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Computer Models of Genetic Drift in Small Populations with Three Different Structures

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COMPUTOR MODELS OF GENETIC DRIFT IN SMALL POPULATIONS WITH THREE DIFFERENT STRUCTURES

By

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ABSTRACT

The effect of population structure on genetic drift was studied using three computor models to simulate the populations of interest. For each model the effective breeding population size was 100, and the initial gene frequency for a locus with two alleles (A, a) was 0.5. These populations were considered to be made up of sexually reproducing diploid organisms. The population size was held constant from generation to generation, and generations were nonoverlapping. It was assumed that selection and mutation were absent. In the panmictic model, mating was at random within the population. In the other two models the populations were subdivided into 10 subpopulations of equal size, each with an initial gene frequency of 0.5. Mating between subpopulations was structured according to an area migration scheme based on the proximity of subpopulations to one another. The two levels of migration were 40% and 5%.

Gametes were simulated by random numbers generated by computational methods. In each model 400 replicates were made by using different sequences of random numbers. Each replicate was run for 200 generations or until one allele was fixed. At every 25th generation the computor printouts included the total gene frequency for the population for each model and the gene frequency in each subpopulation of the subdivided models.

The results showed a significantly reduced cumulative

rate of fixation starting at the 100th generation in the 5% model as compared with the 40% and panmictic models. The latter two were almost identical in fixation rate. The variances among subpopulations for any one generation were computed for the two subdivided models and compared with variances of the panmictic model taken over 10 generations around the generation of interest. The variances of the 5% model were significantly higher than either of the other models for generations 25 through 175 but the variances of the 40% model were significantly different from the panmictic model only through the 100th generation. This indicates that for either subdivided model the variance within any one generation is equal to or greater than that found in the panmictic model in 10 generations. The distributions of gene frequencies over time did not differ significantly among models nor did they deviate from predicted theoretical distributions.

It was tentatively concluded that population structure can alter the effects of random drift on gene frequencies as well as the genetic variability maintained in a population. Further studies employing selection and mutation coefficients are suggested.

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INTRODUCTION

The Hardy-Weinberg law of equilibrium (Hardy, 1908; Weinberg, 1908) stands as a cornerstone of population genetics. The law predicts that gene frequencies will not change from one generation to the next. The fundamental importance of this law is dramatized by the description of speciation as the sum total of deviations from the Hardy-Weinberg law (Merrell, 1962).

The conditions required for the Hardy-Weinberg equilibrium simplify the mathematical relationships, but these assumptions are clearly not valid in natural populations. The law assumes an infinitely large, sexually reproducing population of randomly mating individuals, and the absence of selection and mutation. To have random mating (panmixia), every individual in the population must have an equal chance of mating with any other individual of the opposite sex. These individuals then comprise what is known as a Mendelian population, for they comprise a reproductive community of individuals which share in a common gene pool. Selection and mutation are generally present, and spacial separation of individuals within the population prevents panmixia. Thus constant gene frequencies in a natural population from generation to generation would not be anticipated.

If a population is not infinitely large, but instead is relatively small, random fluctuations of gene frequencies

All the individuals of a species or a population generally do not constitute a panmictic or random mating breeding unit. Panmixia is the second condition for the Hardy-Weinberg law, and thus its absence is a further cause for deviations from the original composition of the population. Dobzhansky (1951) has stated, "Isolation by distance, formation of isolated or partially isolated colonies, and certain combinations of these factors may reduce genetically effective population sizes even in very common species down to values which may make the genetic drift an important agent in evolution." Wright (1939) showed that this was the case with the evening primrose, Oenothera organensis, which with its 500 individuals appeared to be broken up into 50 colonies with an average size of 10 individuals each with 98% of the pollination by members of the colony and 2% from other colonies. Similar observations were made in the sub-species Clematis fremontii riehlii (Erickson, 1945) in which morphological differences between somewhat isolated aggregates were observed which Dobzhansky said may perhaps be attributed to genetic drift. Although this may be the case, genetic drift has come in to disrepute in part due to the sometime indiscriminate use of it to explain observed genetic differences between populations. The role of genetic drift in evolutionary processes is not well understood. Observations of populations are always made in the present, and the lack of knowledge of past population sizes and environmental conditions makes it hazardous to state that drift was the cause of the observed differences in gene

frequencies among closely related populations.

In sub-divided populations of finite size, such as the previously mentioned Clematis, a variety of migration patterns may exist because every individual does not have an equal chance of mating with every other individual of the opposite sex. The genetic effects in such populations have been of interest to population geneticists for the last 35 years. In 1935 the noted probabilist, Kolmogorov, developed a model suggested by Dubinin and Romashov and treated it mathematically. In his paper Kolmogorov commented, "A series of equally interesting schemes of limited crossing (migration) do not submit, so far, to any mathematic process of treatment." As Kolmogorov implies, the mathematical expressions for complex migration schemes rapidly become too complicated for analytical treatment.

Similarly, laboratory studies would not readily yield the desired information for a number of reasons. First, the strict control of variables in a laboratory population is not possible. Second, it is generally desirable to have data on a population for a large number of generations. Third, because the results in small populations are due in part to chance, it would be necessary to run a great number of equivalent populations in order to obtain an accurate view of the probability distributions.

These difficulties can be overcome by the use of the electronic computer as a tool. It is possible to avoid the problems of the mathematician by building a model of the

population structure of interest. The problems of the laboratory are avoided for there are no uncontrolled variables in a computer model. And having many populations of the same type run for many generations is easily achieved with high speed computers. Thus, population geneticists can reduce the simplifying assumptions of the mathematical models and consequently study population structures which more closely approximate those found in nature.

MATERIALS AND METHODS

The computer used in this study was an IBM 360 at the University of New Mexico Research Center. The computer programs written to simulate the three populations were similar in their initial conditions and assumptions. The models were designed such that each population consisted of sexually reproducing, diploid organisms, and had an effective breeding size of 100 with an initial gene frequency of 0.5 for a locus with two alleles (A, a). The population size was held constant from generation to generation in each of the models. Generations were nonoverlapping so that any one generation was formed by gametes of individuals in the preceding generation and not from any other.

The models for the three populations differed only in breeding structure. The first, or panmictic model, assumed random mating of individuals within the population. Because two gametes are required for the formation of any one individual, 200 gametes were required for generation of a population of 100 individuals. It was not necessary to form zygotes as the gene frequency of the next generation depended only upon the component gametes and not upon their combination into zygotes. For example, a population may have all homozygous individuals (1/2 AA, 1/2 aa) or may have all heterozygous individuals (Aa), yet the gene frequency is 0.5 in each case. Figure 1 indicates that for the panmictic model,

Figure 1

Master Plan

Do the following once for each model:

Repeat the following 400 times using
IKT values 1, 3, ... , 799

Initial gene frequency (first generation)

generate 200 gametes

Second gene frequency (second generation)

generate 200 gametes

Third gene frequency (third generation)

.
.
.
.
.
.
.
.

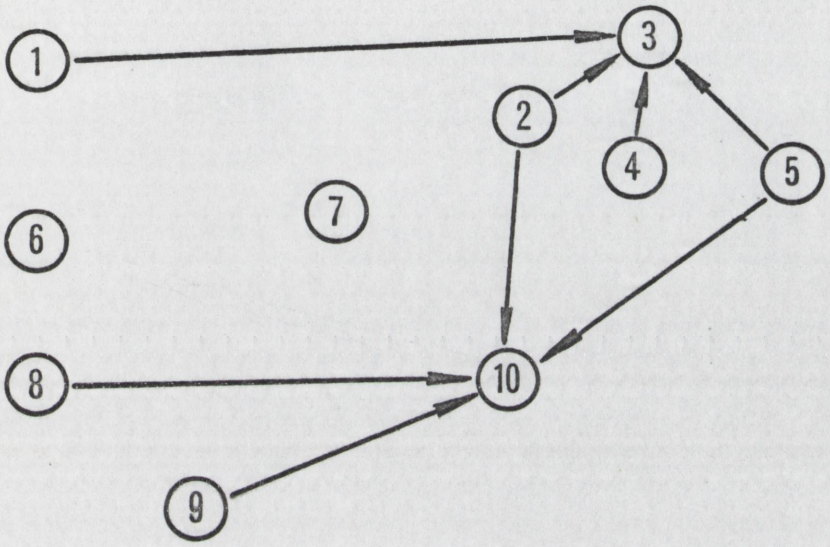
generate 200 gametes

200th gene frequency (200th generation)

as well as for the other models, 200 gametes were formed for each of 200 generations. Because drift is a random rather than a deterministic phenomenon, a large number of replicates were made to provide a good estimate of the probability distributions. Four hundred replicates appeared to give adequate results.

The second and third models were of populations consisting of ten subpopulations each of size ten where each subpopulation had an initial gene frequency of 0.5. A migration scheme was devised based on the proximity of one subgroup to another. Figure 2A shows the arrangement of the 10 subgroups, and Figure 2B shows the complete migration scheme. It can be seen from the arrows in Figure 2A, for example, that the third subpopulation receives gametes from the 1st, 2nd, 4th, and 5th subpopulations. The same information is shown by ●'s in Figure 2B. For the second population model, 40% (8) of the gametes used to form the next generation of each subpopulation came from the four contributing subpopulations, 10% from each. The remaining 60% (12) of the gametes came from the subgroup itself. This is equivalent to 40% migration.

The third model followed the migration scheme of the second with the modification that the migrating gametes (those coming from the contributing subgroups) were limited to 5% (1) of the total of 20 gametes per subgroup. This more limited migration was achieved by randomly choosing only one of the four contributing subpopulations (as shown in the



Contributors										
1	2	3	4	5	6	7	8	9	10	Receiver
	●	●			●		●			1
●		●	●			●				2
●	●		●	●						3
	●	●		●					●	4
		●	●					●	●	5
●						●	●	●		6
●			●		●		●			7
					●	●		●	●	8
				●	●	●			●	9
	●			●			●	●		10

migration scheme) to contribute the one gamete for the next generation of the receiving subpopulation. Thus subpopulation 1 might receive one gamete from subpopulation 3 and the remaining gametes from subpopulation 1 itself. The same procedure was followed for each subgroup in each generation.

A key to understanding the computer models is the random number generator which was used to generate gametes. The numbers generated are not random in the true sense of the word. With a given initializing number, the generator (a subroutine of the main program) will generate, by computational methods, a predictable sequence of numbers lying between zero and one without any repetitions until the order of 10^{29} numbers have been generated. The resulting numbers satisfy statistical tests for randomness. Different initializing numbers provide different sequences of random numbers. Thus it is possible to run the same problem, with the same initial population characteristics, many times and get a distribution of results by initializing the random number generator at different points. It was by this means that the 400 replicates were made for each model. The initializing numbers of the subroutine were required to be odd, positive integers, and are shown as IKT values on the computer printouts. For the first run of 200 generations (see Figure 1), the IKT value was set to 1. The replicates followed using IKT values of 3, 5, ..., 799.

