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The Genetic Structure of an Historical Population: A Study of Marriage and Fertility in Old Deerfield, Massachusetts (Full Text)

Alan C. Swedlund
Prescott College

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THE GENETIC STRUCTURE OF AN HISTORICAL POPULATION: A STUDY OF MARRIAGE AND FERTILITY IN OLD DEERFIELD, MASSACHUSETTS

by

ALAN C. SWEDLUND

Center for Man and Environment, Prescott College
Prescott, Arizona

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CHAPTER I

BACKGROUND OF THE STUDY

Introduction

Data for the present study are derived from vital statistics and genealogical records of the town of Deerfield, Massachusetts. Fieldwork was done during the summers of 1968-1969, and consisted primarily of library research in the Deerfield area, and re-recording the information for computer use. The period of time covered by these records is between 1680 and 1850, or, 170 years.

Massachusetts provides good opportunities for historic population research, since registration of births, deaths, and marriages was made compulsory in 1639 (Spiegelman, 1968:3). Deerfield was selected as the community for study after a number of small towns in northwestern Massachusetts were considered. The reason Deerfield was chosen is because available records appeared to be very complete. The community of Deerfield's own emphasis on its long history, and efforts by such specific groups as the Pocumtuck Valley Memorial Association (founded in 1870), and the Heritage Foundation, provide for a good library with many well preserved records. Although several references concerning Deerfield and Massachusetts are consulted, the major sources for the information presented below are Baldwin's Vital Records of Deerfield, Massachusetts to the Year 1850 (1920); and George Sheldon's History of Deerfield (1896). The major emphasis is on the complete records given in Baldwin

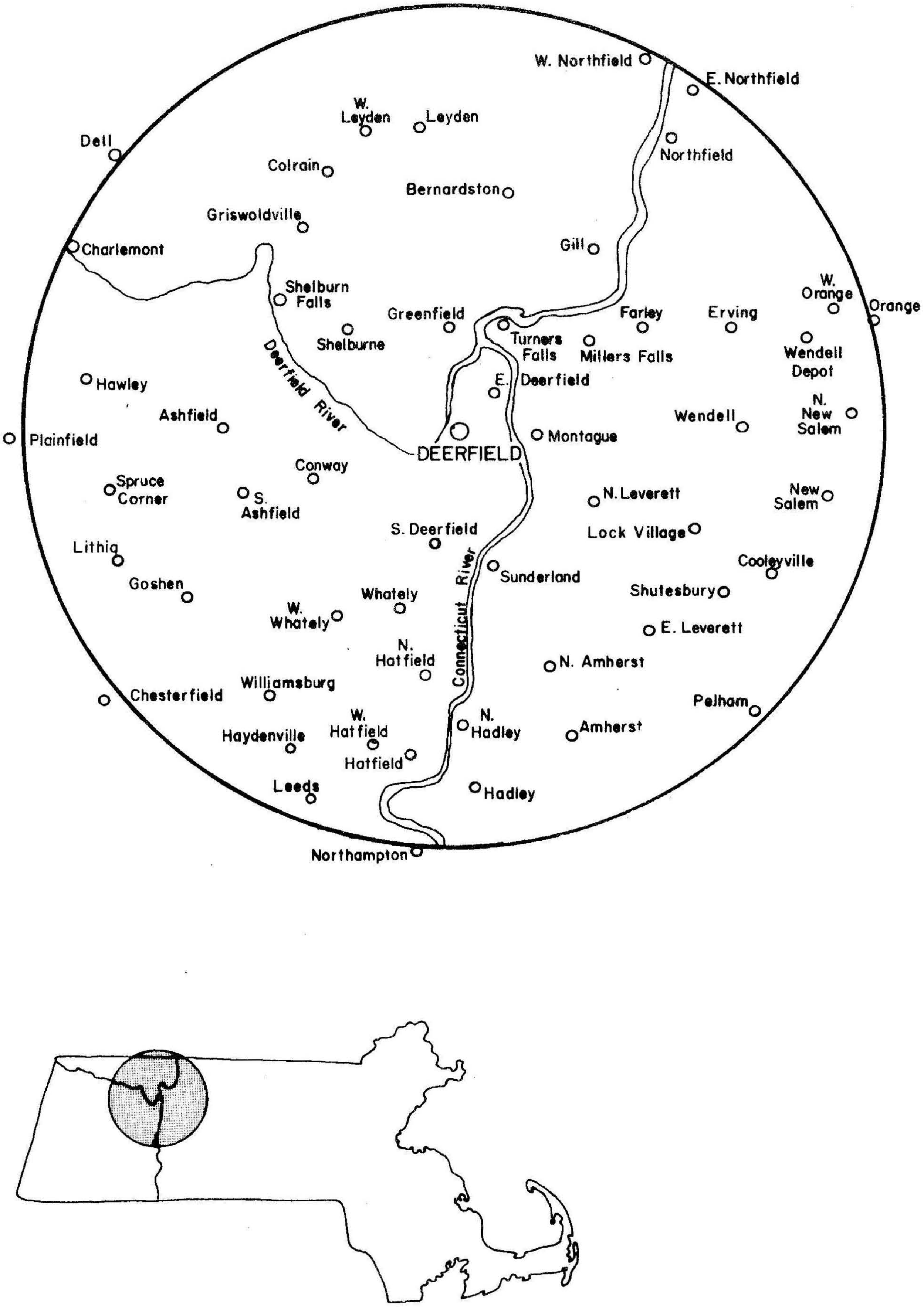
(1920) with supplementary information being added from Sheldon's published genealogies (pp. 4-407, Vol. II). Sheldon's work is considered by many colonial historians to be a very well written and thorough local history. The vital statistics compiled by Baldwin appear to be very complete considering the time period covered and are based on grave inscriptions as well as town and parish records. These statistics include 4943 births, 1485 marriages, and 2204 deaths. In an effort to test the accuracy of the records, the local cemeteries around Deerfield were sample surveyed, and virtually 100 percent of the cemetery markers checked are found in Baldwin.

Description of Deerfield

Deerfield is located in northwestern Massachusetts at the confluence of the Deerfield and Connecticut Rivers, approximately 30 miles north of Springfield (Figure 1.1). The town was formally established in 1673 and has been a rural, largely agricultural community since its founding. Today the town is most well known for its fine preparatory school, Deerfield Academy, and for its attractive and excellent restoration as a colonial town (see McDowell, 1969; Phelps, 1970).

During the early settlement period of the Deerfield region goods and supplies came to the Connecticut Valley (Pioneer Valley) by way of the River; however, many of the early communities were settled by families who trekked through the forests from eastern Massachusetts. Many of the founders came from the Massachusetts Bay Colony or its descendents and were in search of good farming land. Deerfield's first residents tended to come from villages to the south and along the River (e.g.

FIGURE I.1 DEERFIELD AND SURROUNDING AREA



Circle represents a 15-mile radius around Deerfield. The great majority of migration occurs within this radius. Shaded area on map of Massachusetts indicates the primary study area.

Northampton, Hadley, Hatfield), but the original land grant came from the "mother-town" of Dedham, near Boston. Deerfield, or Pocumtuck as the original community was called, was the northwest frontier settlement of New England. Thus, although communication was maintained along the Connecticut River to the south, Deerfield and its nearest neighbors were strongly influenced by the Indian tribes and wilderness to the north and west of them.

The early history of Deerfield did not include the tranquility that prevails today. By virtue of its location, Deerfield played a very prominent role in the history of the Colonial-Indian wars. This period in Early American history has been described in detail by many (e.g. Sylvester, 1910) and one of the most famous incidents is the Deerfield Massacre of 1704. In this raid a group of French-Canadians and Indians attacked Deerfield at daybreak, killed 48 people, and took 111 prisoners to Canada. In spite of this defeat, many of the prisoners ultimately returned to Deerfield and resettled. Following this tragic event Deerfield reestablished itself and through subsequent contacts with Indians and the Revolutionary War remained a very successful community.

Demographic Background

The time depth, growth features, and relative stability of Deerfield make it an ideal community for the proposed study. Although Deerfield suffered the large scale Indian massacre in 1704, and occasional minor uprisings until the 1740's, the town was generally under stable influences in comparison to the coastal and industrial communities of early Massachusetts. The founder population was composed of families, providing for a relatively well balanced sex ratio from the town's inception. Migration tends to be ethnically stable for the time period under study. Economically, the Connecticut Valley is a very fertile farmland and this had positive effects on the health and growth of the local population.

