

Chapter 3

Assortative Mating, Class, and Caste

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Assortative mating in humans has interested human geneticists for decades. It is widely found and it is difficult to make sense out of it. For example, tall people are likely to have tall mates, short people are likely to have short mates, people with more years of education have more highly educated spouses, and so on. These phenomena are usually not treated as selective processes but they can and likely do cause the equivalent of very strong natural and diversifying selection, leading to persistent inherited group differences.

Selection in the Old Order Amish

The Amish are an Anabaptist sect whose members immigrated to Pennsylvania in colonial times, mostly between 1727 and 1770 (Kraybill 2001; Hostetler 1980). Their way of life is unusual; they refrain from using many forms of modern technology, and they generally try to separate themselves from modern society. Some of their customs have biological significance, that we will discuss further. We think that analogous customs—endogamous marriage, in particular—may have occurred often in human history.

The Amish marry within their faith. Although they accept converts, there are a very few, so there is almost no inward gene flow. They descend almost entirely from about 200 eighteenth century founders. On the other hand, there is considerable outward gene flow, since a significant fraction of Amish youth do not choose to adopt the Amish way of life. In recent years, approximately 10–15% of young Amish left the community. In the past, the defection rate seems to have been higher,

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around 18–24%. Defection is up to the individual—there are no barriers against Amish who want to participate in modern society.

Since the Amish have very high birth rates (> six children per family), their numbers have increased very rapidly, even though there is a substantial defection rate. There were about 5000 descendants of the original 200 by 1920, and today (2013) there are about 280,000 Amish.

Every way of life selects for *something*, but the Amish way of life is so different that natural selection in that population should be noticeably different from that in the general US population. It seems likely that the Amish have undergone selection for two specific traits due to their unusual social and reproductive pattern. First, they were almost certainly selected for higher fertility. A recent study (Milot et al. 2011) found evidence of this kind of selection in preindustrial French Canadians, who, like the Amish, went through a very rapid population expansion. Second, and more interestingly, the Amish have probably experienced selection for increased “Amishness”—an increase in the degree to which Amish find their lifestyle congenial, since those who like it least, leave. We term this kind of differential emigration “boiling-off.” Obviously, if some of the soup boils off, what is left is more concentrated.

This boiling off is essentially truncation selection. If we assume a normal distribution, the loss of the least plain 10% corresponds to the loss of everyone more than 1.25 standard deviations (SD) below the Amish mean. If we assume a narrow-sense heritability of 0.3 and use a scale similar to that for IQ, the Amish gain about one point of plainness per generation. Not counting possible selection for this kind of personality in Europe, before they settled in North America, the Amish have spent about 10 generations under this kind of selection. Therefore their “plainness,” their “Amish Quotient” (AQ), might have increased by about 0.6 SD. During most of the period for which we have sufficient information, the defection rate was significantly higher than 10%, so this may be a conservative estimate. Although there are certainly other factors that might influence the defection rate, such as increasing differences between the Amish way of life and that of their neighbors, increasing plainness would tend to reduce the defection rate over time.

The Amish have some genetic problems because of genetic drift in a small population, and these problems have received a fair amount of attention from medical geneticists. However, their social pattern probably drives strong selection for a particular constellation of personality traits, which is fascinating and worthy of further investigation. One could, with difficulty and significant investment, identify personality traits associated with a hypothetical AQ. These traits would likely include affinity for work, perseverance, low status competition, respect for authority, conscientiousness, and community orientation. We proposed (Cochran et al. 2006) a similar mechanism to account for Ashkenazi Jewish evolution in Medieval times selecting for ability and success in white collar occupations.

Recall that there is no selection at all in this model; AQ is selectively neutral. Seen from within the group, this is very strong selection. Mean population fitness does not increase, but mean AQ of Amish increases rapidly. The increase in retention, that is the decline in rate of boiling off, is very likely due to this mechanism of selection as the Amish population’s average affinity for being Amish increases.