It is important to understand the actual role of the random numbers in a simulated population. Because the

population size was not infinite, changes in gene frequency from generation to generation were expected. This is due to a sampling error in the formation of a limited number of gametes which may not accurately reflect the gene frequency of the population from which they came. In the panmictic model with initial gene frequency of 0.5, it was necessary to generate 200 gametes to form a second generation (see Figure 3). A rule was set up to interpret the random numbers as gametes. The rule was: if the random number generated was less than or equal to the gene frequency ($P_1 = 0.5$), the number was interpreted as a gamete containing A and was counted as a one. If the random number generated was greater than the gene frequency, the gamete was interpreted as a and counted as zero. If, of the 200 gametes generated in this way, 90 were A and counted as ones, the sum of all the zeros and the ones would be 90. The quotient 90/200 or 0.45 gives the new frequency of A in the 2nd generation (P_2). This new gene frequency would then serve as the basis for the rule to interpret the next sequence of 200 random numbers. In this example, the rule would be: if the random number was less than or equal to 0.45, the gamete contained A and was counted as one. If the random number was greater than 0.45, the gamete contained a and was counted as zero. This process was continued until 200 generations were formed or until fixation of an allele occurred. As the gene frequency for each new generation, P_g, was computed, a check was made to determine if P_g was equal to either zero or one. If either allele

Figure 3

Generation of Gametes for the Panmictic Model

$$P_1 = .5$$

Generate 200 random numbers, $n_{(1,1)}, n_{(1,2)}, \ldots, n_{(1,200)}$

Rule:

If $n_{(1,x)} \leq .5$ gamete is A and $g_x = 1$

If $n_{(1,x)} > .5$ gamete is a and $g_x = 0$

$$\frac{\sum_{x=1}^{200} g_x}{200} = P_2$$

Generate 200 random numbers, $n_{(2,1)}, n_{(2,2)}, \ldots, n_{(2,200)}$

Rule:

If $n_{(2,x)} \leq P_2$ gamete is A and $g_x = 1$

If $n_{(2,x)} > P_2$ gamete is a and $g_x = 0$

$$\frac{\sum_{x=1}^{200} g_x}{200} = P_3$$

.

.

.

$$\frac{\sum_{x=1}^{200} g_x}{200} = P_{200}$$

P_g = gene frequency of A in the g^{th} generation

$g = 1, \ldots 200$

$n_{(g,i)}$ = the i^{th} random number generated from the g^{th} generation

$g = 1, \ldots 200$

$i = 1, \ldots 200$

g_x = the "value" of the gamete, 0 or 1, depending on the allele.

were fixed, the run was terminated. For this run all future generations were considered to be fixed. For example if in the 7th replicate (IKT = 13) the gene frequency of the 137th generation was 0.955, and the gene frequency of the 138th generation was 1.0, the check would reveal fixation, and the computer would immediately start with the 8th replicate (IKT = 15). The results of the seventh replicate would be understood to be fixation at 1.0 from the 138th through the 200th generation.

The process of generating gametes for the subdivided populations was somewhat more complicated although based on the same principles. Because of the assumption of nonoverlapping generations, it was assumed that the new generations of each of the subpopulations occurred simultaneously. Thus if after the gene frequency of the second generation of subpopulation 1 was computed, subpopulation 1 was randomly chosen to contribute to the formation of the second generation of subpopulation 2, the gene frequency of the first generation of subpopulation 1 would be used to interpret random numbers as contributed gametes. In this way the new gene frequencies for each of the 10 subpopulations were determined before the gene frequencies of the following generation were used in determining gametes. Figures 4 and 5, respectively, show the methods followed in generating gametes for the 40% and 5% migration models. The procedures were repeated for 200 generations or until fixation of an allele occurred. At the end of each generation, the gene frequency for the entire

Figure 4

Generation of Gametes for the 40% Model

Subpopulation 1

$P_{(1,1)} = 0.5$

Generate 12 random numbers

$n_{(1,1,1)}, n_{(1,1,2)} \cdots, n_{(1,1,12)}$

Rule:

If $n_{(1,1,x)} \leq 0.5$ $(P_{(1,1)})$, gamete is A and $g_x = 1$

If $n_{(1,1,x)} > 0.5$ $(P_{(1,1)})$, gamete is a and $g_x = 0$

Following the migration scheme:

(a) $P_{(1,2)} = 0.5$

generate 2 random numbers,

$n_{(1,1,13)}, n_{(1,1,14)}$

Rule:

If $n_{(1,1,x)} \leq 0.5$ $(P_{(1,2)})$, gamete is A and $g_x = 1$

If $n_{(1,1,x)} > 0.5$ $(P_{(1,2)})$, gamete is a and $g_x = 0$

(b) $P_{(1,3)} = 0.5$

generate 2 random numbers,

$n_{(1,1,15)}, n_{(1,1,16)}$

Rule:

If $n_{(1,1,x)} \leq 0.5$ $(P_{(1,3)})$, gamete is A and $g_x = 1$

If $n_{(1,1,x)} > 0.5$ $(P_{(1,3)})$, gamete is a

and $g_x = 0$

(c) $P_{(1,6)} = 0.5$

generate 2 random numbers

$n_{(1,1,17)}$, $n_{(1,1,18)}$

Rule:

If $n_{(1,1,x)} \leq 0.5$ $(P_{(1,6)})$, gamete is A

and $g_x = 1$

If $n_{(1,1,x)} > 0.5$ $(P_{(1,6)})$, gamete is a

and $g_x = 0$

(d) $P_{(1,8)} = 0.5$

generate 2 random numbers

$n_{(1,1,19)}$, $n_{(1,1,20)}$

Rule:

If $n_{(1,1,x)} \leq 0.5$ $(P_{(1,8)})$, gamete is A

and $g_x = 1$

If $n_{(1,1,x)} > 0.5$ $(P_{(1,8)})$, gamete is a

and $g_x = 0$

$$\frac{\sum_{x=1}^{20} g_x}{20} = P_{(2,1)}$$

After all 10 subpopulations have formed second generations:

Subpopulation 1

$P_{(2,1)} = 0.35$ (for example)

Generate 12 random numbers

$n_{(2,1,1)}, n_{(2,1,2)} \cdots, n_{(2,1,12)}$

Rule:

If $n_{(2,1,x)} \leq 0.35$, gamete is A
and $g_x = 1$

If $n_{(2,1,x)} > 0.35$, gamete is a
and $g_x = 0$

Following the migration scheme:

(a) $P_{(2,2)} = 0.45$ (for example)

generate 2 random numbers,

$n_{(2,1,13)}, n_{(2,1,14)}$

Rule:

If $n_{(2,1,x)} \leq 0.45$, gamete is A
and $g_x = 1$

If $n_{(2,1,x)} > 0.45$, gamete is a
and $g_x = 0$

(b) $P_{(2,3)} = .55$ (for example)

.

.

.

.

Subpopulation 10

$P_{(1,10)} = 0.5$

Generate 12 random numbers

$n_{(1,10,1)}, n_{(1,10,2)} \cdots, n_{(1,10,12)}$

Rule:

If $n_{(1,10,x)} \leq 0.5 \ (P_{(1,10)})$, gamete is A and $g_x = 1$

If $n_{(1,10,x)} > 0.5 \ (P_{(1,10)})$, gamete is a and $g_x = 0$

Following the migration scheme:

(a) $P_{(1,2)} = 0.5$

generate 2 random numbers

$n_{(1,10,13)}, n_{(1,10,14)}$

Rule:

If $n_{(1,10,x)} \leq 0.5 \ (P_{(1,2)})$, gamete is A and $g_x = 1$

If $n_{(1,10,x)} > 0.5 \ (P_{(1,2)})$, gamete is a and $g_x = 0$

(b) $P_{(1,5)} = 0.5$

generate 2 random numbers

$n_{(1,10,15)}, n_{(1,10,16)}$

Rule:

If $n_{(1,10,x)} \leq 0.5 \ (P_{(1,5)})$, gamete is A and $g_x = 1$

If $^{n}_{(1,10,x)} > 0.5$ $(P_{(1.5)})$, gamete is a

and $g_x = 0$

(c) $P_{(1.8)} = 0.5$

generate 2 random numbers

$^{n}_{(1,10,17)}$, $^{n}_{(1,10,18)}$

Rule:

If $^{n}_{(1,10,x)} \leq 0.5$ $(P_{(1,8)})$, gamete is A

and $g_x = 1$

If $^{n}_{(1,10,x)} > 0.5$ $(P_{(1,8)})$, gamete is a

and $g_x = 0$

(d) $P_{(1,9)} = 0.5$

generate 2 random numbers.

$^{n}_{(1,10,19)}$, $^{n}_{(1,10,20)}$

Rule:

If $^{n}_{(1,10,x)} \leq 0.5$ $(P_{(1,9)})$, gamete is A

and $g_x = 1$

If $^{n}_{(1,10,x)} > 0.5$ $(P_{(1,9)})$, gamete is a

and $g_x = 0$

$$\frac{\sum_{x=1}^{20} g_x}{20} = P_{(2,\ 1)}$$

After all 10 subpopulations have formed second generations:

Subpopulation 10

$P_{(2,10)} = 0.55$ (for example)

Generate 12 random numbers

$n_{(2,10,1)}, n_{(2,10,2)} \cdots, n_{(2,10,12)}$

Rule:

If $n_{(2,10,x)} \leq 0.55$, gamete is A
and $g_x = 1$

If $n_{(2,10,x)} > 0.55$, gamete is a
and $g_x = 0$

Following the migration scheme:

(a) $P_{(2,2)} = 0.45$ (for example)

generate 2 random numbers,

$n_{(2,10,13)}$ $n_{(2,10,14)}$

Rule:

If $n_{(2,10,x)} \leq 0.45$, gamete is A
and $g_x = 1$

If $n_{(2,10,x)} > 0.45$, gamete is a
and $g_x = 0$

(b) $P_{(2,5)} = .35$ (for example)

.

.

.

.

$P_{g,s}$ = gene frequency of A in the g^{th} generation for the s^{th} subpopulation

$g = 1, \quad 200$

$s = 1, \quad 10$

$n_{i,j,k}$ = the k^{th} random number generated for the i^{th} generation for the j^{th} subpopulation

Figure 5

Generation of Gametes for the 5% Model

for Subpopulation 1

$$P_{(1,\ 1)} = 0.5$$

generate 19 random numbers

$$n_{(1,\ 1,\ 1)},\ n_{(1,\ 1,\ 2)},\ \cdots\ n_{(1,\ 1,\ 19)}$$

Rule:

if $n_{(1,\ 1,\ x)} \leq 0.5$, gamete is A and $g_x = 1$

if $n_{(1,\ 1,\ x)} > 0.5$, gamete is a and $g_x = 0$

to get 1 migrating gamete, generate 1 random number r

Rule:

if $r \leq 0.25$, 2 is the contributing subpopulation

if $0.25 \quad r \leq 0.5$, 3 is the contributing subpopulation

if $0.50 \quad r \leq 0.75$, 6 is the contributing subpopulation

if $0.75 \quad r \leq 1.0$, 8 is the contributing subpopulation

to determine the value of the gamete from the contributing subpopulation;
for example: r is .3752 ... making 3 the contributing subpopulation.

$$P_{(1,\ 3)} = .5$$

generate 1 random number, $n_{(1,\ 1,\ 20)}$

Rule:

if $n_{(1,\ 1,\ 20)} \leq 0.5$, gamete is A and $g_x = 1$

if $n_{(1,\ 1,\ 20)} > 0.5$, gamete is a and $g_x = 0$

$$\frac{\sum_{x=1}^{20} g_x}{20} = P_{(2,\ 1)}$$

population was computed by averaging the gene frequencies of the ten subpopulations, and a check was made for fixation. When the runs were terminated due to fixation or reaching 200 generations, the IKT value of the random number generator was increased by two. This was repeated until 400 replicates were completed for each model.

