

In our example we can see that $S = 5 - 3$, or 2 phenotypic units.

The response (R) to this selection differential is shown in Fig. 12.5b, and may be measured as the difference between the mean of the progeny ($\bar{Y}_R$) and the mean of the parental population ($\bar{Y}_P$). Thus:

$$R = \bar{Y}_R - \bar{Y}_P \quad (\text{Eqn 12.5})$$

In our example, $R = 4 - 3$, or 1 phenotypic unit.

We can also predict the response (R) of the population from the equation:

$$R = h^2_N S \quad (\text{Eqn 12.6})$$

On reflection, this last equation should be intuitively obvious. The heritability (h^2_N) is a measure of the similarity of the progeny to their parents, and if we multiply this by the selection differential (S) we can predict the overall change in the phenotype (or response, R). In our example, $R = 0.5 \times 2$, or 1 phenotypic unit, which is the same as that predicted by Eqn 12.5. Thus, the overall phenotypic score will change, or in this case increase because R is positive, by 1 phenotypic unit. The average phenotypic score of the progeny should be one unit larger than the mean score of the parents, i.e. $3 + 1 = 4$, which is what we observe.

When we repeat the operation, we see that after a second generation of selection at the same intensity ($S = 2$), the average phenotypic score of the population has increased by one more unit and now is 2 units larger than the original population (Fig. 12.5c). Thus, the population responds to selection generation after generation, and the response is directly related to the heritability (h^2_N) and the selection differential (S) being applied. If the heritability had been lower, the response to selection would have been lower. For example if h^2_N was 0.25 and $S = 2$ units, the mean phenotypic score would have increased by 0.25×2 or 0.5 units each generation, rather than the 1 unit observed in Fig. 12.5. Note, that unless the heritability = 1.0, the mean phenotypic score of the progeny will lie somewhere between the phenotypic score of those selected as parents ($\bar{Y}_S$) and the overall phenotypic score of the parental population ($\bar{Y}_P$). This slipping back toward the overall mean is known as regression (toward the mean).

12.5 Empirical examples of selection of quantitative characters

Perhaps the best example of controlled, long-term selection is an experiment on the oil content of corn seed. The experiment was started in 1896 (even before the rediscovery of Mendel's laws) at the Illinois Experimental Station using a base population of 163 corn ears with oil contents ranging from 4% to 6%. Two experimental lines were started, one selecting for high oil content and the other for low oil

