

THE GENETIC BASIS OF QUANTITATIVE TRAITS: EVIDENCE FOR PUNCTUATIONAL  
EVOLUTIONARY TRANSITIONS AT THE INTRASPECIFIC LEVEL.

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**ABSTRACT:** Much of the current major debate on evolutionary transitions concerns morphological change, but the genetics of morphological change has not yet been fully incorporated. Artificial directional selection for morphological change may take traits out of the phenotypic range normally found in natural populations, and the responses to selection may appear analogous to the periods of stasis and punctuational change of the palaeontologist. This is consistent with an underlying genetic architecture of a few genes of relatively large effect predominantly controlling such quantitative traits.

Evidence is now accumulating for analogous genetic architectures for some ecobehavioral traits important in determining the distribution and abundance of organisms, and the same appears true of developmental traits. Even if a trait has an outwardly continuous distribution, more detailed studies often reveal a genetic architecture predominantly involving a few genes.

In summary, the available data on the genetics of quantitative traits appear consistent with the gradualistic and punctuational models within conventional neo-Darwinian theory, whereby natural selection ultimately accounts for most change.

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### Introduction

Darwin's view of evolutionary change consists of natural selection acting upon variation within populations. The neo-Darwinian synthesis that arose from the integration of Mendelian genetics with evolutionary biology occurred when the source of this variation was explained. Some evolutionary biologists and palaeontologists (e.g. Simpson, 1953; Grant, 1963; Mayr, 1963; Eldredge and Gould, 1972; Stanley, 1979; Gould, 1980) have stressed that evolution tends to occur in sudden bursts separated by prolonged periods of morphological stasis. Some (e.g. Eldredge, Gould, Stanley) have presented arguments that such phenomena may be inconsistent with neo-Darwinian theory. However, Charlesworth *et al.* (1982) have recently argued that the punctuational model is entirely compatible with neo-Darwinian theory, whereby most morphological change is due to natural selection.

Much of the fossil record providing the material upon which this ongoing debate is based concerns morphological divergence, measured by body size and related measures. Accordingly, it is important to examine carefully what is known about the genetics of body size. Being a quantitative trait, it has usually been analyzed by the procedures of biometrical genetics, which provide little information upon underlying genes, since they are conventionally assumed to be too small in effect for individual study. In fact, the use of the term polygene (Mather, 1941) helped to remove the study of such traits from Mendelian

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to quantitative genetics. Yet, independent of the biometrical approach, Thoday (1961) "located polygenes" in Drosophila melanogaster for a morphological trait, sternopleural chaeta number. This demonstrates that quantitative traits can be studied at the Mendelian level in certain species (see also Milkman, 1970a,b; MacBean et al. 1971). The object of this paper is to incorporate this literature into the debate on evolutionary transitions, with extensions to ecobehavioral traits important in determining the distribution and abundance of organisms, and briefly to developmental traits.

#### Selection Experiments, Accelerated Responses and Number of Genes

"Polygene-location" studies have mainly been carried out in D. melanogaster on extreme strains following directional selection (Thoday, 1961), but extreme isofemale strains have been used in addition (Parsons, 1980).

