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Chapter 4, Selection

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CHAPTER IV

SELECTION

Introduction

Neel commented in 1958 (p. 43) that our knowledge of the actual workings of natural selection in human populations was almost nil and that few studies, to date, had dealt with the problem; this is largely true today. Although there are scores, or hundreds, of papers dealing with genetic drift, inbreeding, and migration, few have attempted to analyze the role of selection in a subject population.

Although it might appear that the present study is unsuited for the study of selection, some means are available and are investigated in this chapter. The first is an examination of the maximum intensity of selection, introduced by Crow (1958); the second will be an investigation of differential fertility in selected samples.

Selection Intensity

Crow (1958:1) states: "There can be selection only if, through differential survival and fertility, individuals of one generation are differentially represented by progeny in succeeding generations. The extent to which this occurs is a measure of total selection intensity. It sets an upper limit on the amount of genetically effective selection."

Total selection intensity, of course, may only remotely relate to selection on the genotype, but total selection intensity will, as

Crow states, measure the maximum possible amount of selection, and provides a means of using purely demographic data. As a measure of selection intensity Crow has defined the Index of Total Selection (I):

"This means that if fitness is completely heritable, that is, if each offspring has exactly the average of his parents' fitnesses, the fitness of the population will increase at rate I . A trait or a gene that is genetically correlated with fitness will increase in proportion to this correlation. The index therefore provides an upper limit to the rate of change by selection. The actual change in a character will depend also on its heritability and correlation with fitness" (p. 3).

Let V_m equal the variance of mortality and V_f equal the variance of fertility:

$$I = \frac{V_m}{\bar{x}^2} + P_s \frac{V_f}{\bar{x}_s^2} = \frac{V_m}{\bar{x}^2} + \frac{1}{P_s} \frac{V_f}{\bar{x}_s^2} = I_m + \frac{1}{P_s} I_f$$

\bar{x} =total mean offspring. \bar{x}_s =mean surviving offspring.
 P_s =proportion surviving to maturity.

where

$$I_m (=V_m / \bar{x}^2 = p_d/p_s) \text{ and } I_f (=V_f / \bar{x}_s^2)$$

p_d =proportion dying

are the indices of total selection due respectively to mortality and fertility" (p. 3).

For the purpose of determining total selection intensity in the Deerfield population, values were obtained on the population of 1810 concerning fertility and mortality. It should be emphasized that, in using Crow's index, the total mean number of offspring includes

non-productive (non-surviving) parents averaged in as 0. The Deerfield evidence suggests that about 20 percent of the population do not reach maturity, so that mean offspring is adjusted from 8.41 to 6.63 for the parents of 1810. Further evidence suggests that, at least for females born in 1810, an additional 4-6 percent die unmarried; the differences this would make in selection intensity are presented in Table 4.1.

Comparison with other populations (e.g. Hutterites) indicates that when family size is very large and the ratio of mean family size to variance is small, the major component of selection intensity may be mortality; however, in most populations studied, natality is the most important factor. This leads Kirk to state: "The idea that fertility has replaced mortality as the basis of natural selection is wrong in that in premodern as well as in modern societies natality is generally the more important factor" (Kirk, 1966:271).

It is interesting to note that of 30 populations studied by Spuhler (1962) only 8 show indices of total selection below one, and only one population shows a value below the uppermost given for Deerfield (Figure 4.1). This suggests that among populations such as Deerfield and the Hutterites, where large family size and high longevity obtain, the opportunities for selection are not great. Whereas, in spite of cultural advances affecting mortality and the control of fertility, the opportunity for selection in more contemporary populations may remain relatively high. The effect will come from low mean family size, but great variance, common in modern populations--and probably a product of cultural factors.

TABLE 4.1
SELECTION INTENSITY IN DIFFERENT POPULATIONS

| Population | \bar{X} | P_d | I_m | I_f | I_f/P_s | I |
|----------------------|-----------|-------|-------|-------|-----------|-------|
| Deerfield (maturity) | 6.63 | 0.209 | 0.264 | 0.136 | 0.172 | 0.436 |
| " (unmarried) | 6.22 | 0.260 | 0.351 | 0.155 | 0.209 | 0.560 |
| Hutterites* | 7.84 | 0.179 | 0.218 | 0.136 | 0.166 | 0.384 |
| Bengali Villages | 4.80 | 0.313 | 0.456 | 0.217 | 0.316 | 0.722 |
| Switzerland | 1.78 | 0.058 | 0.062 | 1.496 | 1.588 | 1.650 |
| Peri, New Guinea | 1.306 | 0.532 | 1.137 | 1.195 | 2.553 | 3.689 |

All subsequent values from Spuhler, 1962, 1963.

