

Natural selection and the heritability of fitness components

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The hypothesis that traits closely associated with fitness will generally possess lower heritabilities than traits more loosely connected with fitness is tested using 1120 narrow sense heritability estimates for wild, outbred animal populations, collected from the published record. Our results indicate that life history traits generally possess lower heritabilities than morphological traits, and that the means, medians, and cumulative frequency distributions of behavioural and physiological traits are intermediate between life history and morphological traits. These findings are consistent with popular interpretations of Fisher's (1930, 1958) Fundamental Theorem of Natural Selection, and Falconer (1960, 1981), but also indicate that high heritabilities are maintained within natural populations even for traits believed to be under strong selection. It is also found that the heritability of morphological traits is significantly lower for ectotherms than it is for endotherms which may in part be a result of the strong correlation between life history and body size for many ectotherms.

INTRODUCTION

The fundamental theorem of natural selection states: "The rate of increase in fitness of any organism at any time is equal to its genetic variance in fitness at that time" (Fisher, 1930). Fisher's theorem is axiomatic to much of current evolutionary research. It has been variously interpreted but is generally construed to imply that traits that have been closely and consistently associated with fitness will exhibit low additive genetic variances as a result of natural selection (e.g., Hegmann and Dingle, 1982; Lynch and Sulzbach, 1984; Riddel *et al.*, 1981). However, the validity of the fundamental theorem is dependent upon many assumptions that may not usually be met by natural populations (e.g., population equilibrium, weak selection, constancy of genotypic fitnesses over time, and independence of genotypic frequencies) (Charlesworth, 1987). The maintenance of low additive genetic variance has also been inferred to imply low heritability (in the narrow sense); "On the whole, characters with the lowest heritabilities are those most closely connected with fitness, while characters with the highest heritabilities are those that might be judged on biological grounds to be the least important as determinants of natural selection." (Falconer, 1960, 1981.) The most exten-

sive compilation of data in support of this view is that presented in table 10.1 of Falconer (1981). However, these data are rather few and derived primarily from domestic animals, which may be partly inbred. Extension to wild, outbred organisms may be erroneous.

It is possible that some significant amount of additive genetic variance can be maintained within natural populations, even for characters tightly connected to fitness; possible mechanisms include mutation (Lande, 1976; Turelli, 1984), heterozygote advantage (Falconer, 1981), frequency dependence (Bulmer, 1980), fluctuating environments (Ewing, 1979) and migration (Felsenstein, 1976). In addition, zero additive genetic variance in fitness is consistent with positive heritability estimates of fitness components when there exists negative genetic correlations between components (Rose and Charlesworth, 1981).

It is in response to the importance the views of Fisher (1930, 1958) and Falconer (1960, 1981) have reached in the ecological literature, and the concurrent lack of rigorously examined empirical support for these views, that we have undertaken the compilation, analysis, and interpretation of the extensive quantity of data concerning genetic variation within natural populations now available from the published record.

In this paper we address two questions: (a) What is the heritability of traits closely associated with fitness? Do traits that are directly connected to fitness tend to have lower heritabilities than traits more loosely associated with fitness as proposed by Falconer (1960, 1981) and suggested by Fisher (1930, 1958)? If we find this to be not the case a serious reevaluation of current evolutionary thinking would be necessary. (b) Do patterns of genetic variability change from taxa to taxa? If so, this might suggest phylogenetically determined constraints upon rates of evolution.

The data set

The data set comprises 1120 narrow sense heritability estimates collected from 140 sources, representing 75 species. Heritability estimates for the *Drosophila* genus were excluded from the present study as they are treated elsewhere (Roff and Mousseau, 1987). The only prerequisite for inclusion in the data set was that the heritability estimate be derived from a wild, outbred stock; so as to avoid biases potentially introduced through our literature reviewing process, the data were in no other way screened or selected. This compilation is the most extensive of its kind but is not exhaustive. A list of the sources, divided according to species, is given in an appendix.

For the purposes of analysis we define four categories of traits: (a) behavioural traits, (b) life history traits, (c) morphological traits, and (d) physiological traits. We have restricted the term "life history trait" to those characters that are directly and invariably connected to fitness. Some examples of life history traits are fecundity, viability, survival, and development rate. Morphological traits include body size, wing size, and other metric characters. Behavioural and physiological traits are much less widely reported than life history or morphological traits. Examples of behavioural traits are alarm reaction, activity level, and sensitivity to conditioning. Physiological traits include oxygen consumption, resistance to heat stress, and body temperature.

The composition of the data set, divided according to trait type and taxonomic assignment is presented in fig. 1. A total of 341 life history traits, 570 morphological traits, 104 physiological traits, and 105 behavioural traits are represented within the data set. Alternatively, there are 414 heritability estimates for invertebrates, 460 estimates for ectothermic vertebrates (reptiles, amphibians, and fishes), and 246 estimates for endothermic vertebrates (birds and mammals). These taxonomic designations reflect divisions between groupings of biological and ecological significance, and an attempt to maintain statistically sufficient sample sizes within each grouping.

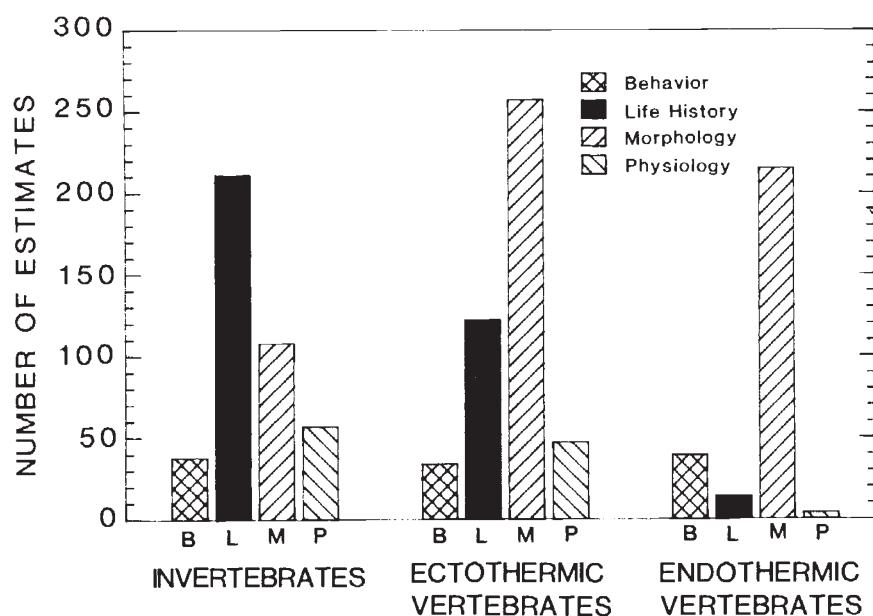


Figure 1 The number of reported heritability estimates grouped according to trait type and taxonomic assignment.