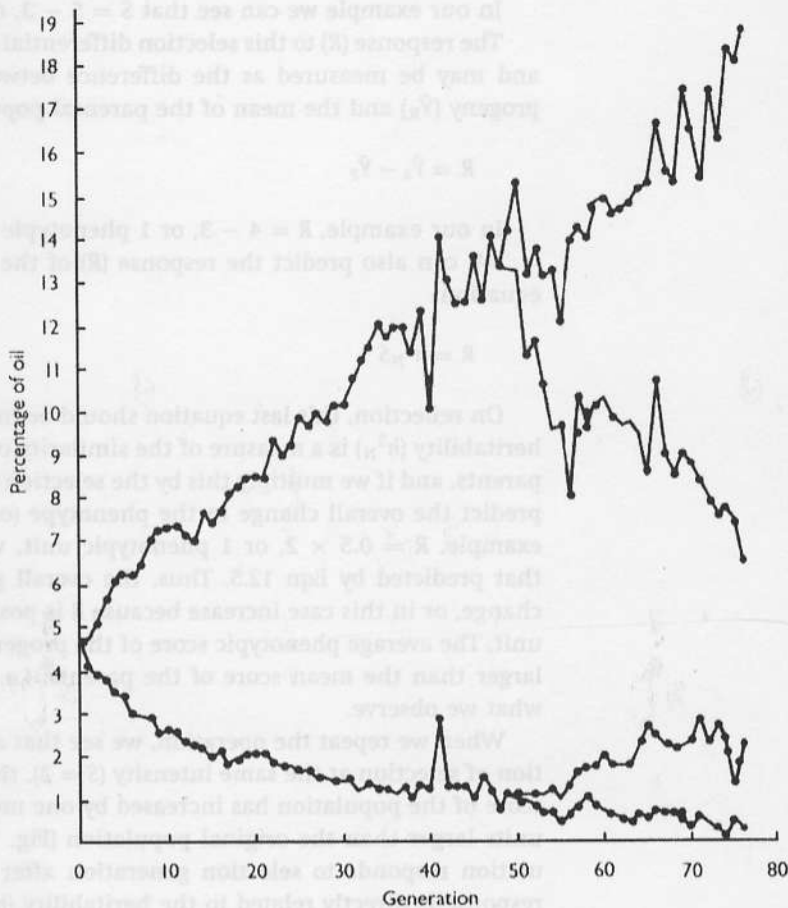


Fig. 12.6 Selection for high and low oil content in the seed of corn (*Zea mays*). The high line was formed from the 24 ears highest in oil content and the low line from the 12 ears with the lowest oil content in an initial population of 163 corn ears. Two additional lines of reverse selection were started in generation 46. (Reprinted from Dudley, J. W., in *Proceedings of the International Conference on Quantitative Genetics* (eds. E. Pollock, O. Kempthorne and T. B. Bailey), pp. 459–73, Copyright 1977, with permission of Iowa State University Press.)

content and the results of the first 78 generations of selection are shown (Fig. 12.6).

It did not take long for the oil content of the two lines to be well outside of the original range of oil content. The low line has changed less than the high line because you cannot have an oil content of below zero. A careful examination of the trends shows that the rate of change was fastest during the first 10 to 20 generations of selection, but the lines are still diverging and so the additive genetic variance has still not been exhausted. Presumably, at some stage all the individuals within a line will come to have the same genotype for oil content, and the heritability (h^2_N) will be zero because there is no additive genetic variance (V_A). At this point there will be no further response to artificial selection unless there are new mutations affecting oil content. Heritability has declined to about one-third of its initial value in both lines (Table 12.3), but will take some time to decline to zero because there are at least 20 genes that affect oil content.

Selection is not always directional, it is often against the phenotypic extremes and intermediate phenotypes have higher fitness. Such selection is called stabilizing selection, because no change may

Table 12.3 The heritability of oil content in corn seed after different numbers of generations of selection in the Illinois corn experiment illustrated in Fig. 12.6

Generations	Heritability of oil content	
	High line	Low line
1 – 9	0.32	0.50
10 – 25	0.34	0.23
26 – 52	0.11	0.10
53 – 76	0.12	0.15

Source: Reprinted from Dudley, J. W. in *Proceedings of the International Conference on Quantitative Genetics* (eds. E. Pollock, O. Kempthorne and T. B. Bailey), pp. 459–73, Copyright 1977, with permission of Iowa State University Press.

be seen in the phenotypic score generation after generation, even though there may be strong selection pressures on the character in question. A good example of this type of selection is seen in human birth weights (Fig. 12.7), where there is strong selection against large and small babies and the average birth weight is similar to the optimum predicted from infant mortality. A similar pattern of stabilizing selection is seen in clutch size in birds (see Chapter 16) where intermediate clutch sizes give rise to largest number of survivors.

12.6 Intelligence, race and societal class

In recent decades there has been a controversy about the reasons for differences in IQ (intelligence quotient) scores between different segments of society, particularly in North America. For example, Jensen (1969) and Herrnstein and Murray (1994) have presented overwhelming evidence that the average IQ scores of people of different colour, and of different socioeconomic classes, are very different. The issue they raise can be stated quite simply: does the low IQ in some racial groups, or in some lower socioeconomic classes, have a genetic or an environmental basis? Thus, we are examining an example of the classic nature (i.e. genes) versus nurture (i.e. environment) debate. In the following discussion we will concentrate on racial differences, because the arguments apply equally to socioeconomic class differences and, in any case, there is frequently a strong association between race and socioeconomic class.

