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Quantitative genetics and fitness: lessons from *Drosophila*

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This paper examines patterns of heritability and genetic covariance between traits in the genus *Drosophila*. Traits are divided into the categories, morphology, behaviour, physiology and life history. Early theoretical analyses suggested that life history traits should have heritabilities that are lower than those in other categories. Variable pleiotrophy, environmental variation, mutation and niche variation may, however, maintain high heritabilities. In *Drosophila* the heritabilities of life history traits are lower than morphological or physiological traits but may exceed 20 per cent. The pattern of variation in the heritability of behavioural traits is similar to that of life history traits. Genetic covariance between morphological traits and between morphological and life history traits are all positive but those between life history traits have variable sign. Negative covariance between traits supports the variable pleiotropy hypothesis but other factors such as environmental heterogeneity, or mutation cannot be excluded.

INTRODUCTION

The quantitative genetic model developed by Fisher (1930) has, over the last two decades, been variously interpreted, modified and extended (O'Donald, 1967; Price, 1970; Slatkin, 1970; Bulmer, 1971; Cavalli-Sforza and Feldman, 1976, 1978; Emlen, 1980; Lande, 1982; Cheverud, 1984). Two principal components of these models are heritability and the genetic covariance matrix. Heritability, the additive component of polygenic variation, dictates, in large measure, the rate at which genetic change will occur, while the genetic covariance determines how traits will change in relation to each other. Early theoretical analyses of quantitative genetic variation suggested that traits associated directly with fitness, such as fecundity or viability, should have low heritabilities and positive covariation between traits (Fisher, 1930; Lerner, 1954; Robertson, A., 1955; Falconer, 1981). Although some evidence has been collated in support of this prediction, (see, for example, table 10.1 in Falconer 1981) the data are largely based on domestic, inbred animals and the collations are not very extensive. Furthermore, it has been suggested that genetic variation may remain high because of negative covariance between traits (Dickerson, 1955; Robertson, F., 1955; Rose, 1982, 1983; Rose and Charlesworth, 1981*b*; Berven and Gill, 1983), environmental variation (Grant and Price, 1981; Rose, 1983), mutation (Dempster, 1955; Lande, 1975; Turelli, 1984) or niche variation (Van Valen, 1965).

The quantitative genetics of *Drosophila* have been extensively studied and in this paper we examine the variation in heritabilities with respect to different categories of traits, and the genetic and phenotypic correlations between traits, both within and between species. We address two questions: first, is there any pattern in the variation of heritabilities and genetic covariance of traits, and second, do traits directly associated with fitness have relatively low heritabilities?

DEFINING THE DATA BASE

For the purpose of this paper we define four categories of traits: (a) morphological traits; (b) behavioural traits; (c) physiological traits and (d) life history traits. Although all of these traits may fall within the purview of life history theory we have retained the term "life history trait" for traits such as fecundity, viability, survival and development rate, that are invariably and directly concerned with fitness. "Classical" theory predicts that life history traits will have lower heritabilities than traits in the other categories. It is certainly possible that certain traits in these other categories are under strong selection and, hence, have low heritabilities: it is for this reason that we compare heritabilities on a group basis and not by pairwise comparison of individual traits.

The data analysed in this paper are extensive but not exhaustive. A listing of the principal sources, divided according to trait, is given in an appendix. Only heritabilities in the narrow sense were accepted. Only six of the 130 studies computed heritabilities by the method of full sibs and these showed no consistent differences from the heritabilities estimated by some other method in the same study and were, therefore, retained.

Is it possible to predict the relative heritabilities of morphological, behavioural or physiological traits? Lee and Parsons (1968) suggest that behavioural traits will be "predominantly under stabilizing selection, but it may be premature to generalize". *A priori* it seems reasonable to suppose that behavioural traits, such as mating propensity, are more closely connected to fitness components than morphological traits. However, this assumption must be viewed with some caution as fecundity and development time in ectotherms are tightly correlated with body size, a morphological trait. These observations stress the unity of the phenotype and the lack of a strict hierarchical structure in traits. For this reason we do not make any predictions concerning the ranking of the