Some Background

For much of the twentieth century, the study of heredity has had two faces reflecting the old conflict between the biometricians and the Mendelians early in the century. The biometricians, associated especially with the Victorian genius and polymath Francis Galton, sought to understand heredity and its workings by collecting a lot of data and measuring everything that could be measured, or so it seems. The Mendelians based their approaches on the newly-discovered laws of inheritance of Mendel. The root of the conflict was whether the path to understanding heredity was to be through careful analysis of quantitative traits, regarding Mendelian mechanisms as side issues, or through elaborated Mendelian analyses, regarding quantitative traits as side issues.

Darwin was the grand inspiration behind this outbreak of biology, but Darwin's own theory of evolution by natural selection was not faring well at the end of the nineteenth and the early twentieth century. Evidence from selection experiments often did not look good for Darwin's theory. For example, Pearl and Surface (1909) conducted selection experiments on egg production by chickens. They found that there was no cumulative effect of selection. They did not realize at the time that chickens had been selected for many generations for egg production and there was little or no genetic variation in the trait left in the chickens.

The divergence in biology was resolved with a single paper by R. A. Fisher (1918) about "the correlation between relatives under the supposition of Mendelian inheritance." The paper is somewhat dense so it does not enjoy the acclaim that it deserves. What Fisher did was to reconcile approaches of the biometricians and the Mendelians, ending at once the disagreements between them. This paper was, in the view of many, the real beginning of evolutionary biology as a coherent discipline.

Fisher proposed a model of an inherited trait whose phenotype was determined by the additive effects of a very large number of Mendelian loci, as well as an effect of the environment. Because of the additivity, the phenotype should have a normal distribution with variance determined by the variance of genic effects across all the loci plus the variance of environmental effects. What Fisher was able to predict was the extent of similarities between relatives. The model worked, it described the world that we observe, and it is widely applicable.

In the years since, the old divide between Mendelian genetics, on the one hand, and Galton and biometrics and quantitative genetics, on the other, has persisted in many ways. Much of academic genetics remains firmly Mendelian in the sense that it focuses on molecular biology, molecular genetics, and biochemistry. The current triumph of this approach is the Human Genome Project and our ability to sequence thousands of complete human genomes at reasonable cost. Human genetics has been concerned, obsessed perhaps, with finding Mendelian roots of medical disorders and diseases. In the trade, this is called the search for "genesfor,"—that is, genes for diabetes or schizophrenia or Obsessive Compulsive Disorder or bad breath. It has occasionally worked out: for example, human skin color is mostly determined by six or so Mendelian loci. On the other hand, it has completely failed in other domains, including fingerprint ridge counts or intelligence or stature, which

otherwise appear to follow closely the Fisher (1918) model. An excellent introduction to and survey of this divide and its history can be found in Razib Khan's (2013) recent blog post.

In this chapter, we explore some simple implications of quantitative genetic transmission of important traits or characteristics within a population with assortative mating. The model is quite general and the implications are startling, at least to us.

A Model of Assortative Mating

We begin by describing a simple model of assortative mating for a quantitative trait. The model is quite general. It may be useful for understanding social phenomena such as change in income inequality over time, social and economic class stratification, assortative mating by education, and the persistence of ethnicity.

We assume that there are two classes in a population called the right class and the left class. These are not necessarily of equal size, but the size of each class, and the size of the total population, is constant over time. There is no selection in this model: everything is selectively neutral.

An important parameter in quantitative genetics is the heritability of a trait, the fraction of the population variance of a trait that is attributable to genetic differences. This idea does not fit well into our model since we are not studying the change in a trait in the population, but the growth of differences in the population. Heritability proceeds from a model in which an individual's genes determine his underlying or genotypic value while the actual value, or phenotype, is the sum of the genotypic value and a random perturbation that is, unfortunately, called "environment." The perturbation reflects many effects, including developmental errors, dominance, gene interactions and interactions among loci, as well as effects conventionally associated with environment, such as nutrition, culturally-transmitted traits, or disease. Low heritability is often taken, among journalists for example, to imply sensitivity to environmental manipulation, but it implies no such thing.