How do we define intelligence? It is highly questionable whether IQ scores give an unbiased and total assessment of intelligence because some things, such as musical skills, are not correlated with IQ. However, IQ tests do evaluate a large range of skills, and the scores correlate reasonably well with the scholastic success of Caucasians, and

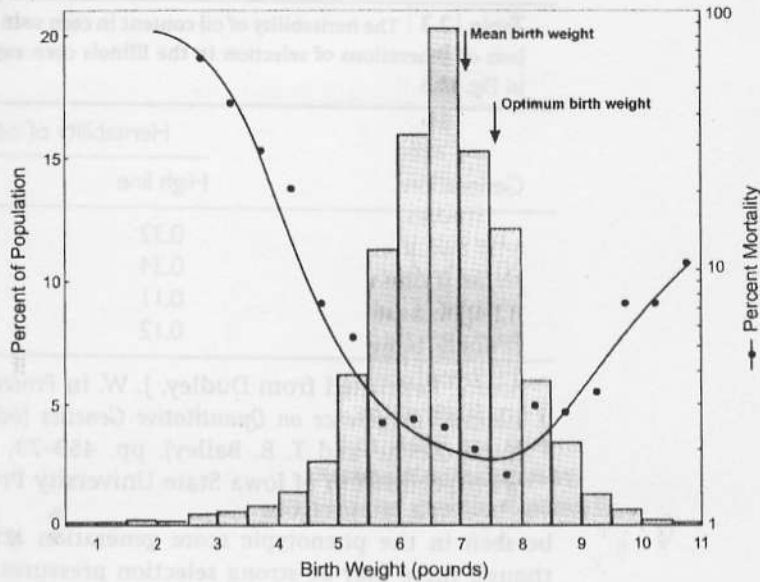


Fig. 12.7 Stabilizing selection for human birth weight (histogram). Early mortality, shown by the points around a fitted curve, is lowest near the mean birth weight. (From *The Genetics of Human Populations*, by L. L. Cavalli-Sforza and W. F. Bodmer © 1971 by W. H. Freeman and Company. Used with permission.)

so they may serve an educational purpose. The form of the present IQ tests was developed soon after 1900 by Alfred Binet, a French psychologist, to identify schoolchildren who would be likely to have difficulty at school. The Binet test was revised in 1916 at Stanford University, and subsequently revised again in 1937 and 1960. It is the standard IQ test in North America.

Interestingly, the 1916 Stanford-Binet test indicated that boys had higher IQs than girls. This was interpreted as a bias favouring males, because of their different experiences, rather than any innate tendency for males to be more intelligent than females. The test was revised to exclude questions where one sex or the other performed better, and so present tests give almost identical IQ distributions for males and females. It is interesting that there has been no successful attempt to eliminate questions where there are different scores for other different racial, cultural or socioeconomic groups.

The test involves answering a large number of questions. The answers are scored and the scores are summed for each individual. These scores are transformed into an IQ test score for each individual by a process of standardization, in which the mean for a large population has a value of 100 and the standard deviation for the population is 15. Thus, the population has a normal distribution of IQs, such that 67% of the population has IQ scores between 85 and 115, 95% of the population has IQ scores between 70 and 130, and 99% of the population has IQ scores between 55 and 145. Naturally, different tests are given to children of different ages. The results of different tests over short time intervals are similar, but the correlation between tests declines as the time interval increases. Some studies have shown that individual IQs vary little between the ages of 2 and 18, but other studies show that

they vary over this time period. For example, one study of Swedish schoolchildren showed that the IQs of students tested at 12 years of age increased by an average of 11 points at the end of high school, if they had been subjected to a demanding curriculum. Thus, IQ scores are not perfectly stable with age, and can be increased with appropriate schooling.