The analysis

I. Methods of heritability estimation

Are estimates of additive genetic variances seriously biased by the methods of calculation? It is widely accepted that published estimates of quantitative genetic parameters are seldom free from biases introduced by inbreeding, assortative mating, dominance, maternal effects, non-additive genetic variances, and non-random sampling of genotypes from natural populations etc. (Mitchell-Olds and Rutledge, 1986). Given the heterogeneous nature of our data set, we commence this investigation with a comparison of heritability estimates generated using different methods of calculation. The outcome of this examination will dictate whether it is necessary to include the method of estimation as a factor in the analyses to follow.

The most commonly employed methods of heritability estimation within our data set are the parent-offspring regression ($n = 341$) and the full-sib correlation ($n = 463$) designs. The realised ($n = 133$) and half-sib ($n = 176$) designs are much less frequently utilized and as a result, insufficiently represented for the analyses to follow.

Theory (Falconer, 1981) predicts that within a given population, for a given trait, estimates generated using the full-sib design will usually be higher or equal to those produced using the parent-offspring method. This results primarily from the covariance of full sibs being inflated by environmental variance between families and by dominance variance (Falconer, 1981).

The simplest and most convincing manner in which to approach this question is to compare heritability estimates calculated using different methods for the same character within a given population. This approach avoids problems related to the sensitivity of heritability estimates to differences between populations in environmental conditions, past and present (Falconer, 1981).

Table 1 lists 33 paired heritability estimates for a variety of characters, obtained from 11 independent studies, for 9 species. We found that on average, the full-sib design produced estimates that were greater by 0.073 than those obtained using the parent-offspring regression method. In addition, full-sib estimates were higher than parent-offspring estimates for 20 of the 33 cases. However, the results of a paired comparison t -test, a Wilcoxon's signed rank test, and a simple sign test revealed no significant differences between estimates generated using these two methods (table 1).

The relationship between pairs of estimates can be described by the following linear regression equation:

$$FS = 0.72 (\pm 0.15) PO + 0.23 (\pm 0.09), \quad r = 0.65,$$

$$MSE = 0.064, \quad t = 4.74, \quad p < 0.0001$$

where FS and PO are the estimates derived from the full-sib and parent-offspring methods, respectively (fig. 2). Since we are concerned with the functional relationship between heritability estimates generated using the full-sib and parent-offspring methods, and the errors of estimation are roughly comparable for both methods, it is appropriate that we determine the slope of the functional regression using Ricker's (1973) formula:

$$v = b/r$$

where v is the slope of the functional regression, b is the slope obtained using an ordinary linear regression, and r is the correlation coefficient of the relationship. Ricker's (1973) formula is used because simple least-squares linear regressions will tend to seriously underestimate the slope (when r is < 1) if the abscissal (X) observations are subject to natural variability of the same magnitude as the Y observations. We find that once corrected, the slope describing the functional relationship between full-sib and parent-offspring estimates equals 1.10, which is not significantly different from unity.

Even if the lack of statistical significance found between estimates generated using different methods of calculation were primarily due to insufficient data, the bias that might be introduced is sufficiently small (< 10 per cent) to justify the pooling of full-sib and parent-offspring estimates. In any case, the various estimates (full-sib, half-sib, parent-offspring, and realised) were roughly evenly represented in the different trait groupings.

Heritability estimates are frequently reported without standard errors; only 738 of the 1120 estimates collected for this study included standard errors. We found the relationship between the standard error and the heritability estimate to be:

$$SE = 0.172 (\pm 0.014) h^2 + 0.088 (\pm 0.007),$$

$$r = 0.41,$$

$$MSE = 0.14, \quad t = 12, \quad p < 0.0001.$$

Although heritability estimates frequently possess large standard errors, an analysis of variance upon the residuals of the above relationship found no significant difference between the standard errors

Table 1 Within study comparisons of heritability estimates calculated using the parent-offspring (PO) and full-sib (FS) methods of analysis. Paired comparison *t*-test: $D = 0.073$, S.E. = 0.046, $t = 1.71$, $p = 0.10$. Wilcoxon's signed rank test: sum of negative ranks = -193, sum of positive ranks = 368, $p = 0.120$. Sign test: $p = 0.15$

