THE DISTRIBUTION OF GENE FREQUENCIES IN WILD POPULATIONS OF COLIAS

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NEARLY all butterflies of the genus Colias have dimorphic female forms—the normal yellow or orange and the "albinic" or white form. The white form in both races of *Colias chrysotheme* in North America is controlled by a dominant autosomal gene which has effect only on the female sex (GEROULD 1923; HOVANITZ 1943a). This seems to be true also for *Colias myrmidone* and *edusa* (=*crocea*) of Europe and the *christina* complex of North America (GEROULD 1923; FORD 1937; HOVANITZ 1943a). The general distribution and abundance of the white female form of *chrysotheme* in North America have been described in detail (HOVANITZ 1943b).

Owing to the ease of identification of the normal and white forms, this material is excellent for the study of gene frequency variations and its biological causes in wild populations. For this purpose, samples of the populations of the orange race were obtained seasonally and geographically in 1941–1942.

METHOD

Counts of normal and white females were made throughout the alfalfa growing districts of central and southern California, southwestern Arizona, and the western Great Basin. The earliest samples obtained were by actually capturing individuals; later, however, counts alone of free-flying individuals were found to give larger numbers and more significant results.

Knowledge of the exact viability of the three genotypes expected in the populations in all locations is necessary before pertinent gene frequency data can be calculated according to the standard formula: $p^2+2pq+q^2$ (HARDY 1908). Since the experimental data suggest that the viability of the dominant homozygote (q^2) may be zero under certain conditions and equal to or better than that of the other genotypes under other conditions, the application of this formula under known conditions of viability is not possible. The data are therefore discussed not as gene frequencies but as phenotype frequencies only.

With no difference in viability between the genotypes, the gene frequency in a population will remain constant, with random fluctuations only (WRIGHT 1932, 1942). With complete lethality of the dominant homozygote, which is probably true in hot environments and in southern regions, the white allele will be eliminated at a rate as given in table 1.

The white allele probably has a selective value under certain environmental conditions which is greater than that of the normal yellow or orange allele. According to the conclusions derived from museum data alone (HOVANITZ 1943b), the white allele should be at an advantage over the normal allele in the north as compared with the south. Therefore, in this detailed analysis of populations, a similar north-south rule should be found. The allelic frequency should vary directly with the change in climate between regions if the two are thus interrelated. In a previous paper (HOVANITZ 1942), it was stated that only by a polygenic or multiple allelic hereditary mechanism can a gradient of morphological, adaptive variation coincide with a gradient of changing environmental conditions. When this kind of hereditary system is not available, similar results may be achieved by varying ratios of two alleles with extremes of 100:0 and 0:100.

TABLE 1

Table showing rate of elimination from a population of a dominant allele which is homozygous lethal, population size being at infinity. Assuming equal viability for the other two genotypes, the elimination will be at the rate shown by the decrease per generation.

FREQUENCY OF WHITE ♀♀, Ww	DOMINANT ALLELE FREQUENCY, W	GENERATION
66.7%	33.3%	1
50.0%	25.0%	2
33.3%	16.7%	3
28.6%	14.3%	4
25.0%	12.5%	5
22.2%	11.1%	6
20.0%	10.0%	7
18.2%	9.1%	8
16.5%	8.3%	9
15.4%	7.7%	10
9.1%	4.6%	20
1.96%	.98%	100
.199%	.099%	1000
.000199%	.000099%	1,000,000

The data presented here illustrate the correlation between the gradient formed by the frequency of the two white alleles and the gradient formed by the climatic conditions of the territory. They also show the effects of migration and random population change upon the gene frequency in various environments. A differential development rate of different genotypes and its effect upon population differences is noted in two populations.

THE FREQUENCIES OF THE WHITE FEMALE IN CALIFORNIA POPULATIONS

The frequencies of white females in California populations of the orange race are shown on the map (fig. 1). The general trend of highest frequencies in the north (69 percent white) and lowest frequencies in the south (13 percent white) is apparent.

The region sampled is divided into five distinct provinces by the local topography of the land. There are from north to south: (1) the San Francisco Bay area in the northwest; (2) the San Joaquin Valley area along the central portion of the state; (3) the Great Basin, represented on the map by Mono Lake and Round Valley; (4) Coastal Southern California, represented by scattered alfalfa fields throughout the coastal valleys; (5) Coachella-Imperial-Colorado River Valley area in the southeast.

The genetic nature of wild populations are studied or visualized only with the aid of maps, climatological information, and a knowledge of the local topography.

To neglect these data would be to eliminate the causal factors in the population differentiation; the cause of the differentiation is the point of this study.

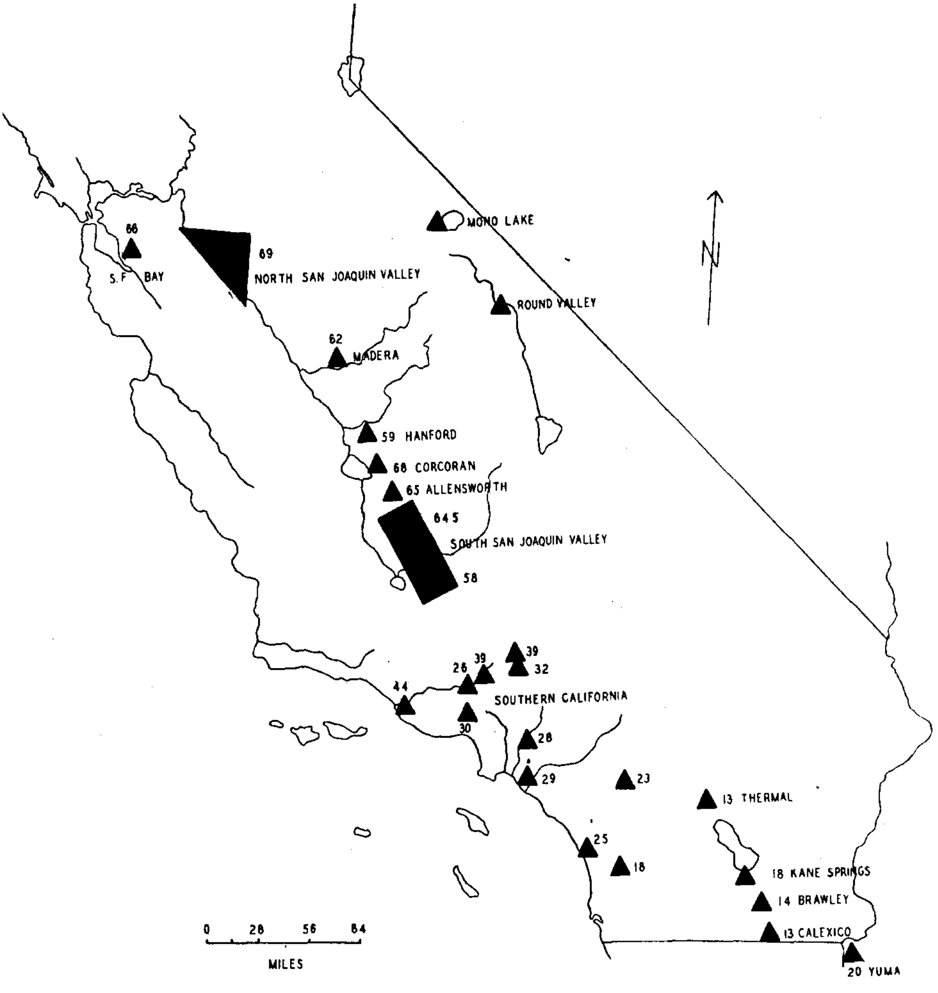

FIG. 1.—Map showing the locations in California and southwestern Arizona of the populations sampled for the white gene frequency and population structure of the races of *Colias chrysotheme.*

The population differences (seasonal and geographical) are described below, starting with a central point, the coastal Southern California populations.

THE COASTAL SOUTHERN CALIFORNIA POPULATIONS

The Coastal Southern California populations sampled are shown on the map (fig. 1) by numbers derived from the white frequency at each place.

The San Gabriel Valley area

The localities known collectively as the San Gabriel Valley area are situated at the lower end of the valley in the vicinity of El Monte, Garvey, and Puente. The locality is marked on the map (fig. 1) by the number 30. The populations are split into two parts, separated by the San Gabriel River, the centers of which are about five miles apart. Unless specified, samples were obtained generally over the area.