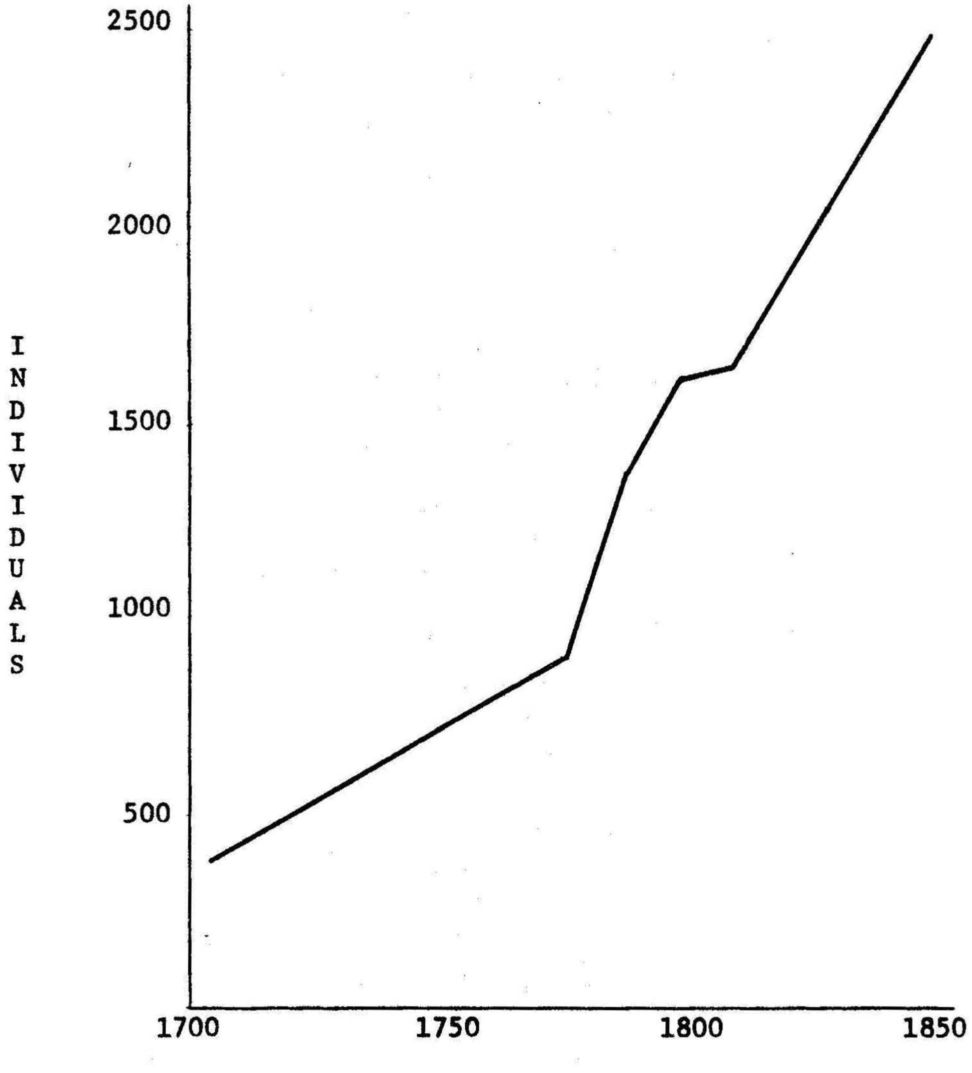
Over the 170 year period covered by the present study, the town experienced steady, rapid growth (Figure 1.2). This growth arises from immigration as well as high local fertility. A comparison of the crude birth and death rates (Figure 1.3) reveal that, on the average, Deerfield had a relatively high birth rate and relatively low death rate for the period under study. The rates would compare favorably, for example, with the rates of Transitional or Advanced countries in the world today (Zelinsky, 1966). A lack of census information for the years 1704-65 produces the straight line effect in Figure 1.2, and this is not a very true reflection of the presumed rates. However, the high mortality of 1704, the result of an Indian massacre, would certainly cause mortality to drop in the direction observed. The slight increase in death rates between 1765-1850 may be explained by two factors: (1) there is the possibility of underenumeration during the earlier years covered; and, (2) a very likely cause is the fact that the population is becoming older and a larger fraction of the population is reaching maximum longevity. In a recently settled population, such as early Deerfield, it is common for the individuals to be relatively young; as stability and growth follow, the population profile changes to include a larger fraction of very young and old.

Suich (1966) in a brief survey of vital statistics for Deerfield in the 1700's, finds the mean age at marriage to be 26.3 for males and

FIGURE 1.2

POPULATION GROWTH IN DEERFIELD

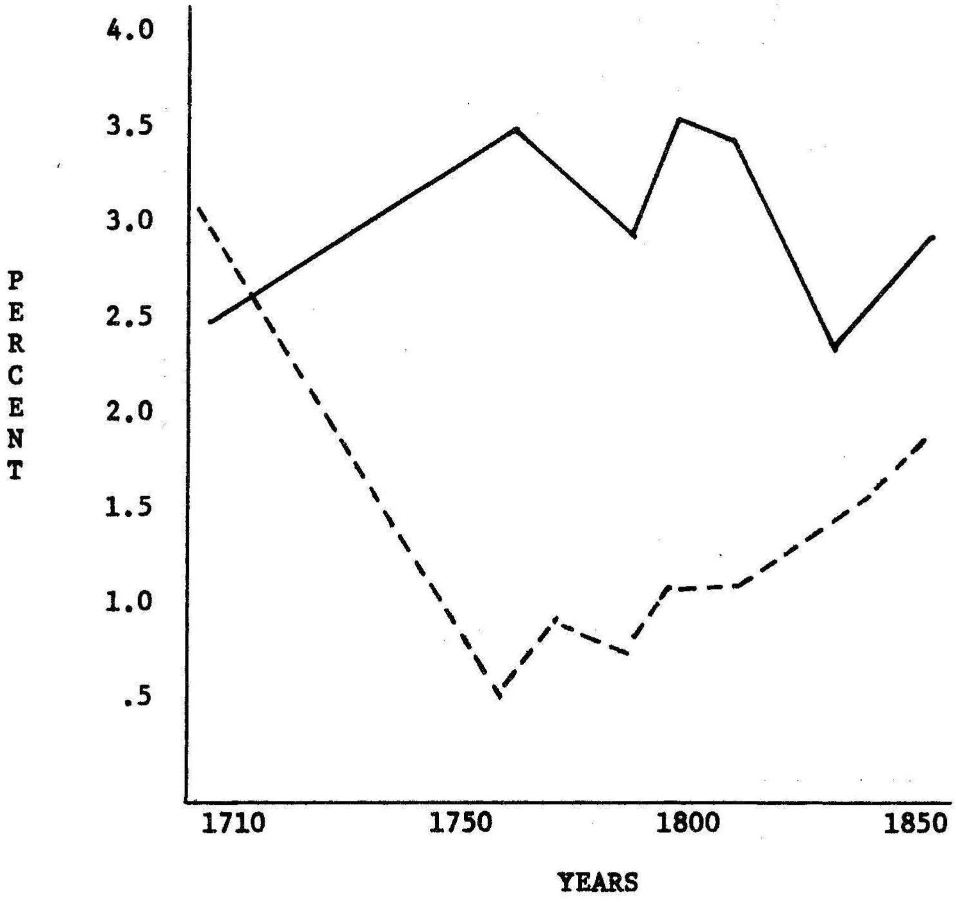
1700-1850



Source: Sheldon, 1896; Dickinson, 1818;
U.S. Bureau of the Census, 1790.

FIGURE 1.3

CRUDE BIRTH AND DEATH RATES* FOR DEERFIELD 1700-1850



Solid Line = Births. Dotted Line = Deaths.

*Rates based on a 3 year average, including the year following and the year preceding dates shown.

22.7 for females. These values are close to those found for other early American populations (Demos, 1965; U.S. Bureau of the Census, 1960). The mean number of children is 7.2 prior to 1765 (Suich:18) and this compares closely with the value of 7.06 which I found for 100 families and including marriages after 1765.

TABLE 1.1

AVERAGE LIFE EXPECTANCY IN DEERFIELD: 1745-1765

Age	Male	Female
Birth	45.0	45.8
1	51.9	52.9
10	59.4	59.3
20	63.8	63.1

Source: Suich, 1966:1

Life expectancy tends to be quite high for Deerfield (Table 1.1) when compared with other available figures. The expectancy of around 45 years for the population at birth, is in contrast to the estimate of 35.5 for the general population of Massachusetts and New Hampshire prior to 1789 (Dublin, 1949:35). The high value for Deerfield is indicative of a quality of life that was probably common for the more prosperous rural communities of early New England. Lower life expectancies would be expected from the more urbanized and industrialized areas. Little information can be found concerning the characteristics of morbidity; however, one report concerning health and mortality for the period 1787-1816 is given by the Gazetteer Dickinson (1818:6): "The number of deaths which have occurred in this place, according to the parish register, since the year 1787, a period of 29 years, have been 510. This upon an average is a fraction over 17 a year. It appears that 59 of these have died of consumption, 66 of dysentary, and 48 of fevers. The greatest number of deaths which have occurred in any one year from consumption is 7, from dysentary 38, and from fevers 22." Thus, although disease and death were certainly problems to be concerned with, the general impression from vital statistics on Deerfield is that it was a very healthy and congenial place to live during most of the 1700 and 1800's.

The Problem

Date for the present study are comprised of: (1) the marriage records from 1680-1849, originally listed in Baldwin (1920) and supplemented by notes from Sheldon (1896); and, (2) selected samples of fertility and other family parameters for the same period. The scope of the present study is more limited and specific than the data collected will eventually permit, and represents an initial analysis of the genetic structure of Deerfield.

In The Problem of the Structure of Isolates and of Their Evolution Among Human Populations, Sutter and Tran-Ngoc-Toan (1957:379) observe that theories of population genetics, in their initial assumptions, often depart greatly from reality. In fact, it is often assumed that the population is supposed to be closed, marriages to take place at random, and fertility to be identical for all couples. The problem which will be discussed in this paper is the empirical determination of departures from these conditions, and their subsequent implications. This is done by an investigation of three relevant areas: (1) population numbers; (2) migration; and, (3) selection.

In experimental breeding populations it is not difficult to control variables to meet assumptions, but with man, and with natural populations of other animals, conditions and assumptions may be highly disparate. Also, in man, another dimension is added, the cultural dimension. In addition to all the biological parameters that may affect population structure, man introduces cultural factors affecting mating, fertility and migration. These cultural factors can have genetic significance and should be taken into account. In the present study I will be concerned with cultural variability that may ultimately have an effect on genetic structure.

The nature of historical samples is such that many question their validity. While poor enumeration is always a possible problem, it may be counteracted by the profits gained in the time-depth which historical analyses permit. My own impression is that the materials from Deerfield are very complete, though certainly not perfect; evidence from cross-referencing sources confirms this impression. In addition, I have attempted to design the analysis of the genetic structure of Deerfield, so that errors of underenumeration will randomly affect the results obtained, and not bias the differences tested. the rejection or acceptance of the findings must, of course, ultimately come from the critical reader.

I should emphasize here that those of us who engage in research using historical records are ultimately dependent upon the temperament, conviction, and morality of the subject population. It should be evident to all that people and names are not genes and that social and biological ancestry are not necessarily one and the same. However, in this last consideration, I place a large amount of faith in the fathers of Deerfield. All the evidence available to me indicates that Deerfield was a community of people that lived and respected the Puritan Tradition. The town was small enough so that the possibility of knowing what other people were doing was great, and the church was judicially as well as spiritually influential concerning morality. An excerpt from Sheldon's Genealogies (1896:106) testifies to the former point regarding a particular Deerfield citizen: "...June 18, 1772, he was arraigned before the church for 'unnecessarily absenting himself from public worship and the ordinance of the Lord's Supper, and accusing the church of oppression;' he acknowledge the truth of the complaint, but professing himself willing 'to be rectified in his sentiments if they were mistaken;' sentence was deferred to the 29th, 'when said Catlin appeared sensible of his error and was restored to good standing.'"