Species	Character	FS	PO	FS - PO	Reference
Invertebrates					
<i>Apis mellifera</i>	chill coma	0.37	0.15	0.22	Hillesheim, 1984
	O ² consumption	0.41	0.13	0.28	Hillesheim, 1984
<i>Eurytemora affinis</i>	temperature tolerance	0.20	0.11	0.09	Bradley, 1982
<i>Eurytemora herdmani</i>	length	0.48	0.12	0.36	McLaren, 1976
	length	0.65	0.54	0.11	McLaren, 1976
<i>Gryllus firmus</i>	wing length	0.64	0.74	-0.1	Roff, 1986b
	wing length	0.62	0.40	0.22	Roff, 1986b
<i>Pseudocalanus</i>	length	0.92	0.98	-0.06	McLaren and Corkett, 1978
<i>Tribolium castaneum</i>	fecundity	0.38	0.36	0.02	Orozco, 1976
	fecundity	0.35	0.30	0.05	Orozco, 1976
Amphibians					
<i>Plethodon cinereus</i>	# of vertebrae	0.57	0.61	-0.04	Highton, 1960
Birds					
<i>Geospiza fortis</i>	weight	0.78	0.91	-0.13	Boag, 1983
	wing length	0.42	0.84	-0.42	Boag, 1983
	tarsus length	0.32	0.71	-0.39	Boag, 1983
	bill length	1.11	0.65	0.46	Boag, 1983
	bill depth	1.12	0.79	0.33	Boag, 1983
	bill width	0.99	0.90	0.09	Boag, 1983
	bill length	0.64	0.35	0.29	Boag, 1983
	weight	0.80	0.91	-0.11	Boag and Grant, 1978
	wing length	0.65	0.63	0.02	Boag and Grant, 1978
	tarsus length	0.27	0.42	-0.15	Boag and Grant, 1978
	bill length	1.34	0.85	0.49	Boag and Grant, 1978
	bill depth	1.41	0.90	0.51	Boag and Grant, 1978
	bill width	0.99	1.03	-0.04	Boag and Grant, 1978
	bill length	0.78	0.41	0.37	Boag and Grant, 1978
<i>Geospiza scandens</i>	weight	0.35	0.58	-0.23	Boag, 1983
	wing length	0.35	0.12	0.23	Boag, 1983
	tarsus length	0.88	0.92	-0.04	Boag, 1983
	bill length	0.30	0.32	-0.02	Boag, 1983
	bill depth	0.56	0.14	0.42	Boag, 1983
	bill width	0.56	0.34	0.22	Boag, 1983
	bill length	0.06	0.60	-0.54	Boag, 1983

associated with estimates generated using the full-sib and parent-offspring methods of calculation ($F = 1.7$, $p > 0.2$, $n = 659$).

The above results suggest that there is no apparent bias introduced to the data set by the method of heritability estimation; Roff and Mousseau (1987) obtained a similar result for *Drosophila* when comparing parent-offspring estimates with half-sib and realised estimates. The method of heritability estimation will not be considered further in this study.

II. Heritability and fitness

Classical theory (e.g., Falconer, 1960; Fisher, 1930) predicts that traits closely associated with fitness

will have low heritabilities while more distantly related traits should have higher heritabilities. If this is indeed the case for natural populations we would expect life history traits to possess, on average, lower heritabilities than morphological traits. It is more difficult to predict *a priori* the relationship between fitness and behavioural and physiological traits. Falconer's compilation (1981, table 10.1, p. 150) would suggest that physiological traits are intermediate between life history traits and morphological traits with respect to average heritabilities. It has been proposed that many behavioural traits will be under strong stabilising selection (Lee and Parsons, 1968), and as a result, possess low heritabilities. It seems only reasonable to suppose that traits such as food conversion

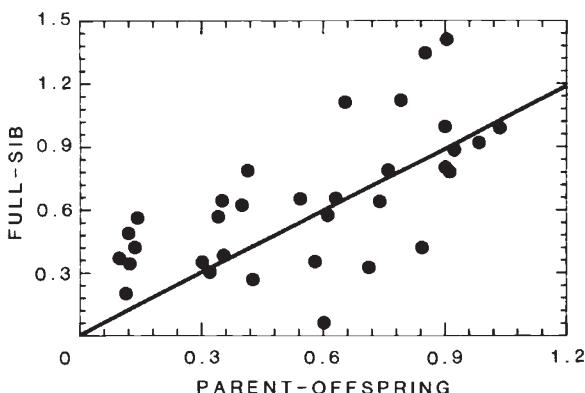


Figure 2 A scatterplot showing the relationship between paired heritability estimates generated using full-sib correlation and parent-offspring regression methods of estimation for the same population ($r = 0.62$). The slope of the plotted line represents a 1:1 correspondence.

efficiency and mating propensity are more closely connected to fitness than morphological traits. However, this assumption must be viewed cautiously as fecundity and development time in ectotherms are tightly correlated with body size, a morphological trait (Kusano, 1982; Peters, 1983; Roff, 1981, 1984, 1986a). For this reason we do not make any predictions concerning the ranking of heritabilities of morphology, behaviour, and physiology, but rather, use the data to discern whatever pattern might exist.

All analyses were performed using an IBM PC; complete descriptions of the statistical tests employed can be found in Sokal and Rohlf (1981). The use of non-parametric statistics (e.g., the Kolmogorov-Smirnov test, and the Kruskal-Wallis test) have been emphasized in our analyses in order to avoid the violation of assumptions associated with the use of more traditional parametric statistics (e.g., normality, homogeneity of variances).

Our analysis of the data has been arranged in a hierarchical manner, organised into four progressively finer scaled lines of investigation: (a) The analysis of the entire data set. (b) The analysis of median heritability values of each character, for a given species. This approach will allow the elimination of biases in the data set due to over-representation of particular characters and species, and will negate the influence held by outliers. (c) The analysis of random subsamples of the data set. The objective of this approach is to assess the stability of any patterns that have emerged from the previous analyses. (d) The paired comparison of life history and morphological traits derived from identical populations and studies.

The entire data set

At this resolution, our analysis is directed towards the illumination of gross patterns of variation. We ignore potential biases introduced via the over-representation of certain species and characters, and the effect of outliers.

Figure 3 shows the cumulative distribution frequencies of the four trait groupings; table 2 lists descriptive statistics and the results of Kolmogorov-Smirnov tests upon paired comparisons of each of the cumulative distributions. The results indicate that life history traits are generally much lower than morphological traits, and that behavioural and physiological traits tend to fall in the middle. This pattern is consistent with the observed means, medians, and cumulative distribution frequencies, and is supported by the results of a one-way ANOVA ($F = 39.7$, $p < 0.0001$, $df = 1119$) and a Kruskal-Wallis test ($H = 106$, $p < 0.0001$, $n = 1120$). Furthermore, the ANOVA and Kruskal-Wallis tests yield significant statistics even when morphological traits are excluded ($F = 5.0$, $p < 0.007$, $df = 549$; $H = 7.22$, $p < 0.027$, $n = 550$).