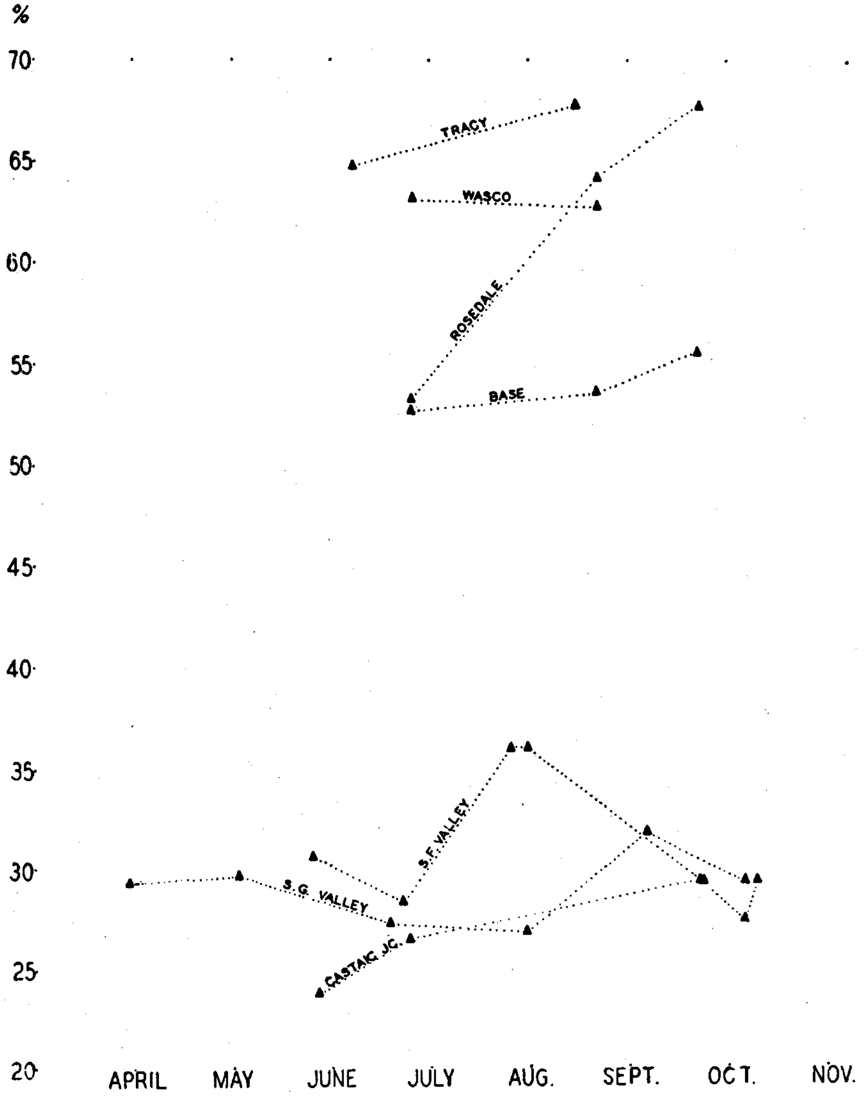

FIG. 2.—Showing the frequencies of white females as compared with orange during the seasons at various localities in California. Compare these minor fluctuations with the large ones of Mono Lake (fig. 6).

The general trend of the frequency variations during the 1942 season is given on the graph (fig. 2) as "S. G. Valley." It is seen that there is little fluctuation during the season. A summary of the data according to the season for 1941–1942 is given in table 2. There are no significant differences in any of the seasons, nor between the two years 1941 and 1942. Were the population number reduced to an exceedingly low value, it might be expected that random changes in gene frequency would occur, but no such variations are present. Apparently the population size is very large, or the environmental selection for the white and orange alleles is rather closely regulated. Both conditions probably prevail.

TABLE 2

Seasonal frequency of white females in the San Gabriel Valley for two years.

SEASON	% WHITE ♀♀	N
1941		
Spring	21.62±6.77	37
Autumn	30.03±1.45	999
Total	29.73±1.42	1,036
1942		
Spring	33.33±7.27	42
Early summer	28.15±1.55	906
Late summer	33.37±1.65	812
Autumn	28.75±1.82	612
Total	30.19±0.94	2,372
Grand Total	30.05±0.78	3,408

In May and June, 1942, separate data were obtained on each side of the San Gabriel River (table 3) to determine if a difference might exist, due to the spatial isolation. This is a test of degree of population movement as well as of size, since a difference in the results would indicate that the area is not well mixed or that random changes have taken place in gene frequency.

TABLE 3

Frequency of white females at two localities on the two sides of the San Gabriel River (in the San Gabriel Valley). 1942. The numbers show the percentage of white females.

	WEST SIDE	N	EAST SIDE	N	TOTAL	N
May	27.27±4.48	99	30.57±3.21	229	29.51±2.51	328
June	25.40±2.10	433	33.10±3.91	145	27.34±1.83	578
Total	25.75±1.89	532	31.55±2.40	374	28.15±1.55	906

In both May and June, the frequency was lower on the west side than the east side. In neither case was the difference equal to or greater than twice the standard error. With the combined data, the difference is 5.80±4.54 percent or considerably less than twice the standard error of the difference.

The San Fernando Valley Populations

The San Fernando Valley populations are located about 30 miles northwest of the San Gabriel Valley. On the map (fig. 1) the place is denoted by the number 30. Between these two localities is located the city of Los Angeles and two "mountain ranges" (Santa Monica mountains and part of the "Puente Hills"). Therefore, there are no alfalfa fields to unite the two places. The chance of much gene exchange across this 30 miles under normal circumstances would seem rather doubtful. However, the species is somewhat migratory, and at times there is probably considerable exchange. The climate at the two places is very similar, being under the same influence of the prevailing westerly winds and ocean fog. There should be very little differential climatic selection.

TABLE 4

White female frequency during the season at San Fernando Valley, Calif. 1942.

DATE	% WHITE ♀♀	N
May 25	30.57±3.04	229
June 22	28.43±2.01	503
July 25	35.97±4.06	139
Aug. 1	35.96±4.50	114
Sept. 7	17.95±6.15	39
May–Sept. 7	30.37±1.43	1,024
Sept. 23–Nov. 7 (see table 5)	30.29±0.43	11,149
Total	30.30±0.42	12,173

The trend of the variations in this region is shown on the graph (fig. 2) as "S. F. Valley." The variations in the populations of the San Fernando Valley are not statistically different. Even the July and August percentages of 35 percent white are not different from the average of 31.48 for this period (table 4).

During the period September 23 to November 7, tests were made to determine if there were a differential development rate between the two types of female. One particular field in the San Fernando Valley had a heavy infestation of Colias and was in full eclosion. Frequencies were obtained in this field at two day intervals of (a) percentage of white females freshly eclosed on that day and (b) percentage of white females free-flying in the population. Frequencies were obtained in local fields nearby to serve as a control.

The graph (fig. 3) shows the variation in frequencies between newly emerged females in one alfalfa field (as judged by the fact that they had wet wings and were in copulation) and the frequency of free-flying females in the same place. There is also shown by dotted lines the frequencies in two control fields about one mile from the former place.

From a high of 36 percent white females which eclosed on September 23, the frequency dropped to 29 percent on each of the two succeeding periods of two days each to a low of 24 percent on September 29. The difference between the extremes is 11.87 ± 4.23 percent or nearly three times the standard error of the difference (table 5).

Two days following the sample of 36 percent of newly emerged females, samples were made of the frequency of free-flying individuals. On September 25, the frequency was 45 percent. This dropped at a rapid rate at first but was slower later until a low of 25 percent was reached on October 5. The difference between these extremes is 19.35 ± 2.50 percent, or nearly eight times the standard error of the difference. Some of the consecutive samples are likewise more than twice the standard error of the difference. For example, that between September 25 and 27 is 6.97 ± 2.93 percent, or over two times. The difference between September 27 and 29 is 4.76 ± 2.78 percent, or just under two times.

TABLE 5

The frequency of white females at a given alfalfa field in the San Fernando Valley during the course of an adult eclosion period. The copulated females were newly eclosed on the day of the sample The control samples were made in fields approximately one mile from the tested field.

DATE	FREE-FLYING %W	N	COPULATED, %W	N	CONTROLS, %W	N
Sept. 23	—	—	35.91 ± 2.96	323	29.24 ± 1.96	537
Sept. 25	44.58 ± 2.04	590	29.22 ± 2.36	373	32.22 ± 2.58	329
Sept. 27	37.61 ± 2.07	561	29.20 ± 3.06	226	27.81 ± 2.31	374
Sept. 29	32.85 ± 1.85	685	24.04 ± 3.01	208	25.12 ± 2.17	414
Oct. 1	29.59 ± 1.59	828	—	16	29.45 ± 2.52	326
Oct. 3	27.75 ± 1.76	645	—		(31.05 ± 1.96 (28.61 ± 2.29	554) 423)
Oct. 5	25.23 ± 1.46	880	—		(27.40 ± 1.99	500)
Oct. 7	29.97 ± 1.47	971	—		(30.08 ± 2.40	359)
Oct. 9	26.90 ± 1.78	617	—		(29.49 ± 2.57	312)
(Nov. 7)	(37.76 ± 4.88	98)	—		—	
Total	31.30 ± 0.61	5875	29.76 ± 1.35	1146	29.00 ± 0.71	4128

On October 7 and 9, the population seems to have leveled off to a standard range of fluctuation, and after the ninth, individuals were scarce. As far as adults were concerned, the population size was greatest between September 23 and 27, when the alfalfa field was literally covered with them. At this period all individuals were exceedingly fresh. From September 27 to October 9, the population size decreased rapidly. Samples of newly emerged adults could not be obtained after September 29 owing to the very rapid drop in eclosions. By October 3, fresh individuals were rare, and by the ninth nearly all were old and worn. The alfalfa field was being cut from about four days before September 23 and was completely cut on the twenty-seventh. At this period thousands of pupae were crushed. By October 9, the shortest average new growth in the field was about one foot high; females rarely lay eggs in a field higher than this.

