing continuously and is worn back at its tip by use. It is conceivable that the consumption of a seasonally changing diet or that additional feeding activity in the spring may produce differential wear on this part (see Davis, 1954). However, measurements of birds that were collected the year around are similar and therefore all have been consolidated for each locality.

Weight records were not adequate to make an analysis of the seasonal weight cycle.

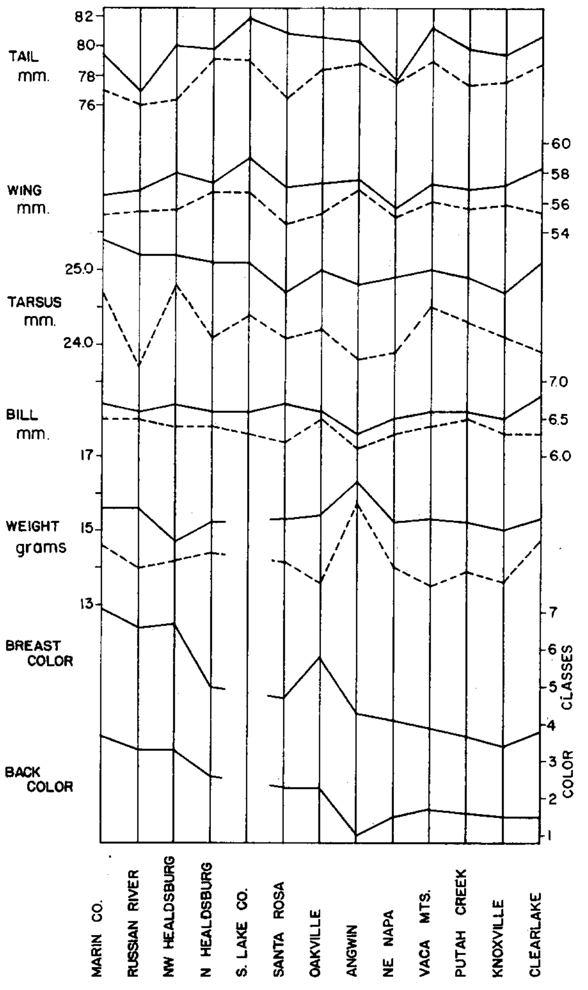

Fig. 2. Summary of mean values for all measurements and color determinations. Breast and back color classes are given some of same numbers but values for the two areas (see text) are not the same. For body dimensions, solid lines indicate males, broken lines, females.

AGE VARIATION

Comparison of the measurements of fall-taken, first-year birds (determined as such by skull examination) with those of adult birds has shown variable differences in dimensional characters. Some samples contain first-year birds that are larger than adults; in others they are smaller. In view of the lack of any consistent deviation of these immatures from the adults, plus the fact that the ages of most of the specimens from museums are not known, it has been judged that first-year and adult age classes may be combined. With regard to color, there is some indication that immatures in most populations average slightly darker than adults. Statistically, however, there is no significance in this difference and for color comparisons the data from all age classes also have been combined.

GEOGRAPHIC VARIATION

Originally, the only significant geographic variation expected was in plumage coloration. However, analysis of measurable characters has shown some definite trends of statistical significance within the limited geographic range studied. The data for the various aspects analyzed are presented in table and graph form in which the localities are arranged in geographic sequences related to the color gradients to be discussed later. These mensural characters are all summarized in figure 2.

Wing length.—The chord of the right wing was measured. The main trends to be

Table 1

Wing Length (mm.)

Locality	Sex	Number	Range	Mean and standard error	Standard deviation	Coefficient of variability
Marin County	♂	71	53.0–60.4	56.50±0.19	1.57	2.8
	♀	60	51.3–58.6	55.07±0.21	1.59	2.9
Russian River	♂	19	54.4–60.5	56.96±0.37	1.58	2.8
	♀	9	52.2–58.5	55.37		
NW Healdsburg	♂	8	57.1–60.1	57.95		
	♀	4	53.2–57.4	55.45		
N Healdsburg	♂	11	55.5–60.0	57.33±0.39	1.24	2.2
	♀	9	54.1–59.5	56.73		
S Lake County	♂	21	56.7–60.6	59.00±0.27	1.19	2.0
	♀	14	54.8–58.6	56.69±0.33	1.20	2.1
Santa Rosa	♂	7	53.7–58.4	57.04		
	♀	6	52.9–56.1	54.48		
Oakville	♂	8	56.1–59.6	57.38		
	♀	5	54.7–55.9	55.34		
Angwin	♂	5	55.8–59.4	57.50		
	♀	4	54.3–58.7	56.83		
NE Napa	♂	8	53.1–57.7	55.62		
	♀	8	53.3–56.7	54.95		
Vaca Mountains	♂	31	54.1–61.3	57.83±0.28	1.55	2.7
	♀	22	53.1–60.6	56.15±0.39	1.78	3.2
Putah Creek	♂	27	54.5–60.3	57.41±0.30	1.52	2.7
	♀	30	53.2–58.8	55.64±0.26	1.42	2.6
Knoxville	♂	18	54.4–61.1	57.66±0.45	1.86	3.2
	♀	14	53.9–58.1	55.91±0.32	1.16	2.1
Clearlake	♂	4	57.2–59.3	58.28		
	♀	2	54.4–56.1	55.25		

seen by scrutiny of table 1 and figures 1 and 2 are toward longer-wingedness northward from Marin County and northward and northwestward from the Napa region. The birds from southern Lake County are significantly longer-winged than all others to the south. Statistical significance between samples in this study is based on the amount of overlapping, or lack of it, of the dimensions encompassed by the means plus or minus twice the standard errors of these means.

Tail length.—This was measured from the skin between the two middle rectrices to the feather tips (see table 2 and figure 2). In general, most of the trends are the same as those for wing length. The males from southern Lake County are significantly longer-tailed than those of all the samples to the south.

Tarsal length.—This was measured from the posterior aspect of the proximal end of the right tarsometatarsus to the distal edge of the last undivided scute. The only sig-

Table 2

Tail Length (mm.)

Locality	Sex	Number	Range	Mean and standard error	Standard deviation	Coefficient of variability
Marin County	♂	68	71.5–89.2	79.54±0.49	4.03	5.1
	♀	57	70.7–86.0	77.03±0.46	3.49	4.5
Russian River	♂	16	71.0–83.5	76.87±0.98	3.77	4.9
	♀	8	68.7–84.6	76.00		
NW Healdsburg	♂	8	75.4–85.2	80.05		
	♀	4	71.1–82.5	76.35		
N Healdsburg	♂	11	74.1–84.0	79.81±0.88	2.78	3.5
	♀	9	70.5–83.0	79.16		
S Lake County	♂	21	75.7–87.8	81.90±0.73	3.24	4.0
	♀	14	73.9–82.7	79.08±0.84	3.04	3.8
Santa Rosa	♂	7	76.8–88.3	80.87		
	♀	6	74.6–78.2	76.42		
Oakville	♂	8	78.0–85.5	80.69		
	♀	5	75.1–80.7	78.48		
Angwin	♂	5	76.2–83.8	80.26		
	♀	4	77.7–81.1	78.90		
NE Napa	♂	8	74.7–82.3	77.69		
	♀	8	74.2–80.2	77.54		
Vaca Mountains	♂	30	73.5–88.7	81.21±0.58	3.20	3.9
	♀	20	74.0–83.2	79.02±0.63	2.73	3.5
Putah Creek	♂	26	74.5–84.4	79.77±0.58	2.91	3.6
	♀	28	72.2–83.9	77.39±0.59	3.11	4.0
Knoxville	♂	17	73.4–85.1	79.36±0.93	3.75	4.7
	♀	13	72.6–84.1	77.61±1.08	3.73	4.8
Clearlake	♂	4	78.0–84.8	80.70		
	♀	2	76.4–81.2	78.80		

nificant difference with respect to this character occurs between the males of the Knoxville-Putah Creek region and those of Marin County in which the birds from the east at Knoxville have shorter tarsi than those of Marin in the west. In between, to the west and south of Knoxville, there is an irregular cline (see table 3 and figure 2). Tarsal length trends in the males seem to correspond most closely to those for color in which the shortest tarsi generally are found in the lightest birds and the longest tarsi in the darkest.

Bill length.—The measurement was taken from the anterior rim of the right nostril to the tip of the culmen. There are no significant differences to be seen here (fig. 2).

Weight.—Average weights lie between 14.7 and 15.6 grams for fall-taken male specimens and between 13.5 and 14.7 grams for female specimens (see table 4 and figure 2). No significant differences appear among the samples, which are admittedly small for seven of twelve localities.

Lengths in relation to weights.—Perhaps of more importance than linear measurements are ratios of these mensural characters to body size expressed as weight. These relationships have been examined in those samples of males in which weights for nine or more specimens are available. Average values for the four mensural characters have each been divided by the respective average weight values to give the mean number of millimeters per gram of body weight. These figures and those for weights are presented in table 5 for five localities studied intensively and are listed in a geographic sequence related to both the coloration gradient and to the average annual temperature gradient. To give a broader scope to this particular aspect, specimens in the Museum of Verte-

Table 3

Tarsal Length (mm.)