Unfortunately for our model of assortative mating, the accounting is very difficult, so we study instead an analogue of heritability that we call h , which is the fraction of matings that are assortative. A fraction $1-h$ are random matings within classes. If h is 0, then there is no assortative mating, while h of 1 implies maximum assortative mating by group. Our results are the outcome of computation rather than of analysis (Mathematica 2012). We have made no progress toward deriving explicit algebraic descriptions of the demographic process that we study.

We begin with the simplest case of two classes that mate assortatively for a heritable trait. Initially, there is a single random mating population in which mating suddenly becomes assortative. We will show our results graphically with a scale of mean of 0 and standard deviation of 1, describing the original distribution of the trait under global random mating. If we were studying stature, the mean would be 70 in. and the standard deviation 2.5 in. Another familiar scale is IQ, with a mean of

100 and standard deviation of 15. We find it helpful to think of these scales when we consider how large the differences that evolve are in familiar and plausible terms.

Figure 3.1 illustrates the process we are modeling. The top panel in both columns shows the initial distribution of the trait, normal with mean of 0 and standard deviation of 1. Speaking of stature for illustration, we think of that mean as at 70 in. rather than at 0 standard units and the standard deviation scaled to 2.5 in. rather than 1 standard unit. Strict assortative mating then occurs. The rule is that everyone shorter than the average moves to the left class and everyone taller than the average moves to the right class. This separates the population into short people in the left distribution and tall people in the right distribution, as shown in the middle panel. Mating occurs within class, and the shuffling that occurs leads to normal distributions *within classes* in the offspring generation, as shown in the bottom panel of Fig. 3.1.

Much of quantitative genetics depends on random mating, but it is not clear what random mating is in this context. It might mean random within class or random over the whole population. The latter will attenuate the effects of assortment: this is shown in the right column of Fig. 3.1. In this column, 5% of the population mates at random from both classes.

The new mating rule has split our single population into two classes. After only a single generation, the classes differ notably. The average stature in the short class is now 68 in. and in the tall class it is 72 in.. The difference is 4 in., 1.6 SD on the original scale. With 5% random mating imposed on each generation, the difference is reduced to 3.75 in.—that is, the effect of the random mating is very slight. Over time it becomes important. Without the random gene exchange, the two classes continue to separate over time, albeit very slowly, on their way to becoming genetic castes. With some random mating between classes the process of separation stops so that over time there is not much change beyond what has occurred in one generation.

We could not quite instantly look at someone and identify their class, since there is overlap as shown in the double-shaded area in the bottom panel of Fig. 3.1. After a few more generations of the process, we will be close to being able to glance at someone and identify their class, absent a large amount of random mating between classes. How do the class differences in genes here compare to differences among major human continental groups? Lewontin (1972) investigated diversity in a collection of genetic markers from human populations around the world and estimated that the fraction of variance that was between-populations was about 15% of overall human diversity, such that 85% of the variance was within populations. His original estimate has held up well for 40 years as the standard data set has gone from a small handful of loci to over a million. However, at the end of his otherwise fine and pioneering paper, Lewontin asserted that this 15/85 ratio implies that human differences must be small and of no significance. Although widely cited, this claim is unsupported by Lewontin's results, and unfortunately gives the impression of being politically motivated.