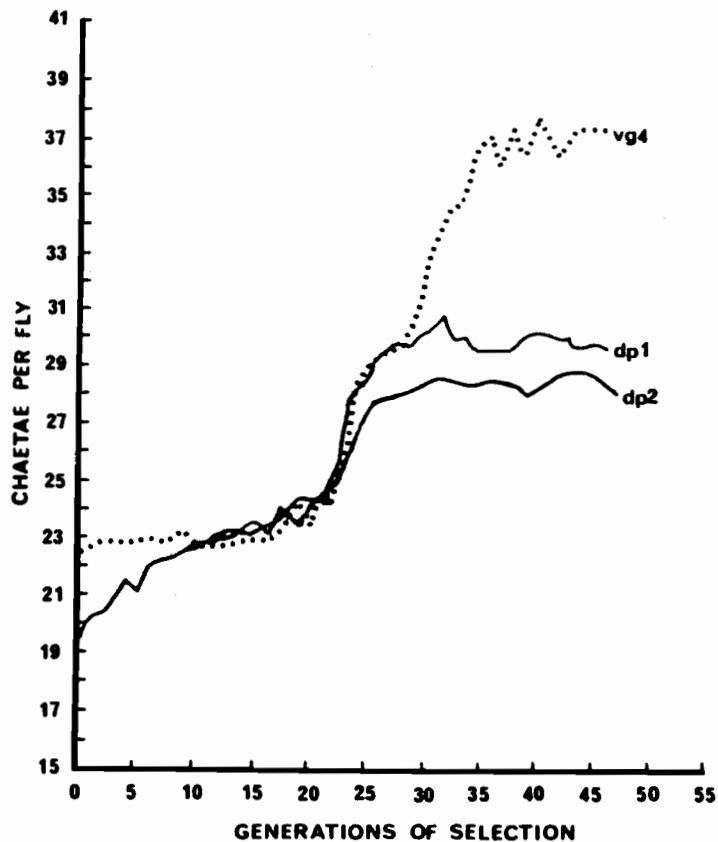


Figure 1. Accelerated responses to selection in Drosophila. The solid curves show the similarity of response of two lines dp1 and dp2. The dotted curve shows the response of a third line, vg4, plotted so that its accelerated response coincides with those of the dp lines. (After Thoday and Boam, 1961)

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 Figure 1 gives the results of selection for high sternopleural chaeta number in two lines of the same origin, dp1 and dp2. Both show accelerated responses from 24 to 28 chaetae and plateaux at about 30 chaetae (Thoday and Boam, 1961).

If + represents a gene for more, and - for fewer chaetae, then assuming that linked polymorphic gametes +- and -+ are segregating in the population, crossing-over in the genotype +/-+ would produce extreme ++ recombinants. Under directional selection these recombinants would be favored increasing rapidly in frequency when formed, and so giving the accelerated response. Since recombination occurs with some degree of predictability, some regularity in accelerated responses would be likely as in Fig. 1. The other line in Fig. 1, vg4, gave an accelerated response that continued to 37 chaetae. This line contained material from the dpl line which may explain the response to 30 chaetae. The dpl line was found to be homozygous for two chaeta loci about four map units apart on chromosome 3 after carrying out the necessary crosses for "locating polygenes". A summary of several experiments reveals 13 loci in a natural population influencing sternopleural chaeta number, one influencing fly size, and one influencing both (Thoday et al., 1963, 1964). In one particular selection experiment, five loci accounted for over 85% of the difference between a high line with a mean of 40 chaetae and a control with 20, so that just five loci take chaeta number out of the range normally found in natural Drosophila populations. It is also important that this variation occurs polymorphically in the natural population upon which selection is based.

Similar qualitative results have been obtained for genes influencing wing vein length (Thompson, 1975, 1977). In addition, in selection experiments for crossveinless, Milkman (1979) found that the total "cve library" is likely to be small enough to catalog, and that a typical cve strain has most cve activity controlled by three to five loci segregating in nature.

A final D. melanogaster example is for scutellar chaeta number which is normally canalized to four chaetae, although occasional isofemale strains have flies with more than four chaetae, usually five or six. MacBean et al. (1971) hybridized four such extreme isofemale strains, and by directional selection increased chaeta number to 16 in less than 60 generations. Figure 2 shows that the response occurred in two accelerated phases of relatively few generations compared with the intervening plateau phase. The increase from 10 to 16 chaetae can be explained by recombination between two closely linked loci just over 1cM apart on chromosome 3 which were segregating in the founder natural population. Once again, the accumulation of "polygenes" by directional selection may lead to phenotypes outside the range found in natural populations, in this case 10 chaetae in excess of the extremes found in nature.

It is reassuring that there are signs of some convergence with theoretical considerations, since Lande (1981) estimated that the minimum number of genes producing a large difference between populations is about 5 to 10, with occasional values to 20. His examples from the literature give the following estimates of effective numbers of factors (in brackets): tomato fruit weight (10), maize kernel oil content (16-22), anthesis date in golden rods (6-7), eye diameter in cane fish (6), and head shape in Hawaiian Drosophila (6-8).

#### Isofemale Strains

Neither the biometrical nor the polygene-location approaches to quantitative inheritance provide much of a guide to phenotypic variability at the population level. However, isofemale strains set up at random from a natural population are proving to be useful for comparing variation within and between populations (Parsons, 1980). Isofemale strains are basically families under test within a population, so that increased accuracy of analysis is obtained in an analogous way to progeny testing. Consistent strain differences originating from the

founder females last for many generations, so that comparisons within and among isofemale strains provide a guide to phenotypic variability for any species that can be conveniently cultured in the laboratory.

