

Genetic latitudinal adaptation of *Drosophila melanogaster*: new discriminative biometrical traits between European and equatorial African populations

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SUMMARY

Five biometrical traits (thorax length, wing length and width, sternopleural and abdominal chaetae numbers) were measured on 13 equatorial African strains and 30 French strains. In all cases highly significant differences were observed between the two geographic groups. These results are added to previously known variations concerning adult weight and ovariole number. In each place, the genetic particularities of the wild populations seem to be maintained by the selective pressure from environmental conditions, resulting in a homeostatic focusing of the best fitted average genotype. Analysis within each group showed that variations between strains were in most cases poorly or not correlated, so that partial or total genetic independence between the various traits measured seems likely.

1. INTRODUCTION

In numerous living species, regular genetic clines occur with latitude (Mayr, 1966; Dobzhansky, 1970). Such changes in species with a broad geographical range are not surprising since many environmental conditions (temperature, light, humidity, etc.) are correlated with latitude. The study of these clines is thus interesting since it affords an opportunity for understanding the effects of natural selection upon wild populations.

Metrical traits usually have a polygenic determinism so that their analysis is difficult. However, regular geographic variations have also been described in the frequencies of structural alleles in *Drosophila* (Johnson & Schaffer, 1973; Vigue & Johnson, 1973; Miller, Percy & Berger, 1975; Band, 1975) and other species of insects (Taylor & Mitton, 1973) which help to bridge the gap between genotype and phenotype (Lewontin, 1974). The study of quantitative characters in wild populations could therefore prove to be more interesting for evolutionary studies than is usually expected.

In the *Drosophila* genus, latitudinal clines for metrical traits have been described in *D. robusta* (Stalker & Carson, 1947), in *D. subobscura* (Prevosti, 1955;

Misra & Reeve, 1964); and recently in *D. melanogaster* and *D. simulans* (David & Bocquet, 1972, 1975*a, b*).

In *D. melanogaster* previous results were obtained only on two traits: adult fresh weight and ovariole number of females. New data concerning five other traits will be presented here. As the known cline in that species ranges from 0° to more than 50° of latitude, it appeared more convenient to compare populations originating in countries at the ends of the cline. Genetic differences between French and equatorial African strains will therefore be considered.

2. MATERIAL AND METHODS

Strains

A population of each of 30 recently collected French strains was founded, starting with several females in each case. The latitudes of origin ranged from 43 to 49°. Only 13 strains from equatorial Africa (Gabon, Congo, Cameroon, Ivory Coast) were available for this comparison. Several of these strains were each founded from a single female. Their origins were 0 to 8° North or South latitude.

Conditions of study

All strains were kept in laboratory conditions for a few generations before being studied. Measurements were made on flies reared under standard, strictly controlled conditions: temperature 25 °C, killed yeast, axenic rearing medium (David & Clavel, 1965), low larval density (30 eggs per culture vial).

Traits measured

Besides fresh weight and ovariole number of females, for which data have already been published (David & Bocquet, 1975*a*), three traits were measured with a Zeiss measuring microscope (precision 0.01 mm): thorax length, wing length and wing width. Sternopleural chaetae were counted on each side of the thorax and added. Chaetae were also counted on the third and fourth sternites and their sum will be called here abdominal chaetae. For each strain, an average was calculated on 30 flies of each sex.

3. RESULTS

Table 1 shows that, for the five traits, the average values in the tropical flies are much lower than in the French strains. In all cases the differences, which are at least 6 times higher than their standard errors (*t* parameter) are highly significant.

Comparison of the averages does not give a clear picture of distribution of the strain values within each geographic group. In each case, we need to know if the frequency distributions are overlapping. If not, the determination of the mean value of a single strain would decide its origin. A graphic analysis of this problem can be made using correlation diagrams between any two traits. In each strain, values of males and females are correlated, so that only data for females will be presented here. For each strain, seven different measures are available (the five indicated in Table 1 plus adult weight and ovariole number previously studied)