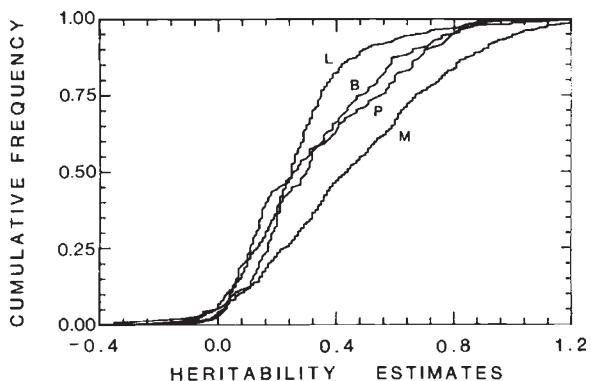


Figure 3 The cumulative frequency distributions of the four trait categories (L = life history, B = behaviour, P = physiology, and M = morphology) for the entire data set. Note that data points are joined by straight lines.

The analysis of median values

Frequently, multiple heritability estimates have been reported for a given character and species. For the following analysis we have confined our interest to the median of the range in estimates reported for each character of each species.

Figure 4 shows the cumulative distribution frequencies of the four trait categories. A summary of descriptive statistics and the results of Kolmogorov-Smirnov tests upon the paired comparisons of each distribution is given in table 3.

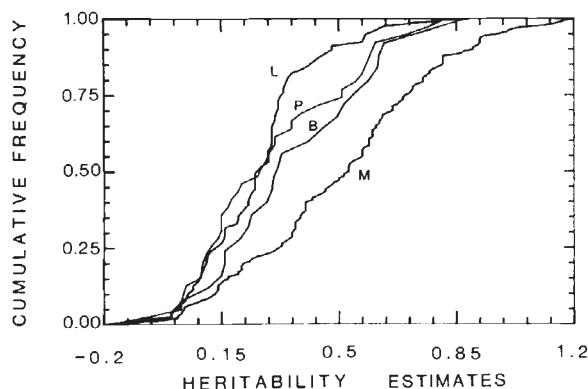


Figure 4 The cumulative frequency distributions of the four trait categories (L = life history, B = behaviour, P = physiology, and M = morphology) for median heritability values for each character of each species. Note that data points are joined by straight lines.

The results of this analysis are qualitatively similar to those obtained for the larger data set; the rankings of the means, medians, and cumulative distributions are identical. The main difference resulting from the use of medians is the lack of significance found by the Kolmogorov-Smirnov test upon comparisons between the cumulative distributions of life history traits and physiological and behavioural traits. Given that the rankings and absolute values are very similar to those obtained for the larger data set, we conclude that this lack of significance is primarily due to the drastically reduced sample sizes and the conservative nature of the Kolmogorov-Smirnov test. The results of a Kruskal-Wallis test and a one-way ANOVA indicate that trait is indeed an important factor governing the patterns of variance within the median data set ($H = 47.4, p < 0.0001, n = 283$; $F = 18.7, p < 0.0001, df = 282$), but only when morphological traits are included in the analysis (without mor-

phology: $H = 3.94, p > 0.13, n = 142$; $F = 2.83, p > 0.06, df = 140$).

Random sampling of the data set

For this analysis, as an alternative to using median values for a character, a representative estimate was selected at random. For example, a total of ten heritability estimates for age at maturity were collected for the rainbow trout *Salmo gairdneri*. Of those 10 estimates, one was randomly chosen to represent this character, for this species. This process was repeated for all characters and species with multiple estimates to generate a randomly selected subset of the larger data set. The entire process was repeated to provide 25 such subsets and all tests were performed individually upon each subset. As with the use of medians, this approach eliminates biases due to the over-representation of particular characters and species.

We found that generally, the results obtained from the random sampling of the data set were statistically similar to those found using median values (table 4). In only one out of 150 comparisons did the results contradict those obtained using medians. Overall, we conclude that the pattern of trait rankings derived from the median data set is robust to the variance contained within the larger data set.

The paired comparison of fitness and non-fitness traits

The objective of this analysis was to make comparisons of traits independently of the species and study from which they were derived. To meet this objective we have collected data from 10 sources and 9 species where estimates for life history and morphological traits have been reported for the same population (table 5). We have confined our

Table 2 Summary of descriptive statistics and Kolmogorov-Smirnov tests (D_{\max}) for all data

	Life history	Physiology	Behaviour	Morphology
n	341	104	105	570
\bar{x}	0.262	0.330	0.302	0.461
S.E.	0.012	0.027	0.023	0.004
median	0.250	0.262	0.280	0.428
D_{\max}				
Physiology	0.199 $p < 0.0003$			
Behaviour	0.154 $p < 0.04$	0.123 $p > 0.3$		
Morphology	0.390 $p < 0.0001$	0.220 $p < 0.0001$	0.338 $p < 0.0001$	

Table 3 Summary of descriptive statistics and Kolmogorov-Smirnov tests (D_{\max}) for character medians

	Life history	Physiology	Behaviour	Morphology
<i>n</i>	79	39	25	140
\bar{x}	0.265	0.308	0.374	0.511
S.E.	0.028	0.040	0.050	0.021
median	0.260	0.270	0.320	0.530
D_{\max}				
Physiology	0.194			
	$p > 0.28$			
Behaviour	0.298	0.199		
	$p > 0.19$	$p > 0.9$		
Morphology	0.562	0.373	0.366	
	$p < 0.0001$	$p < 0.0001$	$p < 0.0007$	

focus to life history and morphological traits because this is the comparison of greatest concern, and also because there were insufficient data to examine the other trait categories. Where multiple estimates were reported for either of the trait types, the median value was used. The results do not differ if means are substituted for medians.