Locality	Sex	Number	Range	Mean and standard error	Standard deviation	Coefficient of variability
Marin County	♂	70	23.3–26.9	25.43±0.09	0.74	2.9
	♀	56	23.2–27.0	24.70±0.10	0.76	3.1
Russian River	♂	18	24.4–25.6	25.17±0.11	0.44	1.8
	♀	8	23.0–24.8	23.59		
NW Healdsburg	♂	8	24.6–25.8	25.24		
	♀	4	24.3–25.2	24.78		
N Healdsburg	♂	9	24.2–25.6	25.01		
	♀	8	23.2–25.1	24.09		
S Lake County	♂	21	23.9–25.8	25.03±0.13	0.59	2.4
	♀	12	23.2–25.5	24.37±0.23	0.76	3.1
Santa Rosa	♂	6	23.6–25.5	24.73		
	♀	6	23.0–24.7	24.05		
Oakville	♂	8	24.5–26.0	25.03		
	♀	5	23.6–25.1	24.22		
Angwin	♂	5	24.2–25.2	24.82		
	♀	4	23.6–24.0	23.83		
NE Napa	♂	7	24.3–25.4	24.94		
	♀	8	23.1–25.1	23.93		
Vaca Mountains	♂	31	22.4–26.4	24.99±0.14	0.78	3.1
	♀	21	23.5–25.8	24.50±0.15	0.67	2.7
Putah Creek	♂	25	23.4–25.9	24.86±0.14	0.70	2.8
	♀	29	23.2–25.4	24.35±0.10	0.53	2.2
Knoxville	♂	18	22.9–25.6	24.71±0.18	0.77	3.0
	♀	13	22.5–25.5	24.13±0.24	0.84	3.5
Clearlake	♂	4	24.8–26.0	25.10		
	♀	2	23.7–24.0	23.85		

brate Zoology representing the northern and southern extremities of the range of the Wrentit were analyzed in the same way to show the ratios for these same characters. These birds represent the races *C. f. phaea* from Oregon (9 males with weights); *C. f. rufula,* from Del Norte and Humboldt counties in northwestern California (14 males with weights); and *C. f. canicauda* from Baja California (37 males with weights). These data are also presented in table 5.

With reference to body weight, which gives an indication of size, it is apparent that shorter wings, tails, tarsi, and bills are present in the north and that there is a fairly even cline southward within the main study area that somewhat parallels certain climatic factors to be discussed later.

The longest wings, tails, and tarsi appear at the southernmost limits of the range of this species. The bills are longer there than in most of the samples from farther north. According to Allen's rule, extremities are relatively shorter in colder regions. This seems to be borne out by these birds, especially over the latitudinal extent of their range which likewise shows a temperature gradient of colder to warmer from north to south. Even within the restricted latitudes of the five study areas used here, there is some increasing length of extremities which correlates with increasing average temperatures.

Calculations of the Spearman rank-difference correlation were carried out. This statistic, rho, shows a correspondence between the rank-ordering of the eight localities with respect to the mean annual temperatures, as arranged in table 5 from cold to warm, and the rank-ordering of birds at these localities with respect to the mean number of millimeters per gram of body weight of the four measurable characters from short to long. The value of rho for wing length and temperature gradient is .926; for tail length,

.972; for tarsal length, .891; and for bill length, .788. The first three are significant at the .01 level and the last at the .05 level. This may be interpreted as a highly significant correlation between these measurements and the mean temperatures to be found at these localities.

Bergmann's rule, which states that animal bodies are relatively larger in colder

Table 4

Weight (grams)

Locality	Sex	Number	Range	Mean and standard error	Standard deviation	Coefficient of variability
Marin County	♂	25	14.3–17.3	15.60±0.19	0.91	5.8
	♀	22	12.9–16.4	14.57±0.19	0.85	5.8
Russian River	♂	6	14.6–16.8	15.57		
	♀	3	13.8–14.2	14.00		
NW Healdsburg	♂	8	13.0–15.6	14.68		
	♀	4	13.7–14.8	14.18		
N Healdsburg	♂	11	14.3–16.1	15.25±0.19	0.61	4.0
	♀	9	13.6–16.3	14.43		
S Lake County	♂	0				
	♀	0				
Santa Rosa	♂	6	14.8–15.9	15.33		
	♀	4	14.1–14.3	14.23		
Oakville	♂	8	13.2–17.5	15.46		
	♀	5	13.3–14.2	13.64		
Angwin	♂	2	14.7–17.8	16.25		
	♀	3	13.9–17.9	15.70		
NE Napa	♂	8	13.3–15.8	15.24		
	♀	8	13.2–15.2	13.99		
Vaca Mountains	♂	24	13.5–16.4	15.33±0.16	0.76	5.0
	♀	16	11.6–15.1	13.52±0.24	0.88	6.5
Putah Creek	♂	26	13.8–16.4	15.20±0.13	0.67	4.4
	♀	30	12.7–15.2	13.92±0.12	0.66	4.7
Knoxville	♂	11	13.0–16.8	14.95±0.35	1.09	7.3
	♀	7	12.7–14.5	13.57		
Clearlake	♂	4	14.2–16.2	15.33		
	♀	2	14.5–14.8	14.65		

Table 5

Measurements in Relation to Weight in Male Wrentits

	Average millimeters per gram				Weight in grams	
	Wing	Tail	Tarsus	Bill	Average	Number
Oregon	3.64	4.86	1.59	.428	15.76	9
NW California	3.51	4.62	1.57	.428	15.66	14
Marin County	3.62	5.10	1.63	.431	15.60	25
N Healdsburg	3.76	5.23	1.64	.435	15.25	11
Vaca Mountains	3.77	5.30	1.63	.431	15.33	24
Putah Creek	3.78	5.25	1.64	.436	15.20	26
Knoxville	3.86	5.31	1.65	.437	14.95	11
Baja California	3.94	5.42	1.68	.435	15.02	37

regions, also appears to apply here since the heaviest Wrentits are found in the north and lighter birds exist toward the south. Within the study area, the heaviest birds were encountered in Marin County where average temperatures are lower than at Knoxville where the lightest birds were found.

The rank-difference correlation between the rank-ordering of the eight localities with respect to mean annual temperatures from cold to warm and the rank-ordering of mean body weight for the birds at these localities from high to low has a value for rho of .937 which is significant at the .01 level.

Interdimensional correlations.—Correlations of habitat factors with these body parts may indicate some significant relationship. The chaparral studied and to be mentioned later shows varying densities. The most dense brush of these localities measured is found at Inverness in Marin County, the least dense at Knoxville. If birds living in the least dense brush tend to fly more, then perhaps longer wings and tails in proportion to weight (as found at Knoxville) may be advantageous and may thus be favored selectively. Likewise, less need to fly in the densest brush may lead to the selection of shorter wings and tails (as found in Marin County). Whether such correlations exist for Wrentits from Oregon and Baja California has not been determined.

Table 6

Coefficients of Correlation (r) in Males

	Wing-tail	Wing-tarsus
Marin County	+.736	+.046
Russian River	+.502	+.367
N Healdsburg	+.547	+.387
S Lake County	+.596	—.228
Vaca Mountains	+.725	—.190
Putah Creek	+.802	+.085
Knoxville	+.749	+.269

Tail and wing lengths show reasonably parallel variations as is indicated by the values of the coefficients of correlation (r) shown in table 6. Presumably these appendages are related in their proportions first because they are made of the same material and very likely respond to the same growth controlling factors in the bird's body, and secondly because they constitute parts of the flight machinery which tend to have basic functional interrelationships of size.

If in dense brush the birds fly less and depend on hopping more than in less dense brush, then wing and tarsal lengths might be inversely correlated. For males they are correlated slightly positively in five samples and very slightly negatively in two samples as shown in table 6. On the other hand, it could also be argued that short tarsi are of advantage to Wrentits in dense brush and the positive values for r that are greater than the negative ones might be called upon to support such an interpretation. The low values of r, however, indicate no significant correlation either way.

Breast color.—Nine Wrentits, selected from the specimens in new plumage collected by the author, were used as color class standards by which to divide the total collection of 267 birds. These nine specimens represent the gamut of color expression within the limited geographic range under consideration and were carefully described by visual comparisons with color dictionaries and a disc colorimeter as well as by means of a photoelectric spectrophotometer to make sure they represented a reasonably objective color gradient. In adjectival color terms, inadequate as they are, the colors run from pale or light yellowish brown to moderate brown. These methods of color analysis have been discussed elsewhere by me (Bowers, 1956). The definition of the colors of all the specimens could in time have been carried out by using the procedures described there. However, it was considered that an adequate expression of the colors could be obtained by simply comparing all the specimens directly with these nine standard birds once they had been selected. The testing of a second set of seven skins in the spectrophotometer gave evidence that fairly good equivalence could be achieved by the method of direct comparison since this second set was chosen by visual determination with reference to the first set.

The nine standard specimens were spread on a table before a large north-facing window in cloud-free daylight. The remainder of the skins, with the locality labels hidden, were then compared one by one with the breast areas of the standards and placed in a row headed by the one which was judged to be the closest match. In this way all the specimens were spread out on the table in nine rows. Some decisions were difficult because there are three dimensions in color and not just one as this kind of separation implies. The main aspect of color on which the decisions of position rested was that of value (darkness and lightness). Some birds that were obviously more yellowish or reddish than the standard that was closest in value were thus possibly placed out of proper position with respect to hue. Since of the three aspects of color the judgment of value is probably the most easily accomplished, it is considered that no great violence was done to the sequence of colors by this selection.

With the whole collection spread out, slightly different viewing positions were taken and a few birds that were seemingly misplaced were rejudged with respect to the other decisions made for that row. Some reassessments were made and better matches were thus found for those specimens in question.

The whole procedure was repeated on another day with the same physical conditions prevailing. For this second trial, 51.5 per cent of the specimens were the same as in the first trial and 95.3 per cent were judged as before or within plus or minus one step. The effects of these differences were shown in the averages of most of the locality samples although the greatest shift was only six-tenths of a color step. None of the color gradients between localities was reversed. These small shifts are thought to be not important since the overall picture still stands. The reproducibility is thus considered to be good especially in view of the problems of color dimensions mentioned earlier and also since there are relatively small steps between adjacent color groups.