CHAPTER II

POPULATION NUMBERS

Introduction

In developing theories of population genetics, the tendency in the past has been to assume that population size is infinite or, if finite, constant. In addition, problems with studying genetic structure have arisen not only because models are inadequate, but also because our knowledge of actual human populations has been deficient (Schull and MacCluer, 1968:282-83). It is quite clear that infinite population size is unrealistic for human population models, and a constant size is probably invalid in a number of specific, empirical situations. Although there are these problems in the concept and definition of population numbers, seldom do studies undertake clarification of the problems involved. In the following chapter the nature of this problem will be investigated in regard to the Deerfield records.

Effective Population Size

In attempting to characterize the genetic structure of human breeding populations, two variables are very commonly investigated: one is the effective population size (e.g. Wright, 1938; Kimura and Crow, 1963) and the other is the coefficient of inbreeding (e.g. Wright, 1931; Crow and Mange, 1965). These measures estimate departures from idealized conditions in the subject population. In a specific, localized, human population mating may not be random;

family size may vary greatly; and the population is not likely to be infinite. The effective population size is a parameter for defining these deviations from Hardy-Weinberg conditions.

The effective population size (N_e) is "...the size of an idealized population that would have the same amount of inbreeding or of random gene frequency drift as the population under consideration" (Kimura and Crow, 1963:279), that is, under panmixia, the number producing the conditions observed in the subject population. As Falconer (1960:70) points out, probably the most common and important deviation from the system of an idealized population is the non-random distribution of family size. Formulae have been developed to estimate variations in family size. Wright (1938) presents a formula given constant population size:

$$N_e = \frac{4N - 2}{V + \bar{k}}$$

where N is the breeding population size, V is the variance in family size, and $\bar{k}$ is the mean family size surviving to maturity; in populations of constant size this is equal to 2. Others (e.g. Kimura and Crow, 1963) have extended this to deal with separate sexes and varying population size.

Among human beings it is necessary to define what is meant by the breeding population, since parents and adults are not necessarily synonymous. Lasker (1954) and others have used the measure of parents with children at a given census time. This estimate can be high if it includes older, non-fertile parents, or low if it omits separated parents (Lasker, 1954:355). Others (e.g. Salzano et al, 1967) have defined the breeding population as composed of those individuals of reproductive age.

This latter definition has been adopted for the present study, and the breeding population is considered to be comprised of all those individuals between the ages of 16-45. This allows for the reality that individuals a "generation" apart may produce viable offspring and yet eliminates all parents who would normally be beyond reproductive age.

It is also necessary to emphasize that variance in family size (V) means variability in number of offspring who themselves reach maturity. This last consideration is very important, since subadult mortality could increase or reduce the variability observed at birth. The variance in family size for the Deerfield population was determined by taking all individuals who were parents in the year 1810, counting their total number of offspring, and then determining the mean and deviation in numbers of offspring for the total sample. 1810 was chosen because it appeared to be in a period of typical reproductive habits for Deerfield, and by taking parents at this time it was possible to include females who gave birth as early as 1789 and as late as 1837. This would compensate for possible fluctuations in social variables, disease, etc. Table 2.1 presents the basic information on the sample.

It may be noted that the family size for Deerfield at this time is very high, even for children surviving to the age of 16; the mean period of productivity for females is 15.9 years. While these values appear quite high, they are not inconsistent with values from other populations (Table 2.2).

The effective population size has been investigated in a few

TABLE 2.1

REPRODUCTIVE HISTORY: PARENTS OF 1810

	All Children	Children Reaching 16 Yrs.
Number of families	41	40
Range of children	3-15	3-11
Mean Children	8.41	6.65
Std. Deviation	2.78	2.45
Variance	7.73	6.00
Mean Reproductive Period*	15.9 yrs.	15.9 yrs.
Deerfield Parents	65	63
Outside Parents	17	17

d=2.288 $P < .01$

*Females

TABLE 2.2

MEAN FERTILITY IN VARIOUS POPULATIONS

Population	Time	N	Source
Deerfield	c. 1810	8.41	Present Study
Plymouth Colony	c. 1700	8.56	Demos, 1965
U.S. Women	c. 1839	5.50	Crow & Morton, 1955
Hutterites	c. 1925	10.90	Henry, 1961*
Norway	c. 1875	8.10	"
Hindu Villages	c. 1945	6.20	"

*In Spuhler, 1963.

human populations, and comparisons have been made between man and other animals. Crow and Morton (1955) calculated $\underline{N_e}$ for man, *Drosophila*, and the snail *Lymnaea* and found it to be between .70 and .95 of breeding size. Morton (1969:57) states that N_e for human females may be typically about two-thirds of breeding size. However, in Crow and Morton's study they considered mean family size at maturity to be two in all three species, since this is often found to be the case in natural populations (p. 211). It is my contention that this is not typical for many human "natural" populations. Even though population growth cannot go unchecked in any environment indefinitely, the fact is that the last 8,000 years of man's evolution have taken place under conditions of rapid increase, the rate of increase is most marked in the last few hundred years (see Huxley, 1956: Deevey, 1960). This trend has no doubt had microgeographic and microevolutionary significance as well as broader effects. As an example, the population of Deerfield grew to 5 times its original size in less than one hundred years, and doubled itself three times in its first 150 years (Figure 1.1). Migration certainly does not account for all this growth and large family size must be a contributing factor. This suggests then that constant population size is an unrealistic assumption for Deerfield and probably for the recent "natural history" of man.

It would thus appear that Crow and Morton (1955) may be too conservative in using the value of two for many human situations, and the results of an increase in mean family size and variance values are twofold: (1) as mean family size increases, the size of the breeding population and effective population size also increase through time. The reason for this is simply that large mean family size ultimately increases the absolute size of all fractions of the population by insuring that each generation will be larger than that preceding. (2) As the mean family size and variance increase the <u>relative proportion</u> of effective size to breeding size decreases at a given point in time. That is, if a particular breeding population is the product of a family size and variance exceeding two, then the proportion of the effective population to breeding population will be less than if the population were not experiencing growth. This latter point is particularly important when investigating actual human populations. For example, the breeding population (individuals between 16-45) of Deerfield in 1810 consisted of 649 individuals. If the population is considered constant in size over time then the effective size is 563 using Kimura and Crow's (1963) formula:

$$N_e = \frac{4N-4}{V^*+2}$$

where V* is the variance for one sex (females=2.6) and N is breeding population size. However, if the actual mean (6.65) is used, and a constant rate of growth, but not size, is assumed, then the effective size becomes 107 using Kimura and Crow's (1963) general formula:

$$N_e = \frac{N_t-2\bar{k} - 2}{\bar{k} - 1 + V^*/\bar{k}}$$

where N_t-2 is the grandparental generation size which, given a constant rate of growth is equal to N_t-1 / $\bar{k}$. In a species with separate sexes, such as man, a pair of alleles in an individual cannot come from the same parent, or from two individuals of the same sex. A pair of alleles may come, however, from the same grandparent. The difference between the two formulae above is that, if population size is constant, the parental and grandparental generation are the same; but if population size is changing, then the N of the grandparents should be used, and the mean ($\bar{k}$) will be greater than 2.

Table 2.3 presents the effective population estimates for Deerfield using the assumed and observed values. The estimates include the effective population size given a mean family size of two, and, in addition, the values given for actual mean family size. The rather dramatic differences between the values are apparent, and relevant in regard to the fact that several past studies have used mean family size of two when other values were observed (e.g. Lasker, 1954; Küchemann et al, 1967; Salzano et al, 1967). Although Deerfield is an extreme example in the sense that family size is so large, it is indicative of the direction and magnitude in which N_e may vary.

TABLE 2.3

EFFECTIVE POPULATION SIZE BASED ON ASSUMED
AND OBSERVED FAMILY SIZE: DEERFIELD, 1810

Total Population Size=1570; Breeding Population=649

	V	X	N_e	%N*	%T
Assumed	2.6	2.00	563	86.7	35.8
Observed	2.6	6.65	107	16.5	6.8

*N=breeding size; T=total size

The effective population size, as presented on the previous page, has a further weakness in the sense that it is based on a strict generational construct. This presents itself in calculation as the myth that 6.65 children, in the case of Deerfield, occur as a single event which all fertile females share in common. As mentioned above, at any given time (e.g. 1810) females bearing young may have also borne children 20 years before or after, and the breeding population is in a constant state of change. The complexity which overlapping generations creates is not easily dealt with in man (Schull and MacCluer, 1968). Kimura and Crow (1963) have defined N_e for overlapping generations <u>with</u> constant population size:

$$N_e = \frac{N^2}{N_o r} = \frac{N}{b\ r}$$

where N is the total population number, N_o is the number born per unit time, $\underline{b}=N_o/N$ is the crude birthrate, and r is the average age of reproduction. Again, the problem arises in populations undergoing growth. In populations which have not reached stability and where age will vary with time, effective population size cannot be viewed as a stable relative proportion of the population. The effective population size will change relatively and absolutely.

A second, very important variable which, although difficult to measure, will affect the effective population size is migration (Morton, 1969:57). Most measures of effective population size are based on the concept of an idealized situation in which no migration is occurring. Lasker (1954) states that in "primitive" or "folk" cultures the breeding population is more or less synonymous with the community

(p. 353). It would appear that "less synonymous" may be most appropriate, since he then goes on to state that over 20 percent of the parents he analyzed in Paracho in 1952 were from outside the community. In calculating N_e it is necessary either to assume that the effects of immigration and emigration are equal, in numbers as well as genotypes, or to make some effort to estimate possible differences. Since N_e is intended to define the sampling variance in gene frequencies between parents and offspring, it is probably most correct to accept the migration existing in the parent group, and to make adjustments for migration by altering the denominator of the equation. Thus, if migration is a factor, then in addition to adjusting mean family size to reflect those who survive to maturity, it is also necessary to account for those who will be gained or lost through migration. For example, if emigration is reducing the number of individuals reaching maturity in the local population, then the rate of this emigration should be added to the rate of mortality between birth and maturity in determining mean family size.