It was found that life history traits tended to possess lower heritabilities than morphological traits. The heritability of morphological traits was higher than life history traits in 11 of the 14 populations. The average difference between the two trait groupings was 0.15, with the results of a paired comparison *t*-test, a Wilcoxon's signed rank test, and a simple sign test statistically supporting the significance of this difference (table 5).

Heritability and phylogeny

In this section of the paper we address the question: Do patterns of heritability vary from taxa to taxa? It is apparent that there exist developmental constraints related to evolutionary history that may have led to differences between taxonomic groups with respect to the additive genetic variance of

various characters. For example, it is well established that fecundity and body size are positively correlated in many ectothermic species (e.g., fish, spiders, salamanders, aquatic ectotherms), and that this correlation is insignificant or negative for birds and mammals (Kusano, 1982; Peters, 1983, p. 279; Roff, 1981, 1984, 1986a). This would suggest that morphological traits related to body size will possess lower heritabilities in ectothermic organisms than in endotherms.

In the following analysis we have examined patterns of heritability variation within four major phylogenetic groupings. Because of the need to maintain sample sizes sufficient for statistical analysis, we have limited our interest to the comparison of invertebrates versus vertebrates and ectotherms versus endotherms for life history and morphological traits.

Kolmogorov-Smirnov tests upon the cumulative distributions (fig. 5) indicate that ectotherms have lower heritabilities for morphological traits than do endotherms ($D_{\max} = 0.23, p < 0.0001$). Thus result is reinforced by a Mann-Whitney U-test ($z = 5.65, p < 0.0001, n_1 = 365, n_2 = 215$) and a *t*-test ($t = -6.0, p < 0.0001, df = 578$). In contrast,

Table 4 Summary of the results obtained from Kolmogorov-Smirnov tests upon comparisons of trait types within randomly generated data sets. The number given represents the number of tests (out of 25) which fell into a given significance level. For example, comparisons between life history and morphological traits yielded a D_{\max} which was significant at $p < 0.0001$ for 25 of the 25 randomly generated data sets

	Life history vs.			Morphology vs.		Behaviour vs.
	Morphology	Physiology	Behaviour	Behaviour	Physiology	Physiology
N.S.	—	25	24	—	—	25
$p < 0.05$	—	—	1*	4	16	—
$p < 0.01$	—	—	—	21	9	—
$p < 0.0001$	25	—	—	—	—	—

* Contrary to results obtained using medians.

N.S. = Not significant.

Table 5 Within study comparison of traits. Estimates represent median values for trait. Sample sizes are given in parentheses. Paired comparison *t*-test: $D = -0.15$, S.E. = 0.061, $t = -2.3$, $p = 0.038$. Wilcoxon's signed rank test: sum of negative ranks = -88, sum of positive ranks = 17; $p = 0.012$. Sign test: $p = 0.029$

Species	Life history	Morphology	L-M	Reference
<i>Crassostrea gigas</i> (oyster)	0.200 (2)	0.325 (14)	-0.125	Lannan, 1972
<i>Dysdercus bimaculatus</i> (cotton stainer bug)	0.193 (6)	0.515 (1)	-0.372	Derr, 1980
<i>Eurytemora herdmani</i> (copepod)	0.115 (12)	0.615 (8)	-0.500	McLaren, 1976
<i>Gambusia affinis</i> (mosquitofish)	0.285 (2)	0.745 (2)	-0.460	Busack and Gall, 1983
<i>Homarus americanus</i> (American lobster)	0.200 (24)	0.360 (20)	-0.160	Fairful <i>et al.</i> , 1981
<i>Oncopeltus fasciatus</i> (milkweed bug)	0.240 (9)	0.375 (2)	-0.135	Hegmann and Dingle, 1982
<i>Pseudocalanus</i> (copepod)	0.385 (6)	0.458 (2)	-0.073	McLaren and Corkett, 1978
<i>Salmo gairdneri</i>	0.230 (1) 0.180 (1) 0.090 (1)	0.405 (2) 0.170 (3) 0.400 (3)	-0.175 +0.010 -0.310	Gall and Gross, 1978a, b Gjerde and Gjedrem, 1984 Gjerde and Gjedrem, 1984
<i>Salmo salar</i> (Atlantic salmon)	0.420 (1) 0.150 (1) 1.000 (1) 0.670 (1)	0.440 (3) 0.540 (3) 0.550 (2) 0.590 (2)	-0.020 -0.390 +0.450 +0.080	Gjerde and Gjedrem, 1984 Gjerde and Gjedrem, 1984 Naevdal <i>et al.</i> , 1976 Naevdal <i>et al.</i> , 1976

neither the mean nor the cumulative distribution of life history traits were significantly different between ectotherms and endotherms (fig. 5; *t*-test $t = -1.63$, $p > 0.1$, $df = 345$; Kolmogorov-Smirnov $D_{max} = 0.37$, $p > 0.05$), although the medians were found to be significantly different (Mann-Whitney U-test: $z = 2.81$, $p < 0.005$, $n_1 = 333$, $n_2 = 14$). The statistical analysis of comparisons between invertebrates and vertebrates (fig. 5) yielded insignificant results for both life history traits (*t*-test $t = 0.76$, $p > 0.4$, $df = 345$; Mann-Whitney U-test $z = -1.16$, $p > 0.25$, $n_1 = 211$, $n_2 = 136$; Kolmogorov-Smirnov $D_{max} = 0.15$, $p > 0.05$), and morphological traits (*t*-test $t = 1.2$, $p > 0.2$, $df = 578$; Mann-Whitney U-test $z = -1.7$, $p > 0.1$, $n_1 = 108$, $n_2 = 472$; Kolmogorov-Smirnov $D_{max} = 0.14$, $p > 0.05$).

DISCUSSION

The notion that traits closely associated with fitness will generally possess lower heritabilities than more distantly related traits, is supported by all segments of our analysis. Our findings extend further support to the views of Fisher (1930, 1958) and Falconer (1960, 1981) concerning the nature of genetic variation within natural populations.

The ranking of trait types that we obtained for animals in general is consistent with that reported for *Drosophila* (Roff and Mousseau, 1987).