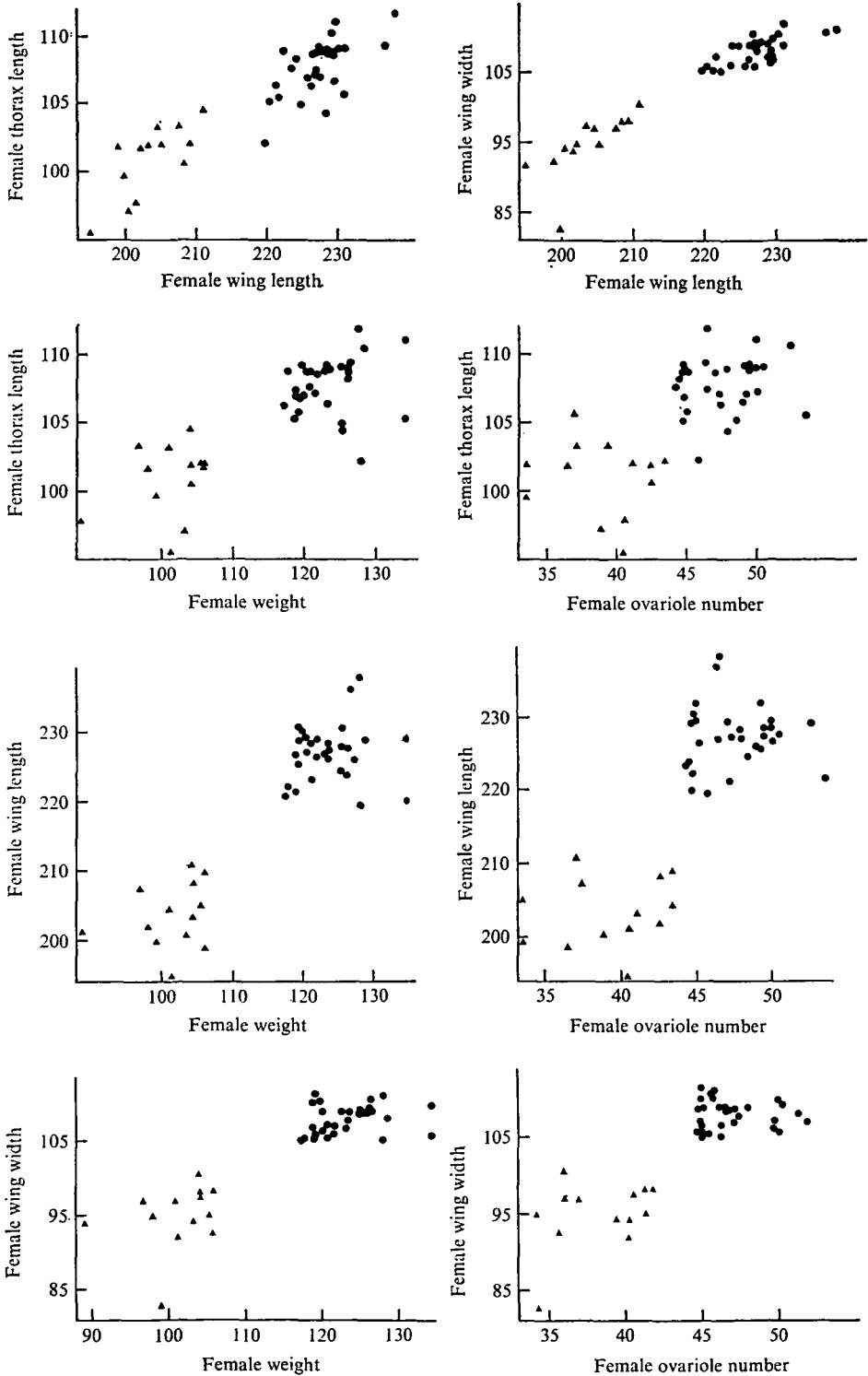


Fig. 1. Correlation diagrams between strain average values of various biometrical traits in females. ▲, African strains; ●, French strains.

