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# Genetic Heterogeneity in Natural Populations of *Drosophila melanogaster* for Ability to Withstand Dessication

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**Summary.** Strains set up from single inseminated females of *D. melanogaster* derived from two wild populations have been shown to differ in their ability to withstand dessication, as measured by mortalities after 16 hours in a dry environment, thus there are genes segregating in wild populations for ability to withstand dessication. A more detailed study on strains from one of the wild populations, showed that strains with high wet and dry weights lose water by dessication relatively less rapidly and have lower mortalities, than strains with lower wet and dry weights.

Variability within and between five inbred strains was studied with results as above. Heritabilities for wet weight, dry weight, and mortality were 0.40, 0.41 and 0.60 respectively, showing the likelihood that the traits would be amenable to further genetic analysis.

The relevance of the results are discussed in relation to stress to high temperatures, and the ecology of the species in general.

## Introduction

Recent work has shown that natural populations of *D. melanogaster* are heterogeneous genetically for a number of physiological stresses, such as resistance to high temperatures (Hosgood and Parsons, 1968; Parsons, 1969), ether (Watt and Parsons, unpubl.), and $Co^{60}$-$\gamma$ rays (Parsons, MacBean and Lee, 1969). In this paper we extend our observations to dessication, i.e. the ability of flies to survive in a dry environment. The study of traits such as resistance to high temperatures and dessication, seems to be of some importance in relation to the ecology of the species.

Not much work has been done on dessication, although Kalmus (1945) and Waddington, Woolf and Perry (1954) described differences between strains for preferences for environments with different humidities. Pittendrigh (1958) found that *D. persimilis* lost water by cuticular transpiration more rapidly than *D. pseudoobscura*, and that males lost water quicker than females.

## Method

The procedures follow some recent work of Parsons and Hosgood (1967), Parsons, MacBean and Lee (1969) etc., who described experiments where a number of strains of *D. melanogaster* derived from single inseminated females collected in the wild led to discrete strains for several quantitative traits, namely scutellar and sternopleural chaeta number, mating speed, duration of copulation, as well as the physiological traits listed above. The differences between the strains were genetic, as was confirmed in some cases by diallel crosses. The genetic heterogeneity between the founder females implies that the population must be polymorphic for genes determining the traits (Parsons, Hosgood and Lee, 1967).

The experiments to be discussed were based on 17 strains collected at Eltham, Victoria in December 1967, and 18 strains collected at Leslie Manor, Victoria, 3 in December 1963 and 15 in December 1965. The strains were all set up from single inseminated females, and were kept in half-pint bottles at 25 °C, and were transferred every 3 weeks to set up the next generation. Experiments on 5 inbred strains maintained in the laboratory by sib-mating for over 100 generations will also be described. These strains can therefore be assumed to be essentially homozygous, and thus permit a comparison of variability within and between strains, from which heritabilities in the broad sense (ratio of genotypic to phenotypic variance) can be obtained for any traits of interest.

In all experiments, flies of different sexes were dessicated in groups of 10 over silica gel at 25 °C. After various trials, 16 hours of dessication was selected as a reasonably critical level from the point of view of discrimination between strains. Flies were 2–3 days old when dessicated. In the experiments it was thought desirable to control levels of larval competition, so as to minimize environmental variations in fly size. Two levels were used, by placing 25 and 200 newly hatched larvae per vial respectively.

## Results

In Table 1, percentage mortalities in the 17 Eltham strains are given for 3 trials each 2 generations apart for experiments carried out in mid-1969, with an analysis of variance of the data after carrying out the angular transformation. The level of larval competition was 25 larvae per vial. The major source of variation is the sexes effect, showing males to be more susceptible to dessication than females. There is no significant overall difference between trials, showing the general reliability of the method adopted for dessication. Of particular interest for this paper is the significant strains effect, showing that in agreement with the evidence cited in the introduction, strains derived from the different founder females are heterogeneous, and so the Eltham population can be argued to be polymorphic for genes determining dessication.