However, the estimated means for each category of trait differed dramatically. The mean (± 1 S.E.) heritability values for morphological, life history, and behavioural traits in *Drosophila* (Roff and Mousseau 1987) were 0.32 (± 0.02), 0.12 (± 0.02), and 0.18 (± 0.03) as opposed to 0.46 (± 0.004), 0.26 (± 0.01), and 0.30 (± 0.03) for animals in general (excluding *Drosophila*). This difference is consistent with the results we obtained from our comparison of ectothermic and endothermic organisms (see table 6), and may be related to the close association between life history traits and body size in many ectotherms (Kusano, 1982; Peters, 1983; Roff, 1981, 1984, 1986a).

Our results show that behavioural and physiological traits have heritabilities more like those of life history traits than those of morphological traits. One interpretation of this finding might be that physiological and behavioural traits are subject to constraints similar to those thought to influence fitness traits. In addition, this discovery supports Falconer's (1981) suggestion that physiological traits generally possess heritabilities intermediate between life history and morphological traits, and Lee and Parsons' (1968) contention that behavioural traits will usually be subject to stabilising selection. However, the magnitude of the average heritabilities of these traits suggests that significant genetic variance is maintained within most natural populations, even for traits closely affiliated with fitness.

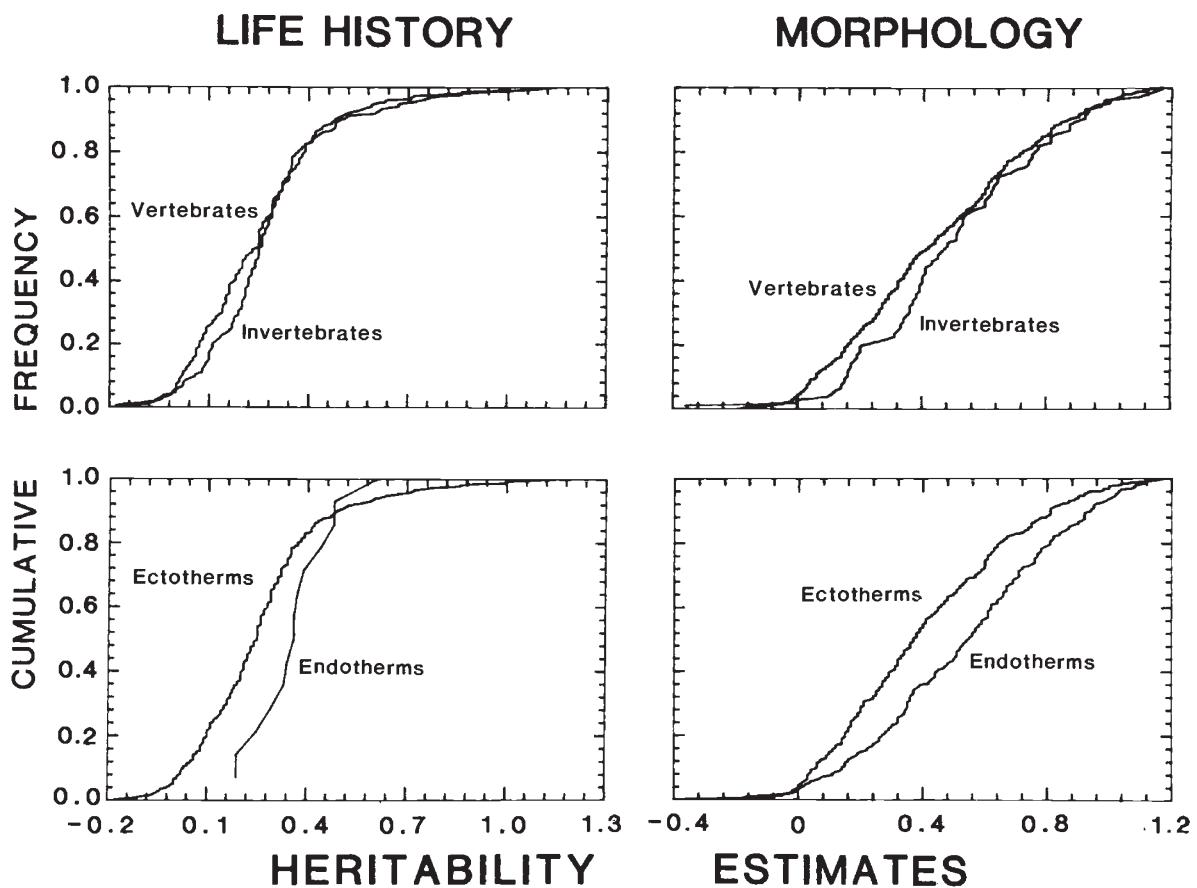


Figure 5 A comparison of the cumulative frequency distributions of ectotherms versus endotherms and vertebrates versus invertebrates for the heritability of life history and morphological traits. Note that data points are joined by straight lines.

Table 6 A comparison of the relative frequencies of heritability estimates. The ectotherm and endotherm data are from this study and are based upon the median by trait data set. The *Drosophila* data are derived from Roff and Mousseau (1987) and is based upon the median by study data set

	# of estimates	Heritability Estimate				
		<20%	20–40%	40–60%	60–80%	>80%
Behaviour						
<i>Drosophila</i>	n = 38	68·4	18·4	7·9	5·3	0
Ectotherms	n = 16	13	38	25	25	0
Endotherms	n = 9	44	22	22	0	11
Life history						
<i>Drosophila</i>	n = 20	80	20	0	0	0
Ectotherms	n = 71	39·4	47·9	8·5	2·8	1·4
Endotherms	n = 8	0	50	37·5	12·5	0
Morphology						
<i>Drosophila</i>	n = 67	16·4	58·2	25·4	0	0
Ectotherms	n = 88	19·3	26·1	23·9	15·9	14·8
Endotherms	n = 52	13·5	17·3	23·1	28·8	17·3