The control samples were gotten in two fields about one mile east of the field being tested. The fluctuations in the control samples are not statistically different but they follow the experimental curves to a certain extent. There is a drop between September 25 and 29 following the drops in the other curves; also a drop followed by a rise between October 1 and 9 following the same in the experimental curve. The control plots were in fields which did not have a high percentage of eclosing individuals. Their population was at least largely composed of individuals which had flown in from elsewhere. This was especially true of the field used between September 23 and 29. The controls are more representative of the valley populations as a whole than the experimental population. Two possibilities may account for the very rapid gene frequency change in the one field: (a) the white individuals are faster in development than the orange so that there are more of them at the earlier stages of the adult eclosion, or (b) the white gene has somehow gotten a rather high concentration in one place due to chance.

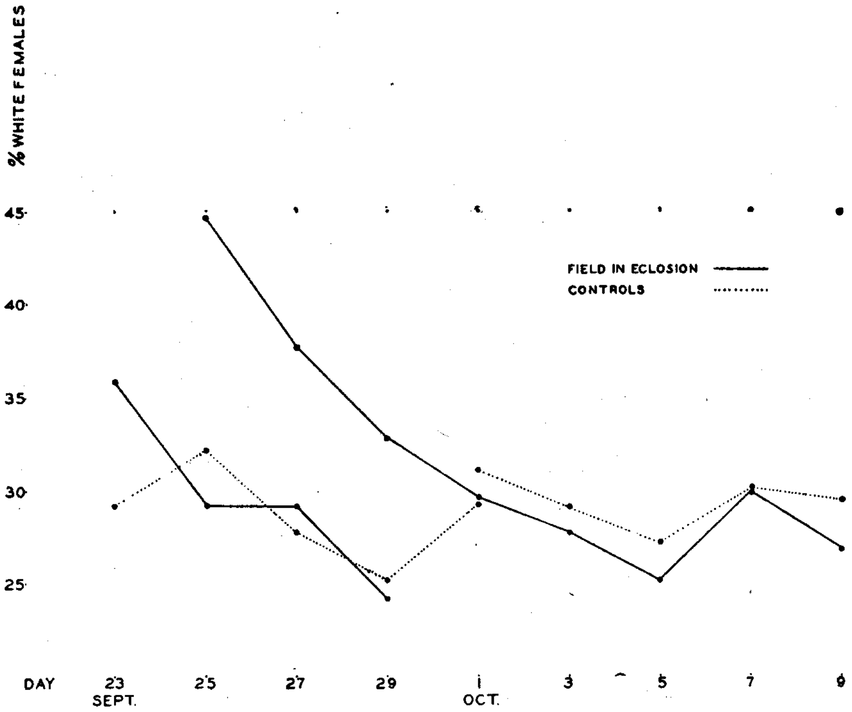

FIG. 3.—Showing the frequency of white females in a San Fernando Valley (California) population during an adult eclosion period (upper heavy line). The lower heavy line represents freshly emerged females with wet wings. The dotted lines represent control samples in other alfalfa fields. The first control was replaced by a second on October 1.

The former possibility seems more likely, because it fits all the data better. One can account for the higher frequency in the beginning in both experimental curves by assuming that more white females emerge at first. Since more orange females would emerge late, it would be expected that the frequency of white females would drop below the average for the region, provided that there was a general exodus of adults from the area. The assumption of decrease in adults is correct, because (a) the number of adults visibly declined from September 27 on, (b) adults were seen to be flying away from the field in large numbers, (c) the area already had a higher concentration of adults than any other place in the valley; therefore, more adults would leave than arrive, and (d) a percentage of the early emergents would have died, thus lowering the number of adults there. As expected, the frequency of whites dropped below the average frequency of 30 percent to a low of 25 percent. In favor of the first possibility also is the drop in frequency in the newly emerged females.

The tendency of the control curves to follow the experimental ones can also be explained by the first possibility (a). Since adults were leaving the field and scattering in all directions, it may be assumed that the higher concentration of whites at the one place may influence those nearby.

On the second possibility, one must assume that a very rare chance concentration of white females had laid the eggs from which the brood arose. The number of females must have been huge considering the size of the brood. The larger the number, the less the chance of getting a concentration fluctuating from the normal. The size of the brood must have been in the millions.

On the basis of the second possibility, there is no way of explaining the drop in frequency in the newly emerged insects unless one assumes that one day a month before the emergence mostly white females had laid eggs in the field and a few days later a higher frequency of orange females laid eggs. The likelihood of this being true seems nil.

The second possibility assumes that the drop in frequency is due to a mixing of the adults with the general valley population. This would entail a great movement of adults into the field. On the contrary, the movement was visibly away from the field. The frequency would not have dropped below the general valley frequency of 30 percent by this method, nor would it have dropped so quickly.

Therefore, unless the development rate of white females is faster than that of the orange, it does not seem likely that the change in gene frequency could have occurred. This conclusion is in agreement with a similar conclusion reached on the basis of breeding data.

Populations of the Santa Clara River Drainage Basin

Airline about 15 miles north of San Fernando Valley along the central part of the Santa Clara River Valley, three samples were made during 1942. This population (Castaic Junction) is located on the map (fig. 1) by the number 27. The fluctuation during the season is not significant but varied from 25 percent white in May to 27 percent white in June to 29 percent white in September. This gradual rise is illustrated on the graph (fig. 2) as "Castaic Jc." It is possible that the frequency has gradually risen during the season, and it could easily have done so by migrations from the extensive populations in the San Fernando Valley. There is, however, a range of hills separating the two places (Santa Susana Hills). Comparing these two localities for the 1942 totals shows that "Castaic Junction" has a frequency which is statistically lower than that in the San Fernando Valley:

		N
Castaic Junction	27.44±1.38 percent	1,046
San Fernando Valley	30.30±0.43 percent	12,173
Difference	2.86±1.44 percent	

"Castaic Junction" is farther north than San Fernando Valley but has a much hotter and dryer climate owing to its sheltered location within the hills and far from the coast. The populations in the San Fernando Valley are at the westernmost and coolest portion of the valley. The inversion of the north-south "rule" in this case may be due to the climatic regularity or possibly to chance alone.

Down the Santa Clara River Valley from Castaic Junction toward the coast is a distance of 40 miles airline. Apparently there are few alfalfa fields between these two places and not very many even at the coast. However, a small sample was gotten at the latter place (Oxnard) with a frequency of 43.75±6.20 percent white females (see map 1 at point marked 44). Climatically, the area is cooler, foggier, and more humid than any of the other Southern California locations. It should have a higher frequency of whites, as is indicated. However, the small number renders the significance of the data doubtful. The frequency is apparently statistically different from the two closest populations by more than twice the standard error of the difference: Difference from Castaic Jc. is 16.31±6.35 percent and from San Fernando Valley is 13.45±6.40 percent.

In one of the branches of the Santa Clara River Valley known as Bouquet Cañon, a sample was gotten in May 1942. This place is about ten miles east of Castaic Junction and is more or less connected with it by occasional alfalfa fields. The frequency found here in May 1942 was 39 percent. The number of individuals again was low, and the frequency, therefore, is once again doubtful. Compared with the populations at Castaic Junction, the difference is nearly four times the standard error of the difference for the month of May and about five times for the seasonal average at the latter place:

		N
Bouquet Cañon	39.34±6.25 percent	64
Castaic Jc. May	23.64±4.05 percent	110
Difference	15.70±4.55 percent	
Castaic Jc. 1942	27.44±1.38 percent	1,046
Difference	11.90±2.45 percent	

The frequency of 39 percent is very close to the frequencies in the Antelope Valley to be considered later and may owe its origin to that source.

The Antelope Valley Populations

The Antelope Valley is located about 25 miles east of the Bouquet Cañon population. It is really the western arm of the Mojave Desert but has considerable agriculture due to the presence of water for irrigation. The northern arm of the San Gabriel Mountains extends between the desert and the coast here, but the elevation is very low, owing to the change in geological structure. Cold winds from the coast blow through the area causing it to be climatically quite different from other parts of the desert. In the summer it may be very hot or may be cold and windy; in the winter it is colder than the Southern California coast.