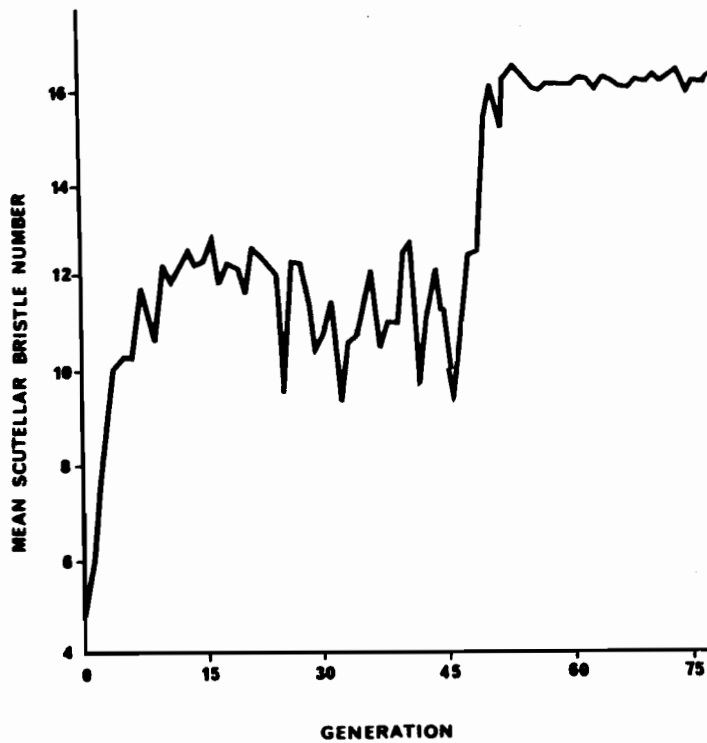


Figure 2. The response to directional selection in females for increased scutellar bristle number over 75 generations. Note the two accelerated responses lasting very few generations in each case. (Modified from MacBean et al., 1971).

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 Extreme isofemale strains have been used in "polygene location" studies for ethanol tolerance, resistance to ether, long term exposure to CO<sub>2</sub>, and to high doses of <sup>60</sup>Co-γ rays. Localization has been taken to the gene level for ethanol tolerance and to specific chromosome regions for the other traits (Parsons, 1980). The results are consistent only with an interpretation of a few relatively major genes having reasonably large and mainly additive effects, as for morphological traits in selection experiment studies.

#### Body Size

As for the above traits, consistent differences among isofemale strains occur for body size measured by wet and dry weight in D. melanogaster (Parsons, 1980). Negative correlations have been found between body weight and both mortality after desiccation and long term exposure to CO<sub>2</sub>. For the latter

trait, analyses of extreme isofemale strains revealed largely additive genetic activity localized to various regions of the X, 2 and 3 chromosomes (Matheson and Parsons, 1973). Somewhat indirectly therefore, it can be inferred that both body size and resistance to desiccation are predominantly controlled by a few additive genes rather than many genes.

Accordingly, it is not necessary to invoke regulatory gene complexes as major components of morphological evolution, as proposed by some (e.g. Wilson et al., 1975; Bush et al., 1977). Indeed, under the punctuational model which typically involves major genetic changes during phases of small population size (references in Introduction), gene interactions involving regulatory genes would tend to be modified or shifted as argued by Carson (1976) when discussing the unit of genetic change in adaptation and speciation. In addition, body size is most likely to be under directional selection in extreme (and new) habitats, where population size is expected highly variable; under these circumstances the development of complex interacting genetic systems would be less likely than in benign habitats where population size varies less (Parsons, 1982).

Therefore in adaptation to new habitats, body size could change quite rapidly, by the reorganization of largely additive genes. While a four-fold increase in less than 60 generations as in Fig. 2 would be difficult to envisage, substantial changes appear possible by the reorganization of "locatable polygenes" up to some ultimate developmental and physiological limit. The possible range of intraspecific variation in some species is in any case often very large as illustrated by certain domestic animals, for example, dogs. In the case of Fig. 2, it is likely that 16 chaetae may be a limit that is difficult to exceed. During the first plateau in Fig. 2, there is substantial variation among generations suggestive of segregating chaeta genes varying in frequency. After the recombinant event that led to the 16 chaeta plateau, there is almost no variation among generations, which suggests that all chaeta genes of major effect have been fixed. A new canalization zone has been entered at 16 chaetae, which is four times that of most flies in natural populations.