Table 1. *Percentage mortalities of 50 flies per sex after 16 hours of dessication (Eltham strains) for 3 trials, each 2 generations apart*

| Strain | Trial 1 | | Trial 2 | | Trial 3 | |
|---|---|---|---|---|---|---|
| | ♀ | ♂ | ♀ | ♂ | ♀ | ♂ |
| E 1 | 12 | 48 | 4 | 52 | 28 | 64 |
| 2 | 20 | 52 | 36 | 96 | 32 | 88 |
| 3 | 52 | 92 | 28 | 100 | 20 | 100 |
| 4 | 0 | 48 | 0 | 64 | 4 | 84 |
| 5 | 28 | 96 | 8 | 88 | 4 | 80 |
| 6 | 4 | 68 | 0 | 76 | 0 | 84 |
| 7 | 36 | 60 | 12 | 36 | 4 | 56 |
| 8 | 20 | 88 | 8 | 96 | 8 | 60 |
| 9 | 12 | 92 | 8 | 96 | 20 | 92 |
| 10 | 28 | 100 | 28 | 92 | 4 | 76 |
| 11 | 0 | 60 | 0 | 16 | 4 | 72 |
| 12 | 0 | 92 | 0 | 92 | 12 | 90 |
| 13 | 28 | 80 | 32 | 48 | 8 | 16 |
| 14 | 68 | 84 | 12 | 100 | 4 | 96 |
| 15 | 44 | 40 | 16 | 24 | 12 | 80 |
| 16 | 16 | 24 | 8 | 64 | 56 | 84 |
| 17 | 48 | 92 | 4 | 100 | 52 | 96 |

Analysis of variance (after applying the angular transformation).

| Source of variation | d. f. | M. S. | F |
|---|---|---|---|
| Strains | 16 | 608.5 | 5.43*** |
| Sexes | 1 | 43162.4 | 385.09*** |
| Trials | 2 | 113.4 | 1.01 |
| Strains × trials | 32 | 182.4 | 1.63 |
| Strains × sexes | 16 | 395.0 | 3.52** |
| Sexes × trials | 2 | 361.2 | 3.22 |
| Error | 32 | 112.1 | |

$^{**}P < 0.01$, $^{***}P < 0.001$.

Table 2. *Percentage mortalities of 50 flies per sex after 16 hours of dessication (Leslie Manor strains) for 3 trials, each 2 generations apar*

| Strain | Trial 1 | | Trial 2 | | Trial 3 | |
|---|---|---|---|---|---|---|
| | ♀ | ♂ | ♀ | ♂ | ♀ | ♂ |
| 1 | 48 | 56 | 100 | 94 | 48 | 84 |
| 2 | 64 | 100 | 84 | 96 | 32 | 96 |
| 3 | 0 | 84 | 40 | 64 | 0 | 88 |
| 20 | 8 | 96 | 92 | 100 | 16 | 92 |
| 21 | 24 | 60 | 24 | 96 | 12 | 80 |
| 22 | 20 | 52 | 96 | 96 | 32 | 96 |
| 23 | 20 | 48 | 44 | 80 | 0 | 92 |
| 24 | 8 | 80 | 8 | 100 | 8 | 100 |
| 25 | 60 | 44 | 76 | 92 | 0 | 100 |
| 26 | 36 | 88 | 72 | 100 | 44 | 100 |
| 27 | 60 | 64 | 60 | 92 | 16 | 84 |
| 28 | 0 | 20 | 68 | 52 | 4 | 66 |
| 29 | 72 | 72 | 88 | 92 | 4 | 84 |
| 30 | 32 | 92 | 92 | 100 | 20 | 100 |
| 31 | 28 | 84 | 84 | 88 | 24 | 80 |
| 32 | 44 | 76 | 68 | 96 | 0 | 84 |
| 33 | 20 | 72 | 76 | 88 | 0 | 48 |
| 34 | 20 | 64 | 64 | 52 | 4 | 44 |

Analysis of variance (after applying the angular transformation).

| Source of variation | d. f. | M. S. | F |
|---|---|---|---|
| Strains | 17 | 617.9 | 4.29*** |
| Sexes | 1 | 26506.4 | 184.07*** |
| Trials | 2 | 5256.2 | 36.50*** |
| Strains × trials | 34 | 131.0 | 0.91 |
| Strains × sexes | 17 | 291.0 | 2.02* |
| Sexes × trials | 2 | 3124.4 | 21.7 |
| Error | 34 | 144.0 | |

$^{*}P < 0.05$, $^{***}P < 0.001$.