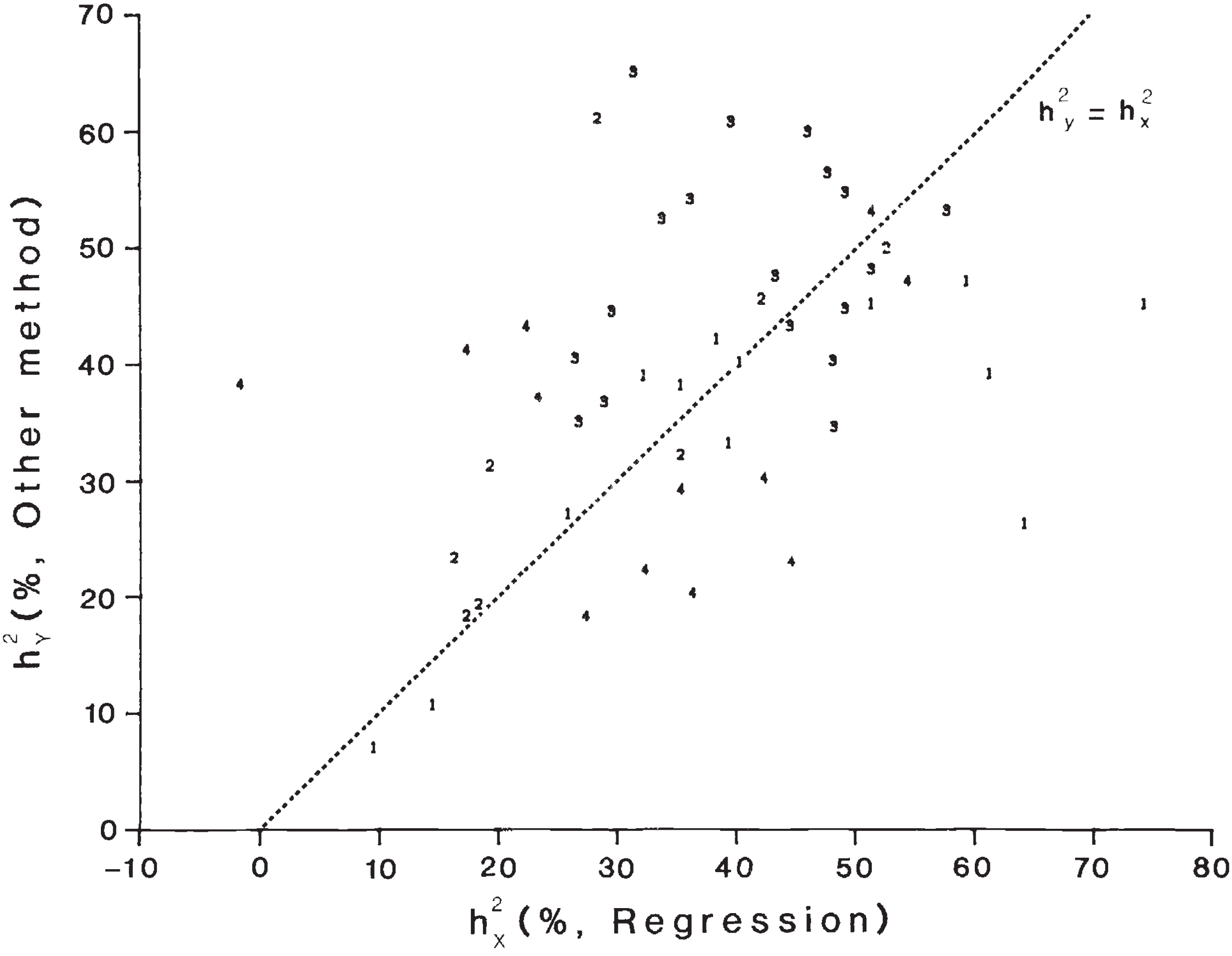

Figure 1 Scatter plot of h^2 estimated by selection (1), half sib (3), full sib (4) or miscellaneous methods (2), (h^2_Y), on h^2 estimated from offspring on parent regression, (h^2_X). Data from Beardmore *et al.* (1975), Clayton *et al.* (1957), Gallego and Lopez-Fanjul (1983), Lopez-Fanjul and Hill (1973*b*), Mackay (1981), Reeve and Robertson (1953), Sheridan *et al.* (1968), Sorenson and Hill (1982, 1983), Tantawy (1956*b*), Tantawy *et al.* (1964), van Dijken and Scharloo (1979).

heritabilities of morphology, behaviour and physiology, but rather use the data to discern whatever pattern might exist.

Most of the studies used wild, outbred strains of flies, though a few used inbred or synthetic strains (made by crossing several lines). The type of strain is indicated in the listing: the conclusions do not differ if only wild, outbred strains are analysed. The number of females used in founding these stocks varied from one to several hundred and the stocks were maintained under laboratory conditions prior to the estimation of heritability for one to many generations. We could find no effect of the size of the founding population or the duration of time within the laboratory and hence these variables will not be considered further.

The data base comprises heritabilities estimated by different methods and in many cases no standard errors are reported. To use these data we must establish: (a) that different methods estimate the same value *or* are not too biased; (b) that standard errors are small enough in those cases in which they have been calculated to suggest that estimates without standard errors are reliable.

For a wide variety of morphological characters and one behavioural trait, alternative estimates of heritability have been reported. These have been grouped into two categories, one being offspring on parent regression and the second, either selection, half sib ANOVA, full sib ANOVA, or "miscellaneous". There is a significant correlation between the h^2 estimated from offspring on parent regression (h_x^2) and that estimated by some other method (h_y^2) ($r=0{\cdot}44$, $t=3{\cdot}42$, $P<0{\cdot}05$, $n=51$, fig. 1). Covariance analysis indicates that inclusion of the alternative method of analysis as a dummy variable significantly reduces the variance, with the slopes being homogeneous ($F_{3,43}=1{\cdot}86$ for the slopes and $F_{1,46}=16{\cdot}83$ for the effect of the alternative method). Since several studies constitute a large fraction of the data set it is possible that the effect is due to study rather than method.

Bias in different methods has also been found by Frankham *et al.* (1968) in their analysis of heritability of abdominal bristle number in *D. melanogaster*. Heritabilities were estimated by full sib and half sib analysis and realised heritabilities computed after 10 generations of selection. The realised heritability consistently underestimated those obtained by the other two methods, though there is statistically significant relationship between them ($r=0{\cdot}51$, $n=27$, $t=2{\cdot}97$, $P<0{\cdot}01$,

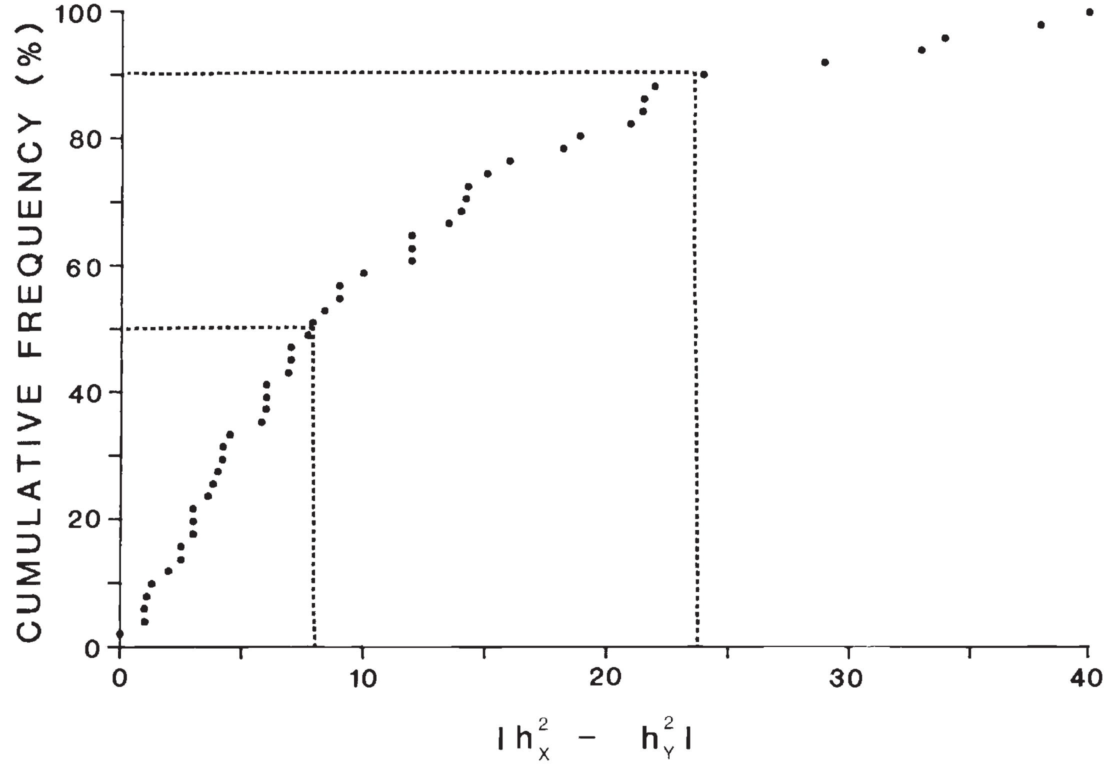

Figure 2 Cumulative frequency plot of the absolute difference between the 2 heritability estimates plotted in Fig. 1 ($h_x^2 - h_y^2$).

$Y = 2{\cdot}47 + 0{\cdot}33X$, where Y is realised h^2 and X the other methods: the slope differs significantly from 1, $t = 6{\cdot}02$: data from table 2 of Frankham *et al.* 1968).