#### Ecobehavioral Changes

The potential importance of behavioral and, more generally, ecobehavioral adaptation in the occupation of new niches or adaptive zones has been stressed frequently (Mayr, 1963, 1974; Parsons, 1982, 1983). Phylogenies based upon ecobehavioral and morphological traits tend to be similar, because both categories are the products of the same genotype, representing a closed genetic program in the sense of Mayr (1974). Accordingly, the expectation is that ecobehavioral traits should have genetic architectures similar to morphological traits. The main distinction between the two categories is that the environment is far more important at the ecobehavioral than at the morphological level, which probably explains the relative paucity of genetic studies on ecobehavioral traits. A few such studies will now be considered.

In D. willistoni, de Souza et al. (1970) found two morphs, one preferentially pupating on moist food surfaces and the other on dry surfaces outside the vial on the floor of a population cage. This behavioral polymorphism is controlled by a pair of autosomal genes, and could favor the occupation of an otherwise unoccupied niche by pupae. Certainly, pupation away from larval sites is known, and in some cases if separate pupation sites are not provided in the laboratory, the maintenance of species is difficult (Carson et al., 1970; Bock and Parsons, 1978). In D. melanogaster, Sokolowski (1980) found a polymorphism controlled by second chromosome genes for larval foraging strategy consisting of "rovers" which traverse a large area while feeding and

"sitters" which cover a small area. Sokolowski argues that this polymorphism may provide a mechanism for rapid genetic change in response to habitat change according to whether food is distributed continuously or discontinuously. In the D. grimshawi complex of Hawaii, Carson and Ohta (1981) studied the evolution of generalism from specialism, and concluded that the data are consistent with a single-gene two-allele system controlling oviposition behavior. This means that shifts from generalism to specialism and vice versa could rapidly occur.

Throckmorton (1975) postulated that Drosophila entered the fermented-fruit habitat from more austere habitats. Some species not attracted to fermented-fruit resources have recently been found to be electrophoretically alcohol dehydrogenase (Adh) null (Holmes, Moxon and Parsons, 1980; Parsons, 1982). One of these species, D. inornata, however, utilizes low levels of ethanol as a resource, and is occasionally attracted to fermented-fruit baits on the edge of urban areas in southern Australia. During such colonizations an active Adh allele could be favored. In fact, certain species of the coracina group of subgenus Scaptodrosophila are polymorphic for a "high-activity" Adh allele and an Adh-null allele, and are spreading into urban/orchard areas (Holmes et al., 1980). Therefore, a change towards generalism may be based upon one gene leading to an ecobehavioral change concerning resources utilized, and so opens up a previously unavailable category of habitats.

Turning to physical stresses, Tucić (1979) selected D. melanogaster for adaptation to cold resistance over 52 generations. Genes on chromosome 2 contributed most to cold resistance of eggs and pupae, while those on chromosome 3 contributed most to larval and egg stages, implying relatively few genes at a given life-cycle stage. A system of major effective factors at different life-cycle stages suggests a high degree of flexibility for cold stress in natural populations.

More generally, Tauber and Tauber (1978) consider that qualitative changes in ecophysiological responses involving the timing of periods of activity and dormancy in relation to annually cycling environmental factors are consistent with relatively few genes. Similarly, based upon rather difficult data from the genetic point of view, Hoy (1978) argues that diapause in insects and mites is frequently controlled by few rather than many genes. More genetic data would, however, be useful in both cases.

The above examples strongly suggest that ecobehavioral phenotypes enabling adaptation to new habitats may be predominantly controlled by a few genes that can be studied individually. Even if a continuous distribution for a trait is found, it may still be consistent with an underlying genetic architecture of a few genes (Thoday and Thompson, 1976), which probably explains why many such traits are regarded as polygenic, especially if genetic analyses have not been or cannot be done.

### Developmental Changes

A small genetic change manifesting itself sufficiently early in ontogeny might engender a cascade of effects through development leading to a large phenotypic change in one step. Goldschmidt (1940) argued that such a punctuational process may be one method of forming a species; this approach has been updated by Gould (1980). Certainly, discontinuous phenotypic changes of perhaps macroevolutionary magnitude can be induced by quite minor environmental manipulations during development leading to phenocopies that mimic the effect of gene mutations. Many of these environmental changes involve temperature and hence rates of reaction; presumably the genes themselves act similarly

(Waddington, 1953). For example, in *D. melanogaster* a short period of high temperature at a certain critical stage in pupal life causes the appearance of crossveinless phenocopies (Waddington, 1953). Selecting flies with the phenocopy ultimately gave flies phenotypically crossveinless, that were not genetically homozygous *cv* (crossveinless). Bateman (1959) produced other wing venation phenocopies and found that a single chromosome was usually responsible, suggesting control by major gene(s). This is consistent with the low number of genes found by Milkman (1979) in his "crossveinless" library.

