Linearity *Versus* Nonlinearity of Offspring-Parent Regression: An Experimental Study of *Drosophila melanogaster*

A. Gimelfarb and J. H. Willis

Department of Biology, University of Oregon, Eugene, Oregon 97403

ABSTRACT

An experiment was conducted to investigate the offspring-parent regression for three quantitative traits (weight, abdominal bristles and wing length) in *Drosophila melanogaster*. Linear and polynomial models were fitted for the regressions of a character in offspring on both parents. It is demonstrated that responses by the characters to selection predicted by the nonlinear regressions may differ substantially from those predicted by the linear regressions. This is true even, and especially, if selection is weak. The realized heritability for a character under selection is shown to be determined not only by the offspring-parent regression but also by the distribution of the character and by the form and strength of selection.

THE following well known formula of quantitative genetics is customarily used to predict the response to selection by a quantitative trait:

$$R = h^2 S, \qquad (1)$$

where R is the response, S is the selection differential and h^2 is the narrow sense heritability. Implicit in this formula is the assumption that the offspring-parent regression is linear. This assumption is rarely questioned. Yet, FRANKHAM (1990) has compiled data illustrating the asymmetry of responses to directional selection on components of reproductive fitness indicating a possibility of nonlinearity in the offspring-parent regression for such traits. It has also been demonstrated theoretically that dominance of allelic effects (BULMER 1985; GIMELFARB 1986a) or skewness in the distribution of the environmental component (NISHIDA and ABE 1974) can cause a nonlinearity in the regression. There are, undoubtedly, other hereditary and developmental mechanisms that can render the offspring-parent regression nonlinear.

The purpose of the current study was to investigate directly the linearity (or nonlinearity) of the offspring-parent regression for a number of quantitative traits in *Drosophila melanogaster*, and to see how nonlinearities, if found, affect our inferences about responses by the characters to selection. The following three traits were involved in the study:

Weight (in milligrams). For this trait, KEARSEY and KOJIMA (1967) have presented evidence of weak epistasis.

Abdominal bristles (on segments 4 and 5 in females and on segments 3 and 4 in males). KELLER and MITCHELL (1962) found evidence of weak dominance and epistasis for this trait. CLAYTON *et al.* (1957) attributed 9% of the total phenotypic variance by the abdominal bristles in a laboratory population to "genetic complexities."

Wing length (in millimeters) measured as the distance between the intersections of the third longitudinal vein

with the wing tip and the anterior crossvein. KELLER and MITCHELL (1962) found no evidence of either dominance or epistasis for the wing length (they measured the distance from the humeral plate at the base of the wing to its tip).

The following notations for the traits will be used in the paper: WTD and WTS for weight of daughters and sons, BD and BS for the number of bristles on daughters and on sons, WGD and WGS for the wing length in daughters and in sons.

MATERIALS AND METHODS

The data on the weight and abdominal bristles were collected from a base population originated from a stock provided to us by BRIAN CHARLESWORTH. The population was maintained in 10 bottles (approximately 150 flies per bottle) with a mixing every two weeks of adult flies between the bottles as described by ROSE and CHARLESWORTH (1981). A batch of 10 families was initiated by collecting 20 virgin females and 20 males (grandparents) from the base population and mating them randomly (one pair in a vial). On the 14th day after mating, 10 virgin females and 10 males (only one fly from each vial) were collected and kept separately. At the age of two days these twenty flies (parents) were weighed, their bristles were scored, and they were randomly mated (one pair in a vial). On the 14th day after mating, two virgin offspring of each sex were collected from each vial. Like their parents, they were kept separately, and their weight and bristle score were obtained on the second day of their life. The total of 22 batches were established, out of which 176 families with complete data have been recovered. The complete data for a family included weights and bristle scores of the mother, the father, two sisters and two brothers. No special effort was made to control for the density other than always removing parents from a vial on the 8th day and collecting offspring on the 14th day. All batches were maintained at $24(\pm1)°$. Collections were made using CO_2, whereas for weighing and bristle scoring the flies were etherized.

The data on the wing length of parents and their offspring (two sisters and two brothers) in 159 families were given to us by JERRY COYNE. They come from the experiment B (parents and offspring reared in the laboratory) reported by COYNE and

A. Gimelfarb and J. H. Willis

TABLE 1

Parameters of parental and offspring distributions

	Weight (mg)		Bristles		Wing (mm)	
	Mean	SD	Mean	SD	Mean	SD
Mothers	1.202	0.112	45.18	3.92	1.540	0.058
Daughters	1.075	0.127	45.21	2.87	1.514	0.056
Fathers	0.862	0.075	38.06	3.35	1.354	0.046
Sons	0.813	0.068	37.83	2.74	1.355	0.044

BEECHAM (1987), and these authors can be consulted for the description of the data and experimental procedures.

Table 1 shows the mean and standard deviation for the characters under consideration. There is a significant difference in the mean of each character between sexes. A significant difference exists also between parents and offspring in their mean weight: the offspring weigh less, on the average, than parents of the same sex. This can be attributed to the fact that the parental parents (grandparents) were not exposed to ether, whereas the offspring's parents were etherized twice in order to weigh them and score their bristles. It has been demonstrated by GIMELFARB and WILLIS (1988) that exposing flies to ether reduces the weight of their offspring. Also, the mean wing length in daughters and mothers differ significantly, but an explanation for this is not known.