In Table 2, percentage mortalities are given for the 18 Leslie Manor strains. These experiments were carried out at about the same time and in the same manner as those above. Again the major source of variation is the sexes effect. There is a significant difference between trials, perhaps due to a constant temperature room fluctuation during the carrying out of trial 2. Even so, the strains effect is significant, showing that the strains derived from the different founder females are heterogeneous as above.

The next step was to look at the effect of dessication as measured by loss of weight, with respect to the mortality of the strains. This was done for the Leslie Manor strains excluding strain 3, which was breeding poorly at the time. In Table 3, mean weights of 10 flies of each sex before dessication (wet weights) $A$ are given for adults derived from the two larval competition levels, namely 25 and 200 larvae per vial. Mean weights $B$ after 16 hours of dessication are also given, with the ratio $B/A$ which measures the relative rate of water loss, the number of flies dead out of 10 at this stage, and mean dry weights after 7 days of additional dessication.

In Table 4a an analysis of variance of wet weights is given, and in Table 4b an analysis of mean dry weights. The wet weights are based on individual flies but the dry weights on groups of 10 flies weighed together, since the accuracy of the balance was not quite adequate to obtain individual dry weights. The wet weights show major differences between sexes and competition levels as is to be expected. The strains effect is significant showing genetic differences between strains. Mean dry weights show similar effects. In both cases, the interaction between sexes and competition levels is significant. One would expect there to be a high correlation between wet and dry weights, and using the overall means for each strain, a correlation coefficient was computed and came to 0.743 (16 d. f.) which is significantly $>0$ at $P < 0.001$.

It was not thought meaningful to present an analysis of variance of the mean weights after 16 hours of dessication, since this would include some dead flies. This is because death itself may alter dessication rates. One relevant observation is that males were more susceptible to dessication than females, since very few males remained alive after 16 hours compared with females (Table 3). Furthermore, considering $B/A$ values in Table 3, $B/A$ for males is less

Table 3. *Mean wet weights A, mean weights after dessication for 16 hours B, with the ratio B/A, the number of deaths out of 10 during this period, and dry weights obtained after a further week of dessication. The data are based on 17 Leslie Manor strains*