Although there may be statistically significant differences between methods it is clear from the scatter plot (fig. 1) that any bias is small relative to the total scatter. Provided comparisons are made on a relatively large number of estimates the effect of bias is unlikely to produce an erroneous conclusion. The size of the data base will depend in part upon the confidence region about each estimate. This will itself be a function of the estimated standard error and any potential bias in the central tendency of the heritability estimate not considered in the method of estimating the standard errors. Consider first the cumulative frequency of the absolute difference between the two estimates (fig. 2): such a plot tells us the probability with which the difference between two estimates will exceed a given value. Thus there is a 50 per cent probability that the absolute difference between h^2 estimated by offspring on parent regression and some other method ($|h_x^2 - h_y^2|$) will exceed 8 per cent. Although this difference is relatively small the cumulative frequency increases slowly and there is one chance in 10 that the difference will exceed 24 per cent. These large differences may reflect bias and/or high uncertainty in the estimates. Of the 51 estimates 29 have associated standard errors, though not in all cases for both estimates of h^2. Consider those estimates in which both standard errors are given; in 14 out of 16 such cases each heritability estimate is within the confidence region of the other estimate. Of the 13 remaining cases in which only the standard error of one estimate is given, the estimate without an associated standard error is enclosed within the confidence region of the other estimate in 10 cases.

In summary, heritabilities estimated by different techniques may vary quite considerably, and there may be small biases in different techniques, but the estimated standard errors reasonably reflect the accuracy with which h^2 is estimated.

THE DISTRIBUTION OF h^2

We shall first consider only those estimates for which standard errors are given. Heritability estimates for life history traits span the full range from 0 to 100 per cent (fig. 3). However, the standard errors associated with h^2 are, in the case of two studies (Tait and Prabhu, 1970; Murphy *et al.*, 1983), far too large to be considered reliable. These two studies have, therefore, been eliminated from the data set. The distribution of heritabilities for three groups (there are insufficient data for the physiological group) are presented in fig. 4: in all but a few cases the associated standard errors are relatively small. It is evident that few morphological traits have heritabilities less than 10 per cent

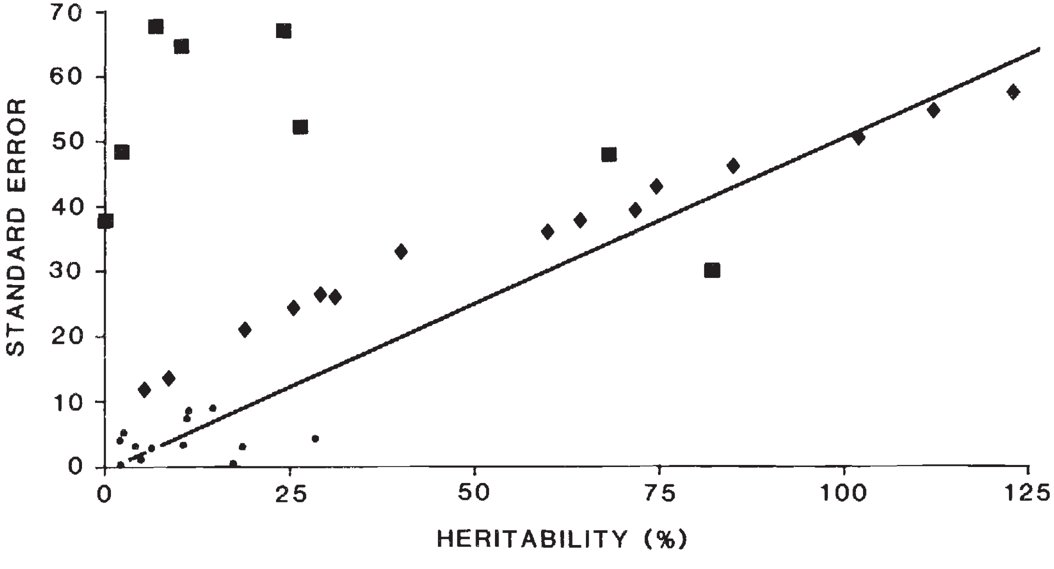

Figure 3 Scatter plots of heritability and associated standard errors for life history traits. Solid line indicates the relationship 2 S.E. = h^2: heritabilities above this line include zero within their confidence region. The closer the heritability is to the x (h^2) axis the more accurate the estimate. ■ Data from Tait and Prabhu (1970); ◆ data from Murphy *et al.* (1983); ● see Appendix.

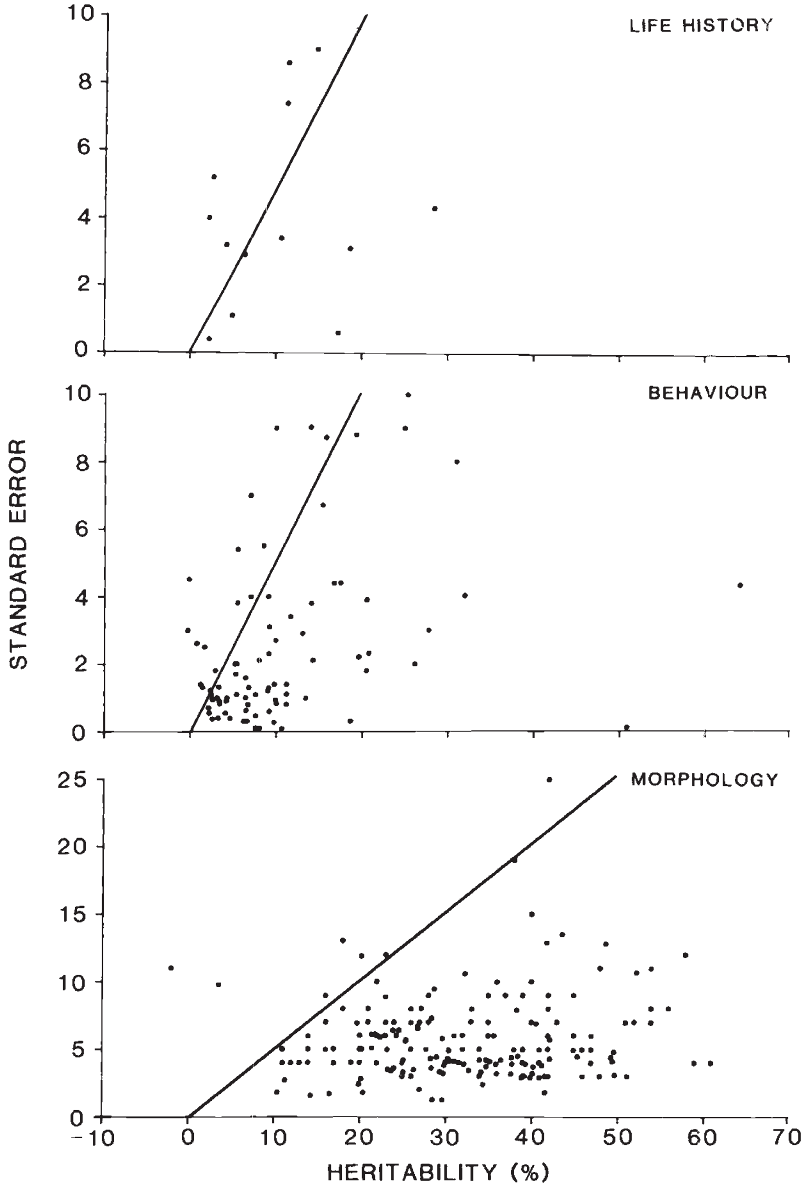

Figure 4 Scatter plots of heritability and associated standard errors. Solid line indicates 2 S.E. = h^2: heritabilities above this line include zero within their confidence region. The closer the heritability is to the x (h^2) axis the more accurate the estimate. For data sources seee Appendix.