The offspring-parent regressions were fitted separately for daughters and for sons. The characters of the two sibs of the same sex were averaged so that an "offspring character" in a regression is in fact the arithmetic average of the character among the two sibs. Also, all characters (in parents as well as in offspring) were standardized prior to fitting a regression by subtracting the mean and dividing over the standard deviation. Hence, each character in a regression has zero mean and unit variance. Statistical analyses were performed using the software SYSTAT (WILKINSON 1990) on a PC 486 computer.

RESULTS AND DISCUSSION

Linear offspring-parent regressions

The coefficient of linear regression of the offspring's character on the character of only one of the parents or on the mid-parental value is often used to estimate the narrow sense heritability and, consequently, to predict the response by the character to selection based on formula (1). In reality, though, the response is determined by the regression on the characters in both parents. For this reason, we fitted the regression

$$f(x, y) = E[z| x, y] \quad (2)$$

of the character in offspring, z, on the character of the mother, x, and of the father, y. Table 2 shows the coefficients of linear regression,

$$f(x, y) = b_m x + b_f y, \quad (3)$$

fitted to the family data for all of the characters. There is no constant term in the regression function since the characters in parents and in offspring are standardized. All of the regression coefficients in the table are significant at $P = 0.001$ level, except for b_f in WTD and WTS which are significant at $P = 0.01$, and b_m for WTS which

is not significant ($P = 0.3$). There is a significant difference ($P < 0.05$) between the regressions of daughters and of sons for all traits.

As has been mentioned earlier, the coefficient of linear regression of offspring on the mid-parental value is used as an estimate of the heritability defined as the ratio of the additive component of variance to the total phenotypic variance. If a character is standardized, this coefficient is equal to the sum of the coefficients in (3). Hence, for the standardized characters discussed in the paper the heritability estimated by the regression on the mid-parental value is

$$h^2 = b_m + b_f. \quad (4)$$

The estimated heritabilities are shown in Table 2. Also shown in the table are the coefficients of determination, R^2. This parameter measures the proportion of the variance among the offspring explainable by the corresponding regression on parents. The higher R^2 is, the more accurate prediction about the character in offspring can be made based on the characters of parents.

Nonlinear offspring-parent regressions

Before fitting nonlinear regressions we have excluded observations that were outliers in the linear regressions (the coefficients reported in Table 3 are, in fact, with the outliers left out). An observation was considered an outlier if the actual value of the character differed by more than 2.5 SD from the value predicted by the regression. It is usually recommended in text books on linear regression to check for outliers as a possible indication of the nonlinearity in the regression. We have decided, however, to be conservative and to make sure that a nonlinearity, if found, is not due to just few outliers but is, indeed, a "solid" nonlinearity. Therefore, the nonlinearities that we have found probably underestimate the nonlinearities in the actual offspring-parent regressions for the characters under consideration.

In the three-dimensional space, the linear regression function $f(x, y)$ in (3) represents a plane. There are many different biological mechanisms that can make the offspring-parent regression nonlinear so that the surface $f(x, y)$ becomes curved rather than plane. For the characters in our study we do not know what mechanisms can be at work making the regressions nonlinear. Moreover, it is almost certain that different mechanisms

TABLE 2

Linear offspring-parent regressions

	Trait					
	WTD	WTS	BD	BS	WGD	WGS
b_m	0.29	0.08	0.35	0.29	0.23	0.45
b_f	0.18	0.18	0.27	0.42	0.37	0.28
h^2	0.47	0.26	0.62	0.71	0.60	0.73
R^2	0.14	0.04	0.18	0.25	0.24	0.36

b_m, b_f, coefficients of regression on mother and on father, respectively; R^2, coefficient of determination of linear regression. All regression coefficients are significant at $P = 0.001$ level, except for b_f in WTD and WTS which are significant at $P = 0.01$, and b_m in WTS which is not significant ($P = 0.3$).

TABLE 3

Polynomial offspring-parent regressions

Trait	Monomials in the regression and their coefficients							R^2_{PN}	P_{NL}
WTD	x^3 0.14	x^4 0.02	y^5 0.03	xy 0.28	xy^3 -0.14	x^2y^3 -0.04		0.21	0.019
WTS	y 0.24	xy^2 0.21	xy^3 -0.07	x^2y^3 -0.06				0.10	0.015
BD	x 0.37	y 0.27	xy^3 -0.08	x^3y 0.04				0.21	0.068
BS	x 0.41	y 0.33	x^4 -0.02	xy 0.32	xy^2 -0.13	x^2y 0.12	x^3y -0.12	0.32	0.010
WGD	x 0.22	y 0.36	x^2 0.17	x^2y^2 -0.09				0.29	0.017
WGS	x 0.43	y 0.28	xy 0.23	x^2y^2 -0.11				0.39	0.053

R^2_{PN}, coefficients of determination of polynomial regression; P_{NL}, significance level for nonlinearity of regression.