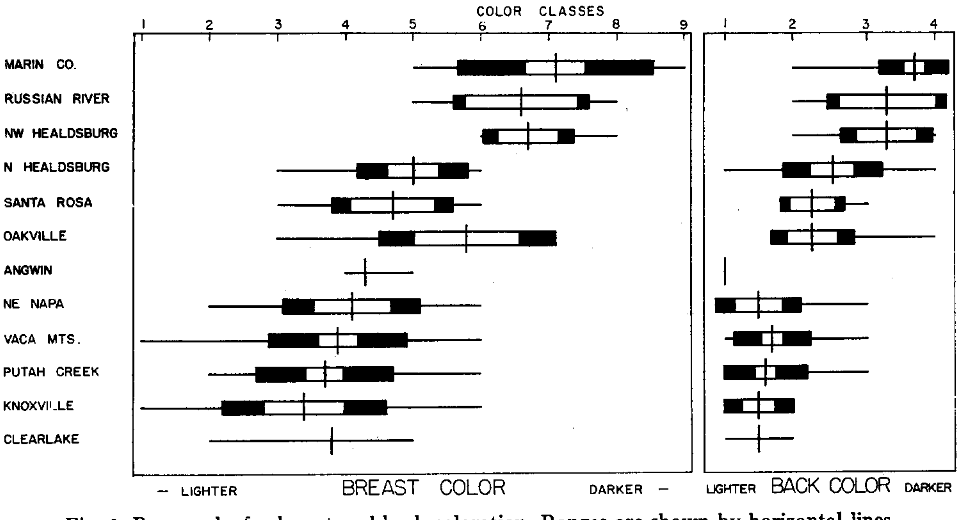

Fig. 3. Bar graphs for breast and back coloration. Ranges are shown by horizontal lines, means by vertical lines, twice the standard errors of the means by open bars, and standard deviations by solid bars.

For the present section the simple terms "darker" or "lighter" will be used to designate collectively the three dimensions of color.

By inspection of table 7 and figure 3, it is to be observed that there is a considerable degree of color separation between some of the samples. By comparing the graph with the map in figure 1, the geographic directions of these clines can be seen. The darkest birds are found in Marin County, the lightest in the Knoxville region to the northeast of Marin County.

Table 7

Breast Coloration

(Light to dark scale—1 to 9)

Locality	Number	Range	Mean and standard error	Standard deviation	Coefficient of variability
Marin County	44	5–9	7.11±0.22	1.44	20.3
Russian River	9	5–8	6.56±0.33	1.00	15.2
NW Healdsburg	12	6–8	6.67±0.20	0.67	10.0
N Healdsburg	22	3–6	5.00±0.18	0.82	16.4
Santa Rosa	11	3–6	4.73±0.27	0.89	18.9
Oakville	14	3–7	5.79±0.36	1.30	22.4
Angwin	4	4–5	4.30		
NE Napa	16	2–6	4.13±0.27	1.03	25.1
Vaca Mountains	54	1–6	3.87±0.15	1.08	27.7
Putah Creek	58	2–6	3.67±0.14	1.07	28.9
Knoxville	19	1–6	3.37±0.28	1.20	35.6
Clearlake	4	2–5	3.75		

The Wrentits from the Russian River, while only nine in number, average half a color step lighter than those from the Marin area but show much overlap with them. The twelve birds from northwest of Healdsburg, farther north, average approximately the same as those from the Russian River. There is good Wrentit habitat between these two collecting stations so that gene flow is probably relatively free between them.

The conspicuous break between those birds from the northwest of Healdsburg and those from directly north to slightly northeast of Healdsburg is striking. There is overlap between the breast color of the two samples only at the extremes of the range of variation of each and yet these collecting localities are fairly close together. There are two agricultural strips between these localities, and the specimens from northwest of Healdsburg were taken within one of these strips. The birds were found in field-side tangles of wild blackberry, poison oak, and *Baccharis*. Dry Creek, which runs northwest from Healdsburg, is flanked by riparian vegetation in which Wrentits were found. The agricultural areas which exist between these two collecting regions, although they contain some scattered Wrentit habitat, evidently contribute to a steepening of the color gradient.

If we consider the back color of these same birds, as shown in table 8 and figure 3, it will be seen that there is no overlap of twice the standard errors for these samples from northwest and north of Healdsburg. Thus in back coloration also there is a significant difference between these samples and the color trend is here steepened and runs in the same direction as that for breast color. The specimens from Marin County, Russian River, and northwest of Healdsburg then appear to form a cluster at the dark end of the color gradient and are set off from the rest of the specimens by the conspicuous discontinuity of the color gradient between the two localities near Healdsburg.

The Wrentits taken near Santa Rosa average lighter in breast color than those from north of Healdsburg, but not significantly so. The birds from the Oakville region average darker than those from Santa Rosa or north of Healdsburg, although they are lighter than those from northwest of Healdsburg. The meaning of these differences is not immediately clear. There is, however, a significant break between the breast color and also the back color of the specimens from northwest of Healdsburg and those from Santa Rosa.

Arrows may be plotted, as in figure 1, from Marin County through Russian River and northwest of Healdsburg, thence southeastward down to Santa Rosa and Oakville to indicate lightening colors. Arrows indicating such color directions would have to be drawn, considering averages only, from Oakville northwestward to Santa Rosa and also to the north of Healdsburg. This would cause confusing directions to appear along the Napa–Sonoma County line. However, since these reversals are not supported by signicant differences, they are only mentioned here and not indicated on the map.

There is almost a full step difference between the averages for north of Healdsburg and northeast of Napa. There is likewise only a slight overlap of twice the standard errors. Of course the distance between these two localities is roughly 40 miles and it could be expected that local conditions are different. Four specimens taken in February from near Angwin in Napa County, about halfway between Healdsburg and Napa, show intermediate coloration. Although these specimens are considered to be too worn for accurate color appraisal, they do indicate that the clinal direction on the map between these localities is correct.

It is of interest to note here that birds from Marin County are three color steps on the average darker than those from northeast of Napa. This difference is statistically highly significant.

The birds of Marin and those from Oakville, while on the average only a little over one color step apart, do show a significant difference. The habitat lying between these two localities is not suitable for Wrentits. There are large stretches of dry grassland and cleared agricultural areas that offer little good cover for the birds. This means that movement of Wrentits across the Petaluma–Sonoma–Santa Rosa region is probably quite restricted. Whatever continuity there is between these populations is maintained over more devious routes. Northward along the coast of Marin and Sonoma counties there is at least low scrubby coastal sagebrush in which the birds are resident. The connecting habitat is then interiorward bordering the Russian River and southward from Healdsburg along the mountains of the Napa–Sonoma County line.

Between Oakville and northeast of Napa there is the agricultural Napa Valley. Here, there are hedgerows and clumps of brush that could afford limited movement to the Wrentits, but the data on breast coloration seem to indicate, as do the data on back coloration, that there is a significant color break between these two localities. Even if the data for the lighter birds from Santa Rosa are combined with those from Oakville there is still a significant discontinuity.

Consideration of these differences and the geographic positions of the localities leads one to conclude that there is the sharpest break in color between the birds so far discussed and those to the east and northeast yet to be mentioned. To be sure the birds from Santa Rosa show considerable overlap with those from northeast of Napa, but there is also considerable distance between the two localities within which is found a population at Oakville that shows much darker color than the population at Napa. There is, however, a significant difference between the birds of Santa Rosa and those to the east from Putah Creek and Knoxville.

From northeast of Napa to Knoxville there is a very even cline toward lightness involving the birds on the Vaca Mountains and along Putah Creek. The Knoxville birds appear to average the lightest of all samples taken although there is overlap of twice the standard errors with those birds to the south. There is a significant break in color between the birds from north of Healdsburg and those from Knoxville, Putah Creek, and the Vaca Mountains.

The four specimens from Clearlake Park in Lake County average lighter than those from north of Healdsburg and slightly darker than those from Knoxville.

Back color.—The analysis of back coloration was carried out in a manner similar to that used for breast coloration. There is, however, not as wide a range of color expression in the back plumage. These colors may be roughly described as differing values (shades) of dusky brown. Comparison of the specimens with the four color-class standards provided results similar to those for breast coloration. The averages of some localities do not fall exactly into the same sequence as for breast color, but there are

Table 8

Back Coloration

(Light to dark scale—1 to 4)

Locality	Number	Range	Mean and standard error	Standard deviation	Coefficient of variability
Marin County	44	2–4	3.70±0.08	0.51	13.8
Russian River	9	2–4	3.33±0.31	0.87	26.4
NW Healdsburg	12	2–4	3.33±0.20	0.67	20.3
N Healdsburg	22	1–4	2.59±0.16	0.73	28.2
Santa Rosa	11	2–3	2.27±0.15	0.47	20.4
Oakville	14	2–4	2.29±0.17	0.62	27.0
Angwin	4	1	1.00		
NE Napa	16	1–3	1.50±0.16	0.63	42.0
Vaca Mountains	54	1–3	1.68±0.08	0.57	33.5
Putah Creek	58	1–3	1.59±0.08	0.62	38.7
Knoxville	19	1–2	1.53±0.12	0.51	34.0
Clearlake	4	1–2	1.50		

no major differences between the seriations for back and breast color (see figure 3 and table 8). The greatest difference between breast and back gradients occurs in birds of the Oakville and Santa Rosa localities. In breast color the sample from Oakville averages about one color step darker than those from Santa Rosa and north of Healdsburg. In back color the averages for birds of Oakville and Santa Rosa are equivalent and both are lighter than those from north of Healdsburg.

Back color shows no overlap of twice the standard errors of specimens from northwest and north of Healdsburg. In breast color there is no overlap even of the standard deviations.

Specimens from Angwin all appeared to be in the lightest color class. Thus they do not fall in line with the back color cline between north of Healdsburg and northeast of Napa as they do for breast color. However, as mentioned earlier, they were collected in February and are more worn than any of the other specimens used for the color analysis.