Examples of the computer programs and print-outs are found in Appendices A through F. For the panmictic model, the print-out includes the gene frequency at each generation. The IKT values for the different runs appear at the upper left-hand corner of each sheet. The print-outs for the 40% and 5% migration models are the same and show the gene frequency of each subpopulation under numbered headings at generation numbers 25, 50, 75, 100, 125, 150, 175, 200. Generation numbers are found under the heading "GEN," and the gene frequency for the total population at that generation is given under the column heading "AVE." The numbers on the right without a heading are IKT values. Following a line of gene frequencies at a given generation number is a line of numbers followed by the word "AVERAGE." These are the average gene frequencies of the individual subpopulations over time.

RESULTS

The results of the computer runs are best shown graphically. It is necessary to accumulate the information from the 400 replicates for each type of population because of the great volume of data produced.

Figure 6 shows generation number plotted against percent fixation. At generation number 50, the percent was determined by including all runs which had fixed at or before the 50th generation. The percent at the 75th generation, was determined by including all runs which had fixed at or before the 75th generation. The result is a monotonically increasing curve.

Figure 7 reflects the distribution of those nonfixed or heteroallelic runs of the panmictic model at different generation numbers. The gene frequency of the total population was recorded at different generation numbers for each replicate. In order to preserve the natural symmetry of the distribution, intervals were chosen around the gene frequencies of 0.1, 0.2, ..., 0.9. Thus the percent of heteroalleles shown at gene frequency 0.5 includes those in the interval of 0.45 to 0.55. At the end points of 0.1 and 0.9, intervals were chosen of 0.05-0.15 and 0.85-0.95, respectively. Runs falling in the terminal portions of less than 0.05 and greater than 0.95 are not shown on the graph. This same process was followed for the subdivided models as well at

Figure 6

Rate of Fixation According to Population Structure

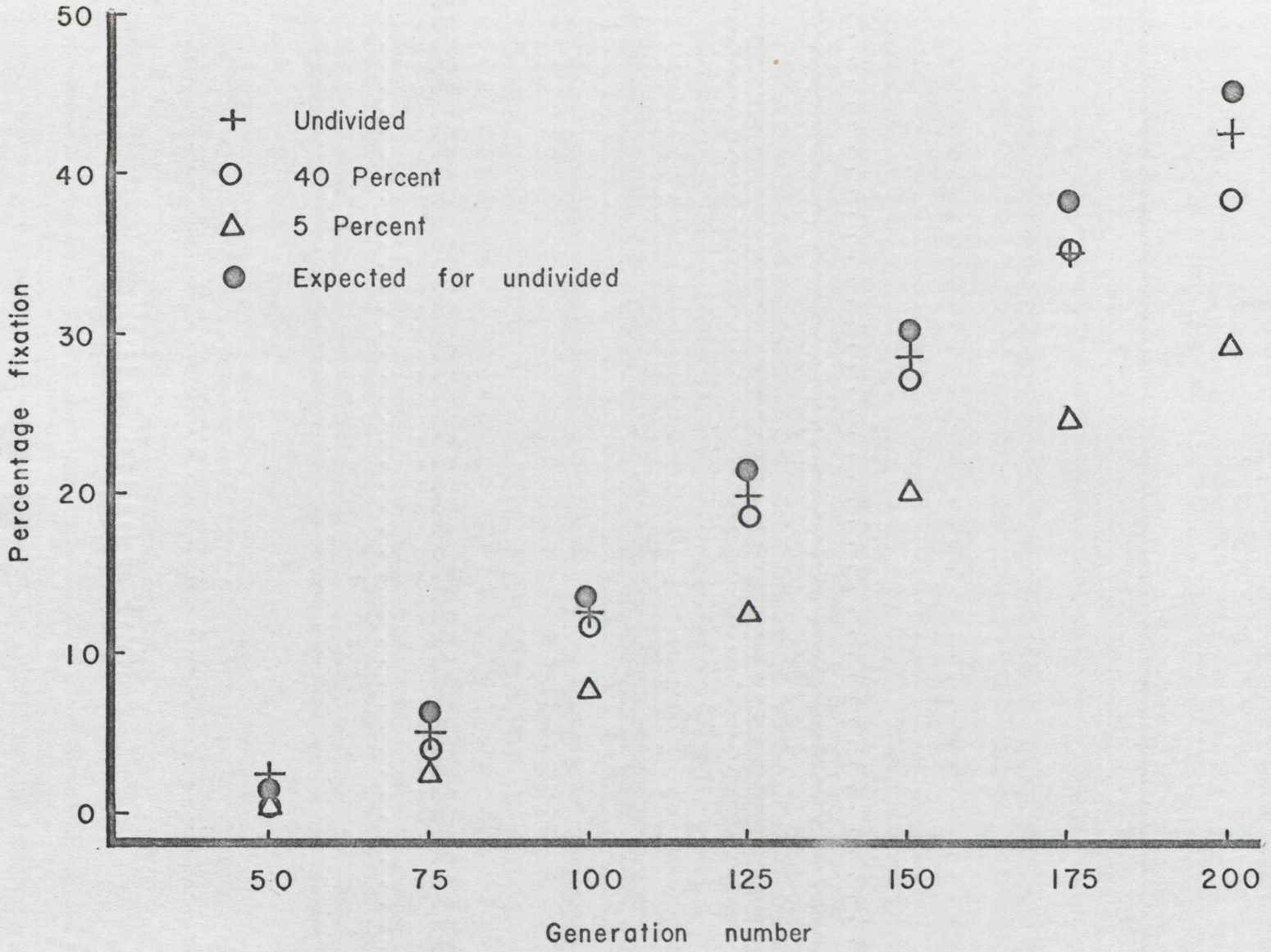

50
40
30
20
10
0
Percentage fixation
Undivided
40 Percent
5 Percent
Expected for undivided
50
75
100
125
150
175
200
Generation number

Figure 7

Experimental Distributions for the Panmictic Model

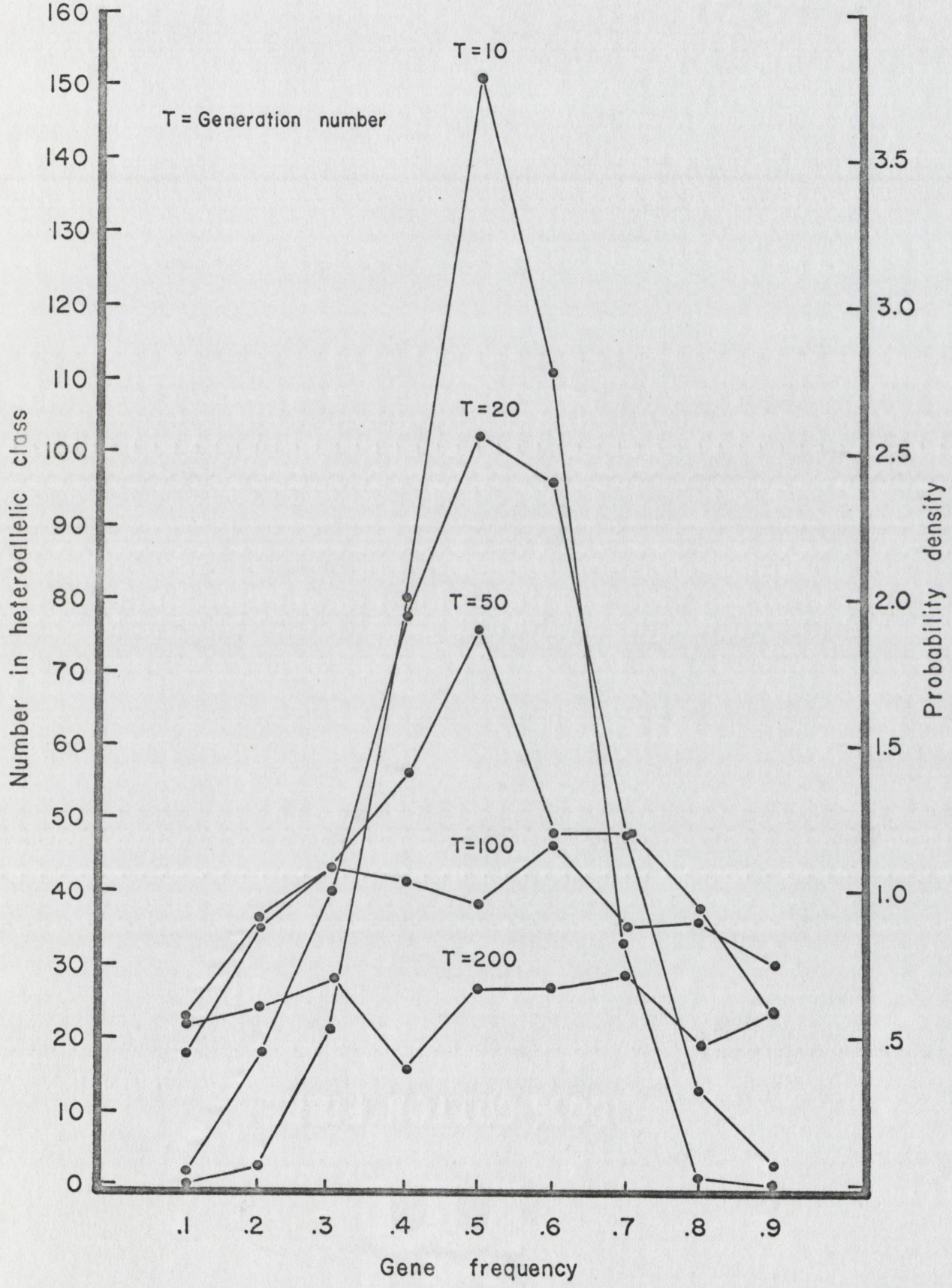
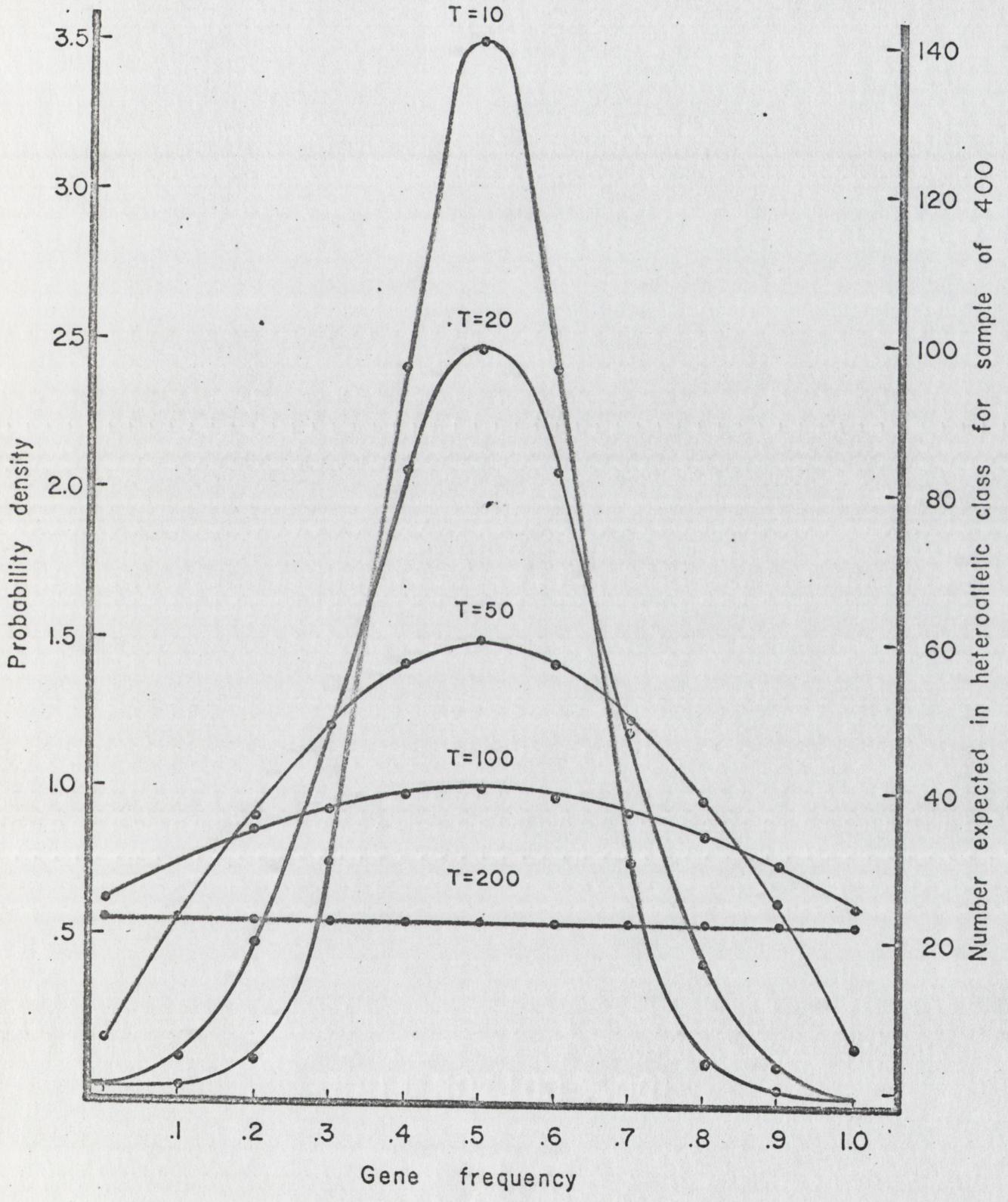