can be responsible for the nonlinearities in different traits. Our purpose, however, is not to model a specific biological mechanism but only to see whether the actual (but unknown to us) regression surface for a particular trait can be approximated better by a curved surface than by a plane. To do that we have fitted for each character a fifth-order polynomial regression function

$$f(x, y) = \sum_i \sum_j b_{ij} x^i y^j \qquad (0 \le i + j \le 5) \qquad (5)$$

in the standardized variables. Stepwise "forward" and "backward" multivariate regression procedures in SYSTAT (WILKINSON 1990) were employed to fit the regression model. The model with the highest coefficient of determination, R^2, and with the significance level of each term in the polynomial lower than $P = 0.05$ was chosen as the "best." The monomial terms included in the polynomial regression functions for the traits under consideration are shown in Table 3. Also shown are the coefficients of determination for the polynomial regressions, R^2_{PN}, as well as the significance levels for the nonlinearity of a regression, P_{NL}. These significance levels were obtained by comparing R^2_{PN} for the "full" polynomial model to R^2 for the "partial" linear model (Table 2) (SOKAL and ROHLF 1981). In cases in which the full

model does not contain a linear term (WTD does not have either x or y, and WTS does not have x), the absent term was added to the model for making comparisons. Tests based on the expanded models could only underestimate the significance of the nonlinearity of the original polynomial models since changes in R^2_{PN} due to such expansions were negligibly small, whereas the number of degrees of freedom in the model increased.

The polynomial model provides a significantly better fit ($P_{NL} \le 0.05$) for almost all characters, except BD, for which the polynomial model is only marginally significant ($P_{NL} = 0.068$). The improvements in the fit by the nonlinear regressions are not very substantial, however. The coefficients of determination for nonlinear regressions are not much higher than those for linear regressions. Even for WTS, in which case R^2_{PN} more than doubles R^2 for the linear regression (0.1 vs. 0.04), its value is still quite low (only 10% of the variation in weight among sons is explained by the nonlinear transmission of the weights by parents).

Figures 1, 2 and 3 show the offspring-parent polynomial regression surfaces in the three-dimensional space for the weight, bristle number and wing length. The regression for daughters and for sons are on the left and right side of each graph, respectively. Also shown
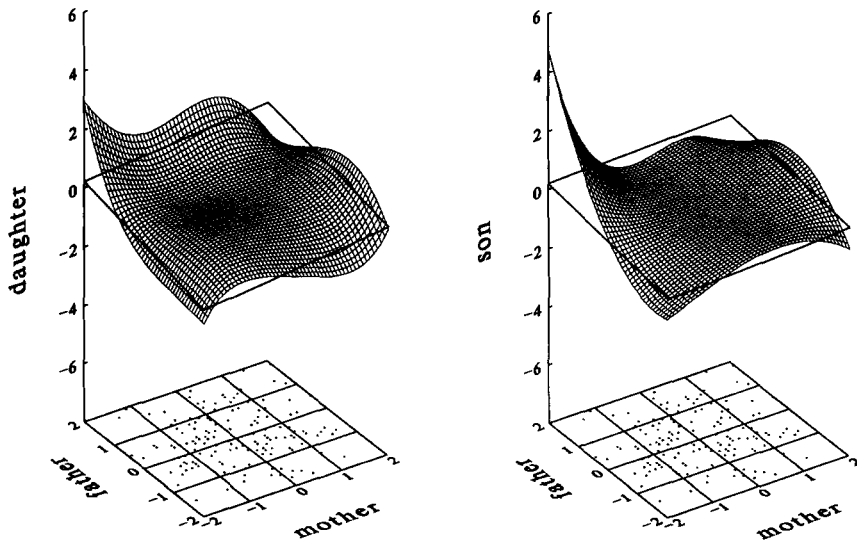
A. Gimelfarb and J. H. Willis

FIGURE 1.—Linear (plane) and polynomial (curved surface) regressions of weight of offspring on the weights of mothers and fathers (scales on all axes are the distances from the mean in standard deviation units).
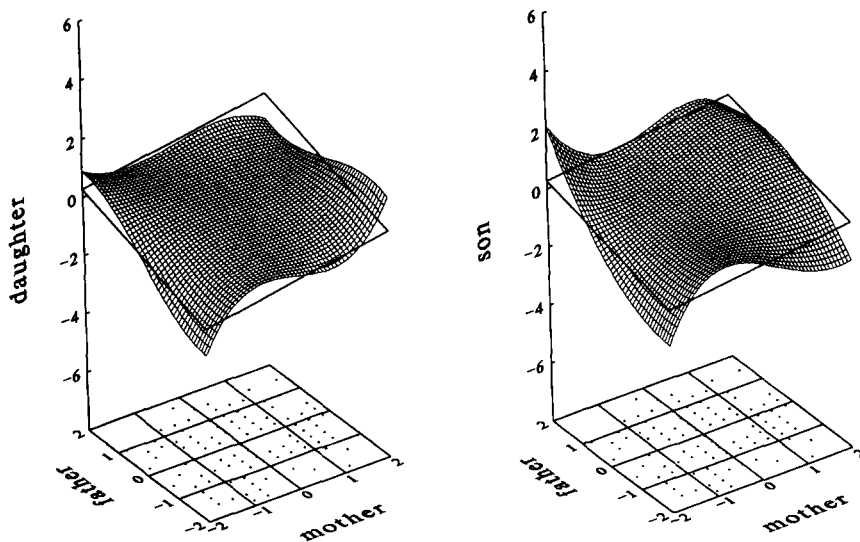
FIGURE 2.—Linear (plane) and polynomial (curved surface) regressions of number of abdominal bristles in offspring on the number of abdominal bristles in mothers and fathers (scales on all axes are the distances from the mean in standard deviation units).