The steepened gradient that was mentioned in connection with breast coloration between the last six localities and the first six, is even more obvious here. In back color there is no overlap of twice the standard errors between these two groups. The last five localities show more homogeneity than any other grouping. (The small sample from Angwin is omitted from this discusssion.) There is a step difference of only 0.2 in back color among their means. In breast color there is a difference of only 0.7 among the means. The birds of these eastern and northeastern localities then appear to be somewhat set apart at the lighter end of the color scales. Since there appears to be correlation between vegetation and Wrentit color, as will be shown later, this break is to be expected since the humid coastal type of vegetation is present interiorward as far as the Napa Valley, with minor exceptions near Angwin and Napa, but it is replaced eastward by the more xeric interior flora with which the lighter birds are associated.

To recapitulate, the darkest Wrentits of those investigated occur along the coast from Marin County to the Russian River region and northeast from there to the area northwest of Healdsburg. These first three localities contain birds that average considerably darker than any others although they are not significantly different from all of them. They are considered taxonomically as belonging to the race *C. f. rufula.*

The next three localities in the geographic sequence outlined harbor birds that lie in the approximate middle of the color span of breast and back. Taxonomically these have been designated the intermediate race *C. f. intermedia.* These Wrentits in turn average darker than those birds found farther east and northeast. In back color this break appears to be statistically significant but more overlap is found in breast coloration.

The birds from Angwin (small sample), Napa, the Vaca Mountains, Putah Creek, Knoxville, and Clearlake (small sample) are all similar and all considerably lighter than other samples to the west. Taxonomically these birds are of the race *C. f. henshawi.* The steepened gradient between these latter samples and those to the west is a reflection perhaps of the partial isolation produced by the agricultural areas between them.

Overall trends are from darkest Wrentits in the west to lightest birds in the east.

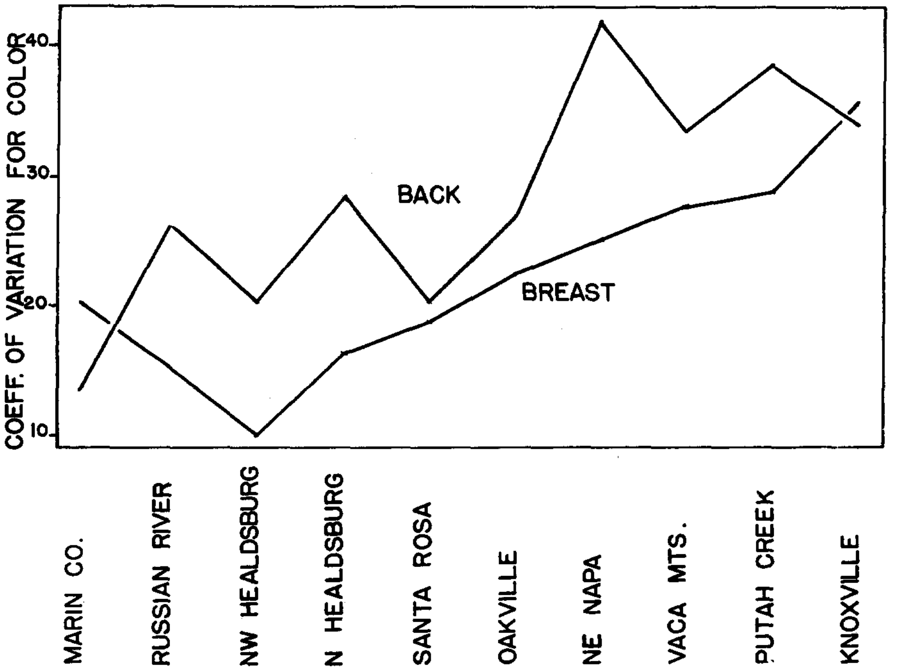

Fig. 4. Coefficients of variation for back and breast coloration.

Pathways between these extremes are not direct but are probably as indicated by the arrows in figure 1.

Color variability.—Variability of coloration is much higher than that of the mensural characters and shows an interesting trend (fig. 4). Generally, the darkest birds have the least variability and the lightest birds show the most. This trend leads one to postulate that the environment which allows selection for the darker plumage is more restrictive or exerts a sharper selection on color expression than the environment in which the lighter birds exist. There is correlation here with weather data, to be discussed later, in which both temperatures and humidities are shown to exhibit wider fluctuations in the interior localities than along the coast. Davis (1951:89) working on *Pipilo aberti* and *P. fuscus* and Selander (1954:79) studying *Chordeiles minor* have found similar situations in which more variable environments contain birds more variable in color than those found in more uniform environments. Pitelka (1951:364) also found population variation and habitat variation to be correlated in *Aphelocoma*.

ANALYSIS OF THE ENVIRONMENT AND CORRELATION WITH PLUMAGE COLORS

COLOR AND ILLUMINATION OF SUBSTRATE

The concept of "substrate" must encompass more of the vertical dimension for brush-inhabiting birds than for ground-dwelling mammals and birds. Hence, it is more complicated to describe this "substrate" and to analyze its color with respect to its possible influence in the selection of color variants in such birds.

The foliage of a tree makes objects under it appear darker by reducing the illumination reaching them. The amount of darkening under a tree depends on the density of the foliage overhead. Hence the measurement of the light reaching the understory beneath different trees gives a measure of the amount of darkening with respect to the open illumination from the sky and thus provides an index for the density of those trees. The fact that Wrentits live in what appear to be variously illuminated areas of chaparral (used loosely here to refer to life form) prompted the measurement of light intensities in several localities.

The assessment of brush density was carried out by using a Weston illumination meter, model number 756, that was built to read directly in foot-candles. The light-sensitive element was covered with a Weston Invercone as an integrating device. The importance of such an addition was pointed out by Wallace (1937). This integrating screen greatly minimizes the effects of the variance of the angle of incidence of light. Experimentation with the present instrument showed likewise that such a filter is indispensable for use under varying sun position, for measuring bright sun flecks beneath the vegetation, and indeed even for measuring the full intensity of the brightest sunlight. The Invercone cuts down the light readings to one-tenth of their value regardless of the actual amount of illumination.

The method used for measuring brush density involved selecting chaparral areas at each of nine localities. Fairly uniform and representative cover in which Wrentits were actually collected or at least seen was desirable. One end of a 100-foot line was tied to a bush, usually in which a Wrentit had been seen, and the cord then was strung out in as nearly a straight line as possible, tightened up, and tied to a bush by its other end. In laying out the line an attempt was made to follow the general direction of the Wrentit as it moved away from the starting bush in order to measure areas of brush that were used by the birds. The cord was marked at five-foot intervals. Light readings were made by placing the light paddle containing the sensitive element at ground level. The sensitive cell was pointed vertically. Readings were taken at five-foot intervals directly beneath the cord and one foot on each side of the cord. Use of the 100-foot line thus gave 60 recordings arranged in a regular pattern throughout the irregularly placed chaparral plants.

The validity of the transect method for plant censusing was tested by Bauer (1943). His system yielded, in a fraction of the time, information which was comparable to forestry service records that contained actual tallies of the plants over whole plots. The transect method used here for light recording is an adaptation of the same basic idea. My transects utilized for density measurement were at the same time used as species census lines.

Light readings obtained beneath the brush have been expressed as percentages of the overhead unobstructed light. It is assumed, although not proven, that plant canopies remove the same percentage of light regardless of the level of the overhead intensity. Thus the percentages become indices of brush density which can be compared roughly under the various illumination characteristics of the sky. Measurements were never made before 9:00 a.m. or after 3:00 p.m., Pacific standard time. If the sun was more than 45 degrees from the zenith no measurements were made.

Possible differences in spectral transmission of the leaves of various species of plants have been disregarded. The visual apparatus of vertebrate predators is relatively insensitive to such qualitative differences in sunlight and only the quantitative sum of whatever light is present is considered of importance. With minor exceptions, the response of the light meter is uniform over the visual range.

The color value of the area under the brush is also produced or effected importantly by a combination of factors other than the amount of visible illumination reaching it. In denser brush, for example, where less evaporating sunlight strikes the ground, there is greater moisture retention resulting in simply making objects appear darker because they are wet. Also, moisture aids the production of dark humus. Moreover there is less bleaching effect of direct sunlight. All these factors contribute to a darker soil surface and the converse effects in less dense brush can be outlined to partly explain the lighter substrate to be found there.

Since animals tend to match the color values of their surroundings, then the darkest habitat should contain the darkest Wrentits and the lightest should harbor the lightest colored birds. The graph of light transmittance (fig. 5) shows the results of the recordings. The localities are arranged to correspond with the breast color seriation from the darkest end of the gradient. It will be seen that the overall trends are somewhat as predicted. The readings from Russian River indicate more dense brush than in Marin County, which inverts the relationship to the coloration of the Wrentits. However, the presence of an overstory or at least bordering individuals of redwood, laurel, and Douglas fir at Russian River may explain the low illumination found there at ground level.

It is of interest that in the study area any sequence of localities from southwest to east or northeast shows decreasing or equal brush density as measured by light transmittance. Likewise any sequence running from the northwest to the east or southeast shows equal or decreasing brush density. The same directional seriations show up in breast and back coloration from dark to light colors. It is also of interest that the measurements for the extreme localities, with respect to east and west, are considerably different.