whereas a significant proportion of behavioural and some life history traits fall within the 0–10 per cent range. The range in h^2 of morphological traits is comparatively large spanning 10 per cent to 60 per cent, with little tendency for the standard error to increase with the estimate. On the other hand, the range in behavioural and life history heritabilities is much smaller, from 0 to 30 per cent. While the heritabilities of behavioural traits tend to be clustered within the region 0–10 per cent those of life history traits are fairly evenly distributed, although the total number of data points is rather low. Therefore, while the data support the "classical" hypothesis that life history traits should have low heritabilities relative to traits less directly concerned with fitness, such as morphological traits, they also suggest that significant genetic variation is maintained and hence that other factors are intervening to present total erosion of variation. At the same time the low heritabilities of behavioural traits suggests that they may be under the same type of selection as life history traits.

The above analysis does not distinguish between traits within each grouping. Further, there are a large number of studies for which standard errors of h^2 are not given. To examine the distribution of heritabilities both within and between traits we have included these studies and consider only the estimate itself (the two studies previously discarded have not been included). In any given study h^2 may have been estimated by several methods or in several different stocks. These separate estimates have been plotted on a number line to indicate the within-study variation in h^2; each trait has been stacked in an orderly fashion to illustrate the

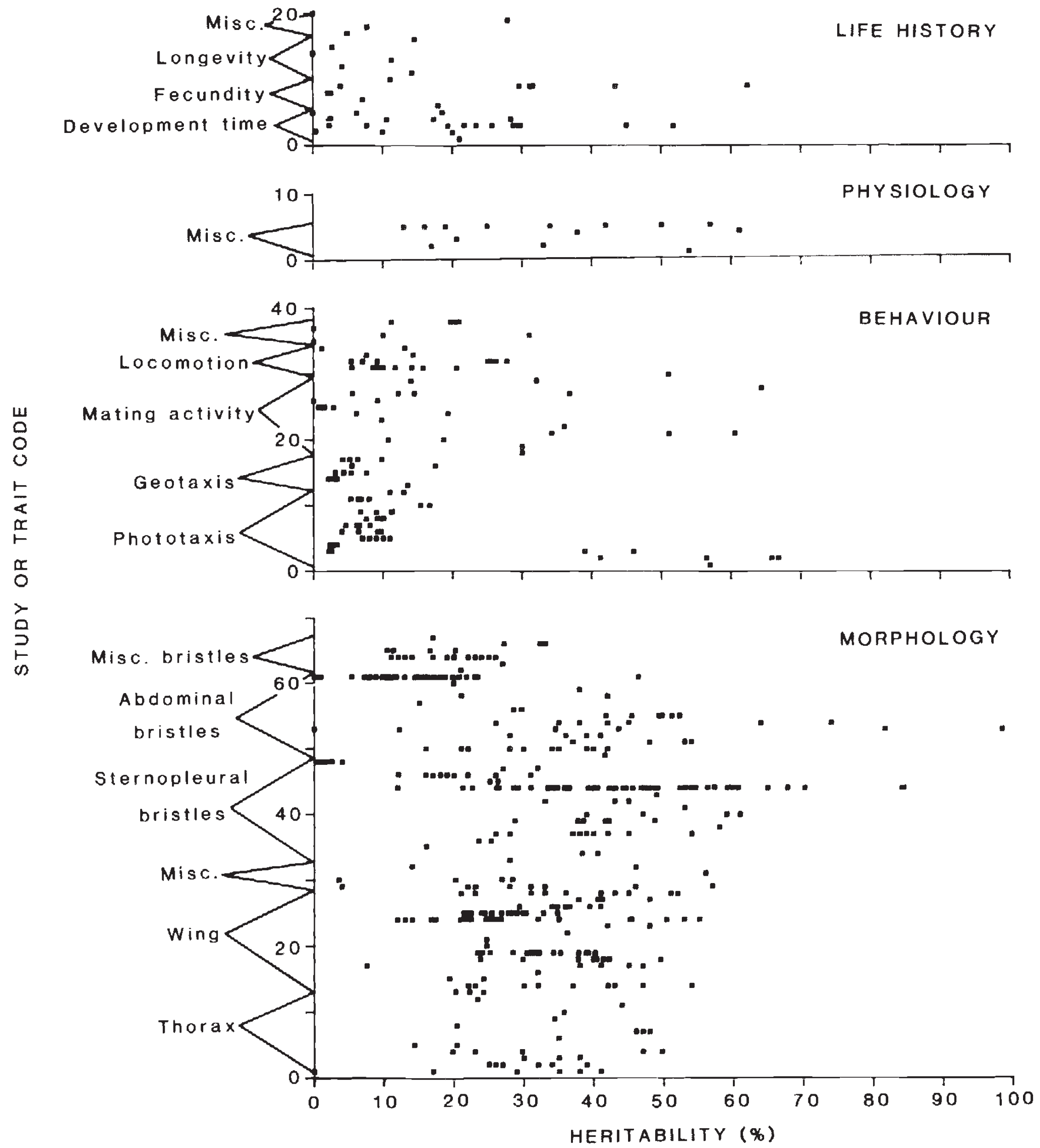

Figure 5 The distribution of heritability estimates within studies, among traits and among categories of traits. Each line consists of all relevant heritability estimates for a given trait from a single study. For data sources see Appendix.

distribution of h^2 within a study, within a trait, between traits and between groups (fig. 5, sources given in Appendix 1). Within the morphology grouping there is no indication that particular traits tend to differ from the rest. *A priori* we might predict morphologies directly related to size to be more closely related to fitness than, say, bristle number. However, Thoday (1958) argued that the number of steropleural chaeta must have adaptive significance since it differs between populations. Reeve (1960) suggested that bristle number *per se* is probably not significant but that the genes controlling bristle development also control some other trait that is under selection. Kearsey and Barnes (1970) demonstrated that chaeta number is under stabilising selection under laboratory conditions and that selection operates in the preadult stage before the bristles have developed, supporting the hypothesis of pleiotropy.

Except for three studies geotaxis and phototaxis appear to have low heritabilities whilst mating activity and locomotion tend to have a wider spread. Physiological heritabilities are scattered more or less evenly between 10 per cent and 70 per cent. The heritabilities of life history traits are more scattered than in fig. 4, ranging from 0 to 60 per cent, though most values lie below 30 per cent. Heritability of development time is variable both within and between studies. Fecundity also tends to be variable. Given the potentially large standard errors associated with the heritabilities of life history traits (figs 3 and 4) the large values in fig. 5 must be viewed with caution. Nevertheless, the same general pattern emerges as previously described, *viz.*, heritabilities of life history traits are generally lower than morphological traits but are not negligibly small and in some cases may be quite large. Behavioural traits appear to be similar to life history traits with respect to h^2 whereas physiological traits more closely match morphological traits.