are the planes corresponding to the linear regressions (Table 2). The scales on all axes are in standard deviation units. A dot on the bottom of a graph represents a family (the value of the trait in mother and in father). The surfaces appear to be sufficiently smooth, without local "wobbling" which means that the polynomial models are not overfitting. The general shapes of the regression surfaces in daughters and sons appear to be similar, even though differences between regressions in two sexes are statistically significant for all traits.

There are noticeable nonlinearities in the regression surfaces for all of the traits. The nonlinearities are more pronounced in the corners of a graph, i.e., if the traits in parents deviate substantially from the mean. Since parents with such traits are underrepresented in a sample, the error of the regression is higher for families with such parents than for families in which parents have traits that are closer to the mean. Consequently, not much credence should be given to a prediction based on

a nonlinear regression of a trait in offspring of parents whose traits deviate substantially from the mean. Let us not forget, however, that the same is true for linear regressions as well. The error of a linear regression is also greater for parents whose traits are farther away from the sample mean and, hence, predictions for the offspring of such parents based on a linear regression are also not reliable. It is not certain whether the error is higher for linear or for nonlinear regression.

Recall that the coefficient of linear regression on mothers was not significant for WTS (Table 2). Thus, judging by the linear offspring-parent regression, mothers do not appear to contribute significantly to the weight of their sons. This has been confirmed by the univariate linear regression of the weight in sons on the weight in mothers which turned out to be also nonsignificant. Notice, however, that this conclusion is contradicted by the polynomial regression. Indeed, the value of R^2_{PN} is twofold higher if the monomials with variable x are present in the regression function (Table
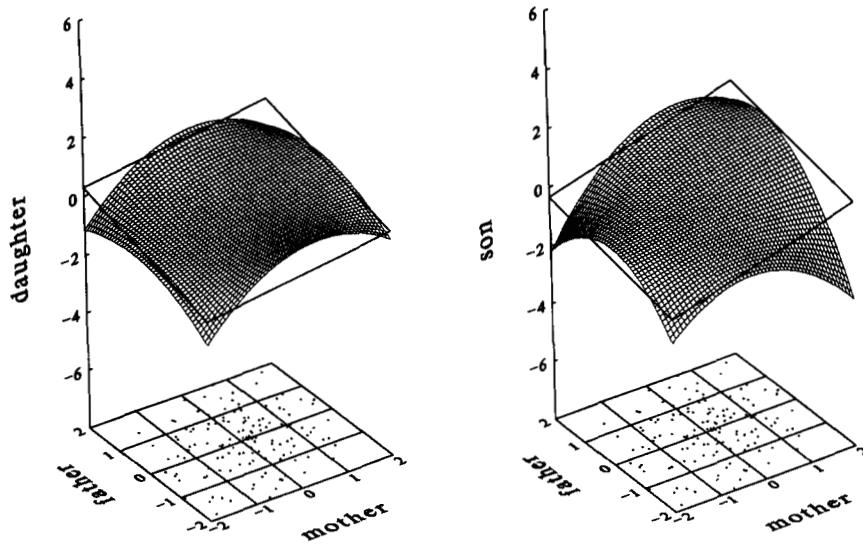
FIGURE 3.—Linear (plane) and polynomial (curved surface) regressions of wing length of offspring on the wing length of mothers and fathers (scales on all axes are the distances from the mean in standard deviation units).

3) than if they are excluded. Thus, mothers do contribute to the weight of their sons, but their contribution is not linear.

Nonlinear regression and realized heritability

We have established that there is a statistically significant ($P \leq 0.05$) nonlinearity in the offspring-parent regression for all considered traits, except the bristles in daughters, BD, for which the nonlinearity is significant at $P = 0.068$. Such a finding is not very interesting in itself since no one expects the regression to be exactly linear for any real trait. It is important to know, however, whether the detected nonlinearities may affect our inferences about the dynamics of the traits. Do, for example, linear and nonlinear regressions predict similar responses by the traits to selection, and, hence, as far as selection is concerned the nonlinearities can be disregarded?

One of the measures of a response to selection by different traits is the realized heritability (FALCONER 1983):

$$h_r^2 = \frac{R}{S}, \tag{6}$$

where S is the selection differential and R is the response to selection. It is quite unfortunate that the term heritability and the notation h^2 are used customarily for both the ratio (6) and the ratio of the additive component of variance to the total phenotypic variance called the narrow sense heritability. It should be kept in mind, however, that the two heritabilities are the same only if the offspring-parent regression is linear, otherwise they may differ. While the narrow sense heritability cannot, obviously, be either greater than one or negative, the realized heritability can. A value of h_r^2 greater than one means only that the response to selection exceeds the selection differential. A negative value means that selection produces a reversed response. GIMELFARB

(1986b) has demonstrated that genotype-environment interaction, for example, may cause a reversed response under strong selection. For a linear offspring-parent regression, the expected realized heritability is the same under any selection as the heritability estimated by the regression itself.