Samples were obtained in May and June at two places, Palmdale and Lancaster. Between these localities, a distance of eight miles, there is no alfalfa, so that the places may be considered as isolated by dry desert. At Palmdale in May the frequency was 39.44 ± 4.1 percent ($N = 142$). In June it was 31.96 ± 2.72 percent ($N = 291$). In June at Lancaster the frequency was 38.83 ± 4.81 percent ($N = 103$). None of these differences approaches statistical significance. The total for Antelope Valley for the season, 35.26 ± 2.08 per cent ($N = 536$) is not different from the closest population, Bouquet Cañon.

At first sight it might seem that the desert should have a low frequency of the white gene. However, this part of the desert is cold in winter and does not always get hot in summer. In 1941, cold winds were almost continuous throughout the summer with only one or two "warm spells."

The Antelope Valley populations are the stepping stones to the San Joaquin Valley populations farther north with frequencies above 50 percent. The more coastal populations of Southern California are separated from the San Joaquin Valley by 70 airline miles of rugged mountains, while Antelope Valley is separated from it by only 20 miles airline across the range. The map does not illustrate the difference, since the Lancaster-Palmdale areas are far to the southeast in the Antelope Valley.

Other Southern California Populations

Samples were obtained at four other coastal localities which are designated on the map (fig. 1) by the white female frequency—namely, Santa Ana, 29 percent, San Pasqual-Escondido, 18 percent, San Luis Rey, 25 percent and San Jacinto Valley, 23 percent.

The Santa Ana population on the map is 20 miles airline directly south of the San Gabriel Valley samples. The area in between is nearly continuously strewn with alfalfa fields in the lower places. The climate is probably a little cooler in the summer and warmer in the winter, since it is closer to the coast; however, this is only very slight. The white female frequency is identical with that of the San Gabriel Valley.

The San Jacinto Valley population is about 50 miles airline due east of Santa Ana (number 23 on fig. 1). Owing to its inland location and higher elevation of 2,000 feet, it has a much warmer and dryer climate in the summer and colder in the winter. The white female frequency is lower here, as is expected considering its climate and location. The significance of the difference between its frequency and adjacent populations follows:

		N
San Jacinto Valley	22.65±1.82 percent	521
Santa Ana	29.41±2.02 percent	510
Difference	6.76±2.71 percent	
San Pasqual-Escondido	18.47±2.19 percent	314
Difference	4.18±2.84 percent	
Thermal	12.95±2.85 percent	139
Difference	9.70±3.78 percent	

The San Jacinto Valley-Santa Ana difference is just over twice the standard error of the difference. The difference with San Pasqual-Escondido is nearly twice while the difference with Thermal is almost three times.

The San Luis Rey frequency (25 percent) is so much like others in the vicinity and the number in the sample is so low that it is hardly different from any adjacent population. The place is located on the coast about 50 miles southeast of Santa Ana. The climate is very similar to that place.

The San Pasqual-Escondido population is located inland about 15 miles southeastward of San Luis Rey. The climate is likely to be warmer than the latter place or Santa Ana and quite similar to San Jacinto Valley. We have seen that the frequency is about twice the standard error of the difference in comparison with the latter place. It is close to or identical with the frequencies in the Imperial-Coachella Valley and quite different from Santa Ana and San Gabriel Valleys. On the coastal side of the mountains, it is the lowest frequency known and is likewise the most southern known.

THE COACHELLA-IMPERIAL-COLORADO RIVER VALLEY POPULATIONS

The Coachella-Imperial-Colorado River Valley is relatively isolated from the other populations considered before by the mountain ranges which include the San Jacinto range, the Santa Rosa range, and the Laguna-Cuyamaca mountains. This region is one of exceptionally low rainfall, receiving less than five inches annually. It must have been completely uninhabited by *Colias chrysotheme* before the period of irrigation, due to the lack of any larval food. The valley floor was covered only by shrubs typical of the Coachella and Colorado deserts before irrigation. The area is largely below sea level, and all samples aside from Yuma were obtained below the level of the sea. At Kane Springs, the elevation is about −200 feet. A few alfalfa fields exist north of the Salton Sea, at which place the sample at Thermal was obtained. Between Thermal and Kane Springs the area is almost all barren desert rock or sand and the water surface of the Salton Sea; this is a distance of about 50 miles. From Kane Springs to Calexico on the Mexican border the area is commonly continuously covered with irrigated alfalfa fields. Climatic conditions are mild in winter so that the populations can be breeding all year. In summer, the temperatures rise to 130°F at times; occasionally, for periods of one or two weeks constantly the temperatures day and night will not drop below 100°F. Such continuous temperatures are sufficient to sterilize the butterflies of the coastal population (at least with a high humidity). Possibly there has been established a physiological race able to withstand such conditions, or perhaps the low humidity of the region allows cooling by evaporation.

The white female frequency in this area is the lowest known, varying from 12.9 to 17.8 percent. The differences in the populations to be described are hardly to be correlated with climatic differences, though such correlations are yet to be made accurately. The valley is climatically very similar from the Mexican border at least to Indio. Farther north, cooling by winds from the San Gorgonio Pass takes place.

The frequency at Thermal, 12.95 ± 2.85 percent is different by nearly three times the standard error of the difference from the nearest "coastal" population at the San Jacinto Valley. They are separated by a mountainous area about 50 miles airline distance in which there are no alfalfa fields. The butterflies breed in the mountain meadows in the summer, however. The next nearest population sampled is at Kane Springs which is not significantly different from it: 17.80 ± 1.49 percent ($N=663$); difference$=4.85 \pm 3.57$ percent.

The Kane Springs frequency of 17.8 percent is obviously not different from the next population about 15 miles south, Brawley, 14.48 ± 2.06 percent ($N=290$). Brawley in turn is not different from Calexico about 20 miles farther south, 12.99 ± 1.57 percent ($N=462$). The extremes, Kane Springs and Calexico, are different by more than twice the standard error of the difference (4.81 ± 2.16 percent).

It should be noted that there are almost continuous alfalfa fields from one place to the other and that the distance is but 35 miles.

The average for the Coachella-Imperial Valley is 15.32 ± 0.91 percent ($N=1554$), which is obviously very different from the average for all of coastal Southern California (including Antelope Valley) of 29.78 ± 0.32 percent ($N=19{,}050$).

Along the portion of the lower Colorado River just south of Yuma, Arizona, on the east side of the river, there is a considerable extent of irrigated agricultural area. Alfalfa fields are strewn throughout the area from Yuma to San Luis on the Mexican border. The sample of the Colias population here was gotten in various fields along the 15 mile airline distance rather than from any particular field (fig. 1).

The climatic conditions in this area are the same as in the Imperial Valley, and it would be expected that the white female frequency would be either the same or lower. This place is about 40 miles airline east of Calexico, but this distance is barren, waterless desert of moving sand dunes and partly creosote-bush vegetation. Without flowers for nectar, adults could hardly travel this distance in the dry atmosphere, especially when it is so hot. In the winter mild weather, however, an exchange of adults may take place. An adult female which was well fed as a larva will live for two or more very active days with no food or water and be capable of laying a hundred or more eggs even with no more food.

The frequency of white females in the Yuma-San Luis area is 19.54 ± 1.91 percent (N = 481). Compared with the Imperial Valley at Calexico, this is two and one-half times the standard error of the difference (Diff. = 6.55 ± 2.37 percent).

It was expected to find the frequency in the lower Colorado River area to be lower than the Imperial Valley. However, the approximate frequencies derived fron the museum material (HOVANITZ 1946b) shows that Arizona as a whole has a frequency of about 39 percent white. Nearly all these data are from the portion of Arizona at the higher elevations. Locations closer to the latter region would be expected to have a frequency varying toward it provided there is some population interchange. Migration could easily take place up and down the Gila River, for alfala fields tend to follow it. This river connects the Yuma area with the Phoenix agricultural area where alfalfa is very commonly grown and where the fields are heavily infested with Colias (WILDERMUTH 1914).

Including the Yuma area in the total, the southeastern region on the map (fig. 1) has a frequency of 16.31 ± 0.82 percent white females (N = 2,035).

THE SAN JOAQUIN VALLEY POPULATIONS

On the map (fig. 1), the San Joaquin Valley lies along the central strip of the state between the places marked North and South San Joaquin Valleys. Actually the San Joaquin Valley is the larger and southern portion of the Great Valley of California which is continuous from the south at the Tehachapi mountains to the Trinity-Cascade ranges in the north. The climate in the San Joaquin Valley is "mild" the year round. Summer days are normally hot (above 100°C) but the nights are cool. Winters are cool but not cold; frost forms for two or three months of the year especially to the north. Rainfall is highest in the north (from ten to 20 inches) and lowest in the south (about five inches or less). Temperatures are higher in the south than in the north, but the humidity is lower in the south than in the north. Alfalfa is grown very extensively in the valley, especially in the region at the northwest (at the big triangle on the map), at scattered areas throughout the central part and very commonly in the southern region near Bakersfield (at the rectangle on the map).