To test the above conclusions further we constructed the cumulative frequency curves for each category using the median heritability from each study (fig. 6). There is a statistically significant difference between the distributions of morphology h^2 and life history h^2 (Kolmogorov-Smirnov $D = 0{\cdot}68$, n (morph.) $= 67$, n (life hist.) $=$ 20, $P < 0{\cdot}01$) but not between the heritabilities of life history traits and behavioural traits ($D = 0{\cdot}16$, n (behav.) $= 38$, $P > 0{\cdot}05$). The mean value of the morphology heritabilities is 31.9 ($\pm 1{\cdot}45$), of the

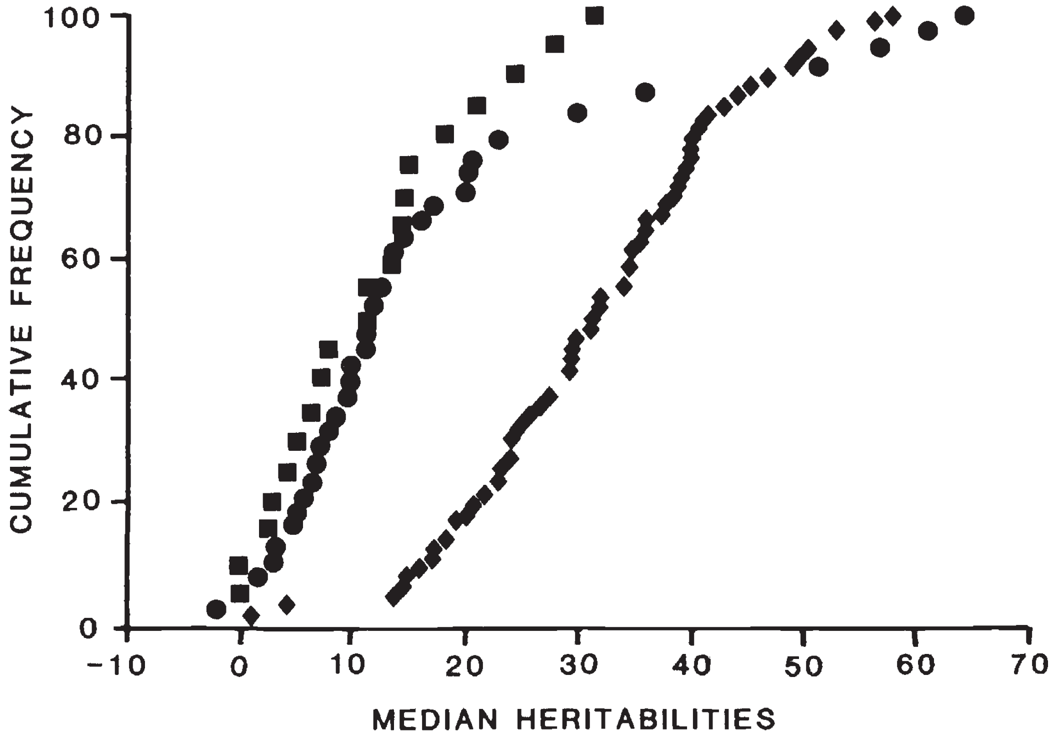

Figure 6 Cumulative frequency plots of the median heritabilities for morphological (◆), behavioural (●) and life history (■) traits. For data sources see Appendix.

life history h^2, 11·94, (±2·05) and of the behavioural h^2, 17·99 (±2.84). The central tendencies of the distributions of the morphology h^2 and life history h^2 are significantly different ($t = 6{\cdot}94$, $P < 0{\cdot}01$; Mann-Whitney $U = 124$, $P < 0{\cdot}01$). Comparison between the central tendencies of the heritabilities of life history and behaviour is slightly complicated by significant differences between the variances ($F_{37,19} = 3{\cdot}67$, $P < 0{\cdot}05$). Using a one-tailed test, based on the proposition that behavioural heritabilities will exceed life history heritabilities, a significant difference is obtained with the t-test for unequal variances ($t = 1{\cdot}73$, df $= 55{\cdot}999$, $P < 0{\cdot}05$) but not with the Mann-Whitney test ($U_{38,20} = 326{\cdot}5$, $z = -0{\cdot}87$, $P > 0{\cdot}05$). Obviously the above statistical analyses must be treated with caution: nevertheless, they do lend further support to the previously drawn conclusion that the heritabilities of life history traits are generally lower than those of morphological traits but approximately the same as behavioural traits.

Maynard Smith (1959) found that, with respect to longevity in *D. subobscura*, the correlations between parent and offspring of the same sex were considerably higher than correlations between parent and offspring of different sex (mean values of 0·241 and 0·078 respectively). Further, the correlations between sibs of the same sex was as large as the correlations between parent and offspring of the same sex suggesting "a negative association between longevity and other components of fitness" (Maynard Smith, 1959). In an extensive investigation of egg to adult viability in various populations of *D. melanogaster* Mukai and his colleagues (Mukai *et al.*, 1974; Mukai and Yamaguchi, 1974; Mukai and Nakana, 1983; summarised in Charlesworth, 1987) found low levels of additive genetic variance. The amount of variation in northern stocks is consistent with maintenance by mutation alone but is far too large in southern stocks to be so maintained. Variable pleiotropy is one mechanism that could account for the excess additive genetic variance (Charlesworth, 1987).

THE PHENOTYPIC, GENETIC AND ENVIRONMENTAL CORRELATIONS

The phenotypic correlation is composed of the genetic and environmental correlations. While it would be most desirable to consider these latter two components separately there are generally very large standard errors associated with the environmental correlation and only a few papers present both correlations. Of the 30 available estimates of environmental and genetic correlations 15 come from a single study, that of Giesel *et al.* (1982). There is no significant correlation between the environmental and genetic correlation with or without this study ($r = -0{\cdot}11$, $t = -0{\cdot}4$, $n = 15$, $P > 0{\cdot}05$ and $r = 0{\cdot}11$, $t = 0{\cdot}6$, $n = 30$, $P > 0{\cdot}05$). Similar results have been found for a wider range of organisms (Bell and Koufopanou, 1986).