Truncation selection: Table 4 shows the realized heritabilities expected under truncation selection for the characters considered in the paper assuming that the actual offspring-parent regressions are polynomial (Table 3). An infinitely large population size and random mating were assumed, and the distribution of a character among females and among males before selection was assumed as a standardized normal (with zero mean and unit variance).

The left column in Table 4 shows the strength of selection expressed as the percentage of individuals being selected. In parentheses are selection differentials (in standard deviation units) produced by truncation selection of the corresponding strength on a normally distributed trait. Positive and negative values of selection differential correspond to positive and negative selection. Only individuals with the character above a specified "threshold" are selected under positive selection, whereas only individuals with the character below the threshold are selected under negative selection. The calculation of the threshold value for selection of a particular strength is discussed in APPENDIX A.

It is seen that for all the traits in Table 4 their realized heritability depends on the strength of selection and it can differ substantially from the heritability estimated by linear offspring-parent regression (shown under the corresponding traits in the table). Also, a linear offspring-parent regression cannot, obviously, predict an asymmetry of responses to positive and negative selection which is not uncommon in selection experiments. On the other hand, at least some degree of asymmetry in responses to selection (realized heritabilities)

TABLE 4

Realized heritabilities predicted by nonlinear offspring-parent regressions under truncation selection

Percent selected (selection differential)	Trait and its estimated heritability					
	WTD 0.47	WTS 0.26	BD 0.62	BS 0.71	WGD 0.60	WGS 0.73
15 (1.55)	0.31	0.04	0.49	0.29	0.42	0.75
15 (-1.55)	0.52	0.62	0.79	0.98	0.72	0.78
30 (1.16)	0.39	0.20	0.56	0.56	0.54	0.90
30 (-1.16)	0.37	0.52	0.73	0.65	0.60	0.63
50 (0.80)	0.39	0.23	0.59	0.68	0.57	0.96
50 (-0.80)	0.37	0.43	0.69	0.59	0.57	0.58
70 (0.50)	0.41	0.23	0.60	0.74	0.56	0.98
70 (-0.50)	0.51	0.36	0.68	0.59	0.58	0.55
90 (0.20)	0.62	0.20	0.62	0.91	0.55	1.07
90 (-0.20)	0.97	0.28	0.66	0.52	0.59	0.47
95 (0.10)	0.83	0.17	0.63	1.10	0.58	1.14
95 (-0.10)	1.36	0.22	0.66	0.41	0.58	0.39

is predicted by polynomial regressions for all of the characters.

For most of the characters the realized heritability predicted under moderate selection (70% selected) appears to be closer to the estimated heritability than that predicted under stronger selection, and the discrepancy between the realized and estimated heritabilities can become quite large when selection is strong (15% selected). The asymmetry of responses seems also to increase with stronger selection, and for most of the characters it becomes quite pronounced under strong selection. The values of the realized heritability predicted for strong selection should be taken, however, with skepticism. Indeed, traits among parents selected under strong selection deviate substantially (more than a standard deviation) from the population mean. At the same time, as has been discussed earlier, a regression function is not a very good predictor of a trait in offspring of parents whose traits deviate much from the mean.

The least squares method of fitting a regression function to sample data ensures that in the absence of selection linear and polynomial regressions predict the same mean value of a character among offspring (zero if the character is standardized). It would seem, therefore, that if the mean is not changed much by selection, *i.e.*, selection is sufficiently weak, linear and polynomial regressions should predict similar responses. Yet data in Table 4 for selection that is relatively weak (between 90 and 95% selected) do not support this conclusion. It is seen that not only the realized heritability predicted under weak selection by nonlinear regressions may differ substantially from the heritability estimated by linear regression, but that the discrepancy between the two heritabilities actually increases with decreasing strength of selection for most of the characters. The asymmetry of

responses is also present even if selection is weak, and for some traits it is more pronounced under weaker selection. These results may appear so bizarre as to suggest a computational error. Yet, there is no error. Indeed, it follows from expressions (A14) and (A15) in APPENDIX A that if a character is distributed with density $p(x)$ over an interval $-B \le x \le B$, and the offspring-parent regression for the character is $f(x, y)$,

$$h_0^2 = \frac{1}{B} \int_{-B}^{B} [f(x, -B) + f(-B, x)]p(x) \, dx$$

(7a)

(positive selection),

$$h_0^2 = -\frac{1}{B} \int_{-B}^{B} [f(x, B) + f(B, x)]p(x) \, dx$$

(7b)

(negative selection),

where h_0^2 denotes the limit of the realized heritability under truncation selection when the strength of selection approaches zero. The first thing to notice is that the absolute values of the integrals in (7a) and in (7b) are not necessarily the same. This means that there can be asymmetry in responses to very weak positive and negative truncation selection. Notice also that if the regression $f(x, y)$ is a polynomial in x and y, the integrals in (7a) and in (7b) are polynomials in B. Consequently, h_0^2 is also a polynomial in B with coefficients that depend on $p(x)$. Thus, the limit of the realized heritability of a character under truncation selection is determined not only by the offspring-parent regression, but also by the width of the interval over which the character is distributed and by the shape of its distribution. The last two rows in Table 5 show the limits of the realized heritability predicted by the polynomial regressions under truncation selection assuming $p(x)$ as truncated normal in the interval $-3 \le x \le 3$. Since h_0^2 is a polynomial in B, the limits of the realized heritability under truncation selection will be higher than those shown in Table 5 if the characters are distributed in an interval wider than $-3 \le x \le -3$. No limit exists if the distribution interval is infinite.