Estimates of the average vertical thickness of the leafy canopy above the transect lines were made in conjunction with the amount of representation of each plant species along these lines. Multiplication of this vertical thickness by the linear footage gives a vertical area of canopy which is an index of the amount of living space available to the Wrentits, since they spend nearly all of their time within this foliage layer. Summation

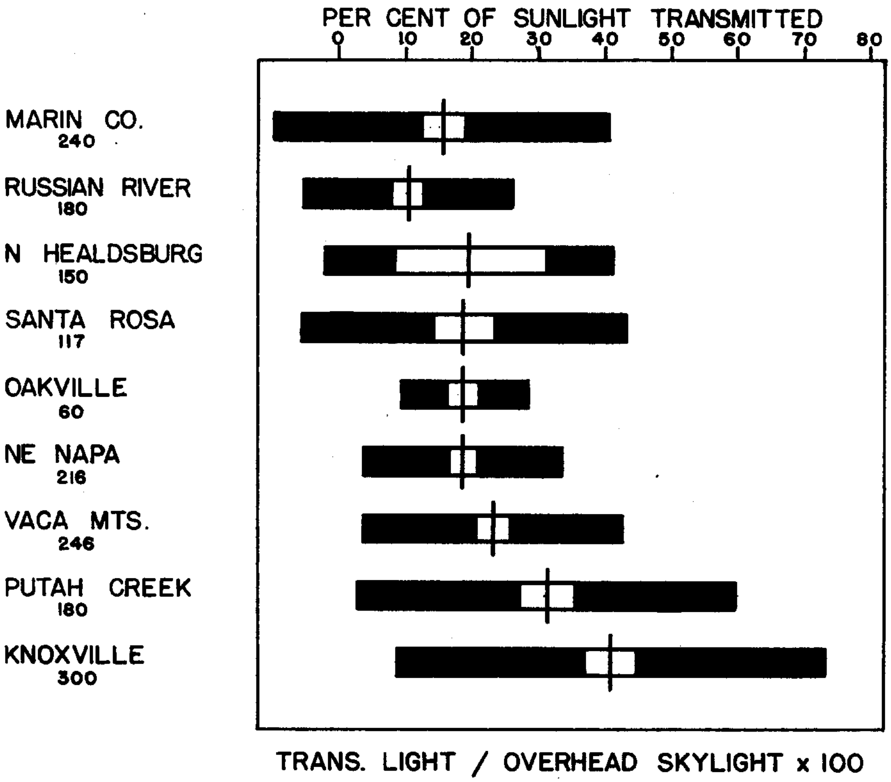

Fig. 5. Bar graphs showing the percentages of skylight transmitted through the chaparral canopies. Higher transmittance occurs through less dense brush and lower transmittance occurs through denser brush. Means, standard errors, and standard deviations as in figure 3.

of these vertical areas allows the calculation of the average number of square feet of vertical area per linear foot of transect for each locality. The results of these calculations are found in table 9.

By comparing these figures with the data for light transmittance, it can be seen that the more objective measurement of density by means of light measurement agrees generally with this somewhat subjective estimate of canopy thickness. The correlation coefficient r is + .698 for light transmittance and canopy thickness. The thickest foliage layer appears to occur in Marin County. The light readings at Russian River were reduced by surrounding trees, but since these trees were not directly above the transects they did not add to the estimates of canopy thickness. Thus, brush density indicated

Table 9

Average Vertical Area of Living Space

Locality	Vertical area per linear foot	Locality	Vertical area per linear foot
Marin County	3.69	NE Napa	2.46
Russian River	3.24	Vaca Mountains	3.29
N Healdsburg	2.80	Putah Creek	2.08
Santa Rosa	2.65	Knoxville	1.86
Oakville	2.65		

by the vertical area figures is not greater than that in Marin County in the way the light readings seem to indicate. One exception, that of the Vaca Mountains, may be explained by suggesting that the canopy there, while almost as thick vertically as that at Marin County, is nevertheless sparse enough to have allowed light readings to be much higher than those at the coast. Disregarding this one exception, the data for vertical area indicate good correspondence with density measurement by light readings and with the color gradient of the Wrentits.

Another aspect of the coloration of the "substrate" is the actual color of plant parts, especially those close to the color of the Wrentits and which provide part of the backdrop against which the birds would be seen. Stems of plants most commonly present were collected from Marin County and the Vaca Mountains for a rough color determination. These are shown in table 10 and are presented in order of abundance as represented by the transect data.

Generally speaking, the lightest Wrentits are quite gray in breast coloration. The darkest birds are deep ruddy-brown. The grays of the stems listed most closely approximate the color of the lightest birds, such as those from the Vaca Mountains, while the

Table 10

Color of Stems of Plants in Two Regions

MARIN COUNTY

Genus	Stem color	Per cent
Ceanothus	dark gray	51.0
Pinus	gray	10.7
Baccharis	gray	9.3
Polystichum	brown	5.8
Arctostaphylos	dark red-brown	5.7
Vaccinium	reddish brown	5.0
Rubus	red-green	4.1
Myrica	gray	2.3
Arbutus	dark red-brown	1.8
Rhamnus	gray	1.5
Pteris	brown	1.3
Corylus	brown	.4
Lonicera	red-brown	.3
Diplacus	brown	.2
Rhus	gray	.2

Totals: gray 75.0 per cent; 6 species
brown 20.5 per cent; 8 species

VACA MOUNTAINS

Genus	Stem color	Per cent
Quercus	gray	30.8
Adenostoma	gray	26.7
Arctostaphylos	dark red-brown	9.1
Photinia	gray	7.8
Cercocarpus	gray	5.0
Garrya	gray	4.7
Ceanothus	gray	4.5
Rhus	gray	4.1
Umbellularia	gray	3.3
Diplacus	brown	1.4

Totals: gray 86.9 per cent; 8 species
brown 10.5 per cent; 2 species

red-browns are closest to the darkest birds as, for instance, those from Marin County. The higher overall percentage of browns and red-browns in plant parts plus the presence of more species with brown bark in Marin County suggest another factor besides density of the brush and its related effects that may influence the substrate color.

All these factors, denser brush, slower evaporation of soil moisture, more humus production, less bleaching of leaf litter, and more dark stems, contribute to darker habitats. Such conditions are found along the coast where weather factors, the details of which are presented later, may be expected to produce heavier vegetation.

CHAPARRAL COMPOSITION

The percentage occurrences and constellations of plant species found at each locality provide clues concerning some aspects of the color distribution of the birds. For example, the abundance of *Adenostoma fasciculatum* (fig. 6) shows a striking correlation with breast coloration. The darkest birds are found where *Adenostoma* is scarce and lighter birds are found where this plant is abundant. Possibly the "substrate" color determined by the *Adenostoma* is one cause of the relationship here. The discussion of Davis (1951: 41) concerning the terms "black chaparral" as applied to *Adenostoma* and "blue chaparral" referring to *Ceanothus* appears not to explain color correlations as well for the Wrentit as for the Brown Towhees since the lightest Wrentits occur where "black chaparral" is most abundant and the darkest are found where "blue chaparral" is most common.

Rhus diversiloba occurs widely and contributes to Wrentit habitat and food supply. This more vine-like plant appears least in the transects where both the extremes of Wrentit color are found and occurs most in those areas where Wrentits are medium in darkness. *Diplacus aurantiacus* shows a similar pattern of occurrence, but apparently it does not contribute appreciably to the living areas of the birds.

Species of *Quercus,* called scrub oak because of their life form, are present in most localities and provide much of the habitat for the Wrentits. The fact that one species of oak does not occur all across the region is an indication of differing environmental conditions. *Quercus wislizenii* is more abundant where Wrentits are darker in color; *Q. dumosa* is more prevalent where Wrentits are intermediate or lightest; *Q. durata* is present mainly where the birds are the lightest.

The picture for *Ceanothus* and *Arctostaphylos* is somewhat more complex. First of all, these two genera are difficult ones taxonomically, and second, the region is sprinkled with several different species of each genus, a further indication of differing conditions. There are great numbers of large-sized plants of *Ceanothus thyrsiflorus* in Marin County and at Russian River. Here this species makes thick canopies and provides dense cover utilized widely by Wrentits. Other species of the genus, although present at all other localities sampled, do not represent as large a percentage of the total vegetation. *Ceanothus cuneatus,* a plant living in dry situations, occurs in only three localities, Oakville, Vaca Mountains, and Putah Creek. In all of these areas Wrentits are intermediate or light. *Ceanothus cuneatus* is present on extremely dry south-facing slopes near Healdsburg, but it did not appear in the transect data.

Arctostaphylos occurs in the transects of seven of the nine localities. At least six different species are represented. At Napa, two species, *A. canescens* and *A. stanfordiana,* grow intermingled to produce sizable, almost pure stands. *Arctostaphylos viscida* comprises similar nearly pure patches in the chaparral at Knoxville. Even though these stands are relatively barren at ground level, Wrentits use them considerably. *Arctostaphylos glandulosa* occurs at the station north of Healdsburg and in the Vaca Mountains. Apparently no other localities share a common species. Manzanitas often grow as isolated individuals and thus may not have been sampled completely.

Umbellularia californica is present in the transects of six localities, but no particular pattern of occurrence appears to correlate with the color trends of the Wrentits.