The genetic correlation is significantly correlated with the phenotypic correlation (fig. 7, $r = 0{\cdot}35$, $n = 53$, $t = 2{\cdot}69$, $P < 0{\cdot}05$), though the relationship is weak. More significantly, both the phenotypic and genetic correlations are positive when the factors are morphology × morphology, or morphology × life history (no behavioural data are available) but may occur in any of the four quadrants for life history × life history traits. Seventeen of these genetic correlations are positive and 14 negative, supporting the variable pleiotropy hypothesis. However, this conclusion can be accepted only tentatively since the majority of the data come from two studies, which give somewhat different results. Rose and Charlesworth (1981) found a preponderance of negative correlations between life history traits in *D. melanogaster* (8 of 11) whereas Giesel *et al.* (1982) working with the same species, but different stock, obtained mainly positive correlations (10 of 15): this difference is barely significant ($G = 4{\cdot}06$, df $= 1$, $P < 0{\cdot}05$). In part, the difference might be due to differences in the traits measured, or they may reflect different evolutionary histories of the stocks. These data suggest that both the magnitude and sign of the correlation may be variable, as is also suggested by the change in sign in inbred stocks (Giesel *et al.*, 1982). Thus data on the genetic and phenotypic correlations between traits in inbred lines, such as those of Mukai and Yamazaki (1971) demonstrating a negative correlation between development time and viability, may not be representative of wild stocks. Inbreeding may, indeed, be expected to produce positive covariation (Rose, 1984). Another factor that may affect the detection of negative genetic covariance is the effect of novel environments (Service and Rose, 1985).

The basic premise of the variable pleiotropy hypothesis is that high heritabilities may be maintained due to the antagonistic interaction between traits. If this is the case we would expect that at least one of each pair of such traits will have a high heritability and there will be a high genetic correlation between the traits, the sign of which will depend upon the particular traits. Estimates of the heritabilities, phenotypic and genetic

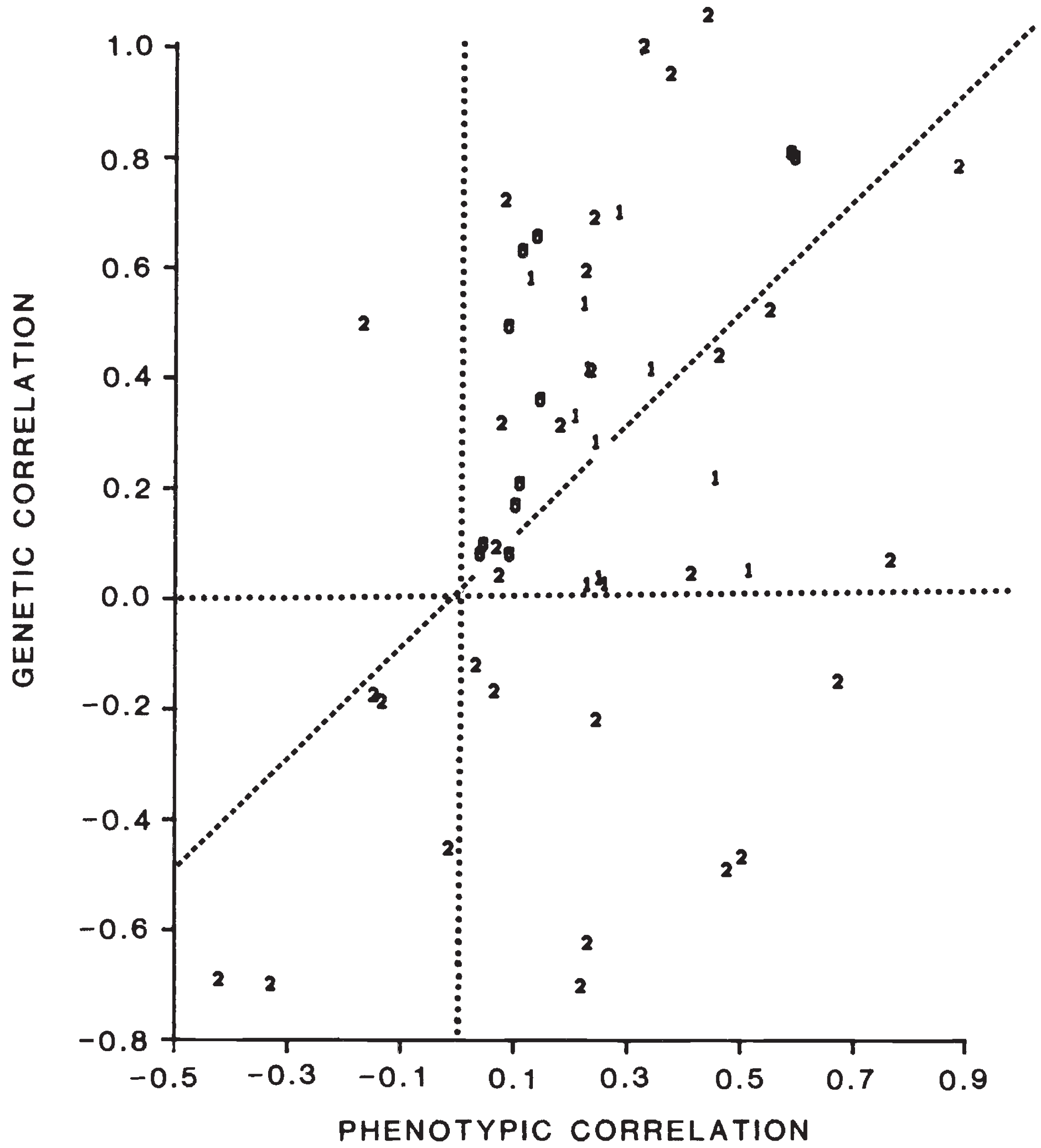

Figure 7 Scatter plot of genetic correlation on phenotypic correlation. 0; correlation between two morphological traits. 1; Correlation between a morphological and life history trait. 2; Correlation between two life history traits. Dotted lines indicate *x* and *y* axes and line of equality. All data from outbred stocks. Data from Clayton *et al.* (1957), Frahm and Kojima (1966), Giesel *et al.* (1982), Mackay (1981), Robertson (1953), Rose and Charlesworth (1981*a*), Sheridan *et al.* (1968), Tantawy and El-Helw (1966, 1970), Tantawy and Rakha (1964).

Table 1 The heritabilities, phenotypic and genetic correlations of egg production and longevity in wild, outbred stocks of *D. melanogaster* and *D. simulans*.

Egg production			Longevity		Phenotypic	Genetic	
	h^2	S.E.	h^2	S.E.	correlation	correlation	Reference
Lifetime	7·2	—	14·2	—	0·78	0·07	Tantawy and El-Helw (1966)
Lifetime	2·6	5·2	11·3	8·6	0·76	0·06	Tantawy and Rakha (1964)
Lifetime (simulans)	11·1	7·4	14·6	9·0	0·40	0·03	Tantawy and Rakha (1964)
Days 1–5	62·3	—	2·8	—	−0·215	-1·43	Rose and Charlesworth (1981*a*)
Days 6–10	29·6	—	2·8	—	0·171	0·30	Rose and Charlesworth (1981*a*)
Days 11–15	31·6	—	2·8	—	0·210	−0·71	Rose and Charlesworth (1981*a*)
Last third	18·9	26·4	56·0	30·2	−0·177	0·49	Giesel *et al* (1982)
Peak	52·9	30·1	56·0	30·2	0·429	1·04	Giesel *et al.* (1982)
Day 2	91·1	29·4	56·0	30·2	0·216	0·578	Giesel *et al.* (1982)