There have been many studies to determine the heritability of IQ scores to assess the genetic and non-genetic aspects of this measure. However, there are problems if one uses the parent-offspring regression technique (see Fig. 12.4) because relatives reared together cannot provide data that discriminate between genetic transmission of the trait and environmental transmission from parent to child. These estimates of heritability are likely to be too high because 'good' genes and 'good' environments are likely to be highly correlated with one another. Better estimates can be made by using the technique of estimating the correlations between monozygotic twins that have been reared apart.² There are four such studies providing estimates of 0.86 (Cyril Burt), 0.77 (J. Shields), 0.73 (Juel-Nielson), and 0.69 (Newman, Freeman and Holzinger). These give a combined estimate of 0.81, which is where the widely quoted estimate of 80% for the heritability of IQ has been derived. However, we now know that Burt's data are fraudulent (he made up most of his data) and Shield's data are less than ideal because over two-thirds of his sample were raised by close relatives. The remaining two estimates are based on small sample sizes, and so their combined estimate of 0.71 is rather uncertain. Finally, studies based on the results of adopted children have provided estimates of between 0.45 and 0.65. Thus, the claim that IQ is 80% heritable is certainly an inflated estimate, and more reasonable estimates would be somewhere in the range of 45% to 70%, or even lower (Feldman 1992). However, as we will see, the precise range of heritability estimates for IQ does not impair our ability to evaluate whether the differences between groups have a genetic or an environmental basis.

Numerous studies have shown that the average IQ of blacks in the USA is 10 to 20 points (average 15 points) below that of US whites (Fig. 12.8). If we ignore the question of how the authors of these studies defined 'white' and 'black' people, this represents a considerable difference between the two groups, equivalent to one standard deviation of the distribution of white IQs. Similarly, the average IQ of people in lower socioeconomic classes is below that of people in higher economic classes.

How do we explain these differences? A group comprising mainly psychologists, called hereditarians, argues that the difference between groups is largely genetic in origin. In their view, one's IQ is mainly innate, and no amount of environmental change will

² Monozygotic twins may be defined as: two individuals that develop by the division and separation of a single fertilized egg into two genetically identical parts (i.e. identical twins).

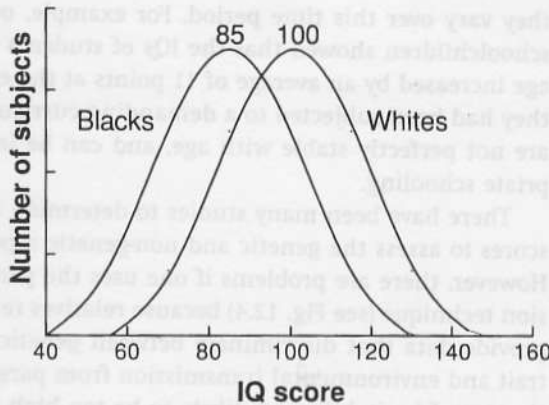


Fig. 12.8 The difference in IQ between idealized samples from blacks and whites in the United States. The mean IQ is shown above the curves for each of the two groups.

eradicate the difference between groups. In case you think that this is merely a racist argument for the genetic superiority of Caucasians, you should be aware that at least one hereditarian, William Rushton of the University of Western Ontario, shows that the average IQ of people of Asian origin is higher than that of Caucasians. On the other hand, many biologists have argued that the differences are mainly due to environmental factors, together with cultural biases in the IQ test questions that favour whites.

The hereditarians' main argument is that the difference in IQ between the two racial groups is mostly genetic in origin, because IQ has a high heritability in both blacks and whites. In other words, hereditarians believe that IQ is mainly genetically determined (as much as 80%), and so this must be the reason for the difference between the two groups. This is a fallacious argument as the following 'thought experiments' make clear.