It should be noted that the fact that the realized heritability may become higher under weaker selection does not mean, of course, that weaker selection yields a stronger response in such instances. In fact, the response to truncation selection approaches zero when the strength of selection goes to zero, but so does also the selection differential.

Exponential and Gaussian selection: Truncation fitness function which is common in artificial selection may not be adequate for describing selection in nature. Such selection may be better approximated either by an exponential fitness function,

$$w(x, Q) = \exp(Qx),$$

(8)

TABLE 5

Limit values of realized heritability when strength of selection approaches zero

Form of selection	Traits and their estimated heritabilities					
	WTD 0.47	WTS 0.26	BD 0.62	BS 0.71	WGD 0.60	WGS 0.73
Exponential	0.52	0.27	0.64	0.69	0.57	0.72
Gaussian ($\theta = 3$)	0.68	0.27	0.64	0.76	0.58	0.79
Gaussian ($\theta = -3$)	0.76	0.27	0.64	0.62	0.57	0.65
Gaussian ($\theta = 1$)	0.60	0.27	0.64	0.86	0.58	0.93
Gaussian ($\theta = -1$)	0.84	0.27	0.64	0.61	0.56	0.51
Gaussian ($\theta = 0.5$)	0.48	0.27	0.64	0.99	0.59	1.14
Gaussian ($\theta = -0.5$)	0.96	0.27	0.64	0.49	0.55	0.30
Gaussian ($\theta = 0.25$)	0.24	0.27	0.64	1.24	0.62	1.56
Gaussian ($\theta = -0.25$)	1.20	0.27	0.64	0.23	0.53	-0.12
Truncation (positive)	2.66	-0.07	0.64	1.87	0.59	1.31
Truncation (negative)	3.69	-0.07	0.64	0.11	0.55	0.22

θ, "optimum" phenotype in standard deviation units.

or by a Gaussian fitness function,

$$w(x, Q) = \exp[-Q(x - \theta)^2] \qquad (Q \geq 0), \qquad (9)$$

with the optimum, θ, away from the mean of the character. The direction of exponential selection is indicated by the sign of Q, whereas the direction of Gaussian selection is indicated by the sign of θ. The strength of selection is determined in both cases by the absolute value of Q.

Regarding the limit of the realized heritability under exponential and Gaussian selection when the strength of selection approaches zero, let

$$a = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} x f(x, y) p(x) p(y) \, dx \, dy, \qquad (10a)$$

$$b = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} y f(x, y) p(x) p(y) \, dx \, dy. \qquad (10b)$$

It follows from equations (A16), (A17) and (A18) (A19) in APPENDIX A that, given the distribution of the character is standardized normal,

$$h_0^2 = a + b, \qquad (11)$$

if selection is exponential, and

$$h_0^2 = a + b - \frac{1}{2\theta} \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} (x^2 + y^2) f(x, y) p(x) p(y) \, dx \, dy, \qquad (12)$$

if selection is Gaussian. Table 5 shows the limits of the realized heritability predicted by the polynomial offspring-parent regressions under exponential and Gaussian selection assuming that the parental distributions are standardized normal. The optima for Gaussian selection are in standard deviation units. If selection is exponential, the limits of the realized heritability are exactly equal to the heritabilities expected from the least squares linear approximations of the polynomial regres-

sions assuming infinite population size and parental distributions as standardized normal (see APPENDIX B). The expected heritabilities differ slightly from those estimated in our samples (shown in Tables 4 and 5 under the corresponding traits). The difference is not surprising given that the sample size is not infinite and the actual parental distributions are not exactly normal.

No general conclusion regarding the limit of the realized heritability can be drawn from Table 5. While for one trait (BD) it is similar to the estimated heritability under any form of selection, for another trait (WTS) it is similar to the estimated heritability under any Gaussian selection but is quite different from it under truncation selection. For the majority of the traits, the limit of the realized heritability depends very much on the form of selection and may differ remarkably from the estimated heritability.

The only general conclusion that can be drawn from Tables 4 and 5 is that predictions of the response by the mean of a character to selection, and to weak selection in particular, based on the estimated heritability of the character may be quite unreliable. The reason for this is simple. If the offspring-parent regression is linear, the mean of a character in offspring population depends only on the mean among parents. Consequently, a response by the mean to selection is completely determined in such a case by the change in the mean among parents (selection differential), and formula (1) is a succinct formulation of this. If, however, the offspring-parent regression is not linear, the mean among offspring depends not only on the parental means but also on higher moments of parental distributions. Consequently, a response by the mean to selection is determined in such a case not only by the selection differential, but also by changes caused by selection in higher moments of the parental

distributions. Hence, the realized heritability for a character with nonlinear offspring-parent regression depends on the parental distribution and on the form and strength of selection.