There are many factors which may be responsible for the maintenance of genetic variance of fitness characters. The rate of origin of variation by mutation alone may be sufficient to maintain substantial additive genetic variance within natural populations (Lande, 1976; Turelli, 1984). Heterozygote advantage (Falconer, 1981), frequency dependent selection (Bulmer, 1980), variable selection in heterogeneous environments (Ewing, 1979), diversifying selection (Thoday, 1972), and migration (Felsenstein, 1976) have been proposed as possible mechanisms for the sustenance of genetic variation. Also, significant heritabilities for fitness characters are not inconsistent with zero additive genetic variance in fitness given negative genetic correlations between fitness components (the antagonistic pleiotropy hypothesis). Much support has been generated for this hypothesis (e.g., Luckinbill *et al.*, 1984; Rose, 1982, 1984; Rose and Charlesworth, 1981; Service and Rose, 1985); however others (e.g., Bell, 1984a, 1984b; Giesel, 1986; Murphy *et al.*, 1983; Stearns, 1983) have challenged its generality.

In conclusion, much of what has been generally accepted in the evolutionary literature concerning patterns of genetic variance in natural populations is verified by this study; fitness components do indeed generally possess lower heritabilities than traits believed to be unconnected to fitness. However, the mechanisms by which the high observed heritabilities of fitness components are maintained remains unclear.

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Appendix Listing of species, traits represented, and sources. B = behaviour, L = life history, M = morphology, and P = physiology.

Species	B	L	M	P	Reference
Invertebrates					
<i>Aedes aegypti</i> (mosquito)	*				Duhrkopf and Young, 1979
<i>Apis mellifera</i> (honeybee)		*	*	*	Hillesheim, 1984
<i>Apis mellifera</i> (honeybee)	*	*	*	*	Collings <i>et al.</i> , 1984
		*	*		Milne and Friars, 1984
		*			Oldroyd and Moran, 1983
	*	*		*	Rinder <i>et al.</i> , 1983
	*		*		Soller and Bar-Cohen, 1967
		*			Zawilski, 1972
		*			Cook, 1965
<i>Arianta arbustorum</i> (snail)					
<i>Asellus aquaticus</i> (isopod)			*		Pashkova, 1978
<i>Cepaea nemoralis</i> (pulmonate)			*		Clarke <i>et al.</i> , 1978
<i>Crassostrea virginica</i> (oyster)	*				Newkirk <i>et al.</i> , 1977
<i>C. gigas</i> (Pacific oyster)		*	*		Lannan, 1972
<i>Culex quinquefasciatus</i> (mosquito)				*	Ferrari <i>et al.</i> , 1982
<i>Deloyala guttata</i> (tortoise beetle)	*				Rausher, 1983
<i>Dysdercus bimaculatus</i> (cotton stainer bug)		*	*		Derr, 1980
<i>Ephestria kuehniella</i> (Mediterranean flour moth)			*		Imura, 1980
<i>Eurytemora affinis</i> (copepod)				*	Bradley, 1982
<i>E. herdmani</i> (copepod)		*	*		McLaren, 1976
<i>Glossina morsitans</i> (tsetse fly)			*		Gooding and Holebone, 1976
<i>Gryllus integer</i> (field cricket)	*				Cade, 1981
<i>Heliconius erato</i> (butterfly)			*		Pansera and Aroujo, 1983
<i>Heliothis zea</i> (corn earworm)				*	Holtzer <i>et al.</i> , 1976
<i>Homerus americanus</i> (American lobster)		*	*		Fairfull <i>et al.</i> , 1981
<i>Hyphantria cunea</i> (fall webworm)	*			*	Finley and Haley, 1983
					Morris and Fulton, 1970

Appendix continued

Species	B	L	M	P	Reference
<i>Lygaeus kalmii</i> (milkweed bug)	*				Caldwell and Hegmann, 1969
<i>Macrobrachium rosenbergii</i> (freshwater prawn)		*			Malecha <i>et al.</i> , 1984
<i>Maniola jurtina</i> (meadow brown butterfly)			*		McWhirter, 1969
<i>Musca domestica</i> (house fly)			*		Bryant, 1977
<i>Oncopeltus fasciatus</i> (milkweed bug)	*		*		Dingle <i>et al.</i> , 1977
			*	*	Dingle <i>et al.</i> , 1980
			*	*	Dingle <i>et al.</i> , 1982
<i>Osmia lignaria</i> (megachilid bee)			*		Hegmann and Dingle, 1982
<i>Partula suturalis</i> (snail)			*		Tepedina <i>et al.</i> , 1984
<i>P. taeniata</i> (snail)			*		Murray and Clarke, 1967
<i>Pseudocalanus</i> (copepod)	*		*		Murray and Clarke, 1967
<i>Spirorbis borealis</i> (polychaete worm)	*				McLaren and Corkett, 1978
<i>Tribolium castaneum</i> (flour beetle)	*				Doyle, 1974
	*				Dawson, 1975
	*				Englert and Bell, 1970
	*				Gall, 1971
	*			*	Halliburton and Gall, 1981
	*			*	Lin <i>et al.</i> , 1979
	*			*	Minivielie and Gall, 1980
	*			*	Orozco, 1976
	*			*	Soliman, 1982
Fish					
<i>Apeltes quadratus</i> (fourspine stickleback)			*		Hagen and Blouw, 1983
<i>Coregonus lavaretus</i> (whitefish)			*		Kirpichnikov, 1981
<i>Cyprinus carpio</i> (common carp)	*		*		Brody <i>et al.</i> , 1981
	*		*		Holm and Naevdal, 1978
	*		*		Kirpichnikov, 1981
	*		*		Moav and Wohlfarth, 1976
	*		*		Nagy <i>et al.</i> , 1980
	*		*		Smisek, 1979
	*		*		Busack, 1983
<i>Gambusia affinis</i> (mosquitofish)	*		*		Busack and Gall, 1983
<i>Gasterosteus aculeatus</i> (threespine stickleback)	*		*		Hagen, 1973
<i>Ictalurus punctatus</i> (channel catfish)			*		Bondari, 1983
			*		Dunham and Smitherman, 1983
			*		El-Ibiary and Joyce, 1978
			*		Reagan, 1980
			*		Reagan <i>et al.</i> , 1976
			*		Ryman, 1972, 1973
<i>Lebastes reticulatus</i> (guppyfish)	*				Kirpichnikov, 1981
<i>Macropodus opercular</i>	*				Saxton <i>et al.</i> , 1984
<i>Oncorhynchus kisutch</i> (coho salmon)		*			McIntyre and Amend, 1978
<i>O. nerka</i> (sockeye salmon)			*		Cramer and McIntyre, 1975
<i>O. tshawytscha</i> (chinook salmon)			*		Kirpichnikov, 1981
<i>Oryzias latipes</i>	*				Kirpichnikov, 1981
<i>Poecilia reticulata</i> (guppy)	*				Kirpichnikov, 1981