Competition level — 25 larvae

| Strain | Females | | | | | Males | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | *A* | *B* | *B/A* | Number dead | Dry weight | *A* | *B* | *B/A* | Number dead | Dry weight |
| 1 | 1.402 | 0.842 | 0.601 | 8 | .399 | .827 | 0.250 | 0.302 | 10 | .222 |
| 2 | 1.358 | 0.824 | 0.607 | 5 | .369 | .844 | 0.226 | 0.268 | 10 | .211 |
| 20 | 1.632 | 1.063 | 0.651 | 3 | .402 | .887 | 0.516 | 0.582 | 6 | .220 |
| 21 | 1.477 | 1.119 | 0.758 | 2 | .384 | .887 | 0.288 | 0.325 | 10 | .216 |
| 22 | 1.510 | 0.986 | 0.653 | 5 | .394 | .855 | 0.290 | 0.339 | 10 | .209 |
| 23 | 1.497 | 0.937 | 0.626 | 5 | .403 | .954 | 0.347 | 0.364 | 9 | .240 |
| 24 | 1.516 | 1.181 | 0.779 | 1 | .430 | .885 | 0.276 | 0.312 | 10 | .237 |
| 25 | 1.374 | 1.011 | 0.736 | 2 | .377 | .849 | 0.318 | 0.375 | 9 | .228 |
| 26 | 1.389 | 0.775 | 0.558 | 8 | .363 | .861 | 0.302 | 0.351 | 10 | .215 |
| 27 | 1.545 | 1.052 | 0.681 | 4 | .427 | .882 | 0.314 | 0.356 | 10 | .232 |
| 28 | 1.518 | 1.044 | 0.688 | 6 | .418 | .957 | 0.357 | 0.453 | 9 | .249 |
| 29 | 1.311 | 0.747 | 0.570 | 8 | .371 | .776 | 0.211 | 0.272 | 10 | .198 |
| 30 | 1.506 | 0.828 | 0.550 | 7 | .384 | .781 | 0.219 | 0.280 | 10 | .199 |
| 31 | 1.310 | 0.620 | 0,473 | 8 | .362 | .829 | 0.251 | 0.303 | 10 | .222 |
| 32 | 1.247 | 0.634 | 0.508 | 8 | .334 | .825 | 0.277 | 0.336 | 10 | .212 |
| 33 | 1.319 | 0.837 | 0.635 | 4 | .355 | .837 | 0.337 | 0.403 | 10 | .216 |
| 34 | 1.396 | 0.947 | 0.678 | 2 | .353 | .799 | 0.264 | 0.330 | 10 | .210 |
| Competition level — 200 larvae | | | | | | | | | | |
| 1 | 1.002 | 0.458 | 0.457 | 8 | .270 | .717 | 0.247 | 0.344 | 10 | .179 |
| 2 | 1.070 | 0.482 | 0.450 | 10 | .262 | .707 | 0.214 | 0.303 | 10 | .115 |
| 20 | 1.146 | 0.711 | 0.620 | 4 | .299 | .701 | 0.297 | 0.424 | 9 | .160 |
| 21 | 1.041 | 0.668 | 0.642 | 2 | .248 | .606 | 0.217 | 0.358 | 10 | .137 |
| 22 | .971 | 0.599 | 0.617 | 5 | .243 | .628 | 0.194 | 0.309 | 10 | .148 |
| 23 | .953 | 0.358 | 0.376 | 10 | .261 | .509 | 0.134 | 0.263 | 10 | .132 |
| 24 | 1.142 | 0.782 | 0.685 | 2 | .290 | .674 | 0.161 | 0.239 | 10 | .154 |
| 25 | 1.004 | 0.600 | 0.598 | 6 | .260 | .625 | 0.183 | 0.293 | 10 | .140 |
| 26 | .961 | 0.257 | 0.267 | 10 | .226 | .527 | 0.140 | 0.266 | 10 | .132 |
| 27 | 1.068 | 0.721 | 0.675 | 4 | .290 | .654 | 0.256 | 0.391 | 10 | .152 |
| 28 | 1.087 | 0.756 | 0.695 | 2 | .273 | .635 | 0.236 | 0.372 | 9 | .153 |
| 29 | 1.162 | 0.854 | 0.735 | 1 | .296 | .693 | 0.293 | 0.423 | 9 | .169 |
| 30 | .954 | 0.411 | 0.431 | 7 | .240 | .690 | 0.166 | 0.241 | 10 | .161 |
| 31 | 1.012 | 0.679 | 0.671 | 2 | .256 | .605 | 0.161 | 0,266 | 10 | .156 |
| 32 | 1.157 | 0.716 | 0.619 | 6 | .287 | .707 | 0.339 | 0.479 | 8 | .162 |
| 33 | 1.040 | 0.548 | 0.527 | 9 | .266 | 679 | 0.179 | 0.264 | 10 | .174 |
| 34 | 1.126 | 0.733 | 0.651 | 1 | .268 | .704 | 0.226 | 0.321 | 9 | .168 |

than that for females, for given strain and competition level, showing their greater susceptibility to water loss than females. In Table 4c, an analysis of variance of the number of flies dead (after applying the angular transformation) is given. It shows a large sexes effect; males being substantially more susceptible to dessication than females. The strains effect is again significant, showing genetic heterogeneity between strains for mortality.

In Table 5, correlation coefficients between the various parameters are given. Because mortalities in males are so high, only correlations for female data are presented. The raw data came from summing the values in Table 3 for the two levels of competition in females for each strain. The high correlations between wet weights, weights after 16 hours of dessication, and dry weights are reasonable, being essentially expressions of the mass of the flies. The significant correlation between the rates of weight loss *B/A* and wet weights, shows that strains characterised by large flies lose proportionately less water than those characterised by small flies, or in other words, large flies are more resistant to dessication than small flies. This fits in with the observation made above that males, which are smaller than females, are more susceptible to dessication as measured by mortality than females. The negative correlation between the numbers dead and wet weights shows that, as expected from the overall differences between the two sexes, dessication leads to death quicker in strains with small flies, and this also indicated by the negative correlation with dry weights although this is not significant.