In addition to changing population size and migration, other factors will have an impact on the effective population size (Salzano et al, 1967:488): (1) concentration of relatives in the founding group; (2) restriction of mate selection within the population; and, (3) differential inheritance of fertility. The imprecisions which attach to effective population size thus become manifold. This has led Morton and Yasuda (1962:188) to state that: "Because of its mathematical simplicity, the concept of a subpopulation with an assignable size N has fascinated population geneticists to such an extent as to retard the development of a more realistic theory."

If a specific community happens to be the focal point of a genetic study, then in spite of the difficulties in quantifying a genetically significant measure of size, some indication of the changes in size of the local breeding population can be useful. Changes in the size will reflect: (1) the growth or decline of the genetically significant reproductive portion of the population; (2) changes in the age structure of the subject population; and, (3) the effects of migration and mortality on the population when viewed through time. The difficulty arises in determining which of these three may be causing any fluctuations observed. Figure 2.1 presents the relative and absolute growth of the breeding population of Deerfield through time. The size of the breeding population appears to be on the increase relatively as well as absolutely. The increase is probably attributable to both high local fertility and immigration, but as indicated above, this high local fertility would have the effect of decreasing the relative effective size of the population.

Coefficient of Inbreeding

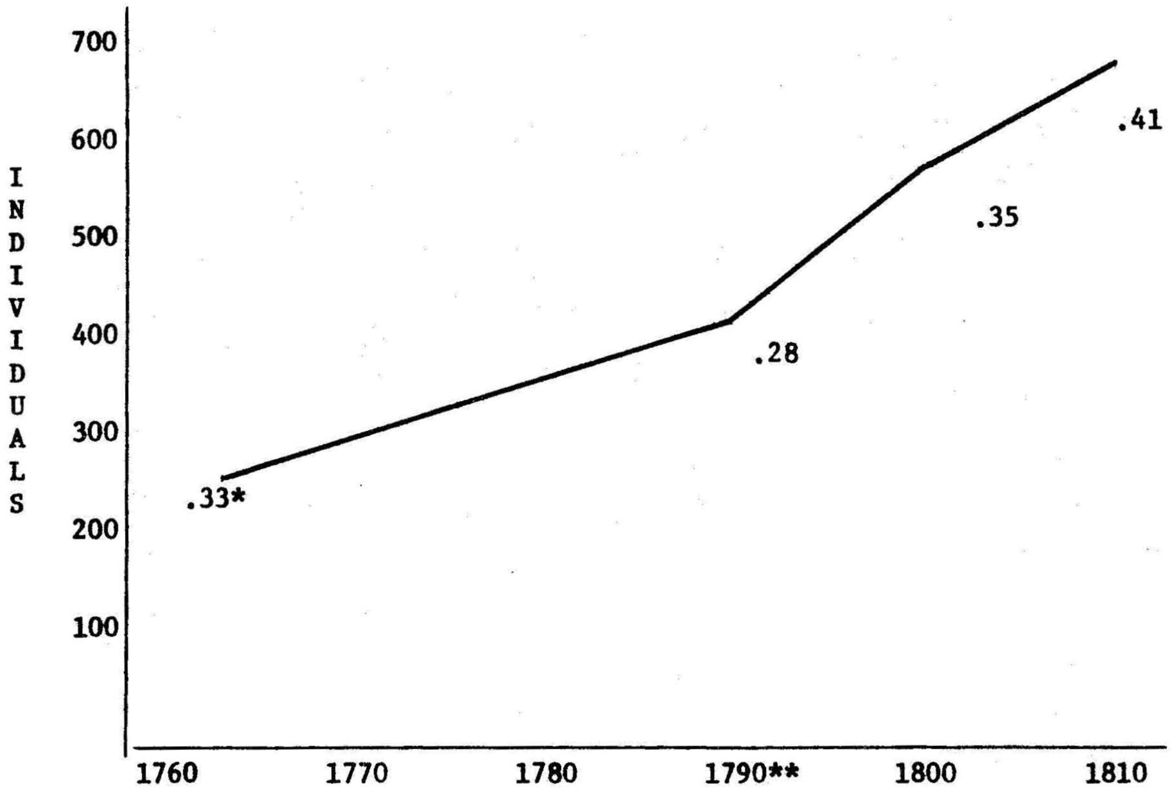
As discussed above, the effective population size is an estimate which ultimately is an expression of inbreeding and gene drift. Inbreeding (F) may be defined as the mating together of individuals related by ancestry. The coefficient of inbreeding is the probability that two genes at any locus in an individual are identical by descent (Falconer, 1960:60-61).

Inbreeding has two components, the random component, which is a sampling product of small population size, and indicative of the

FIGURE 2.1

RELATIVE AND ABSOLUTE GROWTH OF THE BREEDING POPULATION OF DEERFIELD: 1765-1810

Individuals 16-45 years



*Proportion of breeding size to total population.
**Values had to be extrapolated from records not recording exact age breakdown.

opportunity for drift; and a nonrandom component, which in human beings is the tendency for related individuals to marry. Numerous formulae have been developed to estimate inbreeding under various conditions. The most common of these is the model for analysis of individual pedigrees:

$$F = \sum \left[(\tfrac{1}{2})^{n_1+n_2+1} \; (1+F_A) \right]$$

Wright (1922), where n_1 is the number of generations from one parent back to the common ancestor and n_2 from the other parent, and F_A is the inbreeding coefficient of the common ancestor.

One estimation of inbreeding which has been developed for human populations and which can be used for subpopulations where migration occurs is based on the frequency of isonomic marriages (Crow and Mange, 1965). This estimate of inbreeding has recently been applied to several populations and, while caution is warranted regarding the fact that surnames are not genes, isonomy has shown reasonable agreement with other estimates based on European data (Yasuda and Morton, 1967; Morton, 1969). The principle behind the calculation of inbreeding by isonomy is an assumption that all isonomy is a reflection of common ancestry. "Let $\underline{F}$ be the total inbreeding coefficient, $\underline{F_r}$ be the inbreeding from random mating within the population, and $\underline{F_n}$ be that from nonrandom marriages. These are related by

$$F = F_n + (1 - F_n)\, F_r,$$

where

$$F_n = (P - \sum p_i q_i) \;/\; 4\,(1 - \sum p_i q_i)$$

and

$$F_r = \sum p_i q_i \;/\; 4$$

approximately" (Crow and Mange, 1965:201). Where $\underline{p_i}$ is the proportion of males with a certain name, $\underline{q_i}$ is the corresponding proportion in females, and $\underline{P}$ is the proportion of isonomic marriage pairs.

The Deerfield marriage records were analyzed for inbreeding by the above model. A total of four samples were drawn: (1) a sample including all marriages in Deerfield, N=1470, (2) a sample including all endogamous marriages in Deerfield, N=734, and, time based samples for marriages occurring between (3) 1790-1809, N=633, and, (4) 1820-1839, N=677. The results are summarized in Table 2.4.

TABLE 2.4

INBREEDING ESTIMATED BY ISONOMY, DEERFIELD RECORDS

Sample		I*	F_r	F_n	F
Total	1470	.0177	.00207	.00233	.00433
Endogamous	734	.0191	.00273	.00202	.00474
1790-1809	633	.0063	.00045	.00110	.00155
1820-1839	677	.0118	.00055	.00242	.00295

I*=Isonomy frequency

The overall conclusion to be reached from these data (Table 2.4) is that marriage in Deerfield has not been significantly different from random; however, the values also indicate changes in expected directions. For example, the coefficients for endogamous marriages are higher than those for all marriages <u>except</u> for the non-random component. This may indicate a preference for marriage with relatives outside the local community, which has been found to be the case in other populations studied (Morton, 1964; Freire-Maia and Freire-Maia, 1962). The time-based samples also show that inbreeding tends to increase through time. This has been found for other sub-populations (e.g. Hutterities, Yasuda and Morton, 1967) and is an indirect confirmation of the nature of population growth discussed above; that is, large family size would tend to increase the likelihood of relatives marrying each other and thus to decrease the relative effective population size. Thus for Deerfield and other growing populations the localized factors tend to mitigate against a large proportional effective population size. Under the above conditions, elevation of the effective population size will be attained only by migration.

One interesting aspect of the present study is that it is possible to trace the reproductive performance of isonymous pairs and determine whether or not close inbreeding has any notable effects on fertility. Of the total of 26 isonymous pairs, 18 are found to have some biographical information available, the remainder either emigrated at marriage (4 cases), or no information was available (4 cases). Fifteen of the 18 are known cousin pairs, and 12 include what could be considered complete fertility information (of the remaining, two spouses had died within a year of marriage and one had moved away after four years of marriage). The 12 known pairs range from first cousin to second cousin-once-removed matings.

The mean completed family size for cousin marriages (N=N-1) is markedly below that of the females who were parents in 1810 (Table 2.5).

TABLE 2.5

MEAN COMPLETED FAMILY SIZE OF KNOWN CONSANGUINEOUS MARRIAGES AND THE PARENTS OF 1810

Sample	N_p	N_o	$\bar{X}$	Sigma
Consanguineous	12	36	3.27	2.78
Parents of 1810	41	345	8.41	2.78

N_p = parent pairs N_o = offspring

Using a t-test of significance the differences are highly significant between the two means ($t=5.44$, d.f.=50, $P<.001$). These values do not include postnatal mortality which would presumably be higher in consanguineous matings.

Although it is possible to estimate the amount of inbreeding in a human population such as Deerfield, we find that an estimate of population size is very difficult, and perhaps meaningless. Even though the mating pattern in Deerfield is essentially random, there is no close similarity between this community and the isolate or neighborhood model in human genetics. On the other hand, marriage <u>tends</u> to be most frequent among community residents and those in the nearest neighboring communities--so that mating is not entirely random over distances greater than the community. The fact that migration is an important factor in the genetic structure of Deerfield, and presumably most communities, and that patterns of mating and fertility will be affected by migration, requires some means of expressing this significant mechanism.

In the Introduction reference was made to the fact that when a human community is being studied, as opposed to other communities of animals, the possible effects of culture must be considered. In the foregoing discussion it is important to take note of the fact that mating with neighboring communities may be based upon, or may tend to establish, important cultural ties. These ties may, in turn, reinforce interbreeding between neighboring communities. This process will have the effect of increasing the likelihood of inbreeding among individuals in these communities

The attempt in this chapter to define the concept and problem of population numbers leads to the observation that although numbers are very important to an understanding of genetic structure, population size is, at the very best, difficult to quantify. Since population numbers are so closely related to the nature of movements of people, perhaps statements of probability concerning migration are the best form of estimate.

