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The nonlinearity of offspring-parent regression for total sternopleural bristle number of *Drosophila melanogaster*

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Summary. A test of the linearity of the offspring-midparent regression for total sternopleural bristle number showed significant departure from linearity, with a tendency for higher heritability at higher values of the character. Offspring-midparent regression coefficients for each of four subdivisions of the total range of bristle number were not significantly different. The nonlinearity of offspring-midparent regression detected in this study may be due to either chance effects, genotypic asymmetry of genes with large effect, distribution asymmetry, or a combination of these factors. Further work is required to determine the extent and causes of nonlinearity of offspring-parent regression.

Key words: Offspring-parent regression – Heritability – Bristle number – *Drosophila melanogaster*

Introduction

If the heritability of a quantitative character is not constant over the entire range of phenotypic expression for the character, artificial selection in opposite directions may not yield symmetrical responses. Reports of asymmetrical responses to selection over several generations are common (e.g., Falconer 1953, 1955, 1971; Gall 1971; Barker and Karlsson 1974; Frankham and Nurthen 1981).

Relatively few studies have tested for a linear relationship between selection differential and selection response in the first generation, i.e., for linearity of offspring-parent regression. Nishida (1972) reported a highly significant nonlinearity of offspring-midparent regression for body weight in the mouse. Meyer and Enfield (1975) undertook single-generation, two-way selection at three selection intensities for 21-day pupa weight in *Tribolium castaneum* and found a high degree of asymmetry, the realized heritabilities being much larger downwards than upwards. Marked asymmetry was also reported by Robertson (1977) for offspring-midparent regression with assortative mating for sternopleural bristle number in a *Drosophila* population. Robertson (1977) suggested that further work be undertaken in this area using parents at least two standard deviations above and below the mean, respectively. Subsequently, Mäki-Tanila (1982, 1987) discovered a substantial positive curvature in offspring-midparent regression for total sternopleural bristle number in the Dahomey population of *Drosophila melanogaster*. In contrast, two recent studies have found linearity of heritability. Salgado et al. (1989) found linearity of offspring-parent regression for sternopleural bristle number in *Drosophila melanogaster*, using a design that included assortative mating and equal representation of all phenotypic classes of parental values. Weber (personal communication) has conducted replicated single-generation selection experiments at three selection intensities for ethanol vapor resistance in *Drosophila melanogaster* and found no significant departure from linear heritability at extreme high or low selection pressures.

The present study was designed to test the assumption implicit in the selection response equation, $R = h^2 i \sigma_p$ (where R is the expected response to selection, h^2 is the heritability of the selection criterion, i is the intensity of selection, and σ_p is the phenotypic standard deviation), that the regression of offspring on parent remains linear throughout the entire range of parental values. Offspring-midparent regressions with assortative mating for total sternopleural bristle number in

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Drosophila melanogaster were done, involving 614 single pairs of parents selected over the entire range of phenotypic expression for the character.

Materials and methods

Base population

The Armidale strain of *Drosophila melanogaster* was used in the study. The population was derived from 50 inseminated females collected in Armidale, New South Wales. Seven collections were made over a 3-week period in March-April 1981, at three different sites. Individual females were placed into vials for egg-laying. Four female and four male offspring from each of the initial 50 females were collected. Progeny collections were made twice daily and only virgin females were used for the F_1 matings. The four males from wild female 1 were mated to the four females from wild female 2, the males from wild female 2 to the females of wild female 3, and so on. Parents for the F_2 matings were collected and mated in a similar manner. Two offspring of each sex were collected from each of the F_2 matings and the resulting 100 flies of each sex were pooled and randomly allocated to ten bottles, to constitute the base population. The population was subsequently maintained by collecting ten offspring of each sex per bottle, pooling, and distributing as above. All collections and matings were random.

Experimental population

To initiate a population from which the parents for this single generation study could be selected, over 400 virgin flies of each sex were collected at random from the ten population bottles constituting the base population. At that time, the base population had passed through approximately 25 generations since its inception. Forty 140-ml bottles were set up, each with ten pairs of randomly chosen parents. The flies were 4 days old at the start of mating and were mated for 3 days. After the very early emergences were discarded, similar numbers of virgin flies of each sex were collected from each of the 40 bottles, and a total of 614 of each sex were scored for total sternopleural bristle number.

These flies were mated assortatively, as single pairs, in 7.6 x 2.5 cm vials, and were 4 days old at the start of the 3-day mating period.

After the very early emergences in each vial were discarded, six randomly chosen offspring of each sex were scored for total sternopleural bristle number. A total of 7,368 offspring were scored.

Offspring-midparent regressions were estimated over the total range and in each of the four portions of the range, by regression of the mean of all the recorded offspring from a pair of parents on the appropriate midparent record. Nishida (1972) referred to this method of regression estimation as "regression with mean." Regression for the total range was tested for nonlinearity using polynomial regression, with linear, quadratic, and cubic terms extracted.