The rather large differences found between strains for the various parameters discussed, leads one to look further into the genetic control of dessication.

Table 4. *Analyses of variance of wet weights, mean dry weights, and numbers dead out of* 10. *The data are based on* 17 *Leslie Manor strains*

| Source of variation | d. f. | M. S. | F. |
|---|---|---|---|
| a) Wet weights | | | |
| Strains (1) | 16 | 0.067 | 8.84*** |
| Sexes (2) | 1 | 40.56 | 5331.64*** |
| Competition levels (3) | 1 | 14.37 | 1889.00*** |
| (1) × (2) | 16 | 0.022 | 2.94*** |
| (1) × (3) | 16 | 0.047 | 13.77*** |
| (2) × (3) | 1 | 1.27 | 166.75*** |
| (1) × (2) × (3) | 16 | 0.034 | 4.51*** |
| Error | 612 | 0.0076 | |
| b) Mean dry weights | | | |
| Strains (1) | 16 | 0.00067 | 3.74*** |
| Sexes (2) | 1 | 0.32929 | 1839.61*** |
| Competition levels (3) | 1 | 0.14444 | 806.93*** |
| (1) × (2) | 16 | 0.00026 | 1.44 |
| (1) × (3) | 16 | 0.00054 | 3.04* |
| (2) × (3) | 1 | 0.01053 | 58.80*** |
| Error [(1) × (2) × (3)] | 16 | 0.00018 | |
| c) Numbers dead out of 10 (after applying the angular transformation) | | | |
| Strains (1) | 16 | 398.53 | 3.40** |
| Sexes (2) | 1 | 23560.26 | 201.24*** |
| Competition levels (3) | 1 | 43.90 | 0.38 |
| (1) × (2) | 16 | 272.57 | 2.33* |
| (1) × (3) | 16 | 288.13 | 2.46* |
| (2) × (3) | 1 | 64.41 | 0.55 |
| Error [(1) × (2) × (3)] | 16 | 117.08 | |

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

with females. As found in Table 4, the interaction showing most significant effects was that between sexes and competition levels for the two weight parameters, but not for mortalities.

Turning to the strains effect, it is in all cases significant, showing genetic differences between strains for all 3 traits. Heritabilities in the broad sense are given in Table 4d, and are reasonably high, especially for the most direct measure of dessication, which is mortality as expressed by the numbers dead out of 10. The reasonably high heritabilities indicate the likelihood that we are dealing with traits amenable to more sophisticated genetic analyses, and it is hoped to report on these subsequently.

## Discussion

The experiments show that there is genetic variation between strains collected in the wild for ability to tolerate dessication as measured by mortality over 16 hours. This is correlated with wet and dry weights, since heavier strains are more resistant than lighter strains, using mortality as the criterion of the effectiveness of dessication. Taken together, the variation between strains and the reasonably high heritabilities of the three traits mentioned above in this paragraph, suggest that further more detailed genetic analyses on these traits will be worthwhile, and should be carried out, using the techniques of Thoday (1961) and his co-workers in their work on the genetic architecture of sternopleural chaeta number.

In this paper the first of a series of experiments will be reported, namely dessication in 5 inbred strains, in order to look at variability within and between strains, and hence heritabilities in the broad sense. Data analogous to those in Table 3 are given in Table 6, for the 5 inbred strains, and analyses of variance analogous to those in Table 4 are given in Table 7. All 3 traits show a significant sexes effect, indicating lower wet weights and dry weights, and higher mortalities in males than females. Wet weights and mean dry weights are significantly lower at the high level of competition than at the low level as found in Table 4. For mortalities, there is a significant competition effect, but it is much smaller than for the two weight parameters. This is in agreement with Table 4, where in fact the competition effect was not significant. In other words alteration of fly sizes by environmental means, such as competition has no marked effects on mortality, as could have been expected if one considers the higher mortalities of strains with small flies, and of males compared

Table 5. *Correlation coefficients between various parameters* (*d.f.* = 16 *in all cases*) *for female data*

| | Mean weights after dessication B | *B/A* | Mean dry weights | Numbers dead (angularly transformed) |
|---|---|---|---|---|
| Mean wet weights *A* | 0.784*** | 0.597** | 0.791*** | −0.579* |
| Mean weights after dessication *B* | | 0.961*** | 0.705** | −0.902*** |
| *B/A* | | | 0.578* | −0.926*** |
| Mean dry weights | | | | −0.436 |

*$P < 0.05$, **$P \leq 0.01$, ***$P < 0.001$.