The white female frequency throughout this area is over 50 percent as compared with about 30 percent in southern California. The two zones are separated by a mountain barrier which, however, is, not barren of Colias populations. The individuals are merely more scattered, as they must have been over the entire west before alfalfa was grown. The population size must be relatively small; consequently, the gene frequencies would be controlled primarily by migrations from the adjacent alfalfa fields. The population size in the alfalfa fields of California is so huge at the present day that, except in some very isolated places, the gene frequency is probably controlled by them everywhere.

On the map (fig. 1), the general white female frequencies may be observed, these rising from the southern part of the San Joaquin Valley at 58 percent, to 69 percent in the north.

The South San Joaquin Valley Area

Samples were made in this area at points about six to ten miles apart. These data are too detailed for the large maps, and the area represented thereon by a rectangle is shown enlarged (fig. 4). The rectangle represents an area about 60 miles long in a northwest-southeast direction and about 25 miles wide. Alfalfa fields in this area are located in relation to the distribution of the sampled populations. However, there are more fields in the north than the samples would indicate. Near the limits of the rectangle in the southeast and southwest the alfalfa fields are isolated plots surrounded by unirrigated desert. This is true to a certain extent in the central and northern parts, too, but here also there is irrigation of sugar beet farms, beans, etc. Just north of Bakersfield and running southwest between Rosedale and Panama is the Kern River. Its flood basin occupies a wide area in which there are no alfalfa fields. The river itself is no barrier. The area to the north and west of the rectangle is partly dry, unirrigated hardpan soils and partly agricultural. There is no sharp delimitation of the alfalfa-Colias populations in either the west (north of the Kern

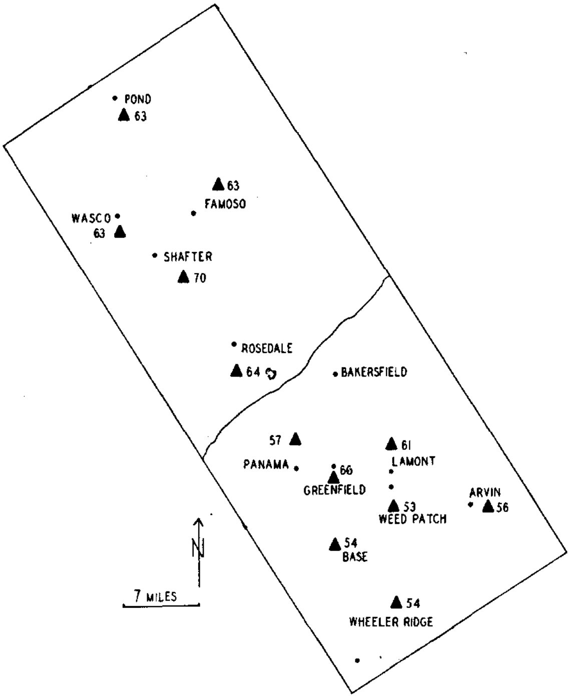

FIG. 4.—The South San Joaquin Valley area, as represented on figure 1 by a rectangle. Dots are locations of towns, and triangles are locations of alfalfa fields sampled. The Kern River is shown by the wavy line through the center.

River), the north, or the northeast. However, the zone directly north of Bakersfield and east of Famoso and Shafter is largely unirrigated lands left in semidesert state. Completely around the east side of Bakersfield, Arvin, Weed Patch and toward Wheeler Ridge, the area is devoid of alfalfa. Much of it is devoid of irrigation. West of Base and Wheeler Ridge, alfalfa is occasionally present, but not too commonly. This spotty distribution of breeding places for Colias is of signal importance in understanding the rapid change in gene frequencies which take place.

The frequencies for the San Joaquin Valley placed on the map (fig. 4) are those obtained on August 21, 1942. Three localities were sampled earlier, on June 25, 1942, and two of these later on September 22, 1942.

The three population samples in June are from north to south:

		N
Wasco	63.19 ± 1.08 percent	1,964
Rosedale	53.33 ± 1.31 percent	1,440
Base	52.68 ± 1.28 percent	1,528

Wasco is obviously quite different from either Rosedale or Base. Being in the north, it is expected that it would have a higher frequency than either of the latter two. However, since the distance is small, chance variations within sub-units of a population could be expected to alter the significance of the north-south rule. In climate, Wasco is but slightly if any different from Base or Rosedale. It might have been expected that Rosedale would have had a frequency exactly intermediate between Wasco and Base, since it is geographically located exactly between the latter two (fig. 4). This was not the case, however, for though it was slightly higher than Base, the difference is not significant even with the large sample.

At the later date (August 21), two months later, these same localities were again sampled. The frequency at Base remained essentially the same (fig. 4); the frequency at Wasco also remained the same. Rosedale, however, had risen and was now equal to Wasco rather than Base:

		N
Wasco	62.85 ± 1.57 percent	942
Rosedale	64.16 ± 1.68 percent	812
Base	53.73 ± 2.51 percent	389

The change in gene frequency necessary to alter the phenotype frequency this much is great. The two months between the sampling dates is long enough in the vicinity of Bakersfield at that time of year for two generations. Therefore, sometime about the 20th of July there was a flight of adults which laid the eggs from which came the August 21, adult flight. Possibly at this time there was a movement of adults southward sufficiently to alter the gene frequency. The population size itself is so enormous that the change could not have come through chance. If selection were the causal factor, it, too, would have had to be very great. Assuming equal viability of the three possible genotypes, the gene frequency for a population of 50 percent white would be

33.5 percent dominant alleles and for 66.7 percent would be 44.4 percent dominant alleles. The selection could have occurred against or for any of the three genotypes. Were the homozygote dominant completely lethal, the change from 50 percent to 67 percent could be accomplished in one generation (see table 1), providing selection against the two remaining genotypes was equal. The former probability of mass movement or shifting of the adult population is considered the most likely explanation for the change (fig. 2), especially considering the spotty distribution of breeding places.

The distribution of frequencies in the areas adjacent to these latter three places is a good key to the verification. Arvin, Weed Patch, and Wheeler Ridge are the western and southernmost localities adjacent to Base. They are 56, 53, and 54 percent respectively. North and east of Base are Lamont 61 percent, Greenfield 66 percent, and Panama 57 percent. The latter two are exactly intermediate to Rosedale. The frequency of Panama is closest to Base, but the locality is closest to Rosedale. The reverse is true for Greenfield. It is possible that a flight of adults from the north came through the area a generation earlier and laid eggs in the freshly cut alfalfa fields. Colias apparently migrate more under certain environmental conditions than under others (HOVANITZ 1943d; WILLIAMS and BISHARA 1929), and it is very reasonable to assume such a mass migration at one time but not another. Females normally migrate to cut fields for egg laying. Since the fields are not all cut at the same time in an area, the infestation will be spotty. Thus, places like Greenfield and Rosedale may get an infestation which arose from farther north and which does not belong to the area. Lamont may have gotten a smaller influx.

The localities north of Rosedale all have a frequency above 63 percent; Shafter is highest at 70 percent. The latter is statistically different from all the populations other than Greenfield.

The average for all the localities north of the Kern River (Rosedale and north) is statistically higher than the area south of the Kern River:

		N
North of Kern River	64.50±0.79 percent	6,450
South of Kern River	57.65±0.69 percent	5,237

It seems that the segregation of a small area like that south of the Kern River could not be maintained at lower gene frequency without either a complete isolation with no selection for any allele, or a selection rate for an allele which is at par with the influx of the other allele. There is no isolation except distance between the above two areas. The only reasonably close populations to this area are in the north; the gene frequencies there are all high. The butterflies are known to fly great distances and to move in great quantities. Therefore, there seems to be no alternative other than to assume *selection against a very high concentration of dominant white alleles in the southern area.* This selection for the area must eliminate as many dominant alleles per year as migrate into the region from the north. There is no higher migration of recessive alleles from any direction into the southern area.

The samples obtained from Rosedale and Base in September were very small, for cold weather had killed most of the brood indirectly (through action of parasites on the eggs and young larvae). The graph (fig. 2) shows that the samples were of nearly the same frequency as in August; the slight increase was not significant:

		N
Rosedale (September)	67.65 ± 2.88 percent	272
Base (September)	55.56 ± 4.86 percent	188

Most of the butterflies were very old and worn at this time, suggesting that these were stragglers from the August emergence. It is quite likely, for the September cool weather would not have allowed a new generation but would have allowed the adults to live longer. Eggs laid in August were noted dead on the alfalfa leaves in great quantities.

June and July averages for the South San Joaquin Valley area are as follows. These are hardly comparable, owing to the additional and different populations sampled in August, but they are statistically different:

		N
June	57.06 ± 0.72 percent	4,932
August	60.50 ± 0.46 percent	8,983

The North San Joaquin Valley Area

Samples were made in this area at distances averaging about the same as those in the South San Joaquin Valley area—namely, six to ten miles. The area is depicted on the large map by a triangle (fig. 1). The details of each sample are shown on the enlarged map (fig. 5). The distance along the hypotenuse of the triangle is about 56 miles; each of the other sides is about 35 miles. Most of the localities sampled lie almost in a straight line along the hypotenuse; this compares with the longest length of the South San Joaquin Valley area. One locality lies at the right angle corner and each of the other two are away from it toward the acute angles. Separating the line of seven populations along the hypotenuse from the other three locations is the meandering San Joaquin River and its flood basin. Owing to this break in the valley agricultural area, the distances between the west San Joaquin River populations and the east San Joaquin Valley areas are nearly twice normal.