T = Generation number
T=10
T=20
T=50
T=100
T=200
Number in heteroallelic class
Probability density
Gene frequency
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
160
.5
1.0
1.5
2.0
2.5
3.0
3.5
.1
.2
.3
.4
.5
.6
.7
.8
.9

Figure 8

Expected Distributions for the Panmictic Model

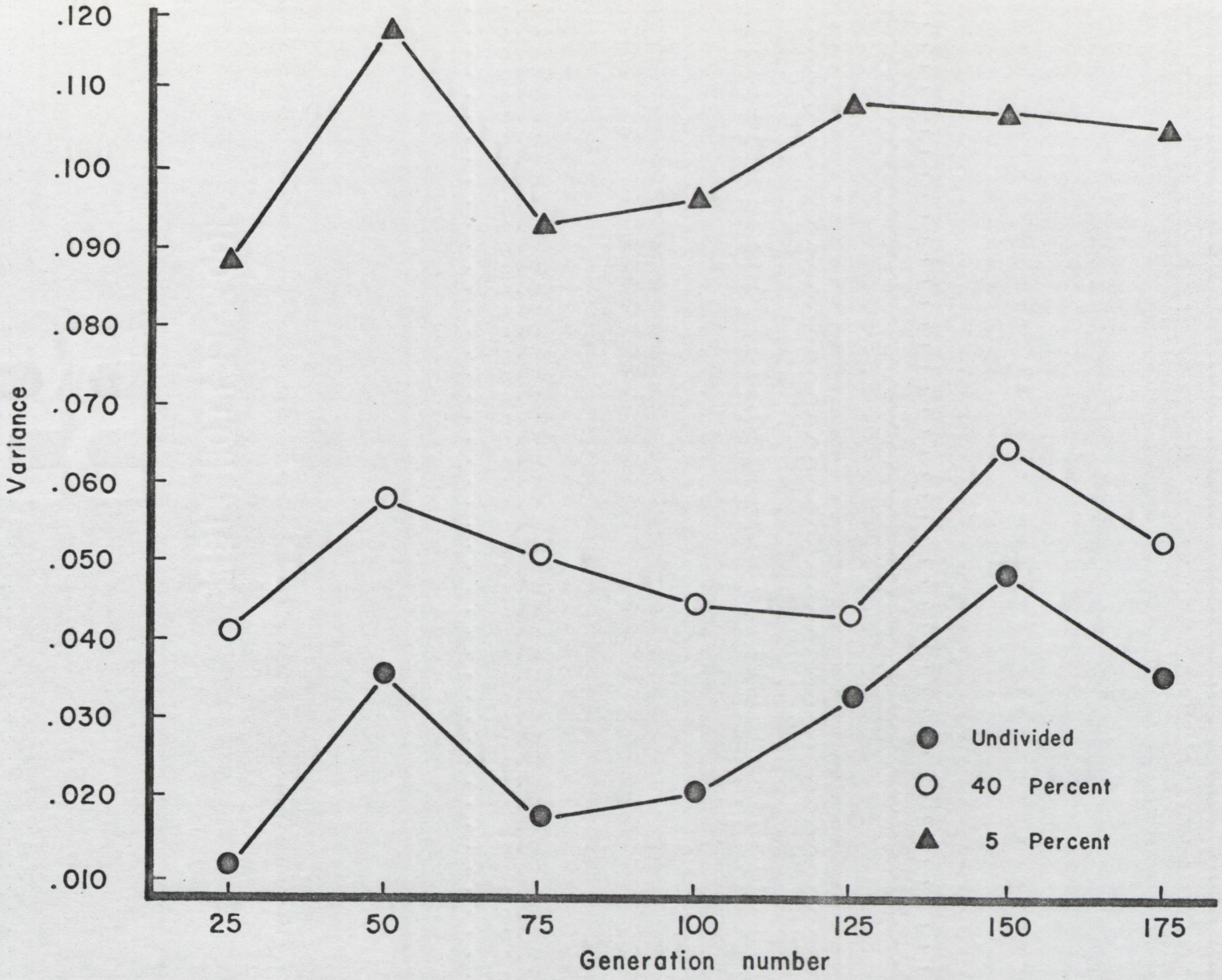

T=10
T=20
T=50
T=100
T=200
3.5
3.0
2.5
2.0
1.5
1.0
.5
Probability density
140
120
100
80
60
40
20
Number expected in heteroallelic class for sample of 400
.1
.2
.3
.4
.5
.6
.7
.8
.9
1.0
Gene frequency

intervals of 25, 50, ..., 200 generations. The results do not differ significantly from the panmictic model.

Figure 9 shows the variances of the three population types at different generation numbers. For the panmictic model, gene frequencies of 10 generations were taken around the generation of interest for 10 IKT values. Thus for generation number 25, the gene frequencies for generations 21 through 30 were taken from 10 IKT values and used to compute the variance. For the two types of subdivided populations, the gene frequencies of each subpopulation for a given generation number were used. This was done with the same IKT values as were used for the panmictic model and yielded 100 numbers. IKT values were chosen to avoid any runs in which fixation occurred before the 180th generation.

Figure 9

Variance According to Population Structure


.120
.110
.100
.090
.080
.070
.060
.050
.040
.030
.020
.010
Variance
25
50
75
100
125
150
175
Generation number
Undivided
40 Percent
5 Percent

DISCUSSION

It is of interest to compare the results of this study with the predictions of other men which came as a result of their theoretical and mathematical studies. There are three papers which relate to this study. Unfortunately, the two papers which refer to subdivided models are not useful for comparisons because they are based on assumptions quite different from mine. Kimura's (1953) stepping-stone model of a population considers two cases of subdivided models, linear and area distributions. Kimura treats the linear case which allows migration only with the two neighboring subgroups as $\cdots \rightleftarrows A \rightleftarrows B \rightleftarrows C \rightleftarrows \cdots$. The area distribution, of which my problem is a type, is not treated.

Kolmogorov (1935) predicted the variance between successive generations under conditions of partial isolation (subgroups and migrations). However, his calculations apply only when three mathematical conditions are met. Because this investigation considered populations of small size, none of the required conditions are met. Thus comparisons with theoretical results can only be made in the case of the panmictic model.

Kimura's (1955) predicted distribution of gene frequencies over time are shown in Figure 8. These curves are generated by using a computer routine (see Appendix) to evaluate the following equation:

$$(x,t) = \sum_{i=1}^{\infty} \frac{(2i-1)(1-r^2)}{i(i-1)} T^1_{i-1}(r) T^1_{i-1}(z) e^{-[i(i-1)/4N]t}$$

where (x,t) is the distribution of gene frequencies with respect to time, r is 1 - 2p ($-1<r<1$) where p is the initial gene frequency of the population, z is 1 - 2x ($-1<z<1$) where x is the gene frequency, N is effective population size, t is generation number, and T^1 is a Gegenbauer polynomial. The ordinate on Figure 8 showing probability density results from Kimura's equation and indicates that the area under any of the curves is equal to the probability that both A and a coexist in the population. The other ordinate gives the number expected out of a sample of 400 which then can be compared to Figure 7. Use of the chi-square test for goodness of fit indicates no significant difference between the observed and expected. This result indicates that a sample size of 400 was adequate in the case of the panmictic model to get a good approximation to the probability distribution.

Because integration of Kimura's curves in terms of the probability densities results in the probability that A and a coexist in the population, one minus this area is equal to the probability that either A or a has fixed. In order to compare the expected rate of fixation with the observed, generation numbers corresponding to those shown in Figure 6 were used in generating Kimura's curves. Numerical

integration was done on the computer, and the results were converted to expected percent fixation which is shown on Figure 6. Chi square tests again showed no significant differences between the observed and the expected.

The next concern is how the parameters of interest of the three different population models compare. Figure 6 shows that the panmictic and 40% migration models are almost identical in the rate of fixation of alleles while the 5% migration model appears to have a lower fixation rate. Two different chi-square tests for homogeneity were used to determine if the observable differences between the panmictic and 5% models are significant. The first test involved nine categories, eight of which were of the following type: number of replicates which fixed within the interval 0-25, 25-50, . . ., 175-200 generations. The ninth category included all those replicates in which fixation did not occur. The results of this test showed no significant difference between the 5% migration model and the panmictic model. However, because fixation at a given generation insures fixation in all later generations, it is reasonable to look at the cummulative fixation rate as shown in Figure 6. The second chi-square test for homogeneity was done by considering two categories at each generation for each of the two models being compared. The categories were the total number of replicates fixed by a given generation and the total number not fixed by a given generation. The results of this test showed significant differences between the two models for generations 100 to 200,

inclusive. This indicates that although the rates for short intervals were not significantly different, the cumulative effect of the differences resulted in significant differences after 100 generations or more. One can conclude that the mating structure of a population can reduce the rate at which fixation occurs as in the case of the 5% migration model, or it may closely approximate panmixia as in the case of the 40% migration model.

In view of these findings, it is rather surprising to note that the distribution of the heteroallelic classes over time was approximately the same for the three models. A chi-square test for homogeneity verified the fact that there are no significant differences among the models at any generation number.

The variances shown in Figure 9 are the only data in which each of the three models gave different results. The 5% migration model maintained a high degree of variability over all generation numbers tested. By the use of Cochran's test (Dixon and Massey, 1957), it was determined that the high variance of the 5% model at the 50th generation does not vary significantly from the other generations. The same test was used to test for significant differences among the models at any given generation number. The results indicate that the variances of the 40% migration and panmictic models were distinct only through the 100th generation. This data is still impressive since the interval for the panmictic model was over 10 generations but for the subdivided models

the interval was one generation. The effect of subdivision and migration is quite strong. The 40% model, which in terms of fixation rate is equivalent to the panmictic model, shows equal or higher variability within one generation than does the panmictic model over 10 generations. The significant differences between the 5% and 40% migration models indicate that variability does not only depend upon subdivision but also upon extent of migration.