The other point is that a trait such as resistance to dessication is presumably of some ecological importance, and may have some influence in determining the distribution of the species in the wild. It is reasonable that there should be some genetic variability for the ability to withstand dessication in natural populations, because during the year, populations would be exposed to various stresses, during which times genetic variability to adapt may be desirable. The variability between strains, implies that there are genes segregating in the population for resistance to dessication. Because of this, such genes would be able to vary rapidly in frequency at appropriate times, and enable adaptation to environmental chan-

Table 6. *Mean wet weights A, mean weights after dessication for 16 hours B, with the ratio B/A, the number of deaths out of 10 during this period, and dry weights after a further week of dessication. The data are based on 5 inbred strains*

| Strain | Females | | | | | Males | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | *A* | *B* | *B/A* | Number dead | Dry weight | *A* | *B* | *B/A* | Number dead | Dry weight |
| Competition level — 25 larvae | | | | | | | | | | |
| OR | 1.325 | 0.695 | 0.525 | 7 | 0.335 | 0.777 | 0.208 | 0.268 | 10 | 0.190 |
| Y 1 | 1.345 | 0.623 | 0.463 | 8 | 0.387 | 0.827 | 0.273 | 0.330 | 10 | 0.222 |
| Y 2 | 1.268 | 0.588 | 0.464 | 9 | 0.318 | 0.839 | 0.221 | 0.363 | 10 | 0.202 |
| Y 4 | 1.123 | 0.369 | 0.329 | 10 | 0.320 | 0.773 | 0.212 | 0.275 | 10 | 0.198 |
| N 4 | 1.223 | 0.377 | 0 308 | 10 | 0.351 | 0.708 | 0.200 | 0.282 | 10 | 0.190 |
| Competition level —200 larvae | | | | | | | | | | |
| OR | 0.778 | 0.494 | 0.635 | 3 | 0.189 | 0.439 | 0.190 | 0.433 | 9 | 0.115 |
| Y 1 | 0.864 | 0.514 | 0.595 | 6 | 0.217 | 0.568 | 0.213 | 0.375 | 9 | 0.158 |
| Y 2 | 0.775 | 0.419 | 0.541 | 6 | 0.180 | 0.496 | 0.136 | 0.275 | 10 | 0.130 |
| Y 4 | 0.675 | 0.287 | 0.425 | 10 | 0.163 | 0.407 | 0.107 | 0.263 | 10 | 0.105 |
| N 4 | 0.645 | 0.229 | 0.355 | 10 | 0.183 | 0.422 | 0.121 | 0.287 | 10 | 0.120 |

ges to occur. Furthermore, such a system of segregating genes (or polygenes) may allow the rapid colonization of new habitats, where dessication stresses may be different. Thus the genetic architecture of flies from different environments varying in dessication levels would be of some interest to investigate. Such detailed genetic analyses will be possible, if actual loci for dessication can be located, at which stage gene frequencies in different environments, artificial and natural, could be studied. In other words, it may be possible to begin preliminary investigations into the ecological genetics of *D. melanogaster*, a field almost entirely neglected in spite of the enormous amount of laboratory work that has been carried out on this species.