The effect of the form and strength of selection on the realized heritability can be seen in Tables 4 and 5. Also, the assumption of normality of parental distributions made in computing these tables implies that all odd moments of the distributions are zero and any even moment is expressed in a particular way through the second moment. This, however, may not be true for distributions other than normal. Consequently, the realized heritabilities for the same traits under the same form and strength of selection may differ from those shown in Tables 4 and 5, if parental distributions are not normal.

The effect on the mean among offspring of changes in higher moments of parental distributions caused by selection may become particularly noticeable if the selection differential is small, *i.e.*, selection on the mean among parents is weak. There can even be a "response" by the mean in offspring to selection that does not affect the parental mean at all. For example, Gaussian selection with $\theta = 0$ does not change the mean in a parental population with normally distributed character, but does change the variance. Given the polynomial offspring-parent regressions (Table 3), it is not difficult to see that the mean among the offspring for WTD, BS, WGD and WGS will be affected by a change in the parental variance, and, hence, the mean for these traits will "respond" to selection even though the selection differential is zero. It is clear that the realized heritability will be infinity in such a case.

CONCLUSIONS

The offspring-parent regression is significantly nonlinear for all of the characters considered in the paper, except the bristles in daughters for which the nonlinearity is marginally significant ($P = 0.068$).

Nonlinear contributions by parents to a character in their offspring may not be revealed by a linear offspring-parent regression, as the weight in sons (WTS) demonstrates.

The response by a character to selection predicted by a nonlinear offspring-parent regression fitted to family data can be quite different from the response predicted by the linear regression fitted to the same family data.

The response by a trait to selection is a result of an intricate interplay between the offspring-parent regression function, the distribution of the character, and the form and strength of selection.

The nonlinearity of the offspring-parent regression can be responsible for the asymmetry of responses to positive and negative selection observed in many experiments.

The discrepancy between the responses by a character to selection predicted by nonlinear and linear offspring-parent regressions can be substantial not only if selection is strong, but also, and even more so, if selection is weak.

Predicting responses by a quantitative character to weak selection can be a very uncertain exercise.

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APPENDIX A

Consider a quantitative character having zero mean and unit variance distributed in an interval $-B \leq x \leq B$ ($B \leq \infty$) with a density function $p(x)$ for both sexes. Let the character be under selection with the phenotypic fitness function $w(x, Q)$. Besides the individual's phenotype, the fitness function also includes a parameter Q characterizing the strength of selection: smaller Q implies weaker selection. There is no selection if $Q = 0$, *i.e.*, $w(x, 0) = 1$. The mean fitness of a population is, by definition,

$$W = \int_{-B}^{B} w(x, Q)p(x) \, dx. \qquad (A1)$$

In the case of truncation selection, the fitness function can be expressed as

$$w(x, Q) = \begin{cases} 1 & \text{if } x \geq -B + Q \\ 0 & \text{otherwise} \end{cases} \quad \text{(A2a)}$$

(positive selection),

$$w(x, Q) = \begin{cases} 1 & \text{if } x \leq B - Q \\ 0 & \text{otherwise} \end{cases} \quad \text{(A2b)}$$

(negative selection).

Substituting these expressions into (A1) yields for the mean fitness

$$W = \int_T^B p(x) \, dx, \quad T = B - Q \quad \text{(A3a)}$$

(positive selection),

$$W = \int_{-B}^T p(x) \, dx, \quad T = -B + Q \quad \text{(A3b)}$$

(negative selection).

The mean fitness under truncation selection is equivalent to the proportion of individuals that are selected. Consequently, the threshold corresponding to a particular proportion of selected individuals can be obtained by solving with respect to T equations (A3a) and (A3b).

Given that the mean of the character before selection is zero, selection differential, S, and response, R, are obtained as

$$S = \frac{1}{W} \int_{-B}^B x w(x, Q) p(x) \, dx. \quad \text{(A4)}$$

$$R = \frac{1}{W^2} \int_{-B}^B \int_{-B}^B f(x,y) w(x, Q) p(x) p(y) \, dx \, dy, \quad \text{(A5)}$$

where $f(x, y) = E[z \mid x, y]$ is the offspring-parent regression function. It is easy to see that if $f(x, y) = ax + by$, i.e., the offspring-parent regression is linear, $R = aS + bS$, and, hence,

$$h_r^2 = a + b \quad \text{(A6)}$$

for any form of selection and character distribution. The realized heritabilities under truncation selection in Table 4 were obtained by first evaluating the integrals (A5) for the regression function corresponding to a particular trait and for the fitness function either (A2a) or (A2b), and then dividing the result by (A4) also computed for the fitness function either (A2a) or (A2b). A package of mathematical programs MATHCAD was used for computing the integrals on a 486 PC computer.