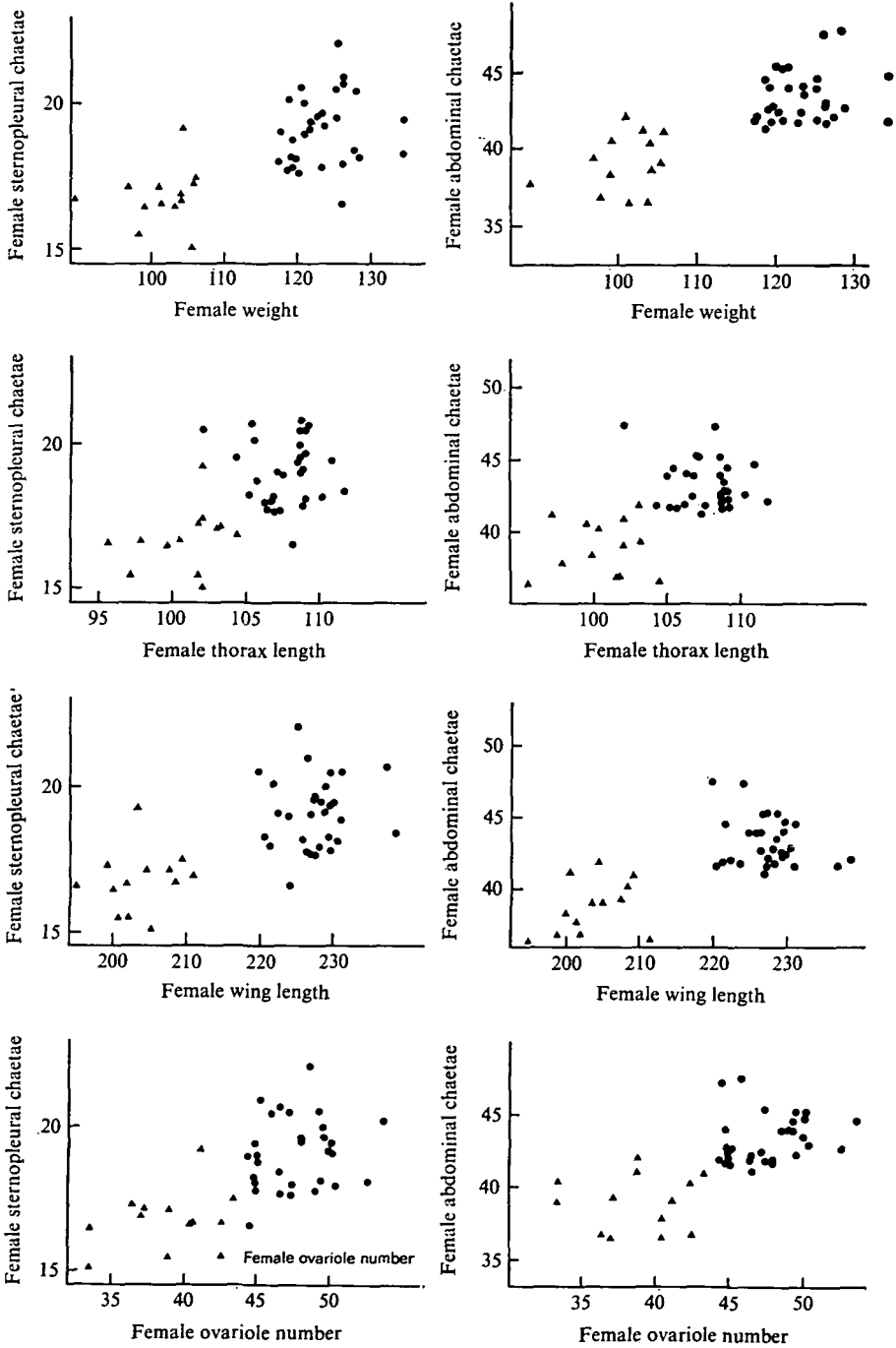


Fig. 2. Correlation diagrams between strain average values of various biometrical traits in females. ▲, African strains; ●, French strains.

so that 21 different diagrams are possible. Among them, 16 were chosen and are given in Figs 1 and 2.

Examining these graphs shows that for several traits (thorax length, wing dimensions, fresh weight and ovariole number) the distributions do not overlap. For sternopleural and abdominal chaetae numbers, a partial overlapping is observed. However, in all cases, when two traits are considered simultaneously, it is possible to separate the two groups of strains.

Table 2. *Within-group correlation coefficients*

(Th.: thorax length; W.l.: wing length; W.w.: wing width; Stp.: sternopleural chaetae; Abd.: abdominal chaetae; F.w.: fresh weight; Ov.: ovariole number. Values significantly different from zero are marked *; $P < 0.05$ or **: $P < 0.01$. Calculations are made on mean values of 30 French and 13 African strains.)

| Traits | Females | Males | Both sexes |
|-----------|---------|--------|------------|
| Th.-W.l. | 0.68** | 0.59** | 0.63** |
| Th.-W.w. | 0.43** | 0.54** | 0.48** |
| Th.-Stp. | 0.00 | 0.35* | 0.18 |
| Th.-Abd. | -0.13 | -0.04 | -0.08 |
| Th.-F.w. | 0.18 | 0.16 | 0.17 |
| Th.-Ov. | 0.04 | | |
| W.l.-W.w. | 0.71** | 0.87** | 0.80** |
| W.l.-Stp. | 0.09 | 0.36* | 0.23* |
| W.l.-Abd. | -0.10 | -0.14 | -0.12 |
| W.l.-F.w. | 0.14 | 0.35* | 0.25* |
| W.l.-Ov. | 0.06 | | |
| W.w.-Stp. | 0.06 | 0.30 | 0.18 |
| W.w.-Abd. | -0.08 | -0.16 | -0.12 |
| W.w.-F.w. | 0.20 | 0.29 | 0.25* |
| W.w.-Ov. | 0.14 | | |
| Stp.-Abd. | 0.04 | 0.35* | 0.19 |
| Stp.-F.w. | 0.14 | 0.34* | 0.24* |
| Stp.-Ov. | 0.20 | | |
| Abd.-F.w. | 0.17 | 0.30 | 0.23* |
| Abd.-Ov. | 0.17 | | |
| F.w.-Ov. | 0.04 | | |

Correlations between traits were not considered at the individual level: fresh weight, wing length and ovariole number, for example, were measured on different flies. It is, however, possible to consider correlated variations between strain averages. Results concerning the within-group correlations are given in Table 2.