The same arguments can be applied to resistance to high temperature stress for which like dessication, there is evidence for variation between strains in natural populations as assessed by the ability of adults to survive 33.5 °C for 24 hours (Hosgood and Parsons, 1968), and the ability of newly hatched larvae to emerge as adults when grown at 30.5 °C. (Parsons, 1969). Like dessication, it seems reasonable that there should be genetic variability in natural populations for this trait, because of the wide ranging environments inhabited by *D. melanogaster*. Thus for both traits, one might expect gene frequency shifts on an annual basis in the same way as found for some of the karyotypes studied by Dobzhansky (1943, 1951) and his coworkers. The situation will be com-

Table 7. *Analyses of variance of wet weights, mean dry weights, and numbers dead out of 10. The data are based on 5 inbred strains*

| Source of variation | d. f. | M. S. | F |
|---|---|---|---|
| a) Weights before dessication | | | |
| Strains (1) | 4 | 0.1774 | 30.07*** |
| Sexes (2) | 1 | 7.0876 | 1201.29*** |
| Competition levels (3) | 1 | 8.5656 | 1451.80*** |
| (1) × (2) | 4 | 0.0264 | 4.47** |
| (1) × (3) | 4 | 0.0079 | 1.34 |
| (2) × (3) | 1 | 0.4561 | 77.31*** |
| (1) × (2) × (3) | 4 | 0.0156 | 2.64* |
| Error | 180 | 0.0059 | |
| b) Mean dry weights | | | |
| Strains (1) | 4 | 0.001427 | 14.98* |
| Sexes (2) | 1 | 0.051309 | 538.68*** |
| Competition levels (3) | 1 | 0.066471 | 697.86*** |
| (1) × (2) | 4 | 0.000190 | 1.99 |
| (1) × (3) | 4 | 0.000060 | 0.63 |
| (2) × (3) | 1 | 0.008201 | 86.10*** |
| Error [(1) × (2) × (3)] | 4 | 0.000095 | |
| c) Numbers dead out of 10 (after applying the angular transformation) | | | |
| Strains (1) | 4 | 629.08 | 31.02** |
| Sexes (2) | 1 | 1662.94 | 82.00*** |
| Competition levels (3) | 1 | 496.71 | 24.49** |
| (1) × (2) | 4 | 288.69 | 14.24* |
| (1) × (3) | 4 | 98.08 | 4.84 |
| (2) × (3) | 1 | 33.67 | 1.66 |
| Error [(1) × (2) × (3)] | 4 | 20.28 | |
| d) Heritabilities in the broad sense | | | |
| Weights before dessication | 0.402 | | |
| Mean dry weights | 0.411 | | |
| Numbers dead out of 10 | 0.600 | | |

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

plicated by behavioural factors, since presumably flies would tend to move away from environments tending to cause stress — thus on a very hot day in Victoria, it is very difficult to trap *D. melanogaster* except in the early morning and evening. Presumably in the middle of the day, when temperatures might approach or even exceed 40 °C., in parts of Victoria, flies would tend to avoid this temperature by seeking out cooler niches, and emerge when the environment becomes more favourable. The same would presumably apply on days of low humidity, and one might often expect a positive correlation between low humidity and high temperature.

It is therefore worth seeing if there is a correlation between the ability to withstand high temperatures and dessication. Using the angularly transformed mortality data in females for the 17 Leslie Manor strains in Table 3, summed over the 2 larval competition levels, and the mortality data given in Parsons (1969), for emergence as adults of larvae grown at 30.5 °C, a correlation coefficient was computed and came to 0.516 for which $P < 0.05$, showing therefore a significant positive correlation between the two stresses. Bearing in mind that the dessication experiments were carried out over a year later than the temperature stress experiments, during which time divergence within strains could have occurred, the conclusion is that there is a strong likelihood of a biological association between the two stresses. Data have also been collected on the same 17 strains on mortality of adults following irradiation with $Co^{60}$-$\gamma$ rays with high intensity doses in the range 90, 000—110, 000 rads. Using the methods of calculating overall mortalities as given in Parsons (1969), the correlation coefficient between mortality after exposure to 30.5 °C and to irradiation came to 0.750 for which $P < 0.001$, showing the likelihood of a similar physiological basis for the resistance to the two forms of stresses as discussed in Parsons (1969). The remaining correlation coefficient, namely that between mortality after $Co^{60}$-$\gamma$ irradiation and dessication came to 0.235, which although not significantly $> 0$, is positive, like the above coefficients. From the ecological genetic point of view, irradiation with $Co^{60}$-$\gamma$ is perhaps of little interest, since the dose rates involved are enormous, however, since it is much easier to obtain reliable results from irradiation experiments than high temperature stress experiments, such work will probably continue to play some part in research on the genetic basis of environmental stresses.

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