Imagine we have a population of dogs which vary greatly in size, and may be black, grey or white (the black and white alleles are codominant). Note that this imaginary genetic system for body colour is simply to make it easy to create pure-breeding groups of black or white dogs. Dog size is a polygenic trait with a heritability of 0.8, and there is no association between dog size and colour. In the first experiment we take a group of young white puppies and feed them on a rich diet. At adulthood, these dogs have a body length that is normally distributed with a mean of 100 cm and a standard deviation of 15 cm. The same is true with the offspring of these dogs. We also take a group of young black puppies and feed them on a reduced diet. At adulthood, these dogs have a body length that is also normally distributed, but with a mean of 85 cm and a standard deviation of 15 cm. The same is true for their offspring. The slope of the parent-offspring regression for body length was 0.8 ($= h^2_N$) in both groups, but the regression line for black dogs was below that of the white dogs. Obviously, we would attribute the difference in size between the two groups of dogs to the difference in their diets, i.e. environmental factors, even though dog size has a high heritability. Thus, even though the variation in dog size *within* each group was

mainly due to additive genetic effects (i.e. V_A is 80% of V_P), this was not the reason for the difference between the two groups. We can also note that dog size had nothing to do with their colour, even though white dogs were significantly larger than black dogs.

In the second imaginary experiment, we select a group of white dogs for increased size, and simultaneously select a group of black dogs for smaller size. After a few generations of selection we observe that the two groups have diverged in average size. We then take the two groups and grow them in the same area, thereby eliminating potential environmental differences between them. We are not surprised that the white dogs are larger on average than the black dogs, and would attribute this difference to genetic differences in the two lines. As a result of the selective process, we might find that the heritability of dog size was reduced to approximately 0.3 in each of the two lines (see Table 12.3). Thus, even though the variation in dog size within each group was mainly a result of a combination of non-additive genetic effects and environmental effects, the difference between the two groups had a genetic basis.

These imaginary experiments demonstrate that there is no foundation to the hereditarian argument: that if IQ has a high heritability, the differences in IQ scores between different population groups must have a genetic basis. However, even though we have shown that the main hereditarian argument is based on a fallacy, this does not settle the question as to whether the difference in IQ between groups has an environmental or a genetic basis. This requires more direct evidence.

Three types of evidence suggest that most of the difference between groups is a result of environmental factors.

1. Studies that compare the IQ of different races usually have poorly matched samples. The samples not only differ in race, but also differ in socioeconomic status, the type of schooling available to the children, and so on. Thus, differences between groups could be a result of associated environmental differences rather than racial differences. Nichols and Anderson (1973) reduced some of the environmental differences in their study by comparing different ethnic groups of children whose parents had the same occupations, education and income (socioeconomic status). They tested two samples of seven-year-old children of blacks and whites in the United States: one group of high socioeconomic status from Boston, and one group of relatively low socioeconomic status from Baltimore and Philadelphia. The Boston whites and blacks had mean IQs of 104.2 and 100.0, respectively, and the Baltimore-Philadelphia whites and blacks had mean IQs of 95.3 and 91.2, respectively. Thus, the 10 to 20 point difference in IQ between blacks and whites, found in most studies (see above), was effectively reduced to about 4 points simply by stratifying the sample design so that potential racial differences were not confounded by differences arising as a result of socioeconomic factors.