Because no natural population exists in the absence of mutation and selection, it is necessary to be cautious in drawing conclusions about the role of population structure and genetic drift in evolution on the basis of this study. However, according to Li (1955), the role of mutation in small populations is negligible, and selection may be completely ineffective if the factor of chance variation dominates the change in gene frequencies in small groups. Thus, even in the absence of comparative data obtained by using a spectrum of selection coefficients, it is possible to make some statements about the genetic effects and the evolutionary implications of drift and population structure on the basis of Li's statements and the data from this study.

The reduced fixation rate for the 5% migration model indicates that the role of drift is not independent of population structure. This would imply that before attributing observed differences between populations to genetic drift, an estimate of the population size and also knowledge of the population structure is necessary.

The markedly increased variability in the divided models, particularly the 5% migration model, is a result of the semi-independent deviations among the subgroups while migrations among the groups retard fixation because alleles can independently fix within the various subgroups of a population. In this respect it is not surprising that the 5% migration model showed a reduced rate of fixation.

The differentiation of gene frequencies among partially isolated subgroups may be adaptive or non-adaptive depending upon chance and the role of selection. As Li (1955) said:

> The selection effect, varying from one locality to another, may be said to be intergroup, which is much more effective than intragroup selection in one population. If the groups are small, some of them will be eliminated by selection while others will flourish. When a group grows large, it may be subdivided again into partially isolated groups. Hence, this condition provides a trial-and error mechanism under which the systems of gene frequencies may finally reach their most favorable equilibrium points. The species may evolve continuously even without substantial changes in environmental conditions. If conditions do change, the total population, with its diversified and flexible subgroups, will be able to cope with the new situation instead of facing extinction.

In the above Li was referring to populations of intermediate size. However, this statement corresponds with the comments of Wright (1931a and b, 1932, 1940a and b, 1948, 1949) indicating that conditions most favorable for progressive evolution exist in species subdivided into large numbers of local populations, at least some of which have medium or small effective sizes. Dobzhansky (1951) further pointed out that perhaps the most important feature of the

subdivided population is the fact that gene combinations with adaptive values somewhat lower than the average of the whole species may be temporarily preserved in some of the groups by genetic drift rather than eliminated as they would be in an undivided population. Given environmental change, the group first reaching the vicinity of the adaptive peak will obviously have the best chance of being the successful one. Thus, conditions are such that differentiation of a single species into derived species may occur as well as evolution of the species as a whole.

These results raise questions which could only be answered by more complicated models and more extensive use of the computer. For example, the differences and similarities between the panmictic and 40% models suggest that investigation of intermediate migration percentages might lead to a better understanding of the role of partial isolation (subdivision). Percentages between 5 and 40 should reveal some sort of gradation as well as the amount of migration necessary to yield results significantly different from the panmictic model at all generations being considered. Migrations of less than 5% might reveal still further reduced fixation rates and increased variability. Also data through the 300th or 400th generation would be very useful in determining with greater certainty the trends in fixation rate and maintenance of variability between generations. It might also be interesting to investigate the gene distributions between generations 1 and 25. Perhaps it is in this

time interval that differences in distributions of gene frequencies exist between the subdivided and panmictic models.

Modification of the models by selection and mutation are also warranted. By using a spectrum of different selection pressures and population sizes, one could draw some conclusions about the magnitude of selection pressure necessary to modify the random fluctuations of drift in populations of different size and mating structure. Thus an entire series of further studies would contribute to understanding the roles of drift, selection, mutation, population size, and population structure in evolution.

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Appendices

Appendix A

Program Listing for the Panmictic Model

```
/JOB TIME=30,GO
/FTC NAME= GENE
      DIMENSION IG(2),P(200),Q(200)
C     IKT SETS INITIAL NUMBER FROM WHICH RANDOM NUMBERS ARE GENERATED IN
C     THE SUBROUTINE.
      IKT=795
C     INITIATE A NEW RUN FOR 100 GENERATIONS.
      LBJ=IKT
102   CONTINUE
      WRITE(6,11)
11    FORMAT(1H1,3HIKT,5X,5(3HGEN,3X,4HFREQ,10X))
      P(1)=.5
C     L IS THE COUNTER FOR GENERATION NUMBER.
      L=1
      WRITE(6,14)IKT
 14   FORMAT(1X,I3)
101   L=L&1
      IF(L-200)20,20,5
C     K IS THE COUNTER FOR THE NUMBER OF HOMOZYGOUS DOMINANT INDIVIDUALS.
 20   K=0
C     J IS THE COUNTER FOR THE NUMBER OF HETEROZYGOUS INDIVIDUALS.
      J=0
C     I IS THE COUNTER FOR THE NUMBER OF HOMOZYGOUS RECESSIVE INDIVIDUALS.
      I=0
C     N IS THE COUNTER FOR NUMBER OF ZYGOTES(IZ) FORMED FROM GAMETES(IG).
      N=0
100   IF(N-100)9,10,8
  9   N=N&1
      CALL RANDU(IKT,NO,A)
C     A IS A RANDOM NUMBER GENERATED BETWEEN  ZERO AND ONE.
      IF(A-P(L-1))19,19,23
 19   IG(1)=2
      GO TO 21
 23   IG(1)=1
 21   CALL RANDU(IKT,NO,A)
      IF(A-P(L-1))17,18,18
 17   IG(2)=2
      GO TO 22
 18   IG(2)=1
 22   IZ=IG(1)&IG(2)
      GO TO (1,2,3,4),IZ
  1   WRITE(6,204)
204   FORMAT(3X,4HIZ=0,3X)
      GO TO 8
  2   I=I&1
      GO TO 100
  3   J=J&1
      GO TO 100
  4   K=K&1
      GO TO 100
C     STATEMENT NUMBER 10 AND THE FOLLOWING TWO STATEMENTS COMPUTE THE NEW
C     VALUE OF P TO BE USED IN PRODUCING THE GAMETES FOR THE NEXT GENERATION.
5     L=L-1
      GO TO 7
 10   IP=2*K&J
      XP=IP
      P(L)=XP/200.
      Q(L)=1.-P(L)
C     THE STATEMENT NUMBERED 13 AND THE STATEMENT PRECEDING IT CHECK TO SEE
C     IF A GENE IS FIXED.
      IF(P(L)-1.)13,7,20
13    IF(Q(L)-1.)15,7,201
200   WRITE(6,202)
202   FORMAT(1X,20HP IS GREATER THAN 1.)
      GO TO 8
201   WRITE(6,203)
203   FORMAT(1X,20HQ IS GREATER THAN 1.)
      GO TO 8
15    GO TO 101
7     LI=L
      WRITE(6,103) (L,P(L),L=1,LI)
103   FORMAT(5(9X,I3,3X,F5.3))
      LBJ=LBJ&2
      IKT=LBJ
      IF(IKT-799)102,102,8
  8   CONTINUE
C     TO MAKE ADDITIONAL RUNS, CHANGE THE INITIAL VALUE OF LBJ AND IKT TO
C     A VALUE  2 GREATER THAN THE LAST IKT VALUE RUN. ALSO CHANGE THE IF
C     STATEMENT PRECEDING STATEMENT 8 SO THAT THE UPPER LIMIT OF IKT IS
C     THAT WHICH YOU WANT.
      END
      SUBROUTINE RANDU(IX,IY,YFL)
      IY=IX*65539
      IF(IY)5,6,6
5     IY=IY+2147483647+1
6     YFL=IY
      YFL=YFL*.4656613E-9
      IX=IY
      RETURN
      END
/DATA
```

