ENVIRONMENTAL VARIATIONS IN EUPHYDRYAS ANICIA EURYTION (NYMPHALIDAE)

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Anyone who has collected butterflies is aware that certain species vary greatly in appearance from one locality to another. In some cases, these variations are due to genetic differences in the populations, but in other cases, particularly where separate localities are encompassed by a small portion of a continuous range of the species, these variations may be caused by environmental conditions such as temperature and moisture. These environmental effects are particularly noticeable in Colorado, since many climatic conditions are found within relatively small areas of the State.

Of course, the best means to discover which variations are caused by particular environmental factors is to raise a single brood under different external conditions and then to compare the phenotypes of the adults. This method was tried with two species during the summers of 1958 and 1959, but none of the caterpillars matured, and conclusive results could not be obtained.

Thus, a less exacting method was employed: the analysis of a number of specimens from localities for which at least one environmental condition is precisely known. Use of this method does not eliminate the possibility that genetic constitution was selected by the particular environmental conditions. Nevertheless, the method can show by noncorrelation that the environmental factors cannot be the cause of the variations. Therefore, the chief aim of this study is to determine if the interpretation of environmental conditions as a causal factor is consistent with actual variations in the butterfly species. In order to insure that correlations are legitimate, one must be careful to select a species that does not tend to wander, so that specimens captured at a particular place will be representative of specimens which mature under conditions associated with that location. Largely for this reason, the species chosen for this investigation is Euphydryas anicia eurytion (Mead), since another Euphydryas has been shown to be sedentary (Ehrlich, 1965). E. a. eurytion is common in the mountainous areas of Colorado.

Figure 1 shows the places from which each examined series was taken. All of these places are within a continuous range of the species. In order to minimize the possibility of inadequate sampling from a particular locality, only series with five or more specimens are used in



FIGURE 1

Map showing locations where the analyzed series were collected.

1. Wilkerson Pass, 2. Glen Cove, 3. Edlowe, 4. Seven Lakes, 5. Cheyenne Mountain, 6. Starr Ranch, 7. Rampart Range Road, 8. Mount Herman, 9. West Creek, 10. Loveland Pass, 11. Shrine Pass, 12. Independence Pass, 13. Cottonwood Pass, 14. Almont.

this study. Except where noted in the tables, specimens collected in different years from the same location are grouped together as one series.

The differing appearance of *eurytion* is due to variations in both size and coloring. Size was determined by measuring the radius of the right forewing with a vernier caliper, and these measurements were reproducible within 0.1 mm. When the size is correlated with the altitude of capture, the coefficient of correlation, r, is -0.66 for the males and -0.61for the females. Tables I and II record both this correlation and the mean size of each series used. The relation between size and altitude is inverse, that is, as one factor (altitude) increases, the other factor (size) decreases. This relation is seen in Figures 2 and 3 which plot size as a function of altitude. The closer r is to 1.0 (its upper limit), the stronger the relation between the correlated factors (Brown, 1951). Taking into account the 11 degrees of freedom for the males, the probability, P, that



FIGURE 2

Graph showing the mean radius of the right forewing of the males as a function of altitude. The numbers refer to localities in Table I.

the relation is not real is less than 0.02 (Fischer, 1950). For the females, P is less than 0.1. At least for the males, one can confidently say that the relation is real. However, since the slopes of the curves in Figures 2 and 3 are the same within the limit of experimental error, one may confidently say that the relation is also real for the females.

The actual cause of the variation is not the altitude itself, but is some condition which varies proportionally to the altitude. The most likely suspect is the average temperature which in Colorado is inversely proportional to the altitude (Ramaley, 1927). For example, the series from



Graph showing the mean radius of the right forewing of the females as a function of altitude. The numbers refer to localities in Table II.

Almont which appears to fall outside the correlation can largely be explained if the differences in average temperature are the real causes for variation. Being on the western slope of the Continental Divide, Almont is generally considered to be colder for its altitude than the other series localities used, all of which are on the eastern slope (Climatological Data of Colorado, 1939). The observation of similar decreases in the size of *eurytion* specimens with an increase in northerly latitude tends further to indicate that temperature is an important contributing cause of these variations in size.



Diagram of wings showing the areas used to measure color differences (see Table III for the color code).