Arbutus menziesii is present only in the transects in Marin County and at the Russian River; these localities contain the darkest birds. One Wrentit from north of Healds-

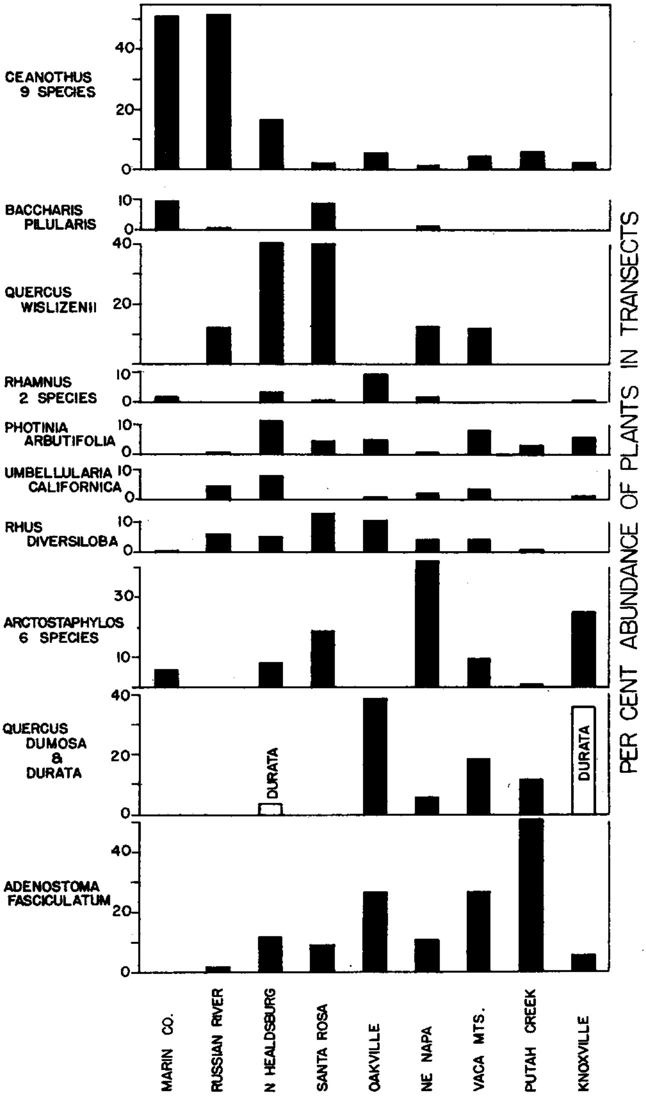

Fig. 6. Histograms showing percentages of the most common plants at nine localities. Species of *Ceanothus, Rhamnus,* and *Arctostaphylos* have been combined only for simplicity of graphing.

burg was taken from madrone although this plant species did not appear in the transects from there. *Arbutus menziesii* is too large and open to be considered a typical chaparral plant. It is most often found in moist areas that also support redwood and Douglas fir trees.

Bracken fern (*Pteris aquilina*) is present in transects at Marin County, north of

Healdsburg, and Santa Rosa. These areas have the darkest and intermediate birds. *Myrica californica* and *Vaccinium ovatum* occur only in Marin County and here provide much used plant food and cover. These plants are most common under the Bishop pine forest and are not widespread in the actual chaparral formation. *Gaultheria shallon* also occurs only in Marin County, but it is a low shrub probably not offering much available living space to the Wrentits.

Rhamnus californica is present in the transects of six localities but represents less than eight per cent in any of them. Wrentits were taken from this species only in the Vaca Mountains where no transect records for the plant occur. *Rhamnus crocea* also occurs in small percentages along Dry Creek near Oakville and northeast of Napa but was encountered at no other locality.

Cercocarpus betuloides appears in the transects north of Healdsburg, Oakville, and the Vaca Mountains. Birds were taken from this species at Oakville, northeast of Napa, and the Vaca Mountains. It grows in rather arid situations although it was not found in abundance.

Garrya fremontii occurs in amounts of less than five per cent at Santa Rosa, Vaca Mountains, and Knoxville but nowhere were Wrentits taken from this species.

Photinia arbutifolia is present at all localities although over ten per cent only at the station north of Healdsburg. It appears to be rather tolerant of environmental conditions since it is so widespread in distribution. Wrentits were taken from this species at six localities. One-third of the specimens from Putah Creek, 19 birds, were taken from *Photinia*. There, these plants filled a dry draw that was surrounded by grassland. These harbored a number of Wrentits in the fall when the red holly berries were being eaten by the birds. Such isolated pockets of habitat were not sampled by transect but did add to the specimen collection.

Baccharis pilularis seems to be confined to fairly moist areas. It was found at Marin County, Russian River, Santa Rosa and northeast of Napa. Wrentits were taken from this plant north of Healdsburg, although it did not appear in the transects there.

A few other plants were encountered at various localities but were not important constituents of the chaparral. Figure 7 summarizes the abundance of the most common plants for six of the localities.

PLANTS FROM WHICH WRENTITS WERE COLLECTED

Records were made of the plant species from which the 267 specimens of Wrentits were collected. With the exception of 32 birds (12 per cent), all Wrentits were taken from plants that appeared in their respective local transects. These exceptions were from relatively rare plants, specialized spots such as fence rows and stream banks, or from plants on the edges of the main chaparral which were not considered as typical of the overall cover type. The degree to which transect sampling of plant species agrees with cover use, as indicated by the plants from which the birds were taken, is shown in the accompanying graphs, figure 7. The plant species are given in per cent of the total transect footage covered at each locality, and the number of birds shot in each plant species is shown as the per cent of the total birds taken from that particular locality. Some obvious parallels occur.

Species of *Ceanothus* are present at all localities and in some measure the number of Wrentits collected from these plants shows a correlation with the linear amount of *Ceanothus* intersected by the transects.

Thus at Marin County and Russian River where *Ceanothus* makes up 50 per cent of the transect tallies, the number of birds taken from plants of this genus makes up almost a third of the birds from each of these localities. At Napa, where species of

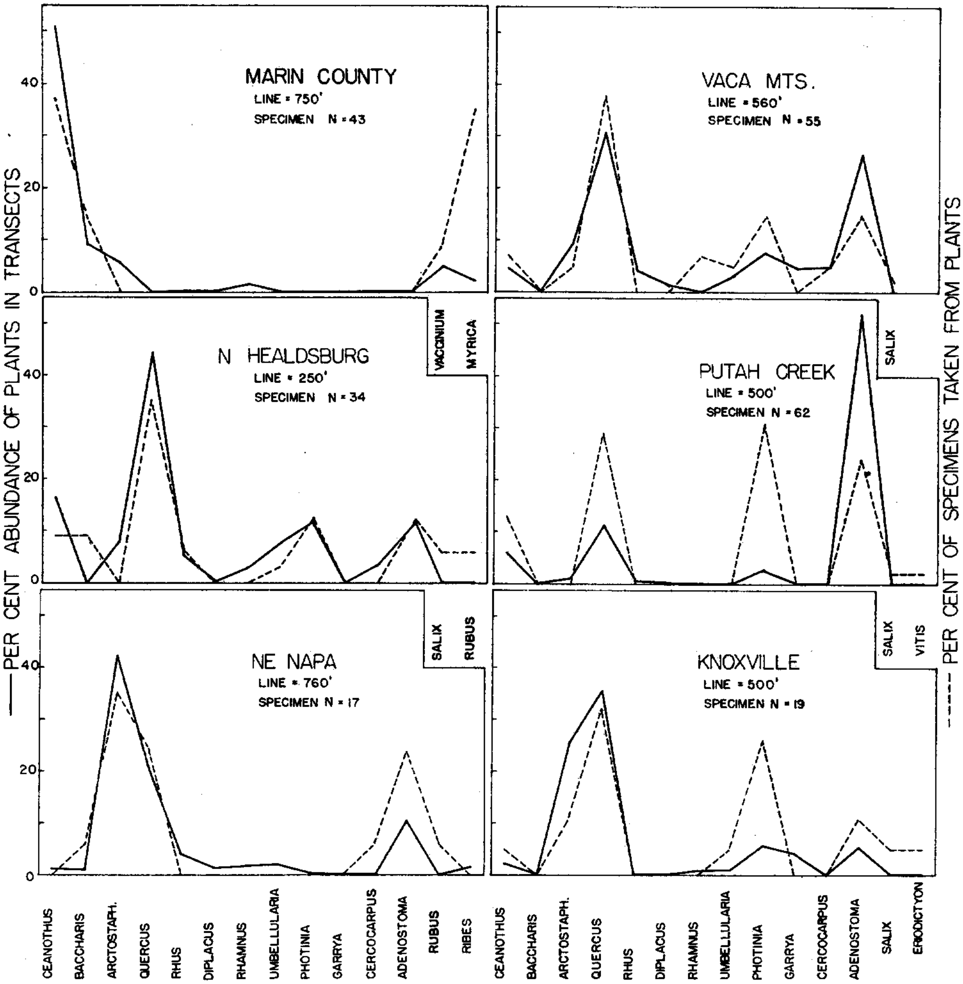

Fig. 7. Graphs representing percentages of plant abundance (solid lines) and the percentages of Wrentits taken from these plants (dashed lines). The plants listed are those most commonly encountered at these localities.

Ceanothus comprise less than three per cent of the lines, no birds were taken from these species. At Knoxville where again *Ceanothus* is present along less than three per cent of the transect lengths, only one bird (5 per cent) was taken from a plant of this genus.

A similar analysis may be made for the several species of scrub oak, *Quercus* sp., which make up considerable portions of the transect data from most of the localities. At the station north of Healdsburg 44 per cent of the line lengths intersected scrub oak and 35 per cent of the birds from this locality were taken in scrub oak. The station northeast of Napa, the Vaca Mountains, and Knoxville all have large percentages of scrub oak and likewise have high percentages of bird collections from this group of plants.

Further correlations may be made for *Adenostoma* especially and for *Photinia* and species of *Arctostaphylos*.

Since collecting of specimens is of a random nature, all these coincident peaks suggest that fairly representative habitat composition figures with respect to Wrentit usage have been obtained. Of course the birds move rapidly from one species to another where there is interspersion of plant kinds.

CLIMATE

Most weather data for California are collected at stations operated by or in cooperation with the United States Weather Bureau, and the data are gathered to give macroclimatic descriptions only. Stations more advantageously placed and operated by a biological investigator would have the disadvantage of being short-term sampling stations. The annual summary of 1952 of "Climatological Data, California section," provides records for the areas concerned in the present study that represent up to half a century of compilation. Here are to be found normal monthly temperature and precipitation figures for eleven stations that lie within or close to the borders of the region investigated. The relevance of averages of temperature and rainfall might be questioned, since it is likely that extremes are more important in influencing biological adaptations. However, mean figures will allow comparisons between different localities that may bring out important environmental trends.