The four portions of the range had approximately equal numbers of single-pair matings (Table 1), and the bristle scores of selected females in portions one, two, three, and four ranged from 17 to 21, 22 to 24, 25 to 27, and 28 to 36, respectively. In portions one to three inclusive, the bristle scores of the selected males were one less than those of the females. In portion four, the bristle scores of the selected males ranged from 27 to 34.

The regression coefficients of the four portions of the range were tested in pairwise comparisons for homogeneity of regression, using a *t*-test (Steel and Torrie 1980).

For stock maintenance and for the experimental single-pair matings, all flies were cultured on a dead-yeast-fortified medium [Medium F of Claringbold and Barker (1961), plus approximately 150 ml of water], at 25 ± 0.5 °C and a relative humidity of 65–70% in a room lit for 12 h per day (6.00 a.m. to 6.00 p.m.).

Results

The correlation coefficients between total sternopleural bristle scores of the female and male parents in portions one, two, three, and four of the range were 0.974, 1.000, 0.986, and 0.868, respectively, and 0.993 over the total range.

The heritability values (± SE) for the total range and for each portion of the range, estimated from offspring-mean midparent regression, are given in Table 1. The heritability value for the total range was 0.5536 ± 0.0142. The heritability estimates within the portions of the range varied from 0.4098 ± 0.0877 in portion one to

Table 1. Estimates of heritability for total sternopleural bristle number over the total distribution and in portions of the distribution

Portion of distribution	Number of single-pair assortative matings	Bristle score of parents (Mean ± SD) ♀	Bristle score of parents (Mean ± SD) ♂	Heritability estimates (± SE) Offspring-mean midparent regression
Total	614	24.6 ± 3.85	23.5 ± 3.60	0.5536 ± 0.0142
1	156	19.9 ± 0.98	18.9 ± 1.00	0.4098 ± 0.0877
2	155	23.0 ± 0.82	22.0 ± 0.82	0.5762 ± 0.1335
3	157	26.0 ± 0.82	25.0 ± 0.82	0.5166 ± 0.1237
4	146	30.0 ± 1.52	28.2 ± 1.42	0.5850 ± 0.0856

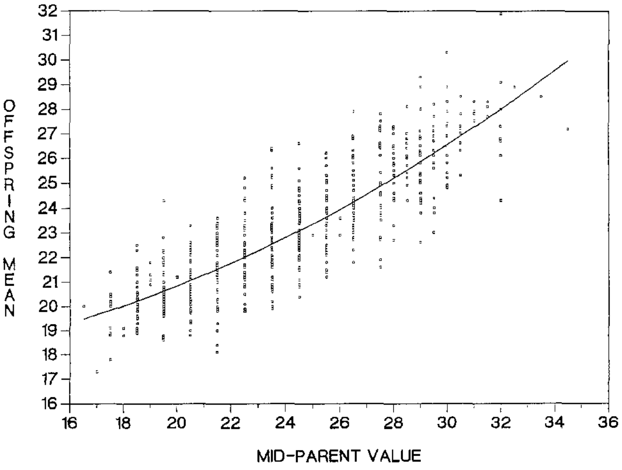

Fig. 1. Quadratic regression of offspring mean on midparent value for total sternopleural bristle number in the Armidale population of *Drosophila melanogaster*

0.5850 ± 0.0856 in portion four. Tests for homogeneity of regression showed that none of the slopes of the regression lines were significantly different.

The test for nonlinearity of regression over the total range indicated that there was a significant departure from linearity. The linear and quadratic terms were highly significant ($F_{1,611} = 1543.74$ and $F_{1,611} = 13.51$, respectively), but the cubic term was not. The equation for the quadratic regression was $Y = 17.4421 - 0.0958\,X + 0.0133\,X^2$, where Y is the predicted offspring mean value and X is the midparent value (Fig. 1).

A check for homogeneity of error variance was done by plotting residuals against fitted values. The assumption of equality of variance was not contradicted.

Discussion

The existence of nonlinearity of offspring-parent regression for total sternopleural bristle number in the Armidale population of *Drosophila melanogaster* complements similar findings by Nishida (1972), Meyer and Enfield (1975), Robertson (1977), and Mäki-Tanila (1982, 1987). However, it should be noted that the results of Nishida (1972) were very inconsistent in the sense that the heritability of body weight of the mouse varied from 0.13 to 0.62 over the 11 age classes (0–70 days), apparently with very large standard errors. The offspring-midparent regression was in some cases linear, in others quadratic (with either convexity or concavity), and in some cases cubic. Nonlinearity of offspring-parent regression also was expected in a case reported by Franklin (1967), in which different distributions for genetic and environmental effects existed for pupa weight in *Tribolium*. A log transformation was appropriate for "normalization" of the genetic variance, but a cube root transformation was required to "normalize" environmental variance.

The finding of a nonlinear relationship between offspring mean value and midparent value, with a tendency to a higher heritability at the higher values of the character, would lead one to predict that observed response for increased bristle number would be higher than expected when the latter is based on the overall linear relationship between offspring and parent. This expectation is in total contrast to the findings from the same population reported by Gifford (1986), who examined the effects of intense selection for increased total sternopleural bristle number in *Drosophila melanogaster* by selecting pedigreed lines for five generations at intensities of 2, 5, and 20%. There was no consistent effect of selection intensity on realized heritability but, overall, observed responses to selection fell between 15 and 25% short of expectation.