Alfalfa fields in this triangular area are most abundant along the zone between the San Joaquin River and the Coast Range hills. The hypotenuse of the triangle roughly designates the edge of the hills. The alfalfa fields are less abundant on the east side of the San Joaquin Valley and disappear beyond Ripon. There are few directly along the San Joaquin River. South of Newman and north of "County Line" the fields are still quite numerous. In the Coast Range hills, there is none for many miles.

A sample was made at Tracy on June 7, 1942. All the other samples, including another at Tracy, were made in the two-day period, August 14 to 16, 1942. One population, Westley, was again sampled on the 18th. The frequency in June at Tracy was not very different from that in August, the slight increase not being significant (fig. 2):

Tracy		*N*
June	64.67±2.37 percent	300
August	67.88±1.36 percent	1,180

The August frequencies suggest a concentration of white genes in the region around Westley. From there to the east and north (and also possibly to the south) the frequency decreases. These differences are statistically significant.

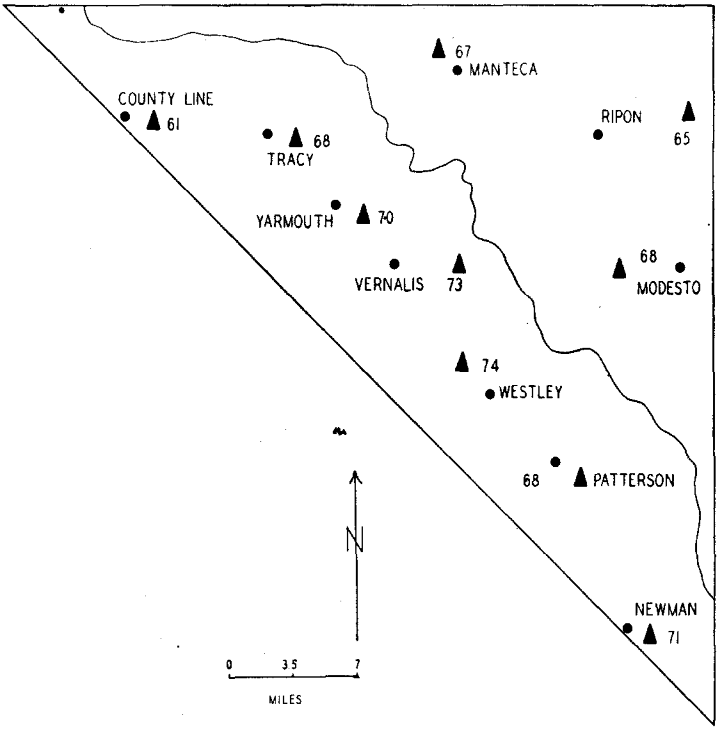

FIG. 5.—The North San Joaquin Valley area as represented on figure 1 by a triangle. The wavy line is the San Joaquin River. The small triangles are locations of alfalfa fields sampled, and the dots are towns or landmarks.

The averages for the three central populations, Westley, Vernalis, and Yarmouth, are shown here for comparison with the two northwestern populations, the three eastern ones and the two southeastern ones:

		N
Central		
(Westley, Vernalis, Yarmouth)	72.25±0.86 percent	2,729
Northwest		
Tracy, County Line)	64.85±1.01 percent	2,202
East		
(Manteca, Ripon, Modesto)	66.77±1.07 percent	1,950
Southeast		
(Patterson, Newman)	66.72±1.55 percent	895

The central area is obviously different from each of the others except the southeast. The standard error of the difference of these two is just twice the difference—that is, 3.53±1.78 percent. Neither of the other three areas are different from one another, though some of the individual differences are great. "County Line" has a low of 61 percent, the lowest in the northern populations; it is statistically different from all the rest.

Judging from visual approximation, the population abundance was also highest in the central area, especially at Westley. At Yarmouth and Westley, the population consisted primarily of newly emerging adults; wet winged individuals were common. At the other localities, the individuals were apparently not so fresh. In a freshly cut alfalfa field, the ratio of males to females is a fair indication of the new emergence. A cut field with no new adults eclosing is nearly barren of males. Females in these places are laying eggs and are quite abundant. On the other hand, a freshly cut field with adults eclosing has a high frequency of males. The frequency of females which have wet wings and are in copulation is very high. Yarmouth and Westley were examples of the latter. The other fields except Tracy were all examples of the former. Tracy was rather intermediate.

At Westley, in view of the correlation between highest frequency of white females and greatest fresh eclosions, a sample of wet-winged (copulated) females was obtained. The following results, which did not seem reasonable at the time, were obtained:

Westley, August 16, 1942		*N*
Free-flying	73.92±1.33 percent	1,112
Wet-winged (copulated)	60.84±3.31 percent	166

It is clear that the frequency is very different. The frequency of white eclosions is lower than the frequency of the free-flying females. This is true despite the contamination of the free-flying population with individuals also eclosed on that day but already in flight. The tentative conclusions were drawn either that white females did not mate so freely with the orange ones (negative sexual selection) or that the brood had already mostly eclosed, with the whites eclosing first. It was for the purpose of testing these conclusions that the San Fernando Valley population already mentioned was analyzed in September–October, 1942, when it was observed that the conditions were fortunately excellent at that one place. Earlier, attempts had been made to get frequencies of copulated females to compare with the general population frequency, this being an analysis of male sexual selection for the different colored females. Such attempts ended in failure, because the females don't often mate after the original copulation at eclosion. A sample was obtained in a field of old females near Rosedale, June 25, 1942, with the following results:

		N
Free-flying	53.33±1.31 percent	1,440
Copulated but not newly emerged	54.17±7.18 percent	48

The number is small but nearly the same in both cases. It is doubtful if the colored forms have any different sexual antipathy.

Two days after the sample described above was taken at Westley another sample was obtained. This time copulated females were more difficult to find. The suggestion is that the emergence was nearing its close. The results were:

Westley, August 18, 1942		*N*
Free-flying	71.12±1.30 percent	1,056
Copulated (with wet wings)	65.38±9.35 percent	26

The number of newly eclosed females is too low this time to have much significance. It is still lower than the general frequency. The frequency in the free-flying individuals has dropped 3 percent, but the significance is doubtful (not quite twice the standard error of the difference: 2.80±1.64 percent).

If the white females had eclosed in a higher frequency earlier in the general population emergence, it would be expected that the white frequency in the general population would drop daily just as it did in the San Fernando Valley population. The above 3 percent drop may represent this difference.

Toward the end of the adult emergence it would be expected that the frequency of white females in the newly eclosing individuals would be lower than that in the general population. This, too, is true just as it was in the San Fernando Valley populations.

On the same grounds, it would be expected that the area where the adult emergence is taking place in greatest quantity would have the highest white frequency. This is true. The central area where the white female frequency is highest is also the area where the adults were emerging in the greatest quantity (especially at Yarmouth and Westley). From this central point of greatest abundance, they were probably flying in all directions. The high frequency at Vernalis where there was no emergence noticeable was due to the trap effect of the "isolated" alfalfa field where the sample was obtained. Being between Vernalis and Yarmouth, it would attract adults flying away from those centers.

These data, therefore, suggest that samples taken at different times of the brood emergence may not be typical of the general region.

The average frequency for the North San Joaquin Valley area is 68.50±0.49 percent (N=9,024). The percentage will be compared with others later.

The Central San Joaquin Valley Area

Four frequency samples were obtained at variously-spaced locations between the North and the South San Joaquin Valley areas. The valley is flat the entire distance, but regions where alfalfa is grown are spotty. Therefore, some of the distance may be said to be a barrier to Colias movement by reason of space alone. The map (fig. 1) illustrates the locations of the places. The two southernmost of these localities have the lowest frequency but are not greatly different than would be expected, nor from what has been found in the more detailed zones. The 65.37±11.29 percent (N=891) Allensworth and the 64.42±8.50

percent (N = 38) at Corcoran are close to the 64 percent average for the north end of the South San Joaquin Valley area. The Hanford 59.48 ± 1.88 percent (N = 686) and the Madera 61.72 ± 1.69 percent (N = 802) are the lowest north of Bakersfield. The following explanation may be suggested for these figures:

(a) These may be just chance changes in the gene frequencies at various places owing to lack of climatic differences between the localities.

(b) Alfalfa fields are not so common in this area, and the populations are more isolated. Therefore, the population size (abundance) may be smaller, allowing chance fluctuations greater leeway.

(c) The smaller population size may be sufficient to eliminate part of the selective advantage the white allele may have.

