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PHENETICS OF NATURAL POPULATIONS

IV. THE POPULATION ASYMMETRY PARAMETER IN THE BUTTERFLY COENONYMPHA TULLIA

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1. INTRODUCTION

RECENTLY Soulé (1967) described a property of insular lizard populations that supports the idea that the average level of developmental stability differs significantly from one population to another. The level of stability was estimated by comparing populations with respect to their relative expression of minor departures from perfect bilateral symmetry—" fluctuating asymmetry "—assuming that every population had an estimable level of asymmetry for a *given set of characters*, *i.e.* a population asymmetry parameter (PAP). The operations used to arrive at the PAP estimates and to assess the reality of the phenomenon are as follows:

1. Choose a number of (preferably) uncorrelated bilateral characters in which differences between the sides can be accurately scored or measured (*e.g.* scale or bristle counts or appendage measurements).

2. Score a sample of individuals from a number of populations for the characters.

3. The absolute difference (d) between right and left sides is determined for each character on each specimen. From the asymmetry distributions the mean asymmetry $(\bar{d})$ is calculated for each character in each population; $\bar{d}$ is an estimate of the PAP.

4. Check for the existence of directional asymmetry and antisymmetry (see Van Valen, 1963), and scale effects that might result from differences in the means of the characters among the populations, and make the appropriate corrections (see Soulé, 1967, for details and references).

5. For each character rank the populations according to the $\bar{d}$ values and determine the Kendall coefficient of concordance, W, in order to verify the hypothesis that the different characters " agree " on the relative levels of fluctuating asymmetry in the populations. Significance* of W means that

* Due to an error the actual value of W was omitted from the earlier paper; it is 0·49; $P < 0·01$.

chance is unlikely to account for the observed concordance of the rankings, and by inference that the different PAP estimates for a sample (as many as there are characters) are all reflecting the same underlying phenomenon.

The interpretation of the PAP rests on the imaginative studies of Mather (1953), Thoday (1953, 1956, 1958) and others who regarded fluctuating asymmetry as developmental accidents reflecting the level of developmental buffering or stability. Although it was not always so, it is now clear that the developmental stabilities of different characters in an individual are independent, and it is not possible to deduce from the asymmetry of one character what the asymmetry direction or level will be in another character (Reeve, 1960; Van Valen, 1962; Ehrlich, *et al.*, 1967). In contrast to the apparently non-existant organism-wide asymmetry property, the occurrence of the PAP favours the hypothesis that different individuals can be well buffered for one character and poorly in others, but that something is regulating or determining the *average* level in a population at least for a given set of characters. Whatever this universal is, it is pervasive enough to be detectable in many different characters. We believe that this underlying variable is the overall compatibility or coadaptation (Mather, 1943; Dobzhansky, 1950) of the genetic elements in the population.

2. MATERIALS AND METHODS

The purpose of this note is to report that the PAP is not a unique phenomenon in lizards, but characterizes the only other animal in which we have sought it—namely, the satyrine butterfly *Coenonympha tullia*. During July of 1964, we made six collections of this small, abundant insect in localities within a 35 km. radius of the Rocky Mountain Biological Laboratory near Gunnison, Colorado. At that time we were still thinking in terms of the organism-wide asymmetry property which turned out to be absent in this and other species of butterflies we investigated.

We chose six bilateral characters for estimating the PAP:
1. maximum length of femurs from the third pair of legs;
2. number of spines in outer rows on uppermost tarsomers of third pair of legs;
3. number of spines in inner rows on uppermost tarsomers of third pair of legs;
4. maximum length of " eyespots " in M_1 cells of forewings measured parallel to the M_1 and M_2 veins on the ventral surface;
5. maximum length of " eyespots " in Cu_1 cells of hind wings measured parallel to Cu_1 and Cu_2 veins on the ventral surface;
6. length of tegulae mounted in 50 per cent. alcohol under coverglass.