Appendix continued

Species	B	L	M	P	Reference
<i>Salmo gairdneri</i> (rainbow trout)	*				Aulstad <i>et al.</i> , 1972
	*				Ayles, 1975
	*				Chevassus, 1976
	*				Gall and Gross, 1978a
	*				Gall and Gross, 1978b
	*				Gall, 1975
	*				Gjerde, 1982
	*	*		*	Gjerde and Gjedrem, 1984
	*	*			Gunnes and Gjedrem, 1981
	*	*			Holm and Naevdal, 1978
	*	*			Kanis <i>et al.</i> , 1976
	*	*			Kincaid <i>et al.</i> , 1977
	*	*	*		Kinghorn, 1983a, 1983b
	*				Klupp, 1979
	*				Linder <i>et al.</i> , 1983
	*				McKay <i>et al.</i> , 1984
	*				Moller and Naevdal, 1973
	*				Moller <i>et al.</i> , 1976
	*				Orska, 1963, Refstie, 1980
					Gjedrem and Aulstad, 1974
<i>Salmo salar</i> (Atlantic salmon)	*	*	*		Gjerde and Gjedrem, 1984
	*	*			Gjerde, 1981
	*				Gunnes and Gjedrem, 1978
	*				Holm and Naevdal, 1978
	*				Kanis <i>et al.</i> , 1976
	*				Kinghorn, 1983a, 1983b
	*				Lindroth, 1972
	*				Naevdal <i>et al.</i> , 1975
	*				Naevdal <i>et al.</i> , 1976
	*				Refstie and Stein, 1978
	*				Refstie <i>et al.</i> , 1977
	*				Riddel <i>et al.</i> , 1981
	*				Ryman, 1972
	*				Blanc <i>et al.</i> , 1979
	*				Kanis <i>et al.</i> , 1976
	*				Kirpichnikov, 1981
	*				Kirpichnikov, 1981
<i>Salmo trutta</i> (brown trout)	*				
<i>Tilapia mossambica</i> (tilapia)				*	
<i>T. nilotica</i> (tilapia)				*	Tave and Smitherman, 1980
<i>Zoarces viviparus</i> (celpout)				*	Kirpichnikov, 1981
Amphibians and Reptiles					
<i>Graptemys ouachitensis</i> (Ouchita map turtle)				*	Bull <i>et al.</i> , 1981
<i>Natrix sipedon</i> (water snake)				*	Beatson, 1976
<i>Plethodon cinereus</i> (red backed salamander)				*	Highton, 1960
<i>Rana pipiens</i> (leopard frog)				*	Underhill, 1968
<i>R. temporaria</i> (grass frog)				*	Chernokozheya, 1983
<i>Thamnophis elegans</i> (garter snake)	*			*	Glushankova, 1982
	*				Arnold, 1981
	*				Ayres and Arnold, 1983
Birds					
<i>Anser caerulescens</i> (lesser snow goose)		*			Findley and Cooke, 1982, 1983

Appendix continued

Species	B	L	M	P	Reference
<i>Branta canadensis</i> (Canada goose)			*		Lessells, 1982
<i>Ficedula albicollis</i> (collared flycatcher)			*		Boag, 1983
<i>F. hypoleuca</i> (pied flycatcher)			*		Boag, 1983
<i>Geospiza conirostris</i> (Darwin's finch)			*		Grant, 1981, 1983
<i>G. fortis</i> (Darwin's finch)			*		Boag, 1983, Boag and Grant, 1978
<i>G. scandens</i> (Darwin's finch)			*		Boag, 1981, 1983
<i>Melospiza melodia</i> (song sparrow)			*		Smith and Dhondt, 1980
<i>Parus caeruleus</i> (blue tit)			*		Smith and Zach, 1979
<i>P. major</i> (great tit)			*		Dhondt, 1982
	*		*		Boag, 1983, Dhondt, 1982
	*		*		Garnett, 1981
	*		*		Greenwood <i>et al.</i> , 1979
	*		*		Jones, 1973
	*	*	*		Ojanen <i>et al.</i> , 1979
	*	*	*		Perrins and Jones, 1974
	*	*	*		Van Noordwijk <i>et al.</i> , 1980, 1981a, 1981b
<i>Puffinus puffinus</i> (manx shearwater)			*		Brook, 1977
<i>Sturnus vulgaris</i> (starling)		*			Flux and Flux, 1982
Mammals					
<i>Macaca mulatta</i> (rhesus macaque)			*		Cheverud, 1981
<i>M. radiata</i> (bonnett monkey)	*				Brooker <i>et al.</i> , 1981
<i>Mus musculus</i> (house mouse)	*				Ebert and Hyde, 1976
	*	*			Hyde and Sawyer, 1980
	*				Smith, 1978
	*				Van Oortmerssen and Bakker, 1981
<i>Peromyscus gambelii</i> (deer mouse)			*		Sumner, 1918
<i>P. rubidus</i> (deer mouse)			*		Sumner, 1918
<i>P. sonoriensis</i> (deer mouse)			*		Sumner, 1918
<i>Rattus norvegicus</i> (Norwegian rat)	*				Hewitt and Fulkner, 1983