correlations of egg production and longevity are given in table 1. The estimates by Tantawy and his coworkers are "best" in the sense of being derived by a reliable method (offspring on parent regression) and having standard errors. The estimates of Rose and Charlesworth (1981*a*) are deficient in not having standard errors (though the data of Service and Rose (1985) suggest that the estimates are not unreliable) while those of Giesel *et al.* (1982) are derived only from full sib analysis and have large standard errors. The data of Tantawy and his coworkers indicate a low heritability for the two traits, a high phenotypic correlation and a low genetic correlation. In contrast, Rose and Charlesworth (1981*a*) found a high heritability for egg production but a low heritability for longevity. In all cases the genetic correlations are much larger in absolute magnitude than those of Tantawy *et al.* and in two cases are negative as expected by the variable pleiotropy hypothesis. Giesel *et al.* (1982) found high heritabilities for both egg production and longevity but the method of estimation and large standard errors make interpretation difficult. In no case is the genetic correlation negative. However, as the outbred lines were obtained by crossing a number of inbred lines (originating from the same geographic location) the results of Giesel *et al.* (1982) may be questionable (Rose, 1984).

These data suggest that, while the variable pleiotropy hypothesis is attractive, more studies, appropriately designed, are required to test its generality.

CONCLUSIONS

The large variability in the data set indicates that no general conclusions can be reached from single experiments, no matter how well designed or executed: it is easy to pick two heritability estimates from among the life history and morphology groups from which one could draw totally opposite conclusions. There is a need for better estimates of the amount of genetic variation in life history traits, these apparently being particularly prone to considerable error.

Despite biases and large confidence intervals about many estimates of heritability the data strongly suggest that life history traits do have consistently lower heritabilities than morphological traits but possibly not behavioural traits. However, there is considerable variation and life history traits may under some circumstances have large heritabilities. Negative genetic correlations between life history traits support the variable pleiotropy hypothesis but do not rule out the influence of other factors such as environmental variability (Mackay, 1980, 1981), or mutation rate (Hill, 1982) in maintaining high heritability of life history traits in *Drosophila*.

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Appendix 1 A listing of the data plotted in figs 3, 4, 5 and 6

Trait/ study code	Species*	Trait	Estimation method†	S.E.‡	Table§	Reference
Morphology						
1	m	thorax length	0, 4	Y	10	Reeve and Robertson (1953)
2	m	thorax length	1	Y	2	Robertson (1955)
3	m	thorax length	1	N	2	Robertson (1960)
4	m	thorax length	1, 4	Y	5, 8	Robertson (1957)
5	m	thorax length	1	Y	p. 210	Baptist and Robertson (1976)
6	m	thorax length	0	Y	1	Tantawy (1956*a*)
7	m	thorax length	0	Y	2	Tantawy (1956*b*)
8	m	thorax length	0	Y	4	Tantawy and Rakha (1964)
9	m	thorax length	0	Y	1	Tantawy and Tayel (1970)
10	m	thorax length	0	Y	7	Tantawy and El-Helw (1970)
11	m	thorax length	0	N	p. 544	van Dijken and Scharloo (1979)
12	s	thorax length	0	Y	4	Tantawy and Rakha (1964)
13	p	thorax length	0	N	5	Tantaway (1961)
14	m	wing length	0, 4	Y	10	Reeve and Robertson (1953)
15	m	wing length	1	N	3	Robertson and Reeve (1952)
16	m	wing length	0	Y	1	Tantaway (1956*a*)
17	m	wing length	0, 1	Y	2	Tantawy (1956*b*)
18	m	wing length	3	Y	3	Tantawy (1964)
19	m	wing length	0	Y	2	Tantawy *et al.* (1964)
20	m	wing length	0	N	1	Tantawy and El-Helw (1966)
21	m	wing length	0	Y	3	Tantawy and Rakha (1964)
22	m	wing length	0	N	1	Tantawy and Tayel (1970)
23	m	wing length	1	N	p. 130	Latter and Robertson (1962)
24	m, s	wing length	1	N	2	Aguadé *et al.* (1981)
25	s	wing length	0	Y	4	Tantawy and Rakha (1964)
25	s	wing length	0	Y	2	Tantawy *et al.* (1964)
26	s	wing length	3	Y	3	Tantawy (1964)
27	p	wing length	0	N	5	Tantawy (1961)
28	sub	wing length	1	Y	1	Prevosti (1967)
29	p	body weight	1, 3	N	1	Frahm and Kojima (1966)
30	m	body weight	0	Y	8	Mackay (1981)
31	m	wing:thorax ratio	1	Y	p. 172	Robertson (1962)
32	m	ovariole Nos.	1	Y	3	Robertson (1957*a*)
33	sub	occelli Nos.	1	N	p. 200	Sondhi (1960)
34	m	sternopleural bristles 2 sides	1, 2	Y	p. 208	Latter (1964)
35	m	sternopleural bristles 2 sides	0	Y	3	Lopez-Fanjul and Hill (1973*b*)
36	m	sternopleural bristles 2 sides	1, 2	N	1	Reeve (1960)
37	m	sternopleural bristles 2 sides	0, 1	Y	1	Lopez-Fanjul and Hill (1973*a*)
38	m	sternopleural bristles 2 sides	0	Y	3	Lopez-Fanjul and Hill (1973*b*)
39	m	sternopleural bristles 2 sides	0	Y	1, 2	Mackay (1981)
40	m	sternopleural bristles 2 sides	0, 1	Y	1	Gallego and Lopez-Fanjul (1983)
41	m	sternopleural bristles 2 sides	?	N	p. 544	van Dijken and Scharloo (1979)
42	m	sternopleural bristles 2 sides	1	N	1	Yousif and Skibinski (1982)
43	m, i	sternopleural bristles 2 sides	1	N	p. 201	Lints *et al.* (1979)
44	m	sternopleural bristles 2 sides	0, 3	N	1, 3, 4	Beardmore *et al.* (1975)
45	m	sternopleural bristles 1 side	1	Y	p. 208	Latter (1964)
46	m	sternopleural bristles 1 side	0, 2	Y	10	Sheridan *et al.* (1968)
47	m	sternopleural bristles 1 side	1, 4	Y	p. 202, 5	Sen and Robertson (1964)
48	m	sternopleural bristles $\lvert L-R \rvert$	2	N	2	Reeve (1960)
49	m	abdominal bristles 2 sternites	1, 2	Y	p. 207	Latter (1964)
50	m	abdominal bristles 2 sternites	0, 2	Y	5	Sheridan *et al.* (1968)
51	m	abdominal bristles 2 sternites	0, 1, 3, 4	Y	p. 135	Clayton *et al.* (1957)
52	m	abdominal bristles 2 sternites	1	N	p. 120	Latter and Robertson (1962)
53	m	abdominal bristles 2 sternites	1	Y	12	Bowman (1962)
54	m	abdominal bristles 2 sternites	0, 1	Y	6, 1	Sorenson and Hill (1982, 1983)
55	m	abdominal bristles 2 sternites	0, 2	Y	4, 5	Mackay (1981)
56	m	abdominal bristles 1 sternite	2	Y	p. 207	Latter (1964)
57	m	abdominal bristles 1 sternite	2	Y	3, 4, 5	Sheridan *et al.* (1968)
58	m	abdominal bristles 1 sternite	1, 4	Y	p. 202, 5	Sen and Robertson (1964)