The change in moisture with altitude and hence its likelihood as another contributing cause is not clear, although some people believe that on the average, the greater the altitude in Colorado, the greater the average surface moisture of the ground. It appears to me that, at best, a consideration of moisture as a contributing cause of size variation would be inconclusive in this study.

In contrast to the correlation of size to altitude, the correlation of coloring to altitude depends upon rather qualitative measurements. One set of spots on the wings apparently changes from red-brown to yellow with an increase in altitude, whereas another set seems to change from red-brown to dark red-brown. In addition, the black overscaling of redbrown areas seems to increase with an altitude increase. Thus, the net effect is a change from a uniformly red-brown appearance to a contrasting checkerboard pattern. The raw data for color variation was collected for almost every area of both the forewing and the hindwing, but it is necessary to take only one representative spot from each set of variable spots for statistical analysis, since the spots within each set vary in exactly the same way. As seen in Figure 4, numbers corresponding to the colors of these spots and to the extent of overscaling were chosen so that the smaller numbers represent those conditions apparently present at higher altitudes. Thus, the sum of these numbers represents the entire apparent color change with altitude. All of these qualitative measurements were made by one person within a continuous period of eight weeks, so the interpretation of "red-brown" and other colors should be internally consistent. The measurement was qualitatively taken for the whole series rather than for each specimen, because series are quite



FIGURE 5

Graph showing the total color factor of the males as a function of altitude. The numbers refer to localities in Table IV.

uniform with respect to coloring, and subjective favoring of the color thesis was avoided by consciously deciding the doubtful cases in a manner least favorable to the hypothesis.

As seen in Table IV, all of the correlations for the males are significant to at least a 5% level. The certainty for the females is not quite so good; nevertheless, from Table V, we see that all but the spot 1 factor are significant to a 10% level. It is difficult to determine the actual cause of the variation, but temperature is a likely possibility: the Almont sample again follows the pattern associated with higher altitudes on the eastern slope. The apparent lack of correlation of the Wilkerson Pass sample may indicate that moisture is an important factor in coloring, for such an interpretation would explain both the Wilkerson Pass sample (the



FIGURE 6

Graph showing the total color factor of the females as a function of altitude. The numbers refer to localities in Table V.

pass being abnormally dry for its altitude) and the Almont sample (Almont being abnormally wet) (Climatological Data of Colorado, 1939). However, such an interpretation must also assume that for the other samples, the moisture increases proportionally to the altitude. Since records are not available from all these areas and since the relation of moisture to altitude does not seem to follow so definite a pattern in Colorado as that for temperature, the contribution of moisture to these color variations must await further studies.

Thus, it is clear that variations in *Euphydryas anicia eurytion* within its Colorado range correlate with the altitude and hence to environmental conditions associated with the altitude—particularly the average temperature. Clearly a decrease in average temperature may affect the

		Altitude		Mean radius		
	Series location	(100 ft)	Ν	of series (mm)	σ	
1.	Starr Ranch	65	6	20.53	0.89	
2.	Cheyenne Mountain	70	9	20.38	1.24	
3.	Almont	80	6	17.35	0.65	
4.	West Creek	80	36	20.33	1.08	
5.	Edlowe	90	5	19.42	0.55	
6.	Rampart Range Road	95	29	20.11	0.95	
7.	Wilkerson Pass	95	8	18.68	0.33	
8.	Seven Lakes	110	6	19.17	0.72	
9.	Shrine Pass	113	9	17.89	0.62	
10.	Glen Cove	115	6	19.00	0.99	
11.	Loveland Pass	123	9	17.10	0.64	
12.	Independence Pass	125	6	17.57	0.89	
13.	Cottonwood Pass	125	35	17.78	1.00	
Mea	an of all series	99		18.79		
σ		21		1.26		
Coe	fficient of correlation			-0.66		
Pro	bability correlation not real			< 0.02		

TABLE I.—CORRELATION	ON	OF	ALTITUDE	WITH	RADIUS	OF		
RIGHT FOREWING-MALES								

chemical development of pigments in wings, so its designation as a major causal factor satisfies a logical test beyond mere correlation. If one tries to show that other conditions than temperature are contributing factors, logical inconsistencies are encountered. For example, although an increase in altitude means a proportional increase in ultraviolet radiation, its designation as a major cause of variation fails to explain