Appendix B

Program Listing for the 40% Model

```
      SUM1=0.
      SUM2=0.
      SUM3=0.
      SUM4=0.
      SUM5=0.
      SUM6=0.
      SUM7=0.
      SUM8=0.
      SUM9=0.
      SUM10=0.
      DO  807  JIR=1,IQ
      SUM1=SUM1+P(1,JIR)
      SUM2=SUM2+P(2,JIR)
      SUM3=SUM3+P(3,JIR)
      SUM4=SUM4+P(4,JIR)
      SUM5=SUM5+P(5,JIR)
      SUM6=SUM6+P(6,JIR)
      SUM7=SUM7+P(7,JIR)
      SUM8=SUM8+P(8,JIR)
      SUM9=SUM9+P(9,JIR)
807   SUM10=SUM10+P(10,JIR)
      AVE1=SUM1/IQ
      AVE2=SUM2/IQ
      AVE3=SUM3/IQ
      AVE4=SUM4/IQ
      AVE5=SUM5/IQ
      AVE6=SUM6/IQ
      AVE7=SUM7/IQ
      AVE8=SUM8/IQ
      AVE9=SUM9/IQ
      AVE10=SUM10/IQ
      JI=0
      WRITE(3,909)  AVE1,AVE2,AVE3,AVE4,AVE5,AVE6,AVE7,AVE8,AVE9,AVE10
909   FORMAT(1X,F5.3,9(1X,F5.3),3X,7HAVERAGE)
407   FORMAT(1X,F5.3,10(1X,F5.3),1X,I4,3X,I4,3X,I5)
      IF(I-199)200,402,402
401   CONTINUE
      CALL EXIT
      END
// EXEC FORTRAN
      SUBROUTINE RANDU(IX,IY,YFL)
      IY=IX*65539
      IF(IY)5,6,6
5     IY=IY+2147483647+1
6     YFL=IY
      YFL=YFL*.4656613E-9
      IX=IY
      RETURN
      END
// EXEC LNKEDT
// EXEC
/&
```

```
// JOB GENETICS     40 PERCENT MIGRATION
// OPTION LINK
// EXEC FORTRAN
      DIMENSION   P(10,201),II(4)
C    IKT VALUE GIVES INITIAL VALUE FOR RANDOM NUMBER GENERATOR.
      IKT=499
      LBJ=IKT
      IJ=0
      IQT=0
C   BA IS EQUIVALENT TO ONE GAMETE WITH A LITTLE A.
      BA=0.
C    BR IS EQUIVALENT TO ONE GAMETE WITH A BIG A.
      BR=1.
C   THE FOLLOWING TEN CARDS INITIALIZE EACH SUBDIVISION WITH A GENE FRENQUENCY OF
C     .5.
      P(1,1)=.5
      P(2,1)=.5
      P(3,1)=.5
      P(4,1)=.5
      P(5,1)=.5
      P(6,1)=.5
      P(7,1)=.5
      P(8,1)=.5
      P(9,1)=.5
      P(10,1)=.5
402   IQT=IQT+1
      IF(IQT-4) 907,906,907
906   IQT=IQT-3
      GO TO 907
907   GO TO (900,901,901),IQT
900   WRITE(3,400)
      GO TO 902
901   WRITE(3,903)
  903 FORMAT(1X,//)
902   JI=0
C     IJ IS THE COUNTER FOR THE NUMBER OF POPULATIONS RUN.
      IKT=LBJ+2
      LBJ=IKT
      IF(IKT-599)199,401,401
199   IF(IJ-100)405,401,401
405   CONTINUE
400   FORMAT(1H1,2X,1H1,5X,1H2,5X,1H3,5X,1H4,5X,1H5,5X,1H6,5X,1H7,5X,1H8
     1,5X,1H9,5X,2H10,3X,3HAVE,3X,3HGEN)
      IJ=IJ+1
C   I IS THE COUNTER FOR GENERATION NUMBER.
      I=0
200   I=I+1
C   IR IS THE COUNTER FOR NUMBER OF GAMETES.
      IR=0
      F=0.
      DO 100  III=1,10
      J=0
      B=0.
      KI=0
C     THE FOLLOWING LOOP GENERATES 12 GAMETES FROM THE PREVIOUS GENERA-
C     TION OF THE SAME SUBPOPULATION.
3     IF(J-12)6,4,5


6     CALL  RANDU(IKT,NO,A)
      J=J+1
      IF(A-P(III,I))2,2,1
1     B=B+BA
      IR=IR+1
      GO TO 3
2     B=B+BR
      IR=IR+1
      GO TO 3
5     WRITE(3,7)
7     FORMAT(1X,23HTROUBLE AT STATEMENT 3.)
      GO TO 401
C   THE FOLLOWING SERIES OF IF STATEMENTS DETERMINES THE MIGRATION PATTERN.
4     IF(III-1)101,102,101
102   II(1)=2
      II(2)=3
      II(3)=6
      II(4)=8
      GO TO 201
101   IF(III-2)103,104,103
104   II(1)=1
      II(2)=3
      II(3)=4
      II(4)=7
      GO TO 201
103   IF(III-3)105,106,105
106   II(1)=1
      II(2)=2
      II(3)=4
      II(4)=5
      GO TO 201
105   IF(III-4)107,108,107
108   II(1)=2
      II(2)=3
      II(3)=5
      II(4)=10
      GO TO 201
107   IF(III-5)109,110,109
110   II(1)=4
      II(2)=3
      II(3)=9
      II(4)=10
      GO TO 201
109   IF(III-6)111,112,111
112   II(1)=1
      II(2)=7
      II(3)=8
      II(4)=9
      GO TO 201
111   IF(III-7)113,114,113
114   II(1)=1
      II(2)=4
      II(3)=6
      II(4)=8
      GO TO 201
113   IF(III-8)115,116,115
116   II(1)=6
      II(2)=7
```

```
      II(3)=9
      II(4)=10
      GO TO 201
115   IF(III-9)117,118,117
118   II(1)=5
      II(2)=6
      II(3)=7
      II(4)=10
      GO TO 201
117   IF(III-10)120,119,120
119   II(1)=2
      II(2)=5
      II(3)=8
      II(4)=9
      GO TO 201
120   WRITE(3,121)
121   FORMAT(1X,7HTROUBLE)
      GO TO 401
C     THE FOLLOWING STATEMENTS GENERATE TWO GAMETES FROM EACH OF FOUR SUB-
C     POPULATIONS OF THE PREVIOUS GENERATION ACCORDING TO THE MIGRATION SCHEME.
201   KI=KI+1
      K=0
      IF(KI-5)12,302,301
12    IF(K-2)10,201,13
10    CALL RANDU(IKT,NO,A)
      K=K+1
      IJ=II(KI)
      IF(A-P(IJ,I))11,11,8
8     B=B+BA
      IR=IR+1
      GO TO 12
11    B=B+BR
      IR=IR+1
      GO TO 12
13    WRITE(3,14)
14    FORMAT(1X,10HTROUBLE IN)
      GO TO 401
301   WRITE(3,303)
303   FORMAT(1X,10HTROUBLE AT)
C     THE FOLLOWING COMPUTES THE NEW FREQUENCY OF THE SUBPOPULATION.
302   P(III,I+1)=B/20.
      F=F+P(III,I+1)
100   CONTINUE
      FI=F/10.
      IF(FI-1.)600,702,600
600   IF(FI-0.)601,702,601
702   IRS=I+1
      WRITE(3,703)IRS
703   FORMAT(1X,9HFI=0 OR 1,3X,I4)
      GO TO 402
601   IQ=I+1
      JI=JI+1
      IF(I-24)498,499,498
499   IF(JI-24)200,1000,13
498   IF(JI-25) 200,1000,13
1000  WRITE(3,407)   (P(III,I+1) ,  III=1,10  ),FI,IQ  ,LBJ
C     THE FOLLOWING COMPUTES THE AVERAGE OVER GENERATIONS WITHIN EACH
C     SUBPOPULATION.
```

Appendix C

Program Listing for the 5% Model

```
/JOB TIME=30,GO
/FTC NAME= GENE40
      DIMENSION   P(10,201),II(4)
C    IKT VALUE GIVES INITIAL VALUE FOR RANDOM NUMBER GENERATOR.
      IKT=725
      LBJ=IKT
      IJ=0
      IQT=0
C  BA IS EQUIVALENT TO ONE GAMETE WITH A LITTLE A.
      BA=0.
C    BR IS EQUIVALENT TO ONE GAMETE WITH A BIG A.
      BR=1.
C  THE FOLLOWING TEN CARDS INITIALIZE EACH SUBDIVISION WITH A GENE FRENQUENCY OF
C     .5.
      P(1,1)=.5
      P(2,1)=.5
      P(3,1)=.5
      P(4,1)=.5
      P(5,1)=.5
      P(6,1)=.5
      P(7,1)=.5
      P(8,1)=.5
      P(9,1)=.5
      P(10,1)=.5
402   IQT=IQT&1
      IF(IQT-4) 907,906,907
906   IQT=IQT-3
907   GO TO (900,901,901),IQT
900   WRITE(6,400)
      GO TO 902
901   WRITE(6,903)
  903 FORMAT(1X,//)
902   JI=0
C     IJ IS THE COUNTER FOR THE NUMBER OF POPULATIONS RUN.
      IKT=LBJ&2
      LBJ=IKT
      IF(IKT-801)199,401,401
199   IF(IJ-100)405,401,401
405   CONTINUE
400   FORMAT(1H1,2X,1H1,5X,1H2,5X,1H3,5X,1H4,5X,1H5,5X,1H6,5X,1H7,5X,1H8
     1,5X,1H9,5X,2H10,3X,3HAVE,3X,3HGEN)
      IJ=IJ&1
C  I IS THE COUNTER FOR GENERATION NUMBER.
      I=0
200   I=I&1
C   IR IS THE COUNTER FOR NUMBER OF GAMETES.
      IR=0
      F=0.
      DO 100  III=1,10
      J=0
      B=0.
      KI=0
C     THE FOLLOWING LOOP GENERATES 19 GAMETES FROM THE PREVIOUS GENERA-
C     TION OF THE SAME SUBPOPULATION.
3     IF(J-19)6,4,5
6     CALL  RANDU(IKT,NO,A)
      J=J&1

      IF(A-P(III,I))2,2,1
1     B=B&BA
      IR=IR&1
      GO TO 3
2     B=B&BR
      IR=IR&1
      GO TO 3
5     WRITE(6,7)
7     FORMAT(1X,23HTROUBLE AT STATEMENT 3.)
      GO TO 401
C  THE FOLLOWING SERIES OF IF STATEMENTS DETERMINES THE MIGRATION PATTERN.
4     IF(III-1)101,102,101
102   II(1)=2
      II(2)=3
      II(3)=6
      II(4)=8
      GO TO 201
101   IF(III-2)103,104,103
104   II(1)=1
      II(2)=3
      II(3)=4
      II(4)=7
      GO TO 201
103   IF(III-3)105,106,105
106   II(1)=1
      II(2)=2
      II(3)=4
      II(4)=5
      GO TO 201
105   IF(III-4)107,108,107
108   II(1)=2
      II(2)=3
      II(3)=5
      II(4)=10
      GO TO 201
107   IF(III-5)109,110,109
110   II(1)=4
      II(2)=3
      II(3)=9
      II(4)=10
      GO TO 201
109   IF(III-6)111,112,111
112   II(1)=1
      II(2)=7
      II(3)=8
      II(4)=9
      GO TO 201
111   IF(III-7)113,114,113
114   II(1)=1
      II(2)=4
      II(3)=6
      II(4)=8
      GO TO 201
113   IF(III-8)115,116,115
116   II(1)=6
      II(2)=7
      II(3)=9
      II(4)=10
```

```
      GO TO 201
115   IF(III-9)117,118,117
118   II(1)=5
      II(2)=6
      II(3)=7
      II(4)=10
      GO TO 201
117   IF(III-10)120,119,120
119   II(1)=2
      II(2)=5
      II(3)=8
      II(4)=9
      GO TO 201
120   WRITE(6,121)
121   FORMAT(1X,7HTROUBLE)
      GO TO 401
C     THE FOLLOWING STATEMENTS GENERATE TWO GAMETES FROM EACH OF FOUR SUB-
C     POPULATIONS OF THE PREVIOUS GENERATION ACCORDING TO THE MIGRATION SCHEME.
201   CALL RANDU(IKT,ND,A)
      IF(A-.25)998,998,992
992   IF(A-.50)997,997,993
993   IF(A-.75)996,996,994
994   IF(A-1.00)995,995,13
998   IJ=II(1)
      GO TO 999
997   IJ=II(2)
      GO TO 999
996   IJ=II(3)
      GO TO 999
995   IJ=II(4)
999   CALL RANDU(IKT,ND,A)
      IF(A-P(IJ,I))11,11,8
8     B=B&BA
      IR=IR&1
      GO TO 302
11    B=B&BR
      IR=IR&1
      GO TO 302
13    WRITE(6,14)
14    FORMAT(1X,10HTROUBLE IN)
      GO TO 401
301   WRITE(6,303)
303   FORMAT(1X,10HTROUBLE AT)
C     THE FOLLOWING COMPUTES THE NEW FREQUENCY OF THE SUBPOPULATION.
302   P(III,I&1)=B/20.
      F=F&P(III,I&1)
100   CONTINUE
      FI=F/10.
      IF(FI-1.)600,702,600
600   IF(FI-0.)601,702,601
702   IRS=I&1
      WRITE(6,703)IRS
703   FORMAT(1X,9HFI=0 OR 1,3X,I4)
      GO TO 402
601   IQ=I&1
      JI=JI&1
      IF(I-24)498,499,498
499   IF(JI-24)200,1000,13
```

```
498   IF(JI-25) 200,1000,13
1000  WRITE(6,407)   (P(III,I&1) ,  III=1,10  ),FI,IQ  ,LBJ
C     THE FOLLOWING COMPUTES THE AVERAGE OVER GENERATIONS WITHIN EACH
C     SUBPOPULATION.
      SUM1=0.
      SUM2=0.
      SUM3=0.
      SUM4=0.
      SUM5=0.
      SUM6=0.
      SUM7=0.
      SUM8=0.
      SUM9=0.
      SUM10=0.
      DO  807  JIR=1,IQ
      SUM1=SUM1&P(1,JIR)
      SUM2=SUM2&P(2,JIR)
      SUM3=SUM3&P(3,JIR)
      SUM4=SUM4&P(4,JIR)
      SUM5=SUM5&P(5,JIR)
      SUM6=SUM6&P(6,JIR)
      SUM7=SUM7&P(7,JIR)
      SUM8=SUM8&P(8,JIR)
      SUM9=SUM9&P(9,JIR)
807   SUM10=SUM10&P(10,JIR)
      AVE1=SUM1/IQ
      AVE2=SUM2/IQ
      AVE3=SUM3/IQ
      AVE4=SUM4/IQ
      AVE5=SUM5/IQ
      AVE6=SUM6/IQ
      AVE7=SUM7/IQ
      AVE8=SUM8/IQ
      AVE9=SUM9/IQ
      AVE10=SUM10/IQ
      JI=0
      WRITE(6,909)  AVE1,AVE2,AVE3,AVE4,AVE5,AVE6,AVE7,AVE8,AVE9,AVE10
909   FORMAT(1X,F5.3,9(1X,F5.3),3X,7HAVERAGE)
407   FORMAT(1X,F5.3,10(1X,F5.3),1X,I4,3X,I4,3X,I5)
      IF(I-199)200,402,402
401   CONTINUE
      CALL EXIT
      END
      SUBROUTINE RANDU(IX,IY,YFL)
      IY=IX*65539
      IF(IY)5,6,6
5     IY=IY+2147483647+1
6     YFL=IY
      YFL=YFL*.4656613E-9
      IX=IY
      RETURN
      END
/DATA
```