The Central San Joaquin Valley area as sampled by these four locations has a white female frequency lower than the north end of the South San Joaquin Valley, 62.52 percent versus 64.50 percent, which is just over twice the standard error of the difference. However, considering the South San Joaquin Valley as a whole, it is higher:

		N
North San Joaquin Valley	68.50 ± 0.48 percent	9,324
Central San Joaquin Valley	62.52 ± 0.97 percent	2,420
South San Joaquin Valley	59.39 ± 0.41 percent	14,375
Total San Joaquin Valley	62.94 ± 0.29 percent	26,119

A rise in white female frequency is apparent from south to the north in the valley.

The San Francisco Bay Area

Alfalfa is apparently grown commonly only at the southeastern portion of the Bay Valley. Hence, the sample was obtained there (fig. 1). Actually, several small areas were investigated, but only the total value is of reasonable size. The average frequency here of 66.04 ± 3.70 percent (N = 159) is in agreement with the 68.50 ± 0.49 percent (N = 9,324) average for the San Joaquin Valley at the same latitude.

A summary of the frequencies in four of the five provinces in California is given in table 6. The fifth province, the Great Basin, is not comparable and will be discussed below.

THE GREAT BASIN AREA

The Great Basin Area was sampled in two locations, Mono Lake Valley, Mono County, and Round Valley, Inyo County (map, fig. 1).

The Mono Lake area

Mono Lake is situated about 180 miles airline directly east of San Francisco (fig. 1). It is a Basin lake at an elevation of 6,300 feet above sea level and has no outlet. The country around it is very high. The Sierra Nevada Mountain range is a continuous wall on the west with peaks up to 13,000 feet in elevation, with no passes lower than 10,000 feet. Mountains 8,000 to 10,000 feet

TABLE 6

Summary of the white female frequencies in the orange race Colias chrysotheme populations in California west of the Sierra Nevada but including the southwestern desert areas.

LOCALITY	% WHITE FEMALES σ	N
1. San Francisco Bay	66.04±3.70	159
2. San Joaquin Valley		
North	68.50±0.48	9,324
Central	62.52±0.97	2,420
South	59.39±0.41	14,375
3. Coastal Southern California	29.86±0.34	18,617
4. Coachella-Imperial-Colorado River Valley area	16.31±0.82	2,035
Grand total	47.77±0.23	47,010

high surround the basin on the other three sides. The country is very arid due to the rain-shadow effect of the western mountain range. Winters are exceedingly cold, going well below 0°F, and snow falls for several months of the year if there is any precipitation at all. Summers are often exceedingly hot but sometimes it may be cold throughout the year. The air is always dry.

Meadows watered by springs and melting snow in the mountains occur in several places around the western edge of the lake. In these meadows, native clovers of various sorts grow, as well as some alfalfa mixed with red and white clover planted by the native residents. The agriculture of the region is primitive; the fields or meadows are grazed by sheep or cattle rather than being cut for hay as in the western valleys. In the meadows, one finds the yellow race Colias at certain times of the year and nearly everywhere one finds the orange race. In the wet meadows both the yellow and the orange race seem to concentrate in the largest numbers, and it is in two of these meadows that the frequencies of the white, yellow, and orange forms were obtained. The yellow form presents an entirely different problem from the white form and will be dealt with separately (HOVANITZ 1943c).[1]

The seasonal fluctuations in the white female frequency were great. Early in the season for that place the frequency was high; in the middle of the sum-

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[1] The white females of the orange and yellow races in the Great Basin region are indistinguishable by phenotypical characters (HOVANITZ 1943b, 1943c). Therefore, without breeding, it is not definitely known whether they are of the one race or the other. The frequencies given in this paper are calculated as if they were all of the orange race. The reasons why it is not believed that extensive error is being introduced into the data are as follows: Breeding and museum data have suggested that the white form is nearly absent in the yellow race in the Mono Lake and Round Valley region. The presence of yellow race adults at Mono Lake, at least, is seasonally controlled (HOVANITZ 1943c). The presence or absence of yellow race adults at this locality has no influence on the fluctuation of the white female frequency. Since more than half of the adults at Round Valley are of the yellow race, the frequency here may be considerably in error. However, no white females from this place which have been bred have given entirely yellow progeny. Also, no yellow females used for breeding purposes from either of the two localities have produced a white form.

mer it was low. Again in the fall, the frequency rose again to nearly its early height. This change is seasonal frequency is illustrated on the graph (fig. 6) for the three years—1940, 1941 and 1942. The fundamental change is the same in all three years. The major portions of the samples making up the curves are statistically significant (table 7). At times it was very difficult to get a reasonable sample, and at first (until the middle of 1941) all samples were obtained by capturing the females with a net.

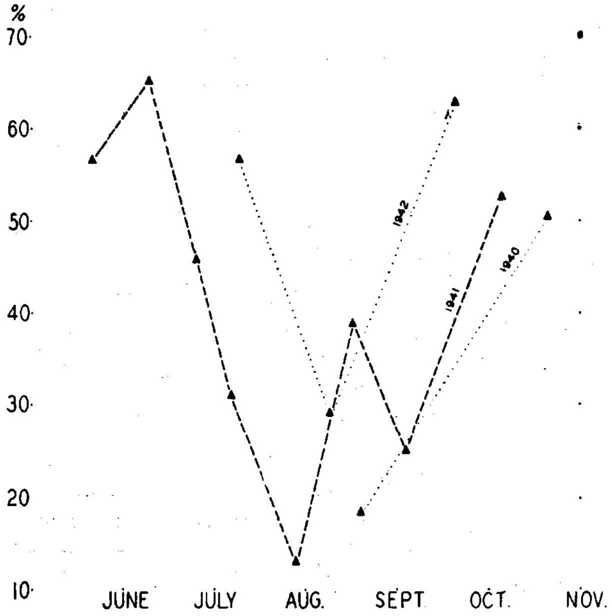

FIG. 6.—The frequencies of white females during the season at Mono Lake, California. The great seasonal change in frequency should be compared with that shown in figure 2.

By way of summary, the 1941 season started out in May and early June at 55–65 percent white females, then dropped through 45 percent in late June, 30 percent the first of July to a low of 15 percent at the end of July. This rose gradually through August and September to a high again of 52 percent in early October.

In 1942, the season started late at Mono Lake for the orange race. In early July, the frequency was at about 58 percent white. By the first of August this had dropped to at least 29 percent and rose again in late September to a high of 62 percent. The samples were not made at as frequent intervals during 1942 as in 1941; hence, the actual low point might have been missed. The 1940 collections are small but, nevertheless, follow the trend perfectly.

This great seasonal change in white female frequency is not duplicated in any of the populations considered heretofore (fig. 2). It is not an effect of the direct influence of the environment upon the phenotype of the adult, for the character is completely under genetic control (HOVANITZ 1943a).

A gene frequency alteration of the proportions needed to change the percentage of white females from 65 percent to 13 percent at Mono Lake is the same as would be necessary to change the population in the North San Joaquin Valley to equal those in the Imperial Valley. This change takes place in as short a period of time as one and one-half months. For the Mono Lake area, it takes place in time equal to the developing period for one generation.

TABLE 7

*The frequency of white females throughout the season at Mono Lake, Calif. This is the frequency as compared with the normal orange females of the orange race.**

DATE	% WHITE FEMALES σ	N
1940		
Aug. 11	18.2 ±11.1	11
Oct. 20	50.0 ±8.48	34
1941		
May 19	56.82±7.45	44
June 8	65.96±4.36	117
June 24	45.75±4.04	153
July 5	31.08±2.22	415
July 26	13.13±3.41	99
Aug. 15	38.74±4.56	111
Sept. 2	25.0	4
Oct. 4	52.27±7.45	44
1942		
July 7	56.30±3.21	238
Aug. 7	29.23±2.82	260
Sept. 16	62.89±3.46	194

* See footnote page 53.

Several possibilities to account for this rapid gene frequency change have been considered.

(a) That there is a tremendous environmental selection in the area against the recessive orange allele in winter due to the very cold winters and in favor of the recessive allele in summer due to the hot, dry weather. The selection during the winter is easy enough to imagine, but the summer change is so rapid that it does not seem possible.[2] Even with the aid of a possible homozygous lethal dominant, which would change the frequency from 66.7 percent to 50 percent in one generation, it is too great a change to expect. The climatic change is not that abrupt or extreme.

(b) That the homozygous dominant white female (and male) is lethal in warmer weather. This would reduce the population very rapidly from 66.7

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[2] DOBZHANSKY (1943) has just shown some similar great changes in the genetic structure of wild populations. As in the present case, his data seem to be best explained by seasonal population migration rather than by seasonal selection.

percent to 50 percent to 28.6 percent to 25 percent, etc., per generation or, in terms of gene frequencies, from 33.3 percent to 25 percent to 14.3 percent, etc. (table 1). It would take more than nine generations to get from 65 percent to 13 percent at this rate, and only one generation is possible.