We can compare this global estimate of group difference to group difference in genes influencing stature between the short people and the tall people in our model. The separation between the group means is about 1.6 graph units, corresponding to

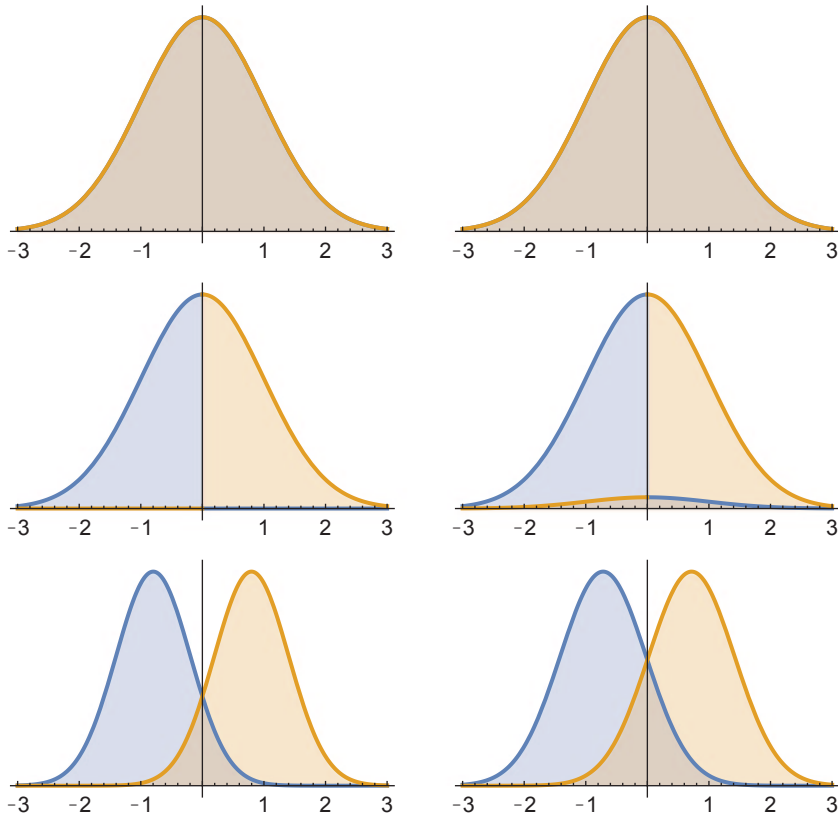


Fig. 3.1 The onset of assortative mating according to class. In the top panels, both classes share the same unit normal distribution of the trait. In the *second row*, everyone with a value greater than 0 has moved to the right class and everyone with a value less than 0 has moved to the left class. Random mating follows and the distribution within each class becomes normal in the *third row*. The *left column* shows the process with no other mating between classes. The *right column* shows the effects of 5% random mating between classes. See text for elaboration

4 in. The standard deviation within each group is about 0.6 on the original scale, or 1.5 in.. These numbers correspond to a ratio of 0.64 for between-group variance relative to total variance. One generation of assortative mating caused the difference between short people and tall people at loci influencing stature to be four times greater than the differences between human continental groups.

The assumption of harsh and immediate imposition of the new mating rule is not realistic. On the other hand, something not so far from that apparently happened after World War II, with the sudden availability of college education and massive college enrollment booms for both men and women. Suddenly both young men and women from Dubuque went off to the state university and met and married each other there. The boys and girls next door who stayed behind ended up marrying each other and, consequently, there was a very rapid assortment for education.