Appendix D

Sample of Data for the Panmictic Model

IKT 1	GEN	FREQ	GEN	FREQ	GEN	FREQ	GEN	FREQ	GEN	FREQ
	1	0.500	2	0.490	3	0.465	4	0.485	5	0.435
	6	0.415	7	0.465	8	0.450	9	0.470	10	0.485
	11	0.515	12	0.525	13	0.485	14	0.530	15	0.520
	16	0.520	17	0.555	18	0.570	19	0.580	20	0.580
	21	0.570	22	0.555	23	0.570	24	0.565	25	0.535
	26	0.555	27	0.605	28	0.590	29	0.625	30	0.650
	31	0.640	32	0.680	33	0.650	34	0.635	35	0.620
	36	0.595	37	0.585	38	0.630	39	0.620	40	0.535
	41	0.510	42	0.510	43	0.515	44	0.475	45	0.480
	46	0.420	47	0.425	48	0.445	49	0.430	50	0.460
	51	0.530	52	0.575	53	0.540	54	0.560	55	0.550
	56	0.535	57	0.565	58	0.550	59	0.540	60	0.505
	61	0.455	62	0.400	63	0.410	64	0.435	65	0.400
	66	0.405	67	0.390	68	0.440	69	0.465	70	0.465
	71	0.450	72	0.475	73	0.510	74	0.470	75	0.410
	76	0.480	77	0.400	78	0.355	79	0.315	80	0.370
	81	0.370	82	0.345	83	0.400	84	0.405	85	0.355
	86	0.345	87	0.320	88	0.315	89	0.275	90	0.270
	91	0.235	92	0.240	93	0.290	94	0.340	95	0.400
	96	0.385	97	0.405	98	0.440	99	0.430	100	0.455
	101	0.455	102	0.520	103	0.420	104	0.440	105	0.390
	106	0.330	107	0.325	108	0.295	109	0.265	110	0.295
	111	0.260	112	0.230	113	0.215	114	0.195	115	0.195
	116	0.205	117	0.165	118	0.180	119	0.180	120	0.195
	121	0.195	122	0.210	123	0.215	124	0.235	125	0.265
	126	0.315	127	0.330	128	0.290	129	0.310	130	0.315
	131	0.235	132	0.255	133	0.245	134	0.275	135	0.300
	136	0.240	137	0.215	138	0.175	139	0.140	140	0.140
	141	0.185	142	0.195	143	0.165	144	0.175	145	0.185
	146	0.170	147	0.215	148	0.255	149	0.245	150	0.210
	151	0.210	152	0.230	153	0.205	154	0.225	155	0.295
	156	0.325	157	0.320	158	0.335	159	0.370	160	0.345
	161	0.300	162	0.295	163	0.280	164	0.335	165	0.300
	166	0.290	167	0.275	168	0.295	169	0.340	170	0.350
	171	0.365	172	0.355	173	0.325	174	0.355	175	0.370
	176	0.385	177	0.345	178	0.285	179	0.345	180	0.325
	181	0.340	182	0.420	183	0.375	184	0.290	185	0.330
	186	0.340	187	0.335	188	0.330	189	0.295	190	0.275
	191	0.250	192	0.230	193	0.190	194	0.210	195	0.195
	196	0.200	197	0.235	198	0.235	199	0.265	200	0.290

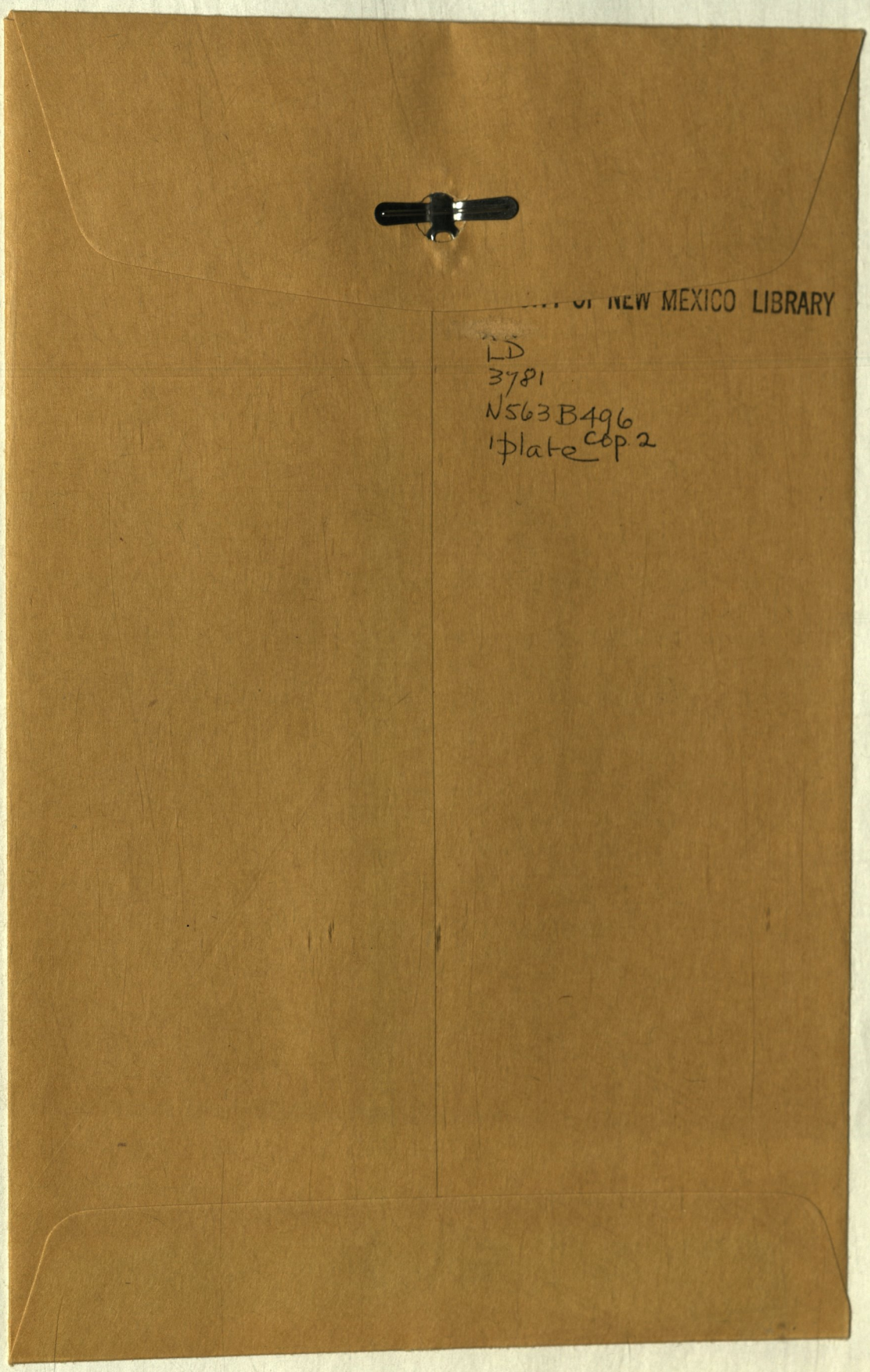
Appendix E

Sample of Data for the 40% Model

1	2	3	4	5	6	7	8	9	10	AVE	GEN	
0.450	0.750	0.450	0.300	0.200	0.350	0.400	0.300	0.500	0.600	0.430	25	1
0.404	0.510	0.394	0.450	0.432	0.452	0.490	0.426	0.486	0.504	AVERAGE		
0.250	0.500	0.450	0.600	0.500	0.250	0.300	0.550	0.450	0.700	0.455	50	1
0.448	0.498	0.426	0.467	0.445	0.505	0.498	0.493	0.511	0.542	AVERAGE		
0.450	0.400	0.450	0.600	0.500	0.300	0.300	0.200	0.600	0.300	0.410	75	1
0.461	0.495	0.457	0.479	0.503	0.453	0.475	0.465	0.551	0.559	AVERAGE		
0.250	0.300	0.350	0.450	0.350	0.200	0.450	0.450	0.350	0.250	0.340	100	1
0.420	0.462	0.427	0.470	0.462	0.416	0.464	0.430	0.505	0.519	AVERAGE		
0.350	0.350	0.250	0.400	0.400	0.250	0.300	0.250	0.250	0.350	0.315	125	1
0.384	0.422	0.400	0.430	0.443	0.385	0.422	0.389	0.469	0.477	AVERAGE		
0.100	0.050	0.250	0.100	0.250	0.200	0.050	0.150	0.200	0.050	0.140	150	1
0.358	0.390	0.377	0.404	0.397	0.349	0.390	0.359	0.420	0.429	AVERAGE		
0.450	0.350	0.500	0.250	0.200	0.100	0.200	0.200	0.100	0.250	0.260	175	1
0.330	0.378	0.360	0.388	0.388	0.323	0.353	0.335	0.398	0.409	AVERAGE		
0.300	0.300	0.350	0.300	0.100	0.100	0.250	0.150	0.150	0.100	0.210	200	1
0.320	0.361	0.341	0.365	0.363	0.300	0.334	0.313	0.363	0.371	AVERAGE		
0.450	0.600	0.300	0.400	0.350	0.600	0.450	0.250	0.300	0.350	0.405	25	3
0.618	0.622	0.578	0.542	0.580	0.630	0.536	0.538	0.498	0.608	AVERAGE		
0.350	0.700	0.350	0.750	0.900	0.550	0.350	0.550	0.600	0.550	0.565	50	3
0.571	0.586	0.557	0.548	0.529	0.600	0.532	0.555	0.534	0.573	AVERAGE		
0.150	0.300	0.500	0.300	0.800	0.250	0.250	0.300	0.350	0.350	0.355	75	3
0.547	0.556	0.561	0.564	0.589	0.552	0.555	0.540	0.554	0.581	AVERAGE		
0.050	0.200	0.050	0.250	0.0	0.100	0.050	0.050	0.0	0.0	0.075	100	3
0.451	0.472	0.480	0.474	0.486	0.460	0.454	0.456	0.450	0.484	AVERAGE		
0.250	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.050	0.0	0.030	125	3
0.382	0.388	0.395	0.391	0.395	0.387	0.373	0.376	0.365	0.390	AVERAGE		
0.0	0.100	0.150	0.100	0.0	0.050	0.050	0.0	0.050	0.050	0.055	150	3
0.334	0.333	0.339	0.332	0.333	0.337	0.322	0.323	0.314	0.333	AVERAGE		
0.0	0.0	0.050	0.050	0.050	0.0	0.0	0.0	0.0	0.0	0.015	175	3
0.290	0.291	0.303	0.292	0.292	0.299	0.282	0.285	0.278	0.293	AVERAGE		
FI=0 OR 1		194										
0.550	0.350	0.150	0.050	0.350	0.300	0.250	0.150	0.350	0.350	0.285	25	5
0.420	0.450	0.374	0.388	0.410	0.440	0.452	0.402	0.420	0.374	AVERAGE		
0.050	0.250	0.050	0.050	0.050	0.150	0.350	0.200	0.100	0.150	0.140	50	5
0.368	0.357	0.320	0.274	0.307	0.337	0.367	0.300	0.295	0.264	AVERAGE		
0.050	0.150	0.350	0.150	0.300	0.300	0.100	0.350	0.450	0.250	0.245	75	5
0.297	0.303	0.258	0.229	0.280	0.283	0.323	0.273	0.281	0.241	AVERAGE		
0.450	0.450	0.600	0.250	0.450	0.600	0.550	0.750	0.350	0.300	0.475	100	5
0.301	0.304	0.280	0.267	0.325	0.310	0.317	0.314	0.304	0.274	AVERAGE		
0.450	0.100	0.550	0.350	0.150	0.200	0.600	0.350	0.350	0.200	0.330	125	5
0.356	0.319	0.324	0.302	0.346	0.337	0.336	0.360	0.312	0.295	AVERAGE		
0.050	0.0	0.100	0.150	0.200	0.0	0.050	0.100	0.0	0.0	0.065	150	5
0.314	0.281	0.288	0.273	0.312	0.309	0.306	0.334	0.295	0.273	AVERAGE		
0.050	0.050	0.0	0.100	0.0	0.050	0.0	0.050	0.0	0.0	0.030	175	5
0.275	0.248	0.255	0.242	0.273	0.272	0.264	0.290	0.259	0.241	AVERAGE		
FI=0 OR 1		192										