The following conditions are straightforward when the strength of selection approaches zero:

$$\lim_{Q \to 0} S = 0, \quad \text{(A7)}$$

$$\lim_{Q \to 0} R = 0, \quad \text{(A8)}$$

$$\lim_{Q \to 0} W = 1. \quad \text{(A9)}$$

Given (A7) and (A8), the limit of $h_r^2 = R/S$ when Q approaches zero is of the indeterminate type $0/0$. It can, however, be evaluated by applying L'Hôpital's rule:

$$\lim_{Q \to 0} h_r^2 = \left(\lim_{Q \to 0} \frac{\partial R}{\partial Q} \right) \bigg/ \left(\lim_{Q \to 0} \frac{\partial S}{\partial Q} \right). \quad \text{(A10)}$$

It can be shown, taking into account (A7), (A8) and (A9), that

$$\lim_{Q \to 0} \frac{\partial S}{\partial Q} = \int_{-B}^B \phi(x) x p(x) \, dx, \quad \text{(A11)}$$

$$\lim_{Q \to 0} \frac{\partial R}{\partial Q} = \int_{-B}^B \int_{-B}^B [\phi(x) + \phi(y)] f(x, y) p(x) p(y) \, dx \, dy, \quad \text{(A12)}$$

where

$$\phi(x) = \frac{\partial w(x, Q)}{\partial Q} \bigg|_{Q=0}. \quad \text{(A13)}$$

For the fitness function of truncation selection, $\phi(x) = \delta(x + B)$ if selection is positive (A2a), and $\phi(x) = -\delta(x - B)$ if it is negative (A2b), where $\delta(\cdot)$ denotes delta function. Substituting such $\phi(x)$ into (A11) and (A12) we obtain

$$\lim_{Q \to 0} \frac{\partial S}{\partial Q} = B p(-B), \quad \text{(A14a)}$$

$$\lim_{Q \to 0} \frac{\partial R}{\partial Q} \quad \text{(A15a)}$$

$$= \left[\int_{-B}^B f(x, -B) p(x) \, dx + \int_{-B}^B f(-B, y) p(y) \, dy \right] p(-B)$$

under positive selection, and

$$\lim_{Q \to 0} \frac{\partial S}{\partial Q} = -B p(B), \quad \text{(A14b)}$$

$$\lim_{Q \to 0} \frac{\partial R}{\partial Q} \quad \text{(A15b)}$$

$$= -\left[\int_{-B}^B f(x, B) p(x) \, dx + \int_{-B}^B f(B, y) p(y) \, dy \right] p(B)$$

under negative selection. Dividing (A15a) by (A14a) and (A15b) by (A14b) yields expressions (7a) and (7b) for h_0^2 in the text.

If selection is exponential (8), the derivative (A13) is $\phi(x) = x$. Given that $p(x)$ is standardized normal, the substitution of such $\phi(x)$ into (A11) and (A12) results in

$$\lim_{Q \to 0} \frac{\partial S}{\partial Q} = \int_{-\infty}^{\infty} x^2 p(x) \, dx = 1, \qquad \text{(A16)}$$

$$\lim_{Q \to 0} \frac{\partial R}{\partial Q} = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} (x + y) f(x, y) p(x) p(y) \, dx \, dy. \qquad \text{(A17)}$$

If selection is Gaussian (9), $\phi(x) = -(x - \theta)^2$, and the substitution of such $\phi(x)$ into (A11) and (A12) yields

$$\lim_{Q \to 0} \frac{\partial S}{\partial Q} = -\int_{-\infty}^{\infty} (x - \theta)^2 x p(x) \, dx = 2\theta, \qquad \text{(A18)}$$

$$\lim_{Q \to 0} \frac{\partial R}{\partial Q} \qquad \text{(A19)}$$

$$= -\int_{-\infty}^{\infty} \int_{-\infty}^{\infty} [(x - \theta)^2 + (y - \theta)^2] f(x, y) p(x) p(y) \, dx \, dy$$

$$= \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} [2\theta(x + y) - (x^2 + y^2)] f(x, y) p(x) p(y) \, dx \, dy$$

Dividing (A17) by (A16) and (A19) by (A18) results in expressions (11) and (12) in the text.

APPENDIX B

The least squares linear approximation of a nonlinear offspring-parent regression is a function $\alpha x + \beta y$ that delivers the minimum of the integral

$$\int_x \int_y [f(x, y) - (\alpha x + \beta y)]^2 \, p(x) p(y) \, dx \, dy, \qquad \text{(B1)}$$

where $p(x)$ and $p(y)$ are the distributions of the character among mothers and fathers, respectively. The minimum of (B1) is delivered by

$$\alpha = \int_x \int_y x f(x, y) p(x) p(y) \, dx \, dy, \qquad \text{(B2a)}$$

$$\beta = \int_x \int_y y f(x, y) p(x) p(y) \, dx \, dy. \qquad \text{(B2b)}$$

Given that the characters in parents are standardized, the heritability expected from such linear approximation is $\alpha + \beta$ (see (4)). It is seen that (B2a) is the same as (11a) and (B2b) is the same as (11b). Hence, h_0^2 under exponential selection is equal to the heritability expected from the linear approximation of the offspring-parent regression.