3. RESULTS

Measurements were made and calculations were performed with the micrometer eyepiece units. No corrections of the raw data were required. There was no indication of directional asymmetry. No *t*-tests (for paired comparisons) for differences between the means of the two sides were significant at the 0·05 per cent. level. Antisymmetry can also be discounted; the few distributions where there was a suggestion of bimodality of the standardised signed asymmetries were not significantly different from the standardised normal distribution using a chi-square test. The absence of correlations

between d's and $\bar{X}$'s from the six populations for each of the characters measured obviated the necessity of making scale corrections.

Two of the characters (Nos. 2 and 3) are often correlated (table 1) and though this might introduce some redundancy into the analysis the choice was intentional because we wished to check whether asymmetries of correlated characters would also be correlated. Table 1 shows that the " neighborhood " effect is non-existent.

TABLE 1

Count and asymmetry correlations for tarsal spines (characters (2) and (3)).
The asymmetries are signed; i.e. right side minus left side

			Correlation coefficients	
Population	N	Elevation in metres	Sum of inner v. Sum of outer	Asymmetry of inner v. Asymmetry of outer
Taylor River	25	2591	0·14	0·09
Slate River	30	2713	0·33	0·03
Twin Lakes	16	2896	0·60*	0·08
Gothic C	16	2926	0·40	0·43
Gothic H	18	2926	0·63**	0·09
Taylor Park	24	3048	0·53**	−0·01

* $P<0.05$;   ** $P<0.01$.

Table 2 presents the character asymmetry sums and rankings for the six populations. The coefficient of concordance (W) for these data is 0·36; $P < 0.05$.

TABLE 2

Average asymmetry and rankings (in parentheses) for six populations of
Coenonympha tullia

	Characters					
Population	1	2	3	4	5	6
Taylor River	0·680 (1)	0·760 (1)	1·080 (4)	2·880 (1)	3·680 (2)	0·960 (1)
Slate River	0·867 (3)	1·167 (6)	0·966 (2)	3·200 (2)	5·066 (5)	2·566 (6)
Twin Lakes	0·875 (4)	1·125 (5)	1·000 (3)	3·437 (3)	4·062 (3)	2·562 (5)
Gothic C	0·857 (2)	0·928 (3)	0·785 (1)	6·141 (6)	4·786 (4)	1·857 (2)
Gothic H	0·944 (5)	0·777 (2)	1·166 (6)	3·666 (4)	3·166 (1)	2·388 (3)
Taylor Park	1·160 (6)	1·083 (4)	1·125 (5)	4·916 (5)	5·834 (6)	2·458 (4)

4. DISCUSSION AND CONCLUSIONS

A significant W means that, if population A is on the average relatively asymmetrical for character X, when compared to population B, then there is a high probability that it will have higher average asymmetries for other characters as well. The above results increase our confidence in the generality of this picture. Many more studies are needed, of course, before it can be concluded that developmental stability in a population can be reliably estimated by these procedures.

Another point worthy of comment is the absence in this case of correlated asymmetry in the spatially adjacent and correlated inner and outer rows of

tarsal spines (in Soulé (1967) it was erroneously stated that such correlations exist). From this we might speculate that the developmental " accidents " which result in asymmetry are very localised events during the morphogenesis of the legs. Furthermore, the absence of the neighborhood effect suggests the restraint of using uncorrelated characters may be unnecessary.

It can be seen in table 2 that the most asymmetrical populations occur at the highest altitudes. If confirmed by future studies, this observation will be useful in testing the hypothesis (Soulé, 1967) that instances of strong directional selection in nature could be detected by relatively high PAP's. Another opportunity this system offers is the separation of genetic vs. environmental contributions to fluctuating asymmetry. A rearing program designed to isolate these components will begin this year.

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THE SIGNIFICANCE LEVEL IN MULTIPLE TESTS MADE SIMULTANEOUSLY

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THE problem of how a certain proportion of " significant " results are to be interpreted when a number of χ^2 tests have been performed on different samples from similar populations often arises in genetics. It is usually understood that when the null hypothesis is correct one result in 20 is expected to fall outside the 95 per cent. level confidence limits. Doubtless, with this in mind, many working at the 5 per cent. level tend to regard one significant result in 20 and results near that figure as chance departures. The opposite is sometimes encountered; anything below 5 per cent. is treated as significant even though the hypothesis has been simultaneously tested on other samples without a significant departure being found. Both practices fail to take