Appendix 1 continued

Trait/ study code	Species*	Trait	Estimation method†	S.E.‡	Table§	Reference
59	m	abdominal bristles 1 sternite	2	N	—	Reeve and Robertson (1954)
60	m	abdominal bristles 1 sternite	2	Y	1	Yoo (1980)
61	m	abdominal bristles 1 sternite	1	N	3	Frankham *et al.* (1968*a*)
62	m	abdominal bristles total Nos.	2	Y	p. 186	Sheridan et al. (1968)
63	m	scuttellar bristles	2	N	3	Latter (1964)
64	m	2nd coxal	0, 2	Y	11, 12, 13	Sheridan *et al.* (1968)
65	m, s	aristal bristles	1	Y	p. 299	Pyle and Richmond (1979)
66	m	interocellar bristles	0	Y	6	Creus (1980)
67	m	interocellar bristles	?	N	—	Marcos (1977) (cited by Creus, 1980)
Behaviour						
1	m	phototaxis	2	N	p. 650	Hirsch and Boudreau (1958)
2	m, s	phototaxis	2	N	p. 1274	Hadler (1964)
3	m	phototaxis	1	Y	2	Choo (1975*a*)
4	m	phototaxis	1	Y	p. 363	Choo (1975*b*)
5	m, s	phototaxis	1	N	p. 284	Markow and Clark (1984)
6	s, s	phototaxis	1	Y	1	Markow and Smith (1977)
7	a	phototaxis	1	Y	1	Markow and Smith (1979)
8	p	phototaxis	1	Y	p. 32	Dobzhansky and Spassky (1967)
9	p	phototaxis	1	Y	5	Dobzhansky *et al.* (1969)
10	p	phototaxis	0	Y	1	Richmond (1969)
11	pers, s	phototaxis	1	Y	2	Polivanov (1975)
12	sub	phototaxis	1	N	2	Kekic and Marinkovic (1974)
13	m	geotaxis	1	Y	p. 78	Watanabe and Anderson (1976)
14	p	geotaxis	1	Y	p. 32	Dobzhansky and Spassky (1967)
15	p	geotaxis	1	Y	5	Dobzhansky *et al.* (1969)
16	p	geotaxis	0	Y	1	Richmond (1969)
17	pers, s	geotaxis	1	Y	2	Polivanov (1975)
18	m	mating speed	1	N	p. 84	Manning (1961)
19	m, s	repeat mating	1	N	p. 136	Pyle and Gromko (1981)
20	m, i	wing vibration	1	Y	p. 582	McDonald (1979)
21	m, s	mating speed	2	N	6	Parsons (1964)
22	m, s	mating speed	2	N	p. 205	Fulker (1966)
23	m, s	copulation duration	2	N	p. 102	MacBean and Parsons (1966)
24	p, s	mating speed	1	Y	p. 424	Kessler (1969)
25	p, s	mating speed	1	Y	1	Spuhler *et al.* (1978)
26	s, s	wing display	1	Y	p. 451	Wood and Ringo (1982)
27	pers, is	mating speed	1	N	4	Spiess and Yu (1975)
28	sub	copulation ability	0	Y	2	Andjelkovic and Marinkovic (1983)
29	merc, s	pulse interval	1	Y	p. 247	Ikedo and Maruo (1982)
30	m	locomotion	0	Y	p. 455	Connolly (1966)
31	m	locomotion	0, 1	Y	2	van Dijken and Scharloo (1979)
32	m	walking speed	1	Y	2	Choo (1975*c*)
33	m, s	walking speed	1	Y	p. 635	Grant and Mettler (1969)
34	m, s	anemotaxis	1	Y	p. 285	Johnston (1982)
35	s, s	pupation height	1	Y	p. 20	Ringo and Wood (1983)
36	m, s	pupation height	1	Y	p. 214	Markow (1979)
37	m, s	oviposition preference	1	N	2	Fogleman (1979)
38	m, s	larval feeding rate	1	Y	1	Sewell *et al.* (1975)
Physiology						
1	mim	water loss	0	Y	4.1.1	Steiner (1974)
2	m	water loss	0	N	p. 434	Eckstrand (1981)
3	m	enzyme activity	2	N	p. 416	Birley and Barnes (1973)
4	m	ether resistance	2	N	p. 212	Deery and Parsons (1972)
5	p	enzyme activity	1	Y	3	Powell and Lichetenfels (1979)
Life history						
1	m	hatching-pupation	1	N	p. 266	Sang and Clayton (1957)
2	m, s	egg-adult	1	N	p. 93, 95	Sang (1962)
3	m	egg-adult	1	N	8	Prout (1962)

Appendix 1 continued

Trait/ study code	Species*	Trait	Estimation method†	S.E.‡	Table§	Reference
4	m	development time (various)	0	Y	7	Tantawy and El-Helw (1970)
5	sub, s	development time	1, 3	Y	p. 72	Clarke *et al.* (1961)
6	m	fecundity	1	N	p. 436	Robertson (1957*b*)
7	m	fecundity	0	Y	4	Tantawy and Rakha (1964)
8	m	fecundity	0	Y	7	Tantawy and El-Helw (1970)
9	m	fecundity	2	N	1, 2	Rose and Charlesworth (1981*a*)
10	s	fecundity	0	Y	4	Tantawy and Rakha (1964)
11	m	longevity	0	Y	1	Tantawy and El-Helw (1966)
12	m	longevity	0	Y	7	Tantawy and El-Helw (1970)
13	m	longevity	0	Y	4	Tantawy and Rakha (1964)
14	m, i	longevity	1	N	p. 200	Lints *et al.* (1979)
15	m	longevity	2	N	1, 2	Rose and Charlesworth (1981a)
16	s	longevity	0	Y	4	Tantawy and Rakha (1964)
17	m	productivity	0	Y	7	Tantawy and El-Helw (1970)
18	m	last day	2	N	1, 2	Rose and Charlesworth (1981a)
19	m	laying rate	2	N	1, 2	Rose and Charlesworth (1981a)
20	m	sex ratio	1	Y	p. 199	Toro and Charlesworth (1982)

*m, *D. melanogaster*; s, *D. simulans*; p, *D. pseudoobscura*; sub, *D. subobscura*; pers., *D. persimilis*; merc, *D. mercatorum*; a, *D. ananassae*; mim, *D. mimica*; ,s, synthetic stock generated by crossing 2 or more strains; i, inbred stock.

† 0, offspring on parent regression; 1, selection; 2, Miscellaneous methods, principally ANOVA; 3, Half sib analysis; 4, Full sib analysis.

‡ Y, at least one h^2 estimate has an associated SE: these are plotted in Fig. 4; N, no S.E. given.

§ Denotes the table or, if prefixed by 'p', the page from whence the data are drawn.