A "MATERNAL EFFECT" ON BODY WEIGHT IN DROSOPHILA

J. C. DeFRIES AND R. W. TOUCHBERRY

Department of Dairy Science, University of Illinois, Urbana, Illinois

Received April 19, 1961

In a study concerning the variability of response to selection for body weight in Drosophila affinis, prima facie evidence was found for the presence of a negative maternal effect (DeFries and Touchberry, unpublished). In this study, the regression of average weight of offspring on the weight of the male parent was found to be higher than that on the weight of the female parent. In addition, the presence of negative paternal half-sib components of variance and a "rebounding" phenomenon, i.e. large responses to selection followed small responses and vice versa, all could be explained by the action of a negative maternal effect.

Recently, Martin (1959) has reported a negative regression of fecundity of offspring on that of the parent in Drosophila melanogaster and suggested that this negative relationship may be due to the positive correlation of fecundity with body weight. It was hypothesized that females which oviposit more eggs inadvertently cause more competition among the resulting offspring and, hence, cause smaller body size. In turn, because of the positive correlation of body size and fecundity, these smaller female offspring are less fecund than average. However, the negative correlation found between body weight and egg size may also be involved in this relationship.

A somewhat similar situation regarding litter size in mice has been described by Falconer (1955). An over-all regression of litter size of the daughter on that of the mother was found to be approximately zero. However, when the body weight of the daughter was held constant a regression of 0.10 was observed. Heritability, as estimated by doubling this latter regression, was found to agree quite closely with that realized from a selection experiment. That the daughter's weight is involved in this relationship was substantiated by the presence of a significant positive regression of litter size of the daughter on her own weight and a significant negative regression of daughter's weight on mother's litter size. Thus, there is apparently a positive genetic pathway and a negative nongenetic, i.e. maternal, pathway involved in the "inheritance" of litter size which tends to cause the overall regression of litter size of the daughter on that of the mother to be essentially zero.

Martin (1959) has also reported that the phenotypic variance of female Drosophila melanogaster weighed between zero and 24 hours after emergence was approximately twice that of females weighed between zero and 12 hours after emergence. However, the phenotypic variance of males weighed at the
different ages did not change appreciably. Thus, the change in the variance due to age in females was attributed to the considerable ovarian development which takes place between 12 and 24 hours after emergence.

The primary objective of the present study is to determine if there is a negative nongenetic pathway involved in the inheritance of body weight in *Drosophila* which operates through offspring number, i.e. number of adults to emerge.

**MATERIALS AND METHODS**

The stock used in this study was derived from a large population of *Drosophila affinis* that was originally trapped in Urbana, Illinois, in 1959. The stock has since been maintained as a large random mating population in the laboratory, the mean daily temperature being maintained at approximately 76°F. All flies from which the data were taken were reared in 100 x 23 mm shell vials containing approximately one half inch of the usual corn meal-karo medium which was slanted and then inoculated with live yeast. The flies were weighed to the nearest microgram on a microbalance which had been found to give highly repeatable results. The intrasex repeatability, as determined by three repeated individual weighings of 25 males and 25 females, was found to be 0.96. As far as possible, all individuals were weighed between zero and 12 hours after emergence in order to reduce the variation caused by different stages of ovarian development in females. Because of differences in the time required for weighing, this interval occasionally was as large as 14 hours. Thus, the average age at which the flies were weighed was approximately six hours. Since the parameters to be estimated in the present study were to relate to a selection experiment, it was felt that the interval from emergence to time of weighing should be as short as possible. With 50 lines involved in this selection experiment, an interval of 12 hours was the shortest interval that was feasible.

**EXPERIMENTAL RESULTS**

Samples of flies were drawn from the large random mating population by removing all flies from their containers, mixing them in an etherizing bottle, spreading them on a flat surface and then choosing individual flies on a basis of closeness to the experimenter until the desired number was obtained. The flies were then weighed and mated as single pairs, without regard to body size. This procedure was followed on each of five different days. From a total of 200 matings, however, only 183 produced at least five male and five female offspring. It was previously planned to use the average weight of the first five male and female offspring to represent offspring weight; therefore, data were collected from only these 183 matings. Offspring number was considered as the total number of adults to emerge within 16 days after the parents were removed from the vials; all parents were discarded when the first pupae appeared. In addition to the data collected from the 183 matings, there was also a considerable volume of data available from another study concerning the weights of parents and offspring; these additional data were included in the present study when relevant. Because
the data included in this study were collected during different periods, the data were analyzed on an intraperiod basis.