Under sufficiently novel or extreme environments as may occur in adaptation to new niches, aberrant phenotypes could perhaps appear as envisaged by Goldschmidt (1940). However, on an evolutionary time scale, there must be sufficient phenotypic selection over a number of generations to permit the assimilation of such phenotypes into the genotype. That is, major phenotypic changes could appear in one generation, but are unlikely to be fixed immediately. Some of the changes considered by Goldschmidt therefore could be incorporated by the accumulation of "polygenes" favored by natural selection over many generations. In addition, Lande (1980) and others have argued that the accumulation of modifiers can lead to the crossing of phenotypic barriers under gradual selection.

### Discussion

Although Stanley (1982) considers that genetics emphasizes gradualism, much of the above evidence is not compatible with this, simply because the genes underlying quantitative traits may have quite substantial effects leading to intraspecific changes that occasionally appear punctuational.

Certainly some authors (see Williamson, 1981a) consider that it is difficult to explain the long periods of stasis between short periods of rapid change as in Figs. 1 and 2. However, in both cases a somewhat rare recombinant event rearranged relatively closely linked chaeta genes, whereupon a short period of rapid phenotypic change occurred away from the plateau. In nature, stabilizing selection during the period of stasis would presumably favor the evolution of a canalized phenotype whereby many genotypes lead to a given phenotype. In agreement, MacBean *et al.* (1972) carried out artificial stabilizing selection for six scutellar chaetae in *D. melanogaster* such that the extra two chaetae were symmetrically on the anterior left and the anterior right position of the scutellum. Ultimately, a selected line was formed with most flies having this chaeta number and pattern i.e. selection for canalization was successful. MacBean *et al.* (1972) concluded that in practice it should be possible to establish canalized symmetrical lines at 6, 8, ... chaetae, but whether this occurs depends upon the genes in the population under selection (Fig. 2 gives a canalized 16 chaeta phenotype).

When stabilizing selection is relaxed or when there is directional selection away from the canalization zone, sufficient phenotypic variability would probably be ultimately produced for the population to change to a new optimum. The response to selection in Fig. 2 is based upon the selection of those few isofemale strains showing deviations from the normal highly canalized four chaeta phenotype of *D. melanogaster*. By going through bottlenecks in the setting up of isofemale strains, certain extreme genotypes were accumulated together artificially, enabling rapid responses to selection. Such a model could apply during bottlenecks caused by climate-induced population crashes, whereby only a few individuals survive that are resistant to the climatic extreme. If extreme phenotypes are heterogeneous for a few genes of large

effect for tolerance to climatic stress, then quite rapid responses to selection could occur, provided that the selection intensity for the extreme is maintained. One test for the possibility of rapid responses to selection in nature would be to find out whether an ecological trait such as resistance to desiccation tracks the seasons, since as argued elsewhere (McKenzie and Parsons, 1974; Parsons, 1982) this would imply rather few genes without significant interactions.

In a sequence of East African fossil beds containing freshwater molluscs, long periods of morphological stability were interrupted by fossil beds in which relatively rapid changes in shell size took place (Williamson, 1981b). During these periods of rapid change there is evidence for major lacustrine regressions when the fauna was probably isolated and stressed. Mayr (1963) emphasized the importance of geographical isolation, environmental stress and small population size as important triggers for rapid evolutionary change as in speciation, as did Lewis (1962) when writing on catastrophic speciation in plants. The size differences among the freshwater molluscs are quite large. However, the populations discussed by Lande (1981) differed by up to 30 phenotypic standard deviations for which the minimum number of segregating genetic factors is argued to be 5 to 10, from which it follows that microevolutionary change need not be gradualistic. Indeed, the plateaux and accelerated responses obtained by artificial selection appear analogous to the periods of stasis and punctuational change of the palaeontologist. Such experimental data need to be incorporated into the debate on evolutionary transitions, especially since ecobehavioral traits determining the distribution and abundance of organisms may be controlled by relatively few genes. Additional knowledge of the biological basis of quantitative traits of all types is essential to understand evolutionary transitions (see also Templeton, 1981), although the data available appear consistent with both the gradualistic and punctuational models incorporated within conventional neo-Darwinian theory.

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