The highest coefficient (0.8) is observed between wing length and width. This is not surprising since the correlation concerns two dimensions of the same organ. Correlations between thorax length and the two wing dimensions are lower (0.63 and 0.48). If we consider the square of the coefficient of correlation as a coefficient of determination, we can conclude that the variability in thorax length explains less than 40% of the variations in wing size. Thorax size is therefore relatively independent of wing dimensions. All the other correlations are still

much lower and often not significant, showing that the traits are almost independent. The lack of correlation between sternopleural and abdominal chaetae confirms previous results of several authors (Clayton *et al.* 1957; Sheridan *et al.* 1968; Jones, Frankham & Sheridan, 1969).

When a global correlation, pooling all strain values into a single group, is calculated, high positive coefficients are obtained in all cases. For example, 0.91 between thorax and wing length, 0.88 between thorax and wing width, 0.68 between thorax and ovariole number, etc. Such results are not surprising since they only reflect the fact that, for all traits, French flies are larger to African ones, as already shown in Table 1.

4. DISCUSSION AND CONCLUSION

In this study, the individual level of variability was not taken into account and the mean value of each strain was considered as a single measure. Differences between strains from the same geographic area are, however, highly significant, as demonstrated by a variance analysis not presented in this paper.

In all experiments, larvae were reared under strictly controlled conditions, reducing the environmental component of variance. In some cases, measurements were repeated on the same strain at various time intervals and the mean values were highly reproducible. Finally, a few crosses were made between different lines and the F_1 flies were always found to be intermediate between their parents. All these observations demonstrate that differences between strains in the same group have a genetic basis. Of course, genetic differences are much more important when the two geographic groups are compared.

Genetic variations between laboratory strains collected in the same country (France for example) are probably the consequence of genetic drift initiated by a small number of founder flies (Bocquet, David & De Scheemaeker-Louis, 1973). Such differences, however, can also derive from limited geographic differentiation of the original populations (Girard & Palabost, 1976). Differences between French and equatorial African populations, on the other hand, certainly reflect their adaptations to different environmental conditions (David & Bocquet, 1972, 1975*a, b*).

It is now well recognized that all wild populations contain a large amount of genetic diversity. Numerous experiments with *D. melanogaster* showed that biometrical traits respond quickly to directional artificial selection. For any trait it would take only a few generations of selection, starting for example from a French strain, to reach the average level of African values. The observation that, in a given area, populations keep the same average genotype, year after year, shows that the best fitted phenotypes and genotypes are permanently favoured by natural selection, resulting in a remarkable genetic homeostasis.

When populations, living in distant places under different climatic conditions, are compared, their average genotypes appear to be very different. Two possible explanations can be given for such an observation. We can first assume that

French and African populations carry different alleles. This hypothesis is very unlikely because *D. melanogaster* probably has a high migration rate due to human transportation. The other, more probable explanation is that the genetic backgrounds are basically the same and that the environmental differences permanently favour different allelic frequencies and genetic equilibria. In other words, the genetic homeostatic focusing is different, resulting in two distinct phenotypic adaptive zones (Lande, 1976).

Compared to equatorial flies, French *Drosophila* can be described simply as being bigger. Such a result would be easy to understand if the two populations differed only by a few 'size polygenes' acting directly on various parts of the body. Such seems, however, not to be the case. From the within-group correlation analysis (Table 2) a partial or total genetic independence between traits can be inferred. Such a conclusion results also from various selection experiments: changing ovariole or chaetae numbers does not seem to modify adult weight or thorax size. A correlated response to selection has only been indicated in the literature between wing and thorax lengths (Robertson & Reeve, 1952; Robertson, 1954; Tantawy & Tayel, 1970). The link between these two traits is, however, not absolute. For example, Tantawy (1956) observed, in a strain selected for long wings, a decrease of thorax length. In *D. robusta*, Stalker & Carson (1947) described an increase of wing length accompanied by a decrease of the thorax.

If we therefore assume that the various traits here measured are genetically mainly independent, two conclusions can be drawn. First, the number of genic differences, or genetic distance, between French and African populations should be high. Second, natural selection must be acting, to maintain the differences, simultaneously upon various traits and genetic systems. In some cases, this conclusion is trivial: larger wings and a larger thorax are obviously needed for a convenient flight of heavier flies. But another interpretation is needed for explaining ovariole number differences which are probably related to reproductive potential (David, 1970, 1971). Finally, the adaptive significance of chaetae numbers, although argued by several authors (Barnes, 1968) still remains to be interpreted. All these observations illustrate a basic difference in the effects of artificial versus natural selection.

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