The relationships between weight of the male parent, weight of the female parent and number of offspring were investigated first. Therefore, only the data from the 183 matings were included in this portion of the analysis. The possibility of a correlation between the weights of the male and female parents was checked and an unexpected, but significant, correlation of 0.17 was found. Standard partial regressions of number of offspring on weight of the male parent, independent of weight of the female parent, and on weight of the female parent, independent of weight of the male parent, were then determined. These standard partial regressions were found to be 0.15 and 0.34, respectively, the former being significant at the 0.05 level of probability and the latter being significant at the 0.01 probability level. The statistical significance of the standard partial regression coefficients in this study was determined according to the method described by JOHNSON (1949).

The proposed relationship of weight of the male parent \((M)\), weight of the female parent \((F)\), number of offspring \((N)\), and average weight of offspring \((O)\) is illustrated as a path diagram in Figure 1. The paths (standard partial regression coefficients) from \(M\) to \(N\) \((b)\) and from \(F\) to \(N\) \((c)\) were determined as previously mentioned. The remaining paths were determined by equating the phenotypic correlations of \(M\) and \(O\), \(N\) and \(O\), and \(F\) and \(O\) to the respective paths contributing to these correlations. These correlations are shown in equations 1–3.

\[
\begin{align*}
    r_{MO} &= a + be + rce + rd \\
    r_{NO} &= e + ba + cd + brd + cra \\
    r_{FO} &= d + ce + rbe + ra
\end{align*}
\]

Values for \(r\) (the correlation between \(M\) and \(F\)), \(b\) and \(c\) were substituted into the above equations. The phenotypic correlation between \(N\) and \(O\) was found to be \(-0.081\) from data of the 183 matings. The additional data concerning 356 comparisons from the other study mentioned earlier were included in calculations regarding \(r_{MO}\) and \(r_{FO}\), however. These latter phenotypic correlations, therefore, are based upon 539 actual comparisons. However, the additional data are from a study covering three different periods, whereas the other data are from five

![Path diagram](image-url)
J. C. DEFRIES AND R. W. TOUCHBERRY

Different periods; therefore, since all analyses were done on an intraperiod basis, these correlations are based on 530 degrees of freedom. The correlations, $r_{MO}$ and $r_{FO}$, were found to be 0.085 and 0.002, respectively. Upon substitution of the respective values into equations 1–3, a set of three equations containing three unknowns resulted. This set of simultaneous equations was then solved, yielding estimates of the paths between $M$ and $O$ ($a$), $F$ and $O$ ($d$) and $N$ and $O$ ($e$). None of these paths was found to be significantly different from zero. Values for the paths and their standard errors are presented in Table 1.

**DISCUSSION**

Several unexpected, but significant, relationships were revealed among the variables by the preceding analysis. The significant positive correlation between $F$ and $M$ indicates that some positive phenotypic assortative mating was involved in the pairing of mates and that these matings were not truly random. The highly significant path between $F$ and $N$ was expected on the basis of MARTIN’S (1959) study, but the significant relationship between $M$ and $N$ was unexpected. This path ($b$) was determined independently of $F$; thus, it should not be attributed to the positive correlation between $F$ and $M$. If a causal relationship actually exists between $M$ and $N$ it would be interesting to learn its basis. It is possible that body weight of males is correlated to sperm production and that this could result in a positive relationship between body weight and offspring number.