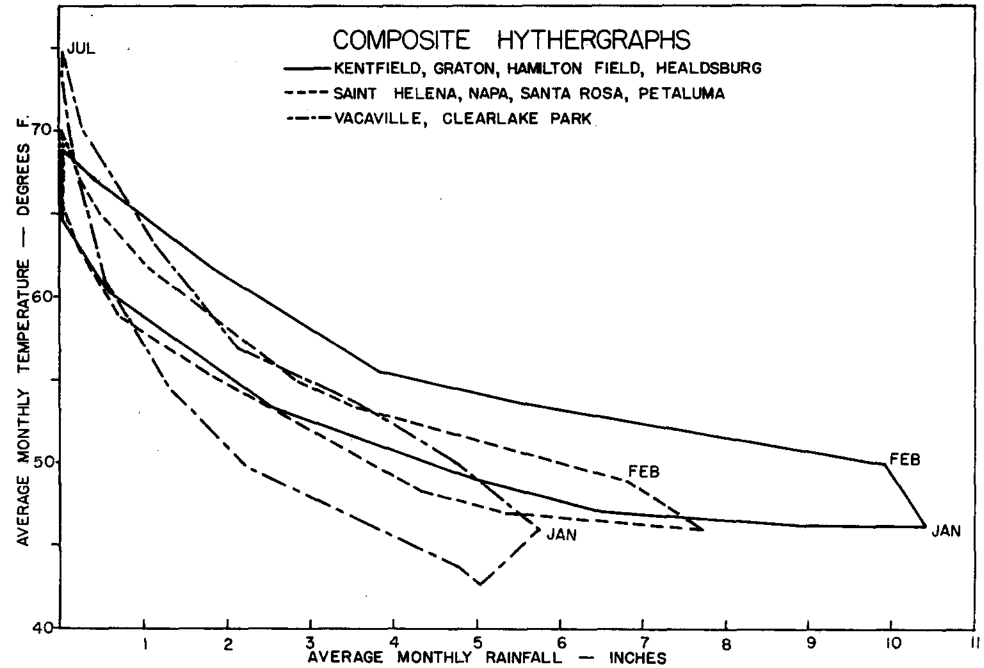

Fig. 8. Composite hythergraphs from United States Weather Bureau data. Solid line represents area in which darkest Wrentits are found; dashed line, area in which intermediate birds are located; dot-dashed line, area in which lightest birds exist.

Hythergraphs for the eleven weather stations were constructed by plotting the normal monthly temperature against the normal monthly rainfall. By connecting these points from January through the months and back to January there is produced a twelve-sided polygon representing some of the aspects of climate for that locality. Larger areas can be roughly compared by circumscribing several polygons for neighboring stations with a line that now describes these aspects of climate for the region included between the separate localities, provided the distance between them is not excessive.

For the present study, hythergraph polygons were circumscribed for the weather stations at Kentfield and Hamilton Field in Marin County, together with those at Graton and Healdsburg in Sonoma County. These stations represent the coastal region in which the darkest Wrentits are found. Polygons for stations at Santa Rosa and Petaluma in Sonoma County and Saint Helena and Napa State Hospital in Napa County were included in a regional representation for the area in which intermediate Wrentits exist. For the region farthest inland containing the lightest Wrentits, polygons for Vacaville in Solano County and Clearlake Park in Lake County were combined.

The following points may be made from a consideration of the three composite hythergraphs shown in figure 8. Rainfall is heaviest during the winter months in the coastal region, moderate in the region of intermediate breast color, and least in the inland region. Summer precipitation provides no differentiation of the areas since there is practically no rain during this season at any of these stations. Winter temperatures average highest in the coastal region, moderate in the intermediate area, and lowest inland. Summer temperatures are lowest along the coast, moderate in the intermediate region, and highest interiorward.

Further search into the available data of the United States Weather Bureau revealed that beginning in 1930 there were sporadically published summarizations of various aspects of California climate in the form of state outline maps with isometers of these weather factors drawn over the surface. Portions of these isometers were enlarged by the author on maps of the region under consideration by using grid lines on a transparent overlay. These maps were evidently drawn originally in a general manner since the Weather Bureau is limited by a lack of stations. Interpolations between the existing stations may thus be inaccurate, but the overall trends should be present. Relative humidity isometers are drawn at ten per cent intervals, temperatures are shown at five degree intervals, and the average number of clear and cloudy days per year are given in 25 and 20 day intervals, respectively. For each of the 12 collecting localities, measures for the various climatic factors were taken from these maps using the value of the whole interval, within which the locality is situated, as the statistic. Where an area fell close enough to an isometer to place its accuracy in doubt, both intervals on either side of the line in question were used as the figure for that locality. These data were tabulated for the collecting localities in the same order as that used in the color seriation of the Wrentits, beginning at the dark end of the gradient.

Cloudiness and fog.—Cloudiness greatly reduces the evaporative and bleaching

Table 11

Average Number of Totally Cloudy Days and Totally Clear Days Per Year and Annual Range of Mean Temperature

Locality	Cloudy days	Clear days	Range of mean temperature (F.)
Marin County	120–140	150–175	10–15
Russian River	80–120	175–200	15–20
NW Healdsburg	60–80	200–225	25–30
N Healdsburg	60–80	200–225	25–30
Santa Rosa	80–100	225–250	20–25
Oakville	60–80	250–275	20–25
Angwin	60–80	250–275	25–30
NE Napa	40–60	250–275	15–20
Vaca Mountains	40–60	225–250	20–25
Putah Creek	60–80	225–250	25–30
Knoxville	80–100	225–250	30–35
Clearlake	60–80	225–250	30–35

radiation that reaches the earth. Since, as mentioned earlier, the amount of moisture retained at ground level has an effect on humus production, and the amount of direct sunlight has an effect on the color of leaf litter via bleaching, wherever the incidence of a cloud cover or fog is high, one would expect to find darker soils and soil coverings than where the skies are more commonly clear.

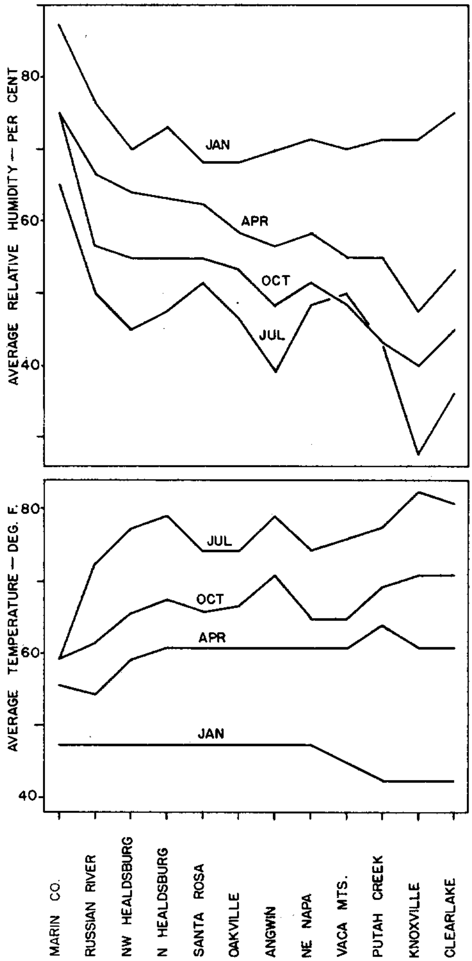

Fig. 9. Summary of average relative humidities and temperatures for four months showing inverse relationship of these weather factors.

From an inspection of table 11 showing the number of clear and cloudy days per year for the various collecting localities, it can be seen that the general trend is somewhat as expected, namely that along the coast there is more cloudiness and fog while inland there are more days that are clear.

Temperature.—Temperatures are treated in the maps of the Weather Bureau for only four months of the year but they may be considered as representative quarterly statements. Mean maxima, means, and mean minima of temperature for January, April, July, and October are available. From these midpoints in the readings were plotted and are summarized in figure 9. Note especially the data for July which show increasing

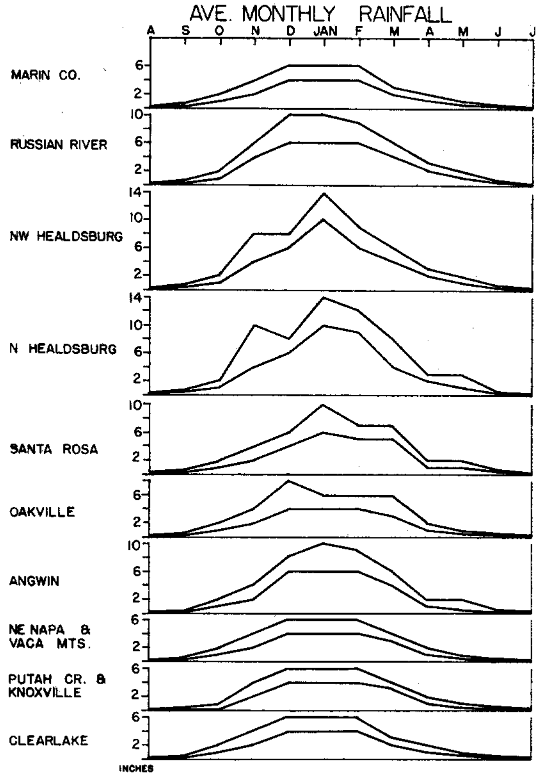

Fig. 10. Graphs showing average monthly rainfall for the collecting localities.

temperatures inland where less dense brush and lighter birds are found. The effect of thermal energy, expressed here as temperature, on evaporation is well known. Where temperatures are consistently low, we would expect less evaporation of soil moisture than in regions of seasonally higher temperatures and the interpretation concerning the effects of this on substrate color may here again be brought out.