CHAPTER III

MIGRATION

Introduction

Migration, in this chapter, refers to the movements of people in the demographic sense, however, it is also ultimately assumed to be occurring between groups with different allelic frequencies. Although the Deerfield migration data provide an excellent example of the nature of gene flow between microgeographic populations, the full genetic implications are not clear. I have assumed that some genetic differences exist between the sub-populations of this area, and although some evidence for differences does exist, the degree or nature of this difference is not quantifiable with the present data. In this chapter I will attempt to define and discuss the events which have occurred in Deerfield, and relate these to our current knowledge of migration patterns. The primary dimensions to be dealt with are space and time, and although the two cannot be treated with any absolute independence, the temporal aspects of migration will be emphasized in the first section, and the spatial aspects below.

The empirical analysis of migration in human populations has not been prevalent until recently (see Morton, 1969). Many past studies of human populations have proceeded to genetic interpretations by studying one variable and holding all others under Hardy-Weinberg assumptions. As Sutter and Tran-Ngoc-Toan (1957) point out, the facts of observation are very different from this approach, and the character of human migration adds a variety of complexities to the analysis of human populations.

In the early history of Deerfield the town may be easily characterized by certain geographic parameters and by the fact that marriage and the production of offspring is most common between local partners. In spite of this discrete quality, however, the community is in no way analogous to an island model of a breeding population in which marriage partners are shared randomly and equitably with all surrounding villages. The relationship between endogamous and exogamous marriages is one of the major forces in the determination of the genetic structure of a population (Küchemann et al, 1967), and Deerfield provides an interesting example of this relationship. Distance between marriage partners has been selected as the measure of migration not only because it is readily ascertained for Deerfield, but also because historically the majority of migration has taken place at marital age (Bogue, 1969; Hollingsworth, 1969); other studies have indicated that most migration takes place at marriage (e.g. Cavalli-Sforza, 1967). The sample used in the present study includes approximately 1460 marriages over a period of 170 years--the complete record of marriages listed in Vital Records of Deerfield, Massachusetts to the Year 1850 (Baldwin, 1920).

Migration in Time

The frequency of exogamous marriages in Deerfield was measured by sorting the marriage records into decades, and by counting the number of marriages in each period. Early in this procedure it became apparent that within a radius of 15 miles of Deerfield the great majority of marriages took place; so, exogamous marriages were coded for each specific village inside this 15 mile radius, and marriages outside the 15 mile limit were coded by zones based on direction and distance. This 15 mile radius may be somewhat arbitrary, but it includes the area within which 85 percent of all outmarriage occurs. The significance of this perimeter lies in the fact that, to the south, it includes the communities of Northhampton, Hadley, and Hatfield. As discussed earlier, these communities are located along the Connecticut River and were established prior to Deerfield (see Figure 1.1). The Connecticut River provided a major route of travel and communities along the River had greater likelihood of intercommunity contacts, including the exchange of marital partners. A second consideration for the probable significance of a radius of 15 miles is that it is about the maximum distance that could conveniently be travelled on foot or by horse in one day. The railroad did not come to this area until the middle 1800's and did not affect travel for the time period under consideration. The temporal distribution of exogamous marriages is given in Table 3.1.

The amount of exogamy has not only increased in absolute frequency, as would be expected with a growing population size, but also the relative frequency has shifted from approximately 14 percent exogamous marriages in 1700, to 65 percent in 1849. This may be seen as a relatively stable trend throughout the 170 year period covered, although at certain intervals the evidence suggests that exogamy decreased (Figure 3.1). Thus, the inhabitants of Deerfield become members of an expanding gene pool. This should not be taken, however, to indicate that the geographic size of the gene pool is correspondingly

TABLE 3.1

FREQUENCY OF DEERFIELD MARRIAGES

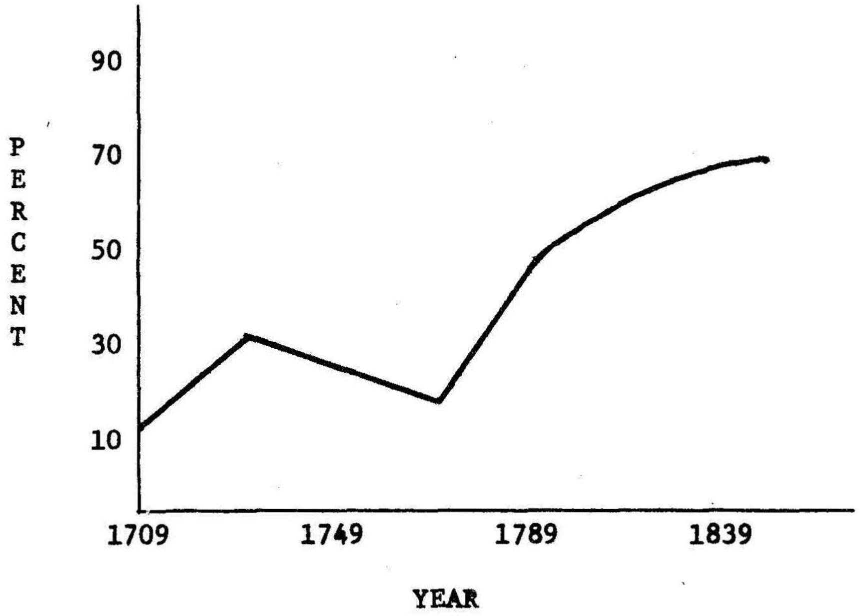
Time	Endogamy(%)	Ex. Males	Ex. Females	Total
1680-89	1 (100)	0	0	1
-1699	15 (78.9)	3	1	19
-1709	24 (85.7)	2	2	28
-1719	15 (71.4)	3	3	21
-1729	17 (68.0)	1	7	25
-1739	25 (89.2)	3	0	28
-1749	40 (74.1)	9	5	54
-1759	43 (71.7)	10	7	60
-1769	59 (88.1)	3	5	67
-1779	57 (76.0)	7	11	75
-1789	40 (50.0)	12	28	80
-1799	76 (48.1)	48	34	158
-1809	61 (38.9)	45	51	157
-1819	70 (46.4)	45	36	151
-1829	62 (37.3)	57	47	166
-1839	58 (33.5)	67	48	173
-1849	68 (34.2)	82	49	199
TOTAL	731 (50.0)	397 (27.2)	334 (22.8)	1462

FIGURE 3.1

FREQUENCY OF EXOGAMOUS MARRIAGES AT

20 YEAR INTERVALS

N=731



expanding. Although it is true that marriages between great distances are somewhat more common in the later periods, the most frequent exogamous marriages remain those within a 15 mile radius of Deerfield. In fact, 84.4 percent of all exogamous marriages prior to 1849 have occurred within this 15 mile radius. Mean marital distance tends to be very low throughout the 170 year period and, in fact, the average marital distance for all periods combined is only 7.44 miles (Table 3.2). Much of the increase in local exogamy may be attributed to basic cultural and demographic factors. During this period Deerfield and the surrounding area is experiencing rapid growth. Population density is increasing

TABLE 3.2

MEAN MARRIAGE DISTANCE FOR DEERFIELD (1690-1849)*

Interval	$\bar{X}$ Miles	N
1690-1719	5.11	54
1720-1739	3.65	52
1740-1759	5.45	113
1760-1779	2.02	135
1780-1799	11.42	221
1800-1819	7.40	315
1820-1839	9.70	335
1840-1849	10.34	216
TOTAL	7.44	1441

*N=number of marriages.
Distance for endogamous marriages = 0 miles. Mode = 0

and many new communities are being founded. The founding residents of these new communities are often former residents of neighbor communities. People from the various villages have much in common, they share the Puritan tradition, and probably become acquainted readily if they do not already know each other. It is clear, then, that the increase in exogamous marriages throughout Deerfield's history is a product of an increasing interaction between local communities rather than a strict distance mobility relationship.

Boyce et al (1968) found this to be true in their study of Charlton, England, and determined that mean marriage distance prior to 1850 was between 4-8 miles.

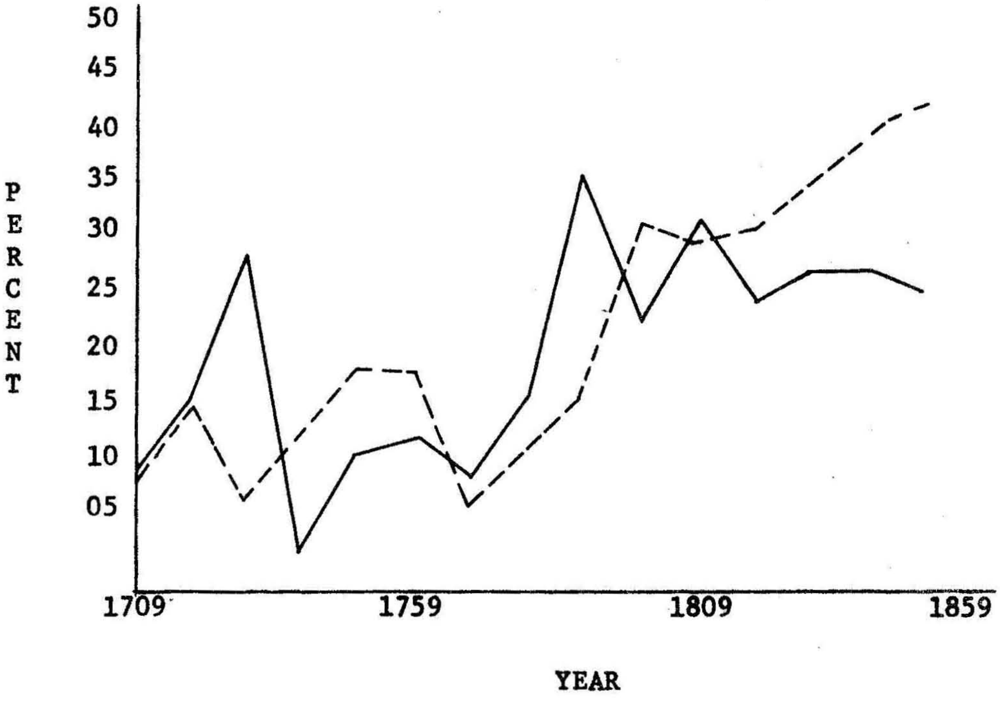
From values derived on the basis of sex, it is apparent that some differential factors are involved in the frequency of exogamy. Of all marriages recorded for Deerfield between 1680 and 1849, 339 males married outside females, and 398 females married outside males. The difference between these values is significant $P < .05$ ($X^2 = 4.723$, d.f.=1), and the effect seems the result of marriages taking place at a distance of greater than 15 miles; that is, a larger proportion of males from greater than 15 miles (n=133) marry Deerfield females than outside females (n=94) marry Deerfield males ($X^2 = 6.70$, $P < .01$). The explanation of this difference may be based on two factors: (1) there is the possibility, even likelihood, that the Western custom of having the marriage ceremony occur at the residence of the bride has resulted in an underenumeration of marriages between Deerfield males and outside females (this was indicated to be the case in the historical study of Charlton, England, by Küchemann et al, 1967). Although this may be viewed as a very possible contributing factor in the Deerfield material, it would not appear to be the single responsible factor. The distribution of frequencies of exogamous marriages, plotted by sex for Deerfield, indicates a relatively even number of outside marriages between males and females until the early 1800's (Figure 3.2). Also, the Deerfield records include a very large number of marriages which actually occurred in other towns, but included a Deerfield individual. (2) Another possibility