The paths "$a$" and "$d$" may be regarded as the genetic pathways between the parents and offspring, whereas "$be$" and "$ce$" are nongenetic pathways. The heritability of body weight in Drosophila may be estimated by doubling the genetic paths, but such a method yields widely different estimates. Heritability, as estimated from the path between $M$ and $O$, is 0.20 and agrees with that reported by MARTIN (1959), whereas that determined from the path between $F$ and $O$ is only 0.04. Neither of the paths was significantly different from zero, and since both are positive in sign and have almost identical standard errors, it is not likely that they are significantly different from each other. However, if the estimates are close to the actual population parameters, it would be possible to rationalize a real basis for a difference. The phenotypic variance of female

<table>
<thead>
<tr>
<th>Path</th>
<th>Value</th>
<th>Standard error</th>
</tr>
</thead>
<tbody>
<tr>
<td>$M$ to $O$ ($a$)</td>
<td>0.10</td>
<td>0.14</td>
</tr>
<tr>
<td>$M$ to $N$ ($b$)</td>
<td>0.15*</td>
<td>0.07</td>
</tr>
<tr>
<td>$F$ to $N$ ($c$)</td>
<td>0.34**</td>
<td>0.07</td>
</tr>
<tr>
<td>$F$ to $O$ ($d$)</td>
<td>0.02</td>
<td>0.15</td>
</tr>
<tr>
<td>$N$ to $O$ ($e$)</td>
<td>-0.11</td>
<td>0.26</td>
</tr>
</tbody>
</table>

* Significant at the 0.05 level of probability.
** Significant at the 0.01 level of probability.
Drosophila is approximately twice that of males (DeFries and Touchberry, unpublished) and much of this larger variance associated with females may be due to environmental differences. There is a considerable ovarian development in females with age, and differences in age at which the females were weighed could add to the environmental component of variance. Although all flies were weighed before 14 hours after emergence, and most within 12, it is possible that enough development occurred in some of the females before being weighed to increase the environmental component of variance and, consequently, reduce the heritability associated with the female parent. Of course, it is also possible that sex linkage or the lack of crossing over in males may also be involved. More data are necessary to determine whether the higher heritability associated with males is due only to sampling errors or if it is a real phenomenon.

The negative path between $N$ and $O$ was predicted, and although it is not significantly different from zero, it is believed to have a real basis. It is felt that competition and crowding can easily take place in the shell vials in which the flies were reared, even when single pair matings are used. Previous experience has shown that crowding certainly causes smaller body size, at least under more extreme conditions. However, it is not known how close the calculated path approximates the true population parameter.

Because of the highly significant path between $F$ and $N$ and because of the likelihood that a negative path exists between $N$ and $O$, it seems that the presence of a negative nongenetic pathway (maternal effect) in the inheritance of body weight has been verified. If the significant path between $M$ and $N$ has a real basis, it would appear that a negative pathway through the paternal side is also operating; however, the cause of a positive relationship between $M$ and $N$ is not as readily apparent as that between $F$ and $N$. As mentioned previously, it is possible that the body weight of males may be positively correlated to number of sperm produced and that this could result in a positive relationship between body weight of males and offspring number. Also, if body weight is positively correlated to sexual maturity, this could possibly account for the observed relationship. However, since all parents were left in the vials until pupae began to appear and since the maximum possible difference in age between flies chosen was 14 hours, it is not likely that this influence could be large. Nevertheless, the possibility of a nongenetic paternal effect is suggested.

As Martin (1959) suggested, it is possible that the negative nongenetic pathway may be caused by competition among the larvae. If competition or crowding is involved, the magnitude of this relationship should change when Drosophila are reared under different levels of environment. Thus, further studies in which containers of varying sizes are used or in which varying oviposition intervals are allowed should indicate whether such factors are involved in this interesting relationship.

SUMMARY

From the results of this analysis, it may be concluded that a negative nongenetic path (maternal effect) exists in the inheritance of body weight in Drosophila.
sophila and that it operates through number of offspring. Path analyses revealed a highly significant positive relationship between body weight of the female parent and number of offspring and a negative relationship between number of offspring and body weight of the offspring. Empirical evidence had previously shown that this latter relationship, although not statistically significant in this study, is almost certainly real, at least under more extreme conditions. A small, but significant, positive relationship between body weight of the male parent and offspring number was also found, indicating the possible presence of a negative "paternal effect". Other relationships between body weight of male and female parent, number of offspring and body weight of offspring were presented. The possibility of a higher heritability regarding body weight in males than in females was also discussed.

LITERATURE CITED