Table 11 gives records taken from a map showing the annual range of mean temperatures. These ranges correspond more closely to roughly concentric rings with their centers in Marin County than to the sequence of localities indicated by the studies of breast coloration. This does show, however, that the darkest birds, which are less variable in color, exist where yearly fluctuations in mean temperature are least and that the lightest birds, which show more variation in color, exist where such fluctuations are greatest.

Relative humidity.—As shown in figure 9, average humidities tend to be higher toward the darker end of the color cline along the coast and lower toward the lighter end inland. While relative humidity may not be as useful as vapor pressure deficit in ecological studies, still these data lend their support to the idea of lower soil moisture evaporation along the coast and greater water loss from the litter farther interiorward.

Precipitation.—It might be supposed that Marin County would receive the largest amounts of rainfall in keeping with its comparatively high humidity values. However, this is not true. In fact figures for Marin County are almost equivalent to those for Napa and the Vaca Mountains (see fig. 10). Other factors in this coastal region then must be sought to explain the humidity levels found there. Proximity to the sea and Tomales Bay is of course a major factor for several reasons. Temperatures in Marin County are consistently rather low because of the nearness of the cold sea water, associated with which are rather high relative humidities. On shore ocean breezes are laden with moisture and are generally more uniform in temperature than terrestrial winds. Coastal fogs and cloudiness likewise prevent solar warming of the area to some extent and in addition hinder evaporation of the surface moisture.

Rainfall in the Healdsburg region according to these maps has almost the highest value of any of the localities for some months. Yet the vegetation there has more the aspect of the arid areas farther east than that of the humid coastal zone along the western portion of Russian River and in Marin County. Healdsburg is of course farther inland than are these latter stations. It should be mentioned that temperatures at Healdsburg average somewhat higher in the summer than for the other collecting localities nearby. It is possible that these comparatively high fire-season temperatures have encouraged more frequent burning of the chaparral in spite of high annual rainfall and thus have hindered more complete regrowth to denser successional stages. Indeed, there are fire-scarred areas evident over large sections of the hills between Healdsburg and Mercuryville to the northeast. The more frequent burning of the plant cover in areas of low summer humidity and high temperature, irrespective of precipitation levels, represents a way in which the brush density is kept lower than in more moist, cooler regions where fire expectation is lower.

DISCUSSION

In the course of describing climate and the plant matrix we have brought out the variations in the color of Wrentits that correlate with variations in some features of the environment. These correlations of course are not to be construed as demonstrating causal relations between climate and color. Gloger's rule, unfortunately, is usually worded in such a way that causality may be inferred from its statement that dark-colored organisms are to be found in humid areas, whereas lighter-colored animals of the same species live in arid areas. There is no mention of any agency or mechanism interposed between humidity and the animals.

We may then analyze possible indirect connections between climate and avian coloration. First, there is a direct relationship between moisture and plant growth that hardly needs documentation. Fairly adequate statements can also be made regarding the influence of humidity on plant density. On the other hand, the effects of the plant cover on humidity are not so well known, but to a degree there is an influence in the sense that humidities are bound to be higher where more plant material is present to absorb from the soil and to release into the air by transpiration the water resources of that soil.

The effects of temperature on transpiration rates and soil desiccation are of course considerable. The correlation of high temperatures with low humidities and the reverse have been pointed out. These connections are most obvious for summer when moisture relations are the most critical for many plant species.

The sparsest chaparral, which occurs at the interiormost localities, very likely has suffered the greatest frequency of burning, since in this region, summer temperatures are highest and humidities are lowest. It is only through long periods free from fire in conjunction with better environmental conditions for growth that the establishment of heavier vegetation is possible, as along the coast.

The darkening effect of moisture on soil color is well known. The habitat for the birds may be effectively darkened by dark and/or moist soil and moist soil may be likewise rich in humus which also has a darkening influence.

In sparse brush, where more sunlight can penetrate to the lower plant and soil levels, there is more lightening of colors by bleaching than in more dense brush. This, correlating with the moisture relations just described, adds another factor in the production of lighter and darker habitats in the various areas.

We now have a reasonable set of correlations that point to the causative mechanism underlying Gloger's rule. The climate has direct effects on the plant matrix, producing different colored substrates in different climatic areas. More specifically, in temperate regions with relatively high humidity, low temperature, and frequent cloudiness, the plants respond by growing luxuriantly; this in turn allows the production of dark, moist soils with abundant humus that is more nearly screened from the bleaching action of the sun than in other situations. Through the agency of natural selection, then, the darker colors of Wrentits in time would be favored and the birds come to match the surroundings in this dark habitat.

The habitat itself, controlled by climate, shows a gradient of structure and density which could afford a graded selective action on the Wrentits. Natural selection is thus the most obvious agent that has caused the differentiation of colors and has enhanced the success and survival of the Wrentits in the differing environments.

SUMMARY

Several types of measurable variation were considered in this study of correlation of the attributes of Wrentits with environments in a west-east transect in central California. It is concluded that linear measurements have their greatest meaning if expressed in terms of body size, represented as weights.

The Wrentits measured fit closely Allen's rule in that they show lengthening of extremities in warm climates.

Bergmann's rule, which reflects an inverse relationship between environmental temperatures and body mass, also is evident in these birds.

There is a steep color gradient over a relatively short geographic range in the back plumage and even more strikingly in the breast plumage of these Wrentits. It can be generally stated that the darker birds inhabit the coastal region and that toward the east, interiorward, the birds become progressively lighter.

The darker birds exhibit less individual variability in coloration than do the lighter birds. This is correlated with less variation in the climatic factors present where the darker birds live and more variation of climate where the lighter Wrentits occur.

The composition of the habitat of the Wrentit, in terms of plant species was sampled using line transects. Some kinds of plants show distributions parallel to climatic gradients and gradients in plumage coloration. Such plants are common at one end of a color cline and tend to disappear toward the other end.

The brush, analyzed in several ways, shows greater density along the coast where this is encouraged by high humidity and low temperatures in conjunction with frequent cloudiness and fog. Interiorward, the brush is less dense because of less moisture and higher temperatures, and there are more cloud-free days per year. Because of conditions more favorable for summer fire in the interior, it is expected that there would have been more frequent burning of the chaparral and thus maintenance of more sparse brush there.

A simple investigation of stem colors has shown more plant species with dark brown stems, as well as a higher representation of these plants, in the western part of the area. Fewer dark brown-stemmed species and lower representation of these is to be found in the eastern areas.

The denser brush possesses a darker living area within it by virtue of higher moisture retention which imparts darker colors to the lower parts of the habitat, encourages greater humus production, and offers better screening of soil litter from the bleaching action of the sunlight. The sparser brush in the east has a lighter living area within it by virtue of lower moisture retention which makes objects appear lighter, inhibits humus production, and provides less screening of soil litter from bleaching.

It has been shown that there is, in fact, good correlation between the color gradient of the Wrentits and several gradients of the physical and biotic environment. This allows a specific expression of Gloger's rule: Where there is high humidity accompanied by other climatic factors which produce dense chaparral, the habitat is dark in color, and there are to be found in it dark-colored Wrentits. Conversely, where humidities are low and in connection with other climatic factors only sparse chaparral develops, the habitat is light in color and there light-colored Wrentits occur. The advantageous matching of light birds with a light environment and of dark birds with a dark environment has in all probability been produced by natural selection.

LITERATURE CITED

Bates, G. L.
1936. The races of *Ammomanes deserti* found in Arabia and near its borders. Ibis, ser. 13, 6:331–334.

Bauer, H. L.
1943. The statistical analysis of chaparral and other plant communities by means of transect samples. Ecology, 24:45–60.

Beebe, C. W.
1907. Geographic variation in birds with especial reference to the effects of humidity. Zoologica, 1:1–41.

Behle, W. H.
1942. Distribution and variation of the horned larks (*Otocoris alpestris*) of western North America. Univ. Calif. Publ. Zool., 46:205–316.

Bowers, D. E.
1956. A study of methods of color determination. Syst. Zool., 5:147–160, 182.

Davis, J.
1951. Distribution and variation of the brown towhees. Univ. Calif. Publ. Zool., 52:1–120.
1954. Seasonal changes in bill length of certain passerine birds. Condor, 56:142–149.

Erickson, M. M.
1938. Territory, annual cycle, and numbers in a population of wren-tits (*Chamaea fasciata*). Univ. Calif. Publ. Zool., 42:247–334.

Grinnell, J., and Miller, A. H.
1944. The distribution of the birds of California. Pac. Coast Avif. No. 27:1–608.

Hamilton, T. H.
1958. Adaptive variation in the genus *Vireo*. Wilson Bull., 70:307–346.

Meinertzhagen, R.
1951. Review of the Alaudidae. Proc. Zool. Soc. London, 121:81–132.

Ogle, C.
1934. Climatic influence on the growth of the male albino mouse. Amer. Jour. Physiol., 107: 635–640.

Pitelka, F. A.
1951. Speciation and ecologic distribution in American jays of the genus *Aphelocoma*. Univ. Calif. Publ. Zool., 50:195–464.

Selander, R. K.
1954. A systematic review of the booming nighthawks of western North America. Condor, 56:57–82.

Sumner, F. B.
1932. Genetic, distributional, and evolutionary studies of the subspecies of deer mice (*Peromyscus*). Bibliographia Genetica, 9:1–106.
1934. A test of the possible effects of visual stimuli upon the hair color of mammals. Proc. Nat. Acad. Sci., 20:397–402.

United States Weather Bureau
1930 and following. Climatological Data, California section. Monthly summaries. Washington, D.C.
1953. Climatological Data, California section, annual summary, 1952, 56:312–330.

Wallace, R. H.
1937. Methods of sampling visible radiation. Plant Physiol., 12:647–666.

Museum of Vertebrate Zoology, Berkeley, California, June 1, 1959.