		Altitude		Mean radius	
S	eries location	(100 ft)	Ν	of series (mm)	σ
1. St	arr Ranch	65	12	23.45	0.78
2. M	ount Herman	70	7	22.69	1.26
3. Cl	heyenne Mountain	75	6	23.15	0.82
4. Al	lmont	80	11	19.99	0.58
5. W	est Creek	85	30	23.80	1.29
6. W	ilkerson Pass	95	11	22.01	0.82
7. In	dependence Pass	125	6	19.55	1.24
8. Co	ottonwood Pass	125	10	20.62	0.97
Mean	of all series	90		21.91	
σ		24		1.65	
Coeff	icient of correlation			-0.61	
Proba	bility correlation not real			< 0.1	

TABLE II.—CORRELATION OF ALTITUDE WITH RADIUS OF RIGHT FOREWING-FEMALES

Kind of factor	Factor	Color interpretation			
Spot 1	3	Red-brown			
Spot 1	2	Red-brown with yellow tinges			
Spot 1	1	Yellow			
Spot 2	2	Red-brown			
Spot 1	1	Dark red-brown			
Overscaling	3	Black overscaling entirely within area (3)			
Overscaling	2	Black overscaling extending into area (2)			
Overscaling	1	Black overscaling extending into area (1)			

TABLE III.—COLOR CODE USED IN MEASUREMENT OF COLOR FACTORS

TABLE IV.—CORRELATION OF ALTITUDE WITH COLOR FACTORS—MALES

	Series location	Altitude (100 ft)	Spot 1 factor	Spot 2 factor	Overscaling factor	Color factor
1.	Starr Ranch	65	2	2	3	7
2.	Cheyenne Mountain	70	3	2	3	8
3.	Almont	80	1	1	3	5
4.	West Creek	85	3	1	3	7
5.	Rampart Range Road	95	3	1	3	7
6.	Wilkerson Pass	95	3	1	3	7
7.	Seven Lakes	110	2	2	3	7
8.	Shrine Pass	113	1	1	2	4
9.	Loveland Pass	123	1	1	2	4
10.	Cottonwood Pass ('53)	125	1	1	1	3
11.	Cottonwood Pass ('54)	125	1	1	2	4
12.	Cottonwood Pass ('55)	125	1	1	2	4
13.	Independence Pass	125	1	1	1	3
Mea	ans of all series	103	1.8	1.2	2.4	5.4
σ 2		22	0.93	0.42	0.77	1.8
Coefficients of correlation			-0.70	-0.61	-0.77	-0.77
Prol	babilities correlations not	real	< 0.05	< 0.05	< 0.05	< 0.05

TABLE V.—CORRELATION OF ALTITUDE WITH COLOR FACTORS—FEMALES

	Series location	Altitude (100 ft)	Spot 1 factor	Spot 2 factor	Overscaling factor	Color factor
1.	Starr Ranch ('31)	65	2	2	3	7
2.	Starr Ranch ('33)	65	3	2	3	8
3.	Cheyenne Mountain	70	2	2	3	7
4.	Mount Herman	75	3	2	3	8
5.	Almont	80	1	1	3	5
6.	West Creek	85	2	1	3	6
7.	Wilkerson Pass	95	3	2	3	8
8.	Cottonwood Pass	125	1	1	1	3
9.	Independence Pass	125	1	1	$\overline{1}$	3
Means of all series		87	1.9	1.6	2.6	6.1
σ		23.5	0.78	0.52	0.88	1.9
Coefficients of correlation		-0.50	-0.60	-0.92	-0.65	
Probabilities correlations not real				< 0.1	< 0.05	< 0.1

both the Almont sample and the observation of similar changes with increasing northerly latitude. Similarly, a consideration of the decrease in pressure as a real causal factor fails to explain these observations.

Some forms of butterflies which are presently designated as subspecies may be no more than opposite ends of a continuous species variation which corresponds to the particular environment in which the specimens matured. I hope that this study illustrates that environment can be an important factor in butterfly variation, although further studies must be undertaken to confirm whether the environmental conditions have created genetic differences between the groups of specimens or whether the variation is caused solely by the conditions under which individual specimens were subjected during their natural development.

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