Differential Fertility

As discussed above, selection can only occur if individuals of one generation are differentially represented in the succeeding generation. In order to assess the possibilities of selection in historic Deerfield, I undertook the analysis of fertility among migrant and non-migrant matings. Definition of marriage-types is as follows: (1) non-migrant (native) matings are those occurring between two individuals from Deerfield, and (2) migrant (non-native) matings are those occurring between a Deerfield and a non-Deerfield individual. The definition of a non-native is based on the place of residence given in records of marriage. Assumptions concerning the data were as follows:

- (1) Migrants are assumed to have been born outside Deerfield.
- (2) Migrants are presumably distinctive from the natives in genotype frequencies, so that,
- (3) A migrant mating normally brings two people together with greater "genetic distance" than a native mating.
- (4) If differences exist in the reproductive performance of the two types of matings--selection is presumably operating.

Hypotheses concerning the data were as follows:

- (1) Null. No difference (significant) exists between the mean family size of migrant and non-migrant matings.

Alternative hypotheses:

- (2) If heterosis is active, offspring from migrant matings should be more viable, and numerous, than those of native matings.
- (3) Local environmental factors select favorably for offspring

of native matings; native offspring will be more numerous and viable because they possess adaptations to local factors (including coadapted alleles).

An initial sample was taken, using the records of the parents of 1810. The sample, as pointed out in Chapter III, consisted of a compilation of the reproductive histories of all parents who had a child in 1810. In all, 17 families were migrant matings, 24 were native. These were compared for mean family size at birth, and at maturity (16 years). Information on the families were compiled from Baldwin (1920) and the genealogies in Sheldon (1896). Findings on the sub-samples are presented in Table 4.2.

TABLE 4.2
FERTILITY OF NATIVE AND MIGRANT MATINGS: PARENTS OF 1810

| Sample | N | \bar{X}_b | s_b | \bar{X}_m | s_m |
|---------|----|-------------|-------|-------------|-------|
| Native | 24 | 8.96 | 2.77 | 6.92 | 2.46 |
| Migrant | 17 | 7.59 | 2.66 | 6.50 | 2.39 |
| | | F=1.08 | | F=1.059 | |
| | | P > .10 | | P > .10 | |
| | | T=1.6006 | | T=.4985 | |
| | | P > .10 | | P > .50 | |

B=at birth.

m=at maturity.

The values, while suggestive, do not indicate any significant differences in fertility. However, there are certain inherent

problems with the sub-samples. In using the parents of 1810, the sample is small and the parents may not have survived their full reproductive years; also, they may have migrated, remarried, or been subject to several other unknown factors. Because of the lack of control in these samples for measuring differential fertility, additional samples were drawn to see if the trends would be the same as those observed for the 1810 parents. These latter samples were collected with better "genetic" controls. One sample of 50 native matings and one of 50 migrant matings were collected. A family was included if:

- (1) Male and female parent survived the complete reproductive period.
- (2) Biographical data of each family was well documented concerning reproductive history.
- (3) Males were all from Deerfield, so that difference between migrant and native was always female.

The method for obtaining a sample was by reading through the alphabetically listed genealogies of Sheldon (1896) and taking each family that met the above criteria. For both samples surnames were drawn from the complete listing of names. It is assumed that any factors of inadequate enumeration are distributed randomly in both samples. Males were drawn for both samples because the subject population is patrynomic and tends to be patrilocal; this suggests that information on migrant females would tend to be more frequent and complete. In addition, control by locality of one sex (male) should minimize social reasons for fertility differences. Marriages included in these samples are distributed from the early 1700's to

the middle 1800's, which should further control for possible fluctuations in social determinants over time. The results of these samples are summarized in Table 4.3.

TABLE 4.3
FERTILITY OF NATIVE AND MIGRANT MATINGS: 1700-1850

| Sample | N | \bar{X}_b | s_b | \bar{X}_m | s_m |
|---------|----|-------------|-------|-------------|-------|
| Native | 50 | 7.74 | 2.95 | 6.36 | 2.95 |
| Migrant | 50 | 6.38 | 3.54 | 5.46 | 2.86 |
| | | F=1.44 | | F=1.06 | |
| | | P > .10 | | P > .10 | |
| | | T=2.266 | | T=1.552 | |
| | | P < .05 | | P > .10 | |

b=at birth.

m=at maturity.