Genetic theory rests on the assumption of an infinite number of loci without epistasis or linkage and with a normally distributed environmental deviation (Bulmer 1980). Departures from this assumption can lead to nonlinearity of offspring-parent regression and asymmetry of selection response. Asymmetrical responses in selection experiments conducted over several generations are common, and the main causes of such effects have been listed by Falconer (1981) as: random drift, differences of the selection differential, inbreeding depression, maternal effects, genetic asymmetry, genes with large effects, scalar asymmetry, and indirect selection.

The nonlinearity of offspring-midparent regression detected in this study may be ascribed to one or more of the following factors.

(i) A crude effect due to limited size of the experiment, especially from limited representation of the extreme phenotypes. Mäki-Tanila (1982), as part of his investigations as to how, to what extent, and under what kinds of models of genetic and environmental variation the offspring-parent regression is likely to depart from linearity, found that only very large experiments have a 90% chance of detecting nonlinearity at the 5% significance level, especially when heritability of the character is low. However, he did suggest that if the true regression was quadratic, the sampling variance of the quadratic coefficient could be minimized for the given limited resources by taking observations at three levels, two as near as possible to the extremes of the phenotypic range and one around the mean, each containing about one-third of the observations. Also, for offspring-midparent regression, assortative mating should occur within each class. In this study a total of 614 pairs, selected from the total phenotypic range for the character, were mated assortatively, and 12 offspring were measured in each family. Representation of the intermediate phenotypes was greater than that of the extreme phenotypes. However, in comparison to the other experiments which reported curvilinearity of offspring-parent regression, this study can be considered as relatively large. For example, Mäki-Tanila (1982) used 45 pair matings over a midparent phenotypic range of 12 to 27 bristles, with each family comprising five offspring of each sex. Nevertheless, he did observe stronger curvilinearity than that in the present experiment.

(ii) Genotypic asymmetry of genes with large effects. Additive genes contribute maximally to the heritability when the gene frequency is 0.5, and recessive genes when the recessive allele has a frequency of $1/\sqrt{2} \sim 0.71$, the so-called "symmetrical" gene frequencies. If all the genes affecting the character were at these symmetrical frequencies in the initial population, two-way selection would not lead to asymmetry of response. However, if the population starts with gene frequencies above or below these "symmetrical" values, two-way selection will lead to opposite trends in the values of both gene frequencies and heritability in the upward and downward selection lines and, therefore, to asymmetry of response. Because genotypic asymmetry is dependent on the differentiation in gene frequencies, it is unlikely to occur in the initial generations of selection. However, in contrast, asymmetry of response in the first generation can result from genotypic asymmetry of genes with large effects, because the large change of gene frequency is equivalent to many generations of selection on genes with small effects. Mäki-Tanila (1982, 1987) reported that, provided the genotypic values and environmental deviations are independently distributed, and assuming a normal distribution of the latter, the most important contributions to nonlinearity of offspring-parent regression are likely to come from rather rare, completely or almost completely recessive alleles segregating at loci with considerable effect on the measurement of the character. Although some initial families in the experiment of Gifford (1986) made extreme contributions to the genetic composition of a particular selection line, the overall results did not clearly establish the existence of genes of large effect on total sternopleural bristle number in the Armidale *Drosophila melanogaster* population.

(iii) Distribution asymmetry. The possibility exists that the genetic and environmental variation may have been skewed to different degrees or in opposite directions. The genetic variation will then make up a larger proportion of the total at one end of the distribution than at the other. In consequence, the offspring-parent regression in the base population will be nonlinear and the response will be asymmetrical in the first generation. The difference in skewness may be a scale effect or it may be due to genotype-environment interaction. Curnow (1960) showed that if the environmental deviations were normally distributed, then the genotypic value is linearly related to the phenotypic value only if the genotypic distribution is normal. In addition, the degree of nonlinearity depends on the ratio of the environmental to the phenotypic variance and on the amount of nonnormality of the genotypic distribution. Nishida and Abe (1974) investigated the relationship between the skewness in the distributions of genotypic and environmental values and the linearity of heritability. They found that a linear regression of genotype on phenotype followed whenever the skewness of the genotypic and environmental distributions was of the same sign and magnitude. However, as pointed out by Mäki-Tanila (1982), this is true only when the genetic and environmental components contribute equally to the phenotypic variation. Nonlinear regression occurs when the two distributions have different skewness, and the larger the difference, the greater the departure from linearity (Nishida and Abe 1974). Furthermore, when the genotypic skewness is greater than the environmental skewness, the regression is curved upwards, and when less, downwards.

As mentioned by Falconer (1981), it is very difficult to accurately identify the cause(s) of nonlinearity of offspring-parent regression. Obviously more work needs to be done in comparing heritabilities at different portions of the phenotypic distribution for a range of characters and in assessing the causes of nonlinearity of offspring-parent regression.

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