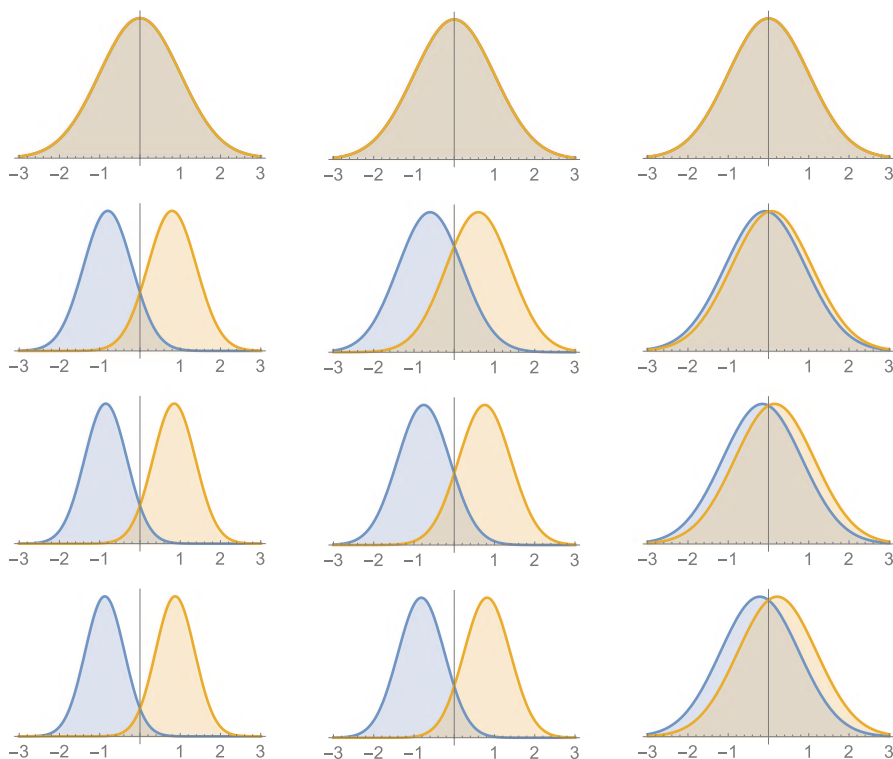


Fig. 3.2 These columns show the accumulating effects of assortative mating over three generations. The *left column* shows changes over time with maximum possible assortment ($h=1$), the *middle column* when half of matings are assortative and the other half random within class ($h=0.5$), and the *right column* when only 10% of matings are assortative and the rest random ($h=0.1$)

Varying Strength of Assortment

The example in Fig. 3.1 illustrated the initial changes when all matings were positively assortative by group in a single generation. The left column of Fig. 3.2 tracks ongoing changes over three generations (corresponding to 75 human years) with the same mating rule. After the first generation, the difference between group means continues to increase at a slower rate. The “raw material” for ongoing change is the area of overlap between the left and right distributions. This area decreases over time as the separation of the left and right distributions grows. After three generations, the difference between group means has only grown to 1.75 SD on the original scale.

The middle column of Fig. 3.2 models the same process, except that only half the matings are assortative rather than all of them. This provides an analogue of a

trait that is moderately heritable. Studies of the heritability of traits like religiosity or aggressiveness usually estimate heritabilities in the neighborhood of 0.50. Differences accumulate more slowly so that after two generations the difference between groups is similar to the difference after a single generation of mating with complete assortment.

The third column shows the process when only 10% of matings are assortative by group and the rest random within groups. The group difference continues to grow, but slowly. After three generations, the difference in means is 0.4 SD on the original scale; think of a one-inch difference in average stature between the groups, or six IQ points. These are not impressive differences compared to the effects of strong assortment, but they are not trivial. How much of income or socioeconomic group differences in stature are consequences of assortative mating by stature? A mere one-inch is not great, but it is surely noticeable.

Unequal Size Groups

Many situations in which we might expect the assortment mechanism to operate are those in which group sizes differ considerably. Figure 3.3 shows the consequences of three generations of assortment, in each column, for complete assortment in the left column, 50% assortment in the center column, and 10% assortment in the right column. Many social concerns focus on large differences in class size: labor and management, poor and rich, etc.

With complete assortment, the right class quickly and prominently separates from the left class, but without much apparent consequence for the left class. Here the mean of the left class decreases by 0.2 SD while the smaller right class's mean has increased by 2 SD. On the stature scale, the left class is one-half inch shorter on average than it was before the assortment while the right class is fully 5 in. taller, on average. On the IQ scale, there is a three-point decrease in the left class, on average, and a 30-point increase in the right class, on average.

The recipe for instant elite creation requires strong assortment. If assortment is 10% rather than 100%, shown in the right column of Fig. 3.3, differences accumulate very slowly. After three generations of low assortment, shown in the bottom right panel of Fig. 3.3, the left class has lost 0.05 SD, on average, or between an eighth and a sixteenth of an inch on the stature scale and less than one IQ point on the IQ scale. The right class mean has gained one-half standard deviation, on average, or three quarters of an inch on the stature scale and seven points on the IQ scale.