2. If the hereditarian view is correct, children of black and white parents should have IQs intermediate between the two groups, but this is not the case. There was no difference in the average IQ of illegitimate children of black and white American servicemen and German women after the Second World War. Similarly, Tizard (1974) found that mixed-race and white English children who had spent part of their early life in institutions had similar IQ scores, although those of the mixed-race children were marginally higher. Finally, the IQ of children of mixed marriages is reported to correlate more with the IQ of the mother than the father, suggesting that cultural traits transmitted to the child during infancy and early childhood are important, because it is the mother who normally has the major influence on the child at this stage.
3. Evidence for environmental effects transmitted by the adoptive parents is also provided by children adopted soon after birth. The effects are quite general and apply equally to the question of racial differences in IQ as well as differences in IQ related to socioeconomic class. A study by Skodak and Skeels (see Bodmer and Cavelli-Sforza 1976) tested the IQs of 100 children, born to white, unmarried mothers from lower classes, that were adopted into middle-class families. The children's IQs showed a higher correlation with those of the biological mothers than with their adoptive parents, showing a strong genetic effect on IQ. However, the average IQ of the biological mothers was 85 whereas the average for the children was 107. The IQ of the biological fathers was unknown, but it is unlikely that all of the 22 point difference was from that source. Probably the increase in IQ was related mainly to the favourable academic environment offered by the foster homes. Finally, a study of black children adopted by white families in Minnesota showed that they had IQs similar to those of white controls, which suggests that there are no genetic differences in IQ between the races.

From this discussion, we can conclude that the hereditarian argument, which states that differences in IQ between different population groups is mainly a result of genetic differences among groups, is based on a misunderstanding of quantitative genetic theory. The available evidence suggests that most, if not all, of the differences among groups are a result of environmental influences.

What if we had discovered that much of the difference in IQs between groups had a genetic basis? Would the genetic fatalism of the hereditarians, and the belief that group differences in IQ cannot be changed, be justified? The simple answer is no. Consider the case of phenylketonuria, a genetic disease which, among other effects, causes severe mental retardation. At one time there was no treatment for the condition, and in the 1960s it accounted for almost 1% of all severely retarded patients in institutions. Phenylketonuria is a metabolic defect resulting from the absence of an enzyme called phenylalanine hydroxylase, which converts the amino acid phenylalanine to

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tyrosine. The phenotypic effects of the condition, only expressed in homozygous recessive individuals, are the result of an excess of phenylalanine and its derivatives. The genetic condition can be treated by restricting the dietary intake of phenylalanine. Individuals that are identified soon after birth with the condition, before the classical phenotypic effects are expressed, and who adopt a rigorously controlled diet can live a normal life. Treatment will not reverse the effects of the disease once they have been expressed. Note, however, that phenylketonuria has a close to 100% heritability, and yet an environmental change (of diet) can effectively abolish its effect on IQ.

Finally, my vigorous attack on the hereditarian position of ascribing the differences in average IQ between racial groups to genetic differences may have led some to conclude that there is no genetic basis to IQ and that only the environment is important. However, although appropriate mental stimulation is necessary to develop our IQ to its full potential, some of us will have a higher IQ than others. We cannot all be as clever as Albert Einstein or Madame Curie, our genetic constitution is also important.

12.7 Summary

When a trait is determined by many gene loci there may be a continuum or a very large number of possible phenotypes. The phenotypic variation of polygenic traits can be partitioned into environmental and genetic components, and the latter further partitioned into additive, dominance and epistatic genetic effects, by suitable breeding experiments.

The response to selection is positively correlated with the proportion of the overall phenotypic variation (V_P) that is determined by the additive genetic effects (V_A). The measure V_A/V_P is called the heritability in the narrow sense of a trait, and when a trait is subjected to intense selection its heritability decreases as inferior alleles are eliminated. This probably explains why traits that are closely related to fitness tend to have low heritabilities, whereas trivial characters tend to have high heritabilities.

The relationship between IQ and race is examined in some detail as an example of the genes versus environment debate. The hereditarian argument that the differences in IQ between groups must have a genetic basis (because the heritability of the trait is high) is shown to be based on a misunderstanding of quantitative genetic theory. The available evidence suggests that most, if not all, of the differences between groups are the result of environmental influences. However, the genetic constitution of individuals has a strong effect on IQ.

12.8 Problems

1. Two highly inbred lines of mice are crossed and give a variance of 2.5 units in tail length in the F_1 generation. The variance in the F_2 generation is 12.5 units, and the parent-offspring regression for tail length is 0.75.