FIGURE 3.2

FREQUENCY OF EXOGAMY BY SEX

IN DEERFIELD, MASSACHUSETTS

N=731



Dotted line is females; solid line males.

is that males simply tend to be more mobile than females, and that during a period when a town is undergoing rapid growth, more males would be expected to settle than females. In the time period from 1800-1849 Deerfield experienced a 56 percent increase in population. And during this same time period females married 69 more outside males than Deerfield males married outside females. It would seem that differential immigration, by sex, is the most likely explanation for the significant difference observed.

In regard to male and female migration patterns, it should be noted here that the result of sexual residence practices could be a very important factor if one were to analyze specific, sex-linked loci in a given exchange between populations. For example, if two populations engaging in gene flow, have two distinct alleles at a given sex-linked locus, then residence patterning will affect the amount of admixture between the two populations. This is a clear case of a cultural practice affecting genetic structure.

To illustrate this factor, let us assume that a population (P_1) exchanges marriage partners with another population (P_2) at the rate of .02 per generation. (1) If matrilocality is the practiced residence pattern, then only males will be exchanged between P_1 and P_2 and the contribution of X chromosomes by one population to the other will be .02. The frequency, then, of the allele P_1 being passed to P_2 will be .02; in the first generation of offspring the males would pass the new allele to 50 percent of their offspring (the females). (2) If patrilocality is the pattern, then only females will be exchanged between P_1 and P_2. The contribution of X chromosomes then becomes

.04. The frequency of allele P_1a contributed to P_2 will also be .04, and 100 percent of the new allele would be transmitted to the first generation of offspring from the exogamous females. (3) And if no residence pattern exists, then equal numbers of males and females will be exchanged at the rate of .02, providing an exchange of X chromosomes (and new alleles) at the rate of .03. In the residence pattern cases, equilibrium frequencies will be reached for the newly introduced allele within a few generations, but the important point here is that the equilibrium frequency for the female migration pattern (patrilocality) will be achieved faster than the male pattern (matrilocality), given the same rates of migration.

In regard to the present study, residence patterns are pertinent. One finds that it was most common in early England and Colonial New England for wives to take residence in the locality of their spouse (patrilocality). Samples of various years of exogamous marriages indicate that this was generally true in Deerfield. This would confirm previous observations that while males are more mobile in exploring for wives, the wives are actually more mobile in the sense of gene flow (Hiorns et al, 1969:248).

If sexual migration is unbalanced, then residence patterning can have other marked effects on the nature of gene flow between populations. For example, if we assume allelic differences between Deerfield and its nearby neighbor villages, then the gene flow rate can be noted as differentially expressed due to residence patterning (Table 3.3). Gene flow has been calculated as:

$$f = \frac{O_m}{2N_m}$$

TABLE 3.3

GENE FLOW RATES INTO DEERFIELD (1690-1849)

N=1462

Pattern	T 1	T 2	T 3	T 4	T 5
Patrilocal	.0024	.0120	.0113	.0089	.0062
Matrilocal	.0133	.0120	.0058	.0054	.0075
TOTAL	.0157	.0239	.0171	.0144	.0137

N = Number of marriages. T = Town. Showing different rates depending upon whether matrilocality or patrilocality is practiced.

TABLE 3.4

FREQUENCY OF MATING TYPES FROM THREE SAMPLES

Sample	Endogamy	Ex. Males	Ex. Females	Total
*Deerfield	734 (50.0)	398 (27.0)	339 (23.0)	1471[1]
*Charlton	297 (66.7)	112 (25.2)	36 (8.1)	445[2]
Xavante	206 (91.2)	20 (8.8)		226[3]

*1650-1850. 1=Present study. 2=Küchemann et al, 1967.
2=Salzano et al, 1967.

where O_m are the number of out-marriages from a particular locality and N_m is the total number of marriages. As can be seen in Table 3.3, if all out-marriages from each of the neighboring communities are ultimately contributing to Deerfield's population, then gene flow is considerable. More important, however, are the variable rates depending on whether patrilocality or matrilocality is practiced. Contributions from Town 2, for example, would be the same regardless of residence pattern; but contributions from Town 1 are noticeably different with matrilocality, providing a more marked effect on the town of Deerfield than patrilocality would.

The rate of endogamy in Deerfield varied from 89 percent (1730's) to 34 percent (1840's), with a mean rate of endogamy for the whole period at 50 percent. The amount of endogamy is thus relatively low and would probably minimize the role of genetic drift, at least in the later periods discussed. A comparison of the frequencies of exogamous and endogamous marriages from various societies point to expected results (Table 3.4). For example, studies done on a group of South American aboriginal communities provide an average endogamy rate of 91.2 percent (Salzano et al, 1967). This is much higher than the rates found for Deerfield and Charlton, England, during the periods 1650-1850 (Table 3.4). We would expect the inter-village mobility in pre-industrial England or the United States to be much greater than in tribal populations of Brazil under previous assumptions (e.g. Neel, 1958:54), however, Salzano et al are quick to point out that even their endogamy frequencies may be unrealistic due to intergroup mobility among the Xavante (1967).

In this section I have indicated that, for Deerfield, the rate of migration increases with time, and this is true of other historical populations studied (Küchemann et al, 1967; Alström and Lindelious, 1966; Cavalli-Sforza, 1967). It must be emphasized, however, that this increase in migration, or exogamy, is not necessarily closely correlated with increasing distance in specific cases.

Migration over Space

As indicated above, any comparisons between village populations, regardless of their degree of cultural development, and the concept of isolated breeding populations are greatly abstracted from reality. However, there is also evidence that while the limits of outbreeding for a village population cannot be considered spatially as its immediate environs, it can be viewed as somewhat limited over space. In this section I will attempt to provide a systematic interpretation of differential migration over space in regard to the Deerfield material.

For some time now it has been recognized that marriage outside a central, home-base tends to decrease in frequency with increasing distance. In addition, the consensus has been that mating distance as a measure of migration follows a leptokurtic distribution, rather than the normal originally proposed by Wright in 1943 (see Schull and MacCluer, 1968). The empirical evidence that mating distance for natural populations of animals is leptokurtic was provided relatively early (Bateman, 1950; Skellam, 1951) and empirical studies demonstrating it for man came shortly thereafter (Sutter and Tran-Ngoc-Toan, 19570. More recent research on man confirms this distribution for several different populations (e.g. Cavalli-Sforza, 1958; Alström, 1958; Morton, 1964; Roberts, 1965; et al). This relationship of migration to distance, of course, relates to the form of gene dispersal for populations of organisms. The function which appears to best fit the observed distributions seems to be the exponential (Morton and Yasuda, 1962; Morton, 1969):

$$y=ae^{-bx}$$

although the geometric has been used as well (Boyce, Kuchemann, and Harrison, 1967; see Morton, 1969). That the exponential function is of general ecological significance in regard to human population density and movement has been suggested (Clark, 1951; Duncan, 1957; Morrill, 1965).