Appendix F

Sample of Data for the 5% Model



1	2	3	4	5	6	7	8	9	10	AVE	GEN	
0.950	0.150	0.300	0.300	0.650	0.900	0.100	0.600	0.300	0.100	0.435	25	1
0.698	0.272	0.578	0.336	0.682	0.498	0.332	0.794	0.180	0.504	AVERAGE		
0.750	0.0	0.400	0.200	0.600	1.000	0.550	0.500	0.700	0.100	0.480	50	1
0.695	0.173	0.425	0.438	0.606	0.654	0.411	0.553	0.413	0.318	AVERAGE		
0.200	0.300	0.0	0.600	0.200	0.350	0.250	0.500	0.050	0.050	0.250	75	1
0.584	0.181	0.361	0.377	0.548	0.675	0.490	0.550	0.393	0.277	AVERAGE		
0.550	0.450	0.450	0.050	0.0	0.450	0.450	0.150	0.300	0.200	0.305	100	1
0.551	0.214	0.327	0.324	0.434	0.660	0.469	0.446	0.370	0.212	AVERAGE		
0.300	0.0	0.0	0.0	0.0	0.050	0.0	0.450	0.0	0.0	0.080	125	1
0.508	0.184	0.274	0.272	0.348	0.582	0.394	0.376	0.342	0.182	AVERAGE		
0.100	0.0	0.0	0.0	0.0	0.050	0.0	0.650	0.200	0.050	0.105	150	1
0.437	0.154	0.229	0.227	0.291	0.491	0.330	0.388	0.313	0.155	AVERAGE		
0.0	0.0	0.0	0.0	0.0	0.450	0.0	0.050	0.0	0.0	0.050	175	1
0.376	0.132	0.196	0.194	0.249	0.458	0.285	0.367	0.279	0.133	AVERAGE		

FI=0 OR 1 189

0.700	0.300	0.100	0.350	0.750	0.400	0.250	0.650	0.250	0.350	0.410	25	3
0.604	0.676	0.336	0.722	0.626	0.378	0.536	0.802	0.376	0.534	AVERAGE		
0.800	0.050	0.800	0.150	0.900	0.400	0.700	0.200	0.250	0.050	0.430	50	3
0.560	0.407	0.409	0.427	0.729	0.366	0.511	0.486	0.281	0.314	AVERAGE		
0.500	0.550	0.050	0.0	0.150	0.250	0.400	0.200	0.100	0.950	0.315	75	3
0.473	0.377	0.452	0.326	0.609	0.376	0.580	0.397	0.257	0.301	AVERAGE		
0.050	0.750	0.200	0.550	0.050	0.050	0.100	0.0	0.050	0.600	0.240	100	3
0.472	0.486	0.371	0.289	0.511	0.352	0.493	0.307	0.212	0.394	AVERAGE		
0.400	0.400	0.950	0.600	0.500	0.0	0.050	0.0	0.050	0.0	0.295	125	3
0.480	0.559	0.451	0.364	0.462	0.288	0.412	0.246	0.174	0.336	AVERAGE		
0.350	0.450	0.950	0.450	0.750	0.0	0.050	0.0	0.0	0.050	0.305	150	3
0.415	0.521	0.521	0.408	0.515	0.241	0.346	0.205	0.181	0.288	AVERAGE		
0.0	0.100	0.350	0.050	0.550	0.0	0.0	0.0	0.0	0.150	0.120	175	3
0.364	0.466	0.551	0.418	0.556	0.207	0.300	0.177	0.159	0.274	AVERAGE		
0.0	0.100	0.0	0.0	0.050	0.0	0.050	0.0	0.0	0.0	0.020	200	3
0.321	0.413	0.522	0.378	0.495	0.181	0.263	0.155	0.139	0.241	AVERAGE		

0.750	0.050	0.450	0.0	0.350	0.800	0.050	0.150	0.050	0.550	0.320	25	5
0.754	0.128	0.288	0.382	0.394	0.642	0.314	0.294	0.336	0.410	AVERAGE		
0.250	0.350	0.250	0.150	0.0	0.0	0.150	0.500	0.0	0.050	0.170	50	5
0.501	0.296	0.259	0.248	0.244	0.436	0.178	0.430	0.189	0.472	AVERAGE		
0.100	0.250	0.200	0.0	0.200	0.050	0.250	0.350	0.100	0.700	0.220	75	5
0.387	0.293	0.194	0.177	0.191	0.298	0.233	0.402	0.165	0.365	AVERAGE		
0.200	0.050	0.900	0.600	0.400	0.350	0.050	0.150	0.500	0.750	0.395	100	5
0.311	0.294	0.264	0.224	0.207	0.268	0.227	0.351	0.178	0.440	AVERAGE		
0.0	0.150	0.350	0.0	0.550	0.0	0.0	0.500	0.0	0.350	0.190	125	5
0.268	0.302	0.324	0.241	0.284	0.237	0.223	0.333	0.153	0.454	AVERAGE		
0.050	0.050	0.250	0.250	0.700	0.050	0.0	0.800	0.0	0.0	0.215	150	5
0.234	0.256	0.304	0.222	0.351	0.202	0.187	0.378	0.133	0.394	AVERAGE		
0.400	0.0	0.050	0.150	0.400	0.150	0.100	0.300	0.0	0.100	0.165	175	5
0.216	0.221	0.283	0.219	0.412	0.177	0.162	0.427	0.121	0.343	AVERAGE		
0.0	0.0	0.0	0.200	0.0	0.0	0.0	0.400	0.0	0.150	0.075	200	5
0.196	0.193	0.253	0.215	0.381	0.166	0.147	0.426	0.112	0.331	AVERAGE		

Appendix G

Listing of Program to Compute Theoretical Distributions

```
      COMMON XNP(6),NOS(6),PR(102),PZ(102),TR(100),TZ(100),PHIXT(100)
      READ 10,(XNP(I),I=1,4)
   10 FORMAT(6F5.2)
      PRINT 11
   11 FORMAT(1H1,3HXNP/)
      PRINT 12,(XNP(I),I=1,4)
   12 FORMAT(1X,6F7.3)
      READ 13,(NOS(J),J=1,4)
   13 FORMAT(6I3)
      PRINT 14
   14 FORMAT(//,1X,3HNOS/)
      PRINT 15,(NOS(J),J=1,4)
   15 FORMAT(1X,6I3)
C COMPUTE PROBABILITY DENSITIES FOR EACH GERERATION.
      DO 7 IK=1,4
      IF(IK-4)20,20,34
   20 PRINT 8,NOS(IK)
    8 FORMAT(1H1,2HT=,I3, //,1X,24HX IS THE GENE FREQUENCY./,1X,33HPHIXT
     1 IS THE PROBABILITY DENSITY./)
      GO TO 16
   21 PRINT 9,NOS(IK)
    9 FORMAT(1H1,2HT=,I1,2H*N//,1X,24HX IS THE GENE FREQUENCY./,1X,33HPH
     1IXT IS THE PROBABILITY DENSITY./)
   16 P=0.5
      R=1.-2.*P
      X=.05
C COMPUTE PROBABILITY DENSITIES FOR EACH GENE FREQUENCY.
      DO 6 IM=1,20
      Z=1.-2.*X
C COMPUTE LEGENDRE POLYNOMIALS.
      DO 1 J=2,100
      PR(1)=1.
      PR(2)=R
      PZ(1)=1.
      PZ(2)=Z
      K=J+1
      L=J-1
      XJ=J-1
      PR(K)=((2.*XJ+1.)*R*PR(J)-XJ*PR(L))/(XJ+1.)
    1 PZ(K)=((2.*XJ+1.)*Z*PZ(J)-XJ*PZ(L))/(XJ+1.)
C COMPUTE GEGENBAUER POLYNOMIALS.
      DO 60 KJ=4,100
      TR(1)=1.
      TR(2)=3.*R
      TZ(1)=1.
      TZ(2)=3.*Z
      KJI=KJ-1
      XKJ=KJ-1
      ZKJ=KJ+1
      IQT=KJ+1
C CHECKS WHETHER OR NOT (1.-R*R) IS ZERO.
      IF(1.-R*R)31,32,31
   32 PRINT 33
   33 FORMAT(1X,17H(1.-R*R) IS ZERO.)
      GO TO 34
   31 TR(KJI)=  XKJ*(XKJ+1.)*(PR(KJI)-PR(IQT))/((2.*XKJ+1.)*(1.-R*R))
C CHECKS WHETHER OR NOT (1.-Z*Z) IS ZERO.
      IF(1.-Z*Z)36,37,36
   37 PRINT 38
   38 FORMAT(1X,17H(1.-Z*Z) IS ZERO.)
      GO TO 6
   36 TZ(KJI)=  XKJ*(XKJ+1.)*(PZ(KJI)-PZ(IQT))/((2.*XKJ+1.)*(1.-Z*Z))
   60 CONTINUE
      PHIXT(1)=(1.5*(1.-R*R)*TR(1)*TZ(1)*EXPF(-1./(2.*XNP(IK))))
C COMPUTE PROBABILITY DENSITIES.
      DO 50 II=2,99
      MO=II-1
      XII=II
      W=XII*(XII+1.)
      V=W/(4.*XNP(IK))
      PHIXT(II)=PHIXT(MO)+((2.*XII+1.)*(1.-R*R)*TR(II)*TZ(II)*EXPF(-V))/
     1W
   50 CONTINUE
      PRINT 53,X
   53 FORMAT(//,1X,2HX=,F4.2/,58X,5HPHIXT/)
      PRINT 54,(PHIXT(II),II=1,99)
   54 FORMAT(1X,10(2X,F10.7))
    6 X=X+.05
    7 CONTINUE
   34 CONTINUE
      STOP
      END
```