In short, a significant difference is found between the migrants and natives at birth, but at maturity the difference has become non-significant. Between birth and 16 years 14.4 percent of the migrant offspring die, while 17.8 percent of the native offspring die. These findings are in the same direction as those observed for the parents of 1810 and would tend to confirm the initial findings. The null hypothesis may be rejected for mean family size at birth, but apparently not at maturity.

Before discussing the results in light of alternative hypotheses,

it would be good to briefly review some previous studies on fertility and heterosis. Traditional studies on populations which have interbred are most often concerned with whether the exchange of alleles was "good" or "bad" rather than whether or not selection operated to produce differential fertility and survivorship. In addition, most of these studies tended to be based on "interracial" samples. Positions concerning the "goodness" or "badness" of cross-breeding were polar, as represented by Shapiro's classic study of the Bounty mutineers and Pitcairn Islanders (1936), in which he found the effects of interbreeding largely good; and, Davenport and Steggerda's study of race crossing in Jamaica (1929), in which they concluded race-crossing was largely bad. This is, generally, an unproductive form of inquiry.

Early studies which have investigated differences in fertility include a study of Hawaiian interracial crosses (Kraus, 1941), American Indians and Anglos (Boas, 1894, 1940), and certain European and American white populations (Hulse, 1957, 1964). The results are interesting: Kraus (1941) found no significant differences in fertility; Boas (1894) found much higher fertility for the Indian-Anglo crosses than for "full" Indians; and, Hulse (1957) found that exogamous marriages were less fertile than endogamous among California and Swiss white populations. A summary statement concerning these findings would be, to say the least, somewhat inconclusive. A more recent study on interracial crosses in Hawaii (Morton, Chung & Mi, 1967) found no significant effects of hybridity.

In two recent studies concerning the fertility of outcrossing the results tend to be less equivocal. T. Yanase (1964, 1965), in a

Carefully controlled study of migration and fertility of two Japanese sub-populations, found that the mean number of children ever born to natives was consistently higher than that of non-natives. This was found to be the case generally over time in both communities. A second study, by J. Bresler (1970) analyzed the frequency of fetal loss among American white families who varied over distance and in diversity of European ancestry. Using a sample of 708 families he found that, as distance or diversity of origin increases, fetal loss increases. The conclusion reached is that heterogeneity in background brings about greater fetal loss in this intraracial sample.

In light of the foregoing, it is tempting to make the following conclusions regarding the Deerfield sample:

(1) Adaptation to local selective factors and maximum compatibility of all polymorphic alleles in the local population, select positively for a large mean family size at birth among native marriages.

(2) Incompatibility of some new allelic combinations (heterozygote disadvantage) and lower fitness to local conditions tend to increase fetal and neo-natal deaths among migrant matings, so that mean family size at birth is lower than for native matings.

(3) Certain new alleles or allelic combinations (heterozygote advantage) are favorably selected for and the viability of offspring of migrant matings who survive birth is greater than that of native offspring, who may carry greater segregation loads and who do not possess favorable new alleles. This results in a tendency for mean family size at maturity to be closer than at birth for native and migrant matings.

(4) It seems reasonable to assume that this can occur in other human populations.

To me it would seem critical to investigate mean family size at maturity whenever possible. Almost all human societies show a common pattern of mortality in which survivorship through the first 10-15 years, and particularly childhood, is less probable than survivorship through the following 20 years. These early years may be the time during which the most significant differential mortality also occurs.

Finally, if past studies of human heterosis seem to be inconclusive, this may only be testimony to good evolutionary reasoning. An evolutionary approach to outcrossing should lead us to the conclusion that outcross matings will at times be more fertile, and at times less fertile, than the two original populations; and this difference will depend on the intensity of local selection and the fitness of the migrant group to the new conditions. Not surprisingly, studies on non-human animals tend to support this: studies cited by Ehrlich and Raven (1969), and Bresler (1970), and based on such diverse forms as insects, amphibians, and mammals, tend to show decreased fertility among the hybrids. On the other hand, many past studies on non-human animals, as Penrose suggests (1955), have indicated the hybrids were more fertile; others indicate intermediacy.

If anything, in evolutionary perspective, may be concluded about heterosis in man, it is that, generally, a group migrating into a new selective area could be expected to profit from interbreeding with the local, adapted population. In turn, any new variability or adaptation the migrant group introduces may be favorably selected for in subsequent generations of mixed matings.