(c) That white females are at a predatory disadvantage and are likely to be eliminated in the summer more than at the colder parts of the year. The degree of bird attacks on adult butterflies of Colias was closely and carefully observed during the sampling of all the populations in 1941 and 1942. It must be considered that predatory attacks are negligible, though not completely absent.

(d) That there is an alternation of generations during the season such that spring and autumn individuals represent a really different population from the midsummer one. In some of its aspects, this is the conclusion accepted. However, it is not believed that both "populations" live and breed at Mono Lake. If they did there would have to be almost no intermixing in order to prevent gene interchange. No break of this sort is observed at Mono Lake in the orange race. Instead there is a population "high" in midsummer and decrease toward spring and fall, rather than discrete broods.

(e) That the individuals at Mono Lake have migrated there from some other place so that at certain times of the year the individuals are representative of some other locality. This would really be an alternation of "generations," at the locality. At first, this possibility seemed unlikely but later evidence has made it seem very credible. The reasons are as follows:

1. The exceptionally rapid gene-frequency alteration is most reasonable on these grounds. The presence of individuals from a high-frequency population at one time of the year and from a low-frequency population at another time is the easiest explanation.

2. Populations of high frequency (60 to 70 percent) exist just west of the Sierra Nevada from where migrations could have had their origin (San Joaquin Valley). The Great Basin and Mountain Region have a low dominant gene frequency (14 percent—$N=635$) as judged by museum data (HOVANITZ 1943b). Nevada and eastern California have frequencies of 19 and 17 percent, respectively ($N=43$ and 65). Much of the latter material is probably yellow race, since there is only 29 percent orange race calculated in the above figures. Apparently the environmental conditions in the dry mountain and basin region are most favorable for the lower dominant allele frequency. It is not believed that there is any migration of individuals into the Mono Lake area from low-frequency areas but rather that the low-frequency individuals represent the resident population.

3. When the white frequency is high, the individuals are invariably old and worn. When low, the individuals are much fresher and newly eclosed as if they had been bred in the vicinity.

4. At the times of high frequency early and late in the season the adults flying are of a phenotype development which could not have occurred in the cold weather of the Mono Lake climate. Were the pupae or larvae exposed to the cold night temperatures of the vicnity, they would be reduced forms com-

parable to "spring forms" in the low lands. A very few "spring form" individuals do occur early in the season and especially in the autumn. These are the resident individuals. Most adults at those times are worn "summer form" and were probably grown at a lower elevation. Later, as the resident population increases in size, it masks the high white frequency of the immigrant population. This would account for the gradual rise in the recessive orange allele frequency with a lack of a definite series of broods during the season as is found in the San Joaquin Valley (MICHELBACHER and SMITH unpublished). It was originally assumed that the adults found at Mono Lake in May were overwintering individuals because of the "summer" phenotype development they possessed. Such a supposition had been made as long ago as the nineteenth century by MEAD and EDWARDS (Edwards 1863–1898). They found that adults high in the Colorado Rockies early in the season were also "summer" individuals. The high improbability that Colias adults can overwinter in the true sense is shown by the length of time they can be kept in a cold room at extremely high humidities and normal low humidities. At 2°C, females will live inactive for three to four weeks or possibly a little longer at an extremely high humidity. At a normal low humidity they will die in one to two weeks at that temperature. The dryness of the Mono Lake atmosphere would kill the butterflies there quickly if the cold did not.

That Colias of the orange race can fly distances as great as the 100 miles from the San Joaquin Valley to Mono Lake is illustrated by the many migratory individuals taken in the far northern parts of North America (Hudson Bay, Northern Manitoba, Alberta, etc.), where overwintering populations do not exist. "Summer-form" individuals of the orange race have been taken in the New England states very early in the season. They must have flown in from the South. The ability to travel is great in the orange race of *Colias chrysotheme* (HOVANITZ 1943d). Summer form females have been observed laying eggs high in the San Jacinto mountains of Southern California in May and June where temperatures in the day are cool and at night near freezing. They could not have overwintered there but must have come from the alfalfa fields in the valleys below.

The orange race is fairly abundant in the Hudsonian and Alpine life-zones of the Sierra Nevada in midsummer. It is exceedingly doubtful that they could have overwintered in such a cold place but it is more likely that they have been re-introduced into the mountains seasonally. Apparently, a re-introduction takes place in the north such as in Alberta every few years (BOWMAN 1942). *Colias behri* is the resident Colias of the Hudsonian meadows in the Sierra Nevada, to which place it is restricted.

The question of why the Mono Lake population never reaches equilibrium with the San Joaquin populations probably involves several factors. The resident individuals may be better able to withstand the cold winters just as the orange race in the north-eastern United States can now better withstand the winters there. Or, the low frequency of the populations throughout the Basin and Mountain area may just absorb the excess white genes coming from the valley. Climatic selection in the area may be sufficient to reduce the frequency after a period of time. Or, the low white allele frequency in the yellow race of the area may absorb and eliminate many of the genes through intercrossing. The yellow race is apparently better adapted to resident life in this region judging from its frequency of 71 percent for the mountain area in the museum data. Or, the dominant gene may have a disadvantage in the genome typical of the Basin region which would render the homozygote-dominant lethal or reduce the white heterozygote frequency.

The average frequency of white females at Mono Lake is 43.16 ± 1.18 percent (N = 1,724).

The Round Valley Area

Round Valley is south of Mono Lake 60 miles. It is part of Owens Valley and is 2,000 feet lower than Mono Lake, or 4,500 feet. The winters are not quite so cold a Mono Lake, and the summers are very much hotter. The warm season is several months longer. The general relationship to the Sierra Nevada range and San Joaquin Valley is the same as Mono Lake. There are, however, more alfalfa fields in the vicinity, especially to the south in Owens Valley. Round Valley itself is a big meadow with mixed native clovers, white clover, red clover, alfalfa, and grass fields kept green by irrigation and springs.

TABLE 8

*The frequency of white females throughout the season at Round Valley, Calif. This is the frequency as compared with the normal orange females of the orange race. However, in 1942 66 per cent of the females other than white at this place were of the yellow race.**

DATE	% WHITE FEMALES σ	N
1941, season from May–Oct.	35.13±7.84	37
1942		
April 1	28.6	7
April 25	50.0 ±10.2	24
June 12	53.85±9.78	26
July 8	58.46±4.32	130
Aug. 6	65.22	8
Sept. 16	51.61±8.98	31
Total	56.64±3.42	226
1941–42 total	53.61±3.04	263

* See footnote page 53.

The frequencies of white females obtained at this locality were purely incidental to the study of the orange-yellow relationships. Therefore, the numbers in the samples are small (table 8). Apparently, however, the frequency may not fluctuate seasonally as at Mono Lake, since in July of 1942 a frequency of 58 percent was procured. This may be accounted for by the more desert environment around Round Valley such that the orange race population is completely restricted to alfalfa fields. Apparently, there is a great migration of Colias over the Sierra Nevada to Round Valley just as to Mono Lake. Without a native population of orange race other than that one in alfalfa fields, the high white frequency is not reduced much by swamping of the genes.

The average of white females during 1941 and 1942 was 53.61 ±3.04 percent (N=263). This is statistically higher than Mono Lake's 43.16±1.18 percent (N=1,724). The north-south rule is reversed, and the climatic expectancies are also reversed. However, possible reasons for this condition have already been covered. (Probable lack of resident population.) The frequency of the total for Mono Lake and Round Valley is 44.53±1.06 percent (N=1,987). This total is much higher than the 17 percent determined from museum material for the eastern Sierra Nevada, but the latter was based on 70 percent yellow race contamination. White females in the yellow race at Mono Lake and Round Valley are either totally absent or close to it.

SUMMARY AND CONCLUSIONS

The frequency distribution of white females in the orange race of *Colias chrysotheme* (*=eurytheme*) has been shown to change from 74 percent in the North San Joaquin Valley to 13 percent in the Imperial Valley. This change in frequency has been shown to be largely correlated with the change in climatic conditions through the area.

The greatest change in frequency between populations takes place where there is complete isolation between populations as well as a climatic difference. However, an environmental selection for the alleles controlling the characters is shown to be present even when no isolation other than distance exists between populations (San Joaquin Valley).

Wild population changes in gene frequency of various magnitudes have been illustrated. Most of these are shown to be due to population movement and others to a differential development rate of the genotypes.

The causes of population differences have been shown to lie in any of the following: (a) possible random deviation, (b) climatic selection, (c) differential population movement and migration, and (d) different age of the adult population after eclosion.

The faster development rate of white females (heterozygous plus homozygous dominant) over the orange (homozygous recessive) is deduced from some of the population analyses.

No differential sexual selection by the males for the polymorphic females is noted.

The calculation of actual gene frequencies from wild population phenotype frequencies in any organism can never be accurate so long as knowledge of the viability of the three genotypes ($p^2+2pq+q^2$) under known environmental conditions cannot be controlled; only good estimates can be made of the true gene frequency.

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