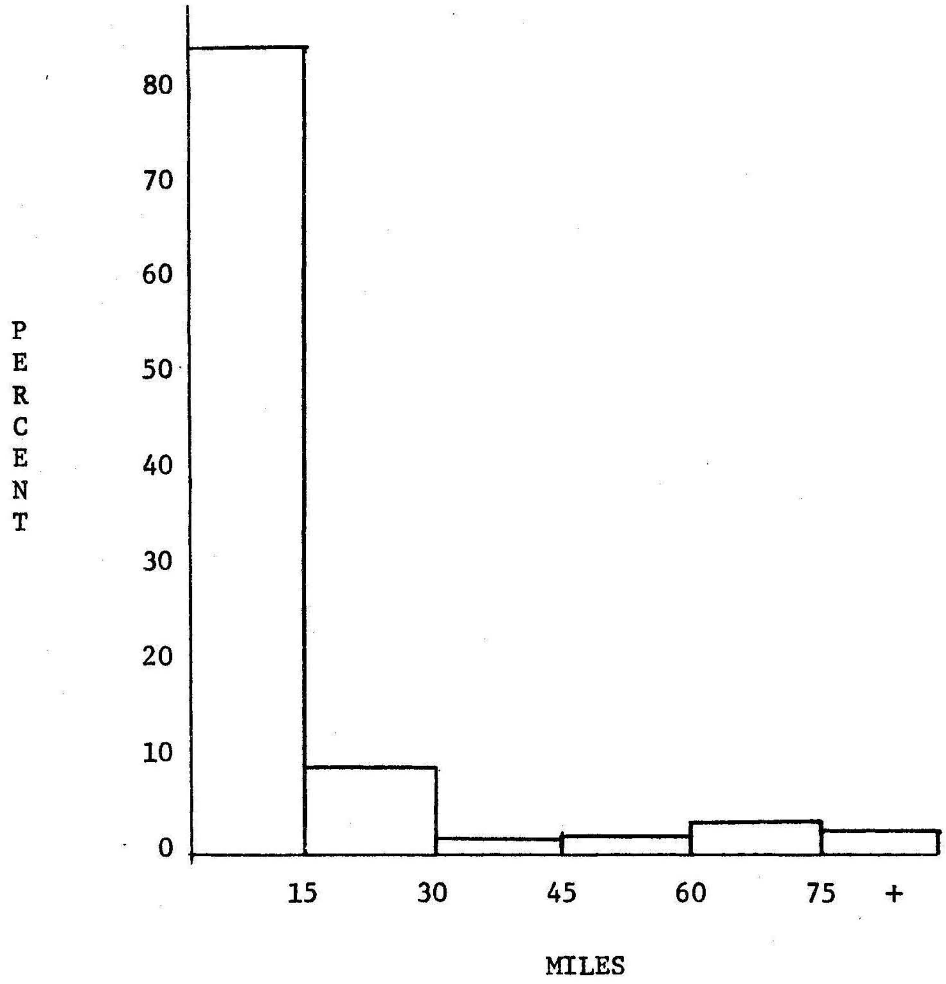
For the present analysis, a sample was obtained by taking all marriages registered for Deerfield individuals in 20 year intervals. As indicated above, exogamous marriages have been classified by zones surrounding Deerfield. These primary zones are located at 15 mile intervals, so that an individual will be identified by a number indicating his exact distance if under 15 miles from Deerfield, or, as being from 15-30 miles away, 30-45, 45-60, 60-75, and greater than 75 miles away. Since only 29 marriages occurred with an individual from greater than 75 miles for the entire 170 year period (.18 individual/year), marriages from this "outside world" perimeter were not included in the sample. The mean marriage distances are presented in Table 3.2, indicating the very low average distance between Deerfield matings. The leptokurtic nature of mating distance may be clearly seen in Figure 3.3, where we find 85 percent of all marriages occurring within 15 miles of Deerfield.

In order to focus specifically on the relationship between

FIGURE 3.3

DISTRIBUTION OF DEERFIELD MARRIAGES (1690-1849)

N=1462



migration and space, another sample was gathered which controlled for time. This second sample is based on the total number of marriages occurring between 1810-1819; in collecting the information this way, the frequency of matings should reflect the nature of a breeding population for a specific point in time, and indicate the degree and kind of interaction between local populations during this time. The data include: (1) all matings occurring within a distance of 15 miles. Since for any 10 year period in Deerfield matings at greater than 15 miles are very few, I concluded that a study of the properties of mating distance would be most easily understood within the 15 mile parimeter, where controls and sample size were maximum. (2) The contribution of each neighbor village expressed in spouse's per 1000 inhabitants (village size was based on the census of 1810). (3) No assumptions are made about the ultimate residence of the marriage pairs, the sample is designed to analyze the number of "marriage contacts" between various subpopulations, and the only criterion for inclusion in the sample is that an individual have married a Deerfield citizen in the years 1810-1819. These data were collected specifically for the purpose of comparison with previous studies on migration distance.

Findings: A recent study by Boyce, Küchemann, and Harrison (1967) represents one of the few attempts to develop an explanatory model for the observation that the frequency of marriage decreases exponentially with distance. Their model is based on the concept of "neighborhood knowledge," and in order to test this concept, the Deerfield sample was drawn to be comparable to the model sample.

The assumptions concerning "neighborhood knowledge" are as follows (p. 33-36):

(1) "...the frequency of marriages with the numbers of a village in the neighborhood of the home base is directly proportional to the number of inhabitants and to the frequency of visits to that village. The frequency of marriage when divided by the number of inhabitants is thus directly proportional to the number of visits."

(2) "...the frequency of visits to a village at a particular distance from the base is equal to the frequency of visits to all villages at that distance divided by the number of villages at that distance..."

(3) "...the frequency of visits to villages at a particular distance from the home base is equal to twice the frequency of journeys to and beyond that distance (since each outward journey is followed by an inward journey)."

(4) "...it is assumed that the frequency of journeys to villages at a particular distance from the home base is inversely proportional to a power of twice that distance."

"It therefore follows, from the above assumptions, that the frequency of marriages with the inhabitants of a village at a particular distance from the home base, when allowance is made for the number of inhabitants, is inversely proportional to that distance to the power b. Under the above model therefore, there is an exponential relationship between frequency of marriage and distance" (p. 336).

Boyce, Küchemann and Harrison's empirical test of this exponential relationship (1967), made on the parish of Oxfordshire, England (1861 census), provided the expected distribution. On the basis of 23 surrounding communities and their respective contributions of marriages to Oxfordshire, a geometric curve was fitted that indicates agreement with the assumed relationship ($y=4.75x^{-1.88}$).

The 1810-19 marriage frequencies for Deerfield were compared with those of Oxfordshire in regard to exogamous unions. The Oxfordshire sample was, as stated above, comprised of 23 surrounding communities. These were located within a 6 mile radius of Oxfordshire parish. To achieve a similar number of surrounding communities in the Deerfield study, it was necessary to expand this radius to 15 miles ($n=17$). Thus, the population density in the Deerfield area is considerably less. In addition, it was found that the proportion of marriages per 1000 inhabitants corresponded to the proportion of marriages per 100 inhabitants in the Oxfordshire sample.

Fitting a curve to the Deerfield observations gave $y=22.4x^{-1.05}$, using the family of curves $y=ax^{-b}$. The value of 1.05 is much lower than the 1.88 found for Oxfordshire; however, it is close to the total value for all periods found for Oxfordshire (Boyce, Küchemann, and Harrison, 1968), which was close to 1. The constant of 22.4, as compared to 4.75 for Oxfordshire, relates to the greater distance units used for Deerfield (see Figure 3.4). Using the following function for the Deerfield material:

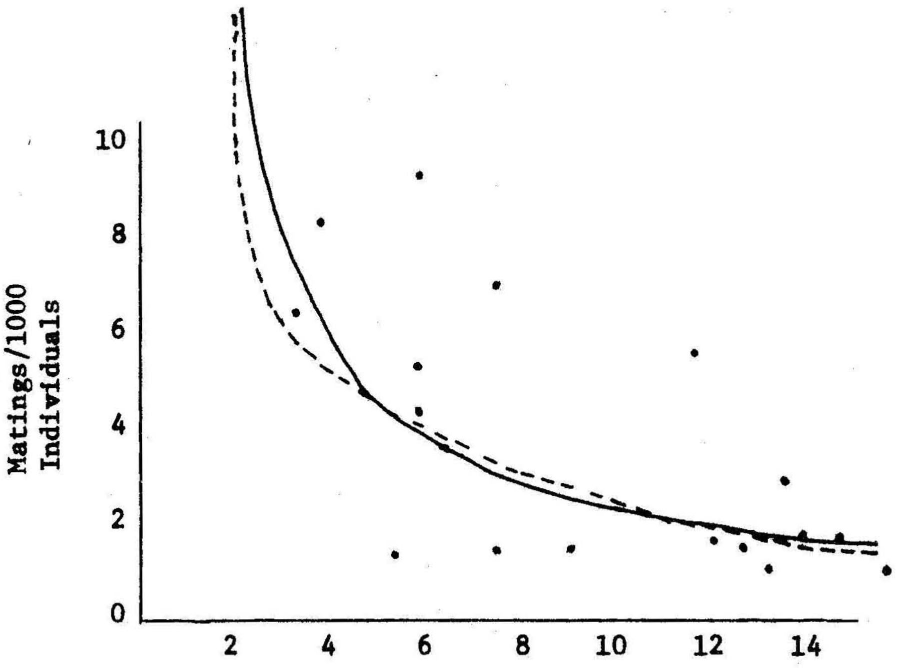
$$y=ae^{-bx}$$

the value of $\underline{a}$ is found to be 8.331 and $\underline{b}$ is -.1324. A comparison of the two curves (Figure 3.4) shows their very similar shape. X^2 values for the two curves indicate a slightly better fit with the

FIGURE 3.4

COMPARISON OF THE GEOMETRIC AND EXPONENTIAL

CURVES FOR MARRIAGE DISTANCE: DEERFIELD



MILES

Dots represent 17 communities surrounding Deerfield. Dotted line=Exponential curve. $X^2=23.96$, d.f.=15, $P > .05$. Solid line=Geometric curve. $X^2=25.98$, d.f.=15, $P < .05$.

exponential ($P > .05$). Morton (1969) has suggested that X^2 is often significant for these curves, and that possibly no better fit can be expected in light of the various factors affecting human migration. In the present analysis the small number of observations may also be considered, and the visual fit is good. In any event it is clear that the evidence from these two studies corroborates the observation that mating distances tend to follow a leptokurtic distribution and that distance is expressed by an exponential relationship. What neither study provides is data concerning the actual, observed, frequencies of types of journeys from a home base.

While the information from Deerfield basically confirms the observations of Boyce, Küchemann, and Harrison (1967), certain assumptions must be more closely scrutinized. As they note (p. 335), although neighborhood knowledge is certainly an important factor when considering human population movement, village density and distance are of critical importance as determinants of neighborhood knowledge. Demographers have noted the significant effect of distance for many years: Ravenstein (1885) as quoted by Lee (1966:48) states: "The great body of our migrants only proceed a short distance" and "migrants enumerated in a certain center of absorption will... grow less [as distance from the center increases]." Zipf (1946) defined the obstacles that mitigate against migration as an inverse function of distance. So that a prime determinant in the possibility of obtaining marital partners, or of migrating, is the distance over which man can travel in a given unit of time. As Boyce, Küchemann and Harrison further point out (p. 335), for thousands of years man's ability to travel has been confined to animal transport of his own feet, and this will necessarily limit the frequency and magnitude of migrations. In the United States, even as late as the 1960 census, the great majority (63%) of all migration was *intracounty* (Bogue, 1969:757). Also, as the Deerfield material suggests, the simple facts of population density will, in part, determine the distance travelled for marriage partners or other migration motives.