Applications?

Patterns like these generated by assortative mating would warm the hearts of Victorian eugenicists and might inspire governments not in the mold of modern liberal democracies. An implication is that a totalitarian regime could impose mating rules



Fig. 3.3 In this model, the left group in each column is 10 times the size of the right group. The volumes of the left and right distributions reflect the difference in group size. The *left, middle, and right columns* show results for h equal to 1.0, 0.5, and 0.1, respectively

and create an instant (i.e., in a quarter to a half century) elite class to populate its universities and professions, with little social disruption and damage to anyone. When assortment is strong, most of the effects happen within a generation or two, at the beginning of the process, so this mechanism is an attractive target for social improvers, just as it was a century ago before eugenics went out of fashion in favor of the compelling new fad of social science.

Richard Herrnstein (1973), late professor of psychology at Harvard University, was concerned for much of his career with the process we present in this chapter, wary that society was fragmenting with the creation of a meritocracy that would be a hereditary meritocracy. With Charles Murray, he published *The Bell Curve* (Herrnstein and Murray 1996) in 1995, a data-intensive exploration of the social and personal correlates of intelligence. A central focus of the book was the creation of a meritocracy in America. Unfortunately, they included a chapter on race differences that touched the American nerve and the message of the book was obscured by the cacophony from the politically correct. More recently Murray (2013) published a kind of ethnographic exploration of the lives of the new right and left

classes in America, titled *Coming Apart*. He does not include much explicit discussion of the quantitative genetics of what he describes, but he would certainly find such data congenial to his arguments.

The President of the USA recently declared that income inequality is the “defining challenge of our time,” referring to the large and growing income and wealth gap between the wealthy and the rest in the USA. There are also many references in the press to the vanishing middle class, a phenomenon which is expected with strong assortment, as we have discussed in this chapter.

Economists have a lively interest in income comparisons between parents and their children. There are serious issues with data quality and availability for empirical study of these issues, however. For example, one can find data on father’s and son’s incomes, but the son may be aged 30 and the father aged 60, so researchers must rely on cumbersome corrections and adjustments. A classic paper (Zimmerman 1992) from 1992 investigated transition rates between income quartiles, a convenient trick since quartiles are by definition the same size. The general pattern showed that retention rates in the bottom and top quartiles—the probability that a son is in the same quartile as the father—were about 40% for the top and bottom quartiles and about 30% for the second and third quartiles. Several years later, a comparison of mobility between the USA and Sweden (Björklund and Jäntti 1997) gave compatible results for the USA and showed that retention rates of the wealthy and poor groups were somewhat lower in Sweden, implying greater income mobility in Sweden. This is to be expected since the level of income variation in Nordic countries is much less than that in the USA.

An important study of trends over time in educational assortative mating in the USA was published by Schwartz and Mare (Schwartz and Mare 2005) in 2005 using census data. The researchers generated tables of matings between couples by complete education of the partners. Overall attainment changed over time; in 1940, most marriages were between people with 10 or fewer years of schooling, whereas in 2000 the most common marriage was between two college graduates. In a blog post (Harpending and Cochran 2013), we used a simple technique to estimate underlying “attraction” to remove the effect of changing average overall population levels, estimating in effect which marriages would occur if all educational levels were equally frequent in the overall population. The results were remarkable: the tables were essentially identical for all periods from 1944 to 2000 in spite of the great increase in population average educational attainment.

Data on educational attainment offer an excellent platform for investigating our proposed mechanisms in detail. Unfortunately, the data provided by Schwartz and Mare are too coarse for our purposes; the categories of educational attainment established in the 1940s are less useful today when a huge fraction of the population graduates from college. A check on our model would require the ability to drill into educational attainment to investigate differences between Liberal Arts and STEM graduates, for example, adding another category or two at the top.

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