An additional factor to which Boyce, Küchemann, and Harrison (1967) did not originally allude, is that man may also migrate selectively in regard to direction, regardless of village distribution or density. As they point out in a later paper (1968), the distribution of roadways and rivers caused differential migration in relation to direction. Thus, communities of the same distance may not be visited with equal frequencies, due to a number of cultural and physical heterogeneities, and the second assumption is subject to several non-random factors for man. This, as noted, is reflected in the Deerfield sample. The fourth assumption, that frequency of visits and presumably matings is inversely proportional to the square of the distance, does not seem to fit well with the available data. Neither the English sample (Boyce, Küchemann, and Harrison, 1968), the present study, nor work done on parishes in France (see Sutter and Tran-Ngoc-Toan, 1957) indicate a good fit with 2 as the power of *b*. Nevertheless, the concepts and assumptions involved in the "neighborhood knowledge" model seem generally to correspond well with existing empirical data.

Neighborhood knowledge, and the simple effects of distance, can only be expected to operate in a highly predictable way within a limited radius of the home base. Long range migration of genetic significance is presumably controlled by additional factors. For example, the tendency that demographers have noted for migration to be selective in favor of urban centers (e.g. Bogue, 1969) has probably affected man for the last several thousand years. Also there is the possibility that the frequency of long-range marriages may be proportional to long range visits with consanguineous relatives, presumably a selective factor for travelling long distances (Morrill, 1965; Morton, 1969:102).

These possibilities are evidenced in the Deerfield material. The higher frequency of matings with individuals from the Boston area (58.9%) as opposed to the 7 other zones at the same distance is evidence of this urban trend. Further, the number of marriages outside the 15 mile radius seems to correlate to increased contact with relatives who have outmigrated or who form the original enclaves of Deerfield families (discussed above in relation to inbreeding).

This kind of distance model is well suited to <u>populations who migrate</u> and who can be classified by some common home base; it is not, however, entirely suitable to <u>migrant populations</u> such as studied by Morton (1964). The migrant population, which has no common origin in regard to at least one spouse of each married pair, may tend to corroborate that mating distance is generally leptokurtic and small in total distance for man, but it cannot relate to a specific class of settlement pattern which may be deterministic in mating distance;

or account for other non-random factors which any specific geographic locality may present. Homogenizing several specific localities may actually obscure the operation of significant evolutionary mechanisms.

In the study of human migration, of great importance is the nature of settlement pattern. Early human organization, and even most non-human primate organization seems to be oriented around a home base from which migration takes place. Even hunting and gathering societies who exploit large territories tend to have clear boundary zones between distinctive geographic and cultural units. The fact that Boyce, Küchemann, and Harrison (1967) relate mating distances to population size, and the fact that the Deerfield material point to the importance of village density clearly suggest reasons for variability in the frequency of matings observed in different regions, such as Italy and Sweden (e.g. see Cavalli-Sforza, 1967; Alström, 1958).

Recently the discontinuity between populations of plant and non-human animal species has been noted, with evidence that very little gene flow between such populations occurs (Ehrlich and Raven, 1969). Man is frequently referred to as the social animal in contrast to other animals. This social propensity of most of the anthropoids must be assumed to enhance the spread of genes as well as good and bad will. Nevertheless, as the present study and others indicate, the <u>distance</u> from which any "discrete" population's genes are spread, generally, is probably very little. On the other hand, <u>between</u> sub-populations of a given microgeographic region, gene flow is probably great. The effect in the past has probably been that in newly settled areas "homogenization" has taken place rapidly (see Hiorns et al, 1969), but between areas of great distance, or where cultural or geographic barriers intervene, differences are likely to be great.

In light of the foregoing statements, it is difficult to accept the results of certain recent investigations. Cavalli-Sforza (1958, 1962, 1969) has noted significant allele frequency differences, using blood group data, for a group of village populations in the Parma Valley, Italy. The explanation invoked for these differences is genetic drift, and demographic data were collected to try and reject or substantiate this explanation. The full substantiation of drift is not really accomplished and it remains to be seen whether or not drift actually determines the frequencies observed. Localized selection, problems associated with sampling, and incomplete mixture of sub-populations (see Kalmus, 1969) are possible alternative explanations. The fact that 80 percent of children were found, in the actual analysis, to be born in the same village as their parents, would indicate a reasonably high rate of migration, mitigating against drift.

Whereas some models (e.g. Malecot, 1969) attempt to account for limitations in the island and neighborhood (isolation by distance) models, as Bodmer and Cavalli-Sforza point out (1967:566): "... real populations are almost very irregular in their geographic distribution. Population size, density, and mobility are not constant with respect to space and time." Thus, although the desirability and need for simulation models is clear, it also remains clear that the empirical demonstration of evolution in human populations will require use of empirical data on specific populations. Recent attempts (e.g. Cavalli-

Sforza, 1967; MacCluer and Schull, 1970) to derive information from actual populations, and then simulate temporal effects, while provocative and very useful, are nevertheless hypothetical. At this time it would seem important that investigators having the opportunity to study real populations should attempt to discover and explain real events.

What emerges from Deerfield and other recent studies, however, is that it is possible to view human migration systematically. While many variables are different in specific cases, the nature of migration distance is predictable; given certain controls, quantifiable. Future empirical studies may be expected to corroborate the leptokurtic distribution, and future models to incorporate the exponential curve.

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:

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

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

where

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

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 nonsignificant. 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 <u>who survive birth</u> 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.

CHAPTER V

SUMMARY AND CONCLUSIONS

Introduction

The evidence from Deerfield which is presented in the foregoing chapters would tend to confirm the observation of Sutter and Tran-Ngoc-Toan (1957), that the departure of human populations from genetic models may often be great. This has been demonstrated particularly in regard to population numbers and the problems of fertility and migration. As Neel (1958) pointed out and Spuhler has reiterated (1959) there is very little information on selection in human populations, yet selection is a very significant and relevant departure from the conditions normally assumed in human populations. Observations and conclusions concerning the evidence from Deerfield may be summarized as follows:

Population Numbers

1. Although the "effective population size" is a useful parameter in concept, it is extremely difficult to actually quantify in man. The nature of internal population growth, migration, and generational overlap in human beings makes estimates subject to a variety of errors. The Deerfield sample demonstrates that if constant population size is assumed, the tendency is to overestimate the effective population size. Further, a failure to include the effects of migration will introduce errors in estimating the size of the breeding population and ultimately the effective population size.

2. The importance of knowing population numbers, in regard to genetic structure, is primarily for an understanding of the possibilities of non-random mating in the subject population. In the present study estimates of inbreeding, and the opportunities for drift, are based on an analysis of isonomy, or the tendency for people of like surname to marry. Observations for Deerfield include: (a) inbreeding tends to be low and mating is essentially random during the period studied; (b) there may be a tendency for exogamous marriages to commonly occur between related individuals; (c) close consanguineous marriages are less fertile than non-consanguineous marriages; and, (d) inbreeding tends to increase through time. This may confirm previous observations concerning effective population size, namely, that large family size increases the likelihood of relatives to marry each other, which subsequently decreases relative effective population size.

3. It would appear from the evidence from Deerfield and other communities studied (e.g. Alström and Lindelius, 1966; Küchemann et al, 1967) that migration is the most significant variable in attempting to define population numbers and that measurement of migration is very important in community studies.

Migration

1. Exogamous marriages occurring in time and space form the basis for a study of migration in Deerfield. The frequency of outside marriages increases relatively and absolutely in time, and the mean marriage distance increases only very slightly in time. By far the majority of exogamous marriages occur with members of nearby

neighboring communities.

2. The Deerfield population tends to be patrilocal but this is by no means an exclusive pattern. The general implications of the effect residence patterning has on sex-linked loci is discussed. If only females are exchanged between populations in gene flow, then the equilibrium frequency of newly introduced alleles will be achieved faster than if only males are exchanged, or if migration is equal with respect to sex.

3. The migration in Deerfield is plotted with respect to frequency over space and related to the geometric and exponential curves. The exponential curve provides a slightly better fit and is probably most often the best approximation of human migration. Several past studies have found migration to show a leptokurtic distribution over space, as is true of Deerfield.

4. The nature of migration observed for Deerfield compares closely with that found for historic English villages (Küchemann et al, 1967). The concept of "neighborhood knowledge" provides a formal explanation of the nature of migration and both population density and settlement pattern are important variables affecting migration.

Selection

1. Crow (1958) has defined the Index of Total Selection which measures the maximum possible amount of selection. Evidence from most studies (e.g. Spuhler, 1962; Kirk, 1966) suggests that the component of fertility is greater than that of mortality in the total selection intensity. However, in the Deerfield example and others (e.g. Hutterites), where family size is large and the ratio of mean family

size to variance is small, the mortality component is likely to be greater. As the ratio of family size to variance increases, as with many modern populations, the total index of selection will tend to increase.

2. In an analysis of selection and heterosis it is found that endogamous marriages in Deerfield are more fertile than exogamous marriages. However, if mean family size is measured at maturity, differences in fertility become non-significant. Speculation in regard to these results is as follows: (a) 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; (b) incompatibility of new allelic combinations 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; and, (c) certain new alleles or allelic combinations 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.

3. Past studies on heterosis in man and animals are somewhat equivocal in regard to expected results. This suggests that no single outcome from outcrossing is predictable, and that the outcome in any specific situation will depend on the fitness of the two parent populations to the selective environment in which the offspring are produced

and raised. Although this may appear to be a simplistic and obvious statement, it is seldom made by human geneticists.

The study of Deerfield has brought to light an important recurring factor, this is the effect cultural patterns may have on population structure and ultimately genetic structure. In the present study evidence on human migration, residence practices, settlement patterns, and other aspects of mating behavior suggests significant non-random occurences. These events can have a definite effect on the distribution of genotypes and the microevolution of a breeding population. This brings to the attention of physical anthropologists who are working on a population at a specific point in time, the importance of having knowledge of the demographic and ethnographic history of the subject population.

I have attempted, by using Deerfield as an example, to demonstrate the way in which actual populations may differ from the conditions commonly assumed in genetics models. It would be overstating my case to imply that geneticists are not aware of the way in which actual populations depart from the "simplifying assumptions," for much of the recent literature in human genetics is concerned with this very problem (see Schull and MacCluer, 1968; Morton, 1969). It is, however, very clear that the need for comprehensive studies of local populations, including historic ones, is great. The expansion and refinement of mathematical-genetical models is dependent upon a better empirical base from which generalizations may be made.

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