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The maintenance of polymorphisms at two loci in house mouse Mus musculus populations.

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THE MAINTENANCE OF POLYMORPHISMS AT TWO LOCI IN HOUSE MOUSE (*MUS MUSCULUS*) POPULATIONS

by

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ABSTRACT

An examination of house mouse (Mus musculus) populations collected from corn cribs in southwestern Ontario revealed further evidence for the widespread distribution of a polymorphism at the T locus. The overall frequency of the t alleles at this locus is 0.081. These same mice were examined for a polymorphism at the hemoglobin β chain (Hbb) locus. The overall frequency of the more common allele (Hbb^s) at this locus is 0.70. Ecologic data suggest that house mouse populations are structured, with little gene flow between units.

A stochastic model was developed, and accounts for the polymorphism at the T locus when male transmission ratio is 0.95, and interdemic migration is 5 percent. Varying the number of breeding units or demes per population had no significant effects on the t allele frequency.

The model was applied to the Hbb locus to see how well the model could explain the data from natural populations. The observed frequencies and frequency variances at the Hbb locus could not be explained simply by gene flow between populations. Strong selective pressures were required to establish a stable polymorphism with the same frequency and frequency variance in the model as are observed at the Hbb locus in natural populations.

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I INTRODUCTION

Until recently most of the genetic variants known in the house mouse were discovered and studied in mice bred in the laboratory. Since wild house mice show limited variability in morphological traits under simple genetic control and useful in the study of genetic aspects of natural populations, attention was turned to electrophoretic patterns of proteins. Surveys of wild house mouse (Mus musculus) populations have revealed that many biochemical systems are polymorphic (Berry and Murphy, 1970; Heinecke and Wagner, 1964; Petras, 1967a; Petras et al, 1969; Roderick et al, 1971; Selander et al, 1969). To account for this variation two general theories have been proposed. The balance theory emphasizes natural selection as the evolutionary force responsible for maintaining or even increasing variation. The neoclassical theory asserts that when selection occurs it is almost always purifying, that is, it acts to decrease variation, and that there is a class of mutations which is not subject to natural selection, and in the case of these neutral mutations variability is maintained by gene flow between populations.

The magnitudes of population size, migration and selection so important to distinguishing between these two theories, are difficult to measure in natural populations of Mus musculus. Estimates of these parameters have been made

but these are indirect, based on allelic frequency data and on physical movements of animals in their habitats. Subdivision of house mouse populations is indicated by the analysis of allelic frequency data (Selander, 1970) and of aggressive behaviour (Anderson and Hill, 1965). The breeding unit size appears small, perhaps as low as 10 individuals (Petras, 1967a). Furthermore, migration between populations appears to be a rare event, an idea supported by several studies (Brown, 1953; Rowe et al, 1963; Southern and Laurie, 1946).

Since the important parameters are difficult to measure in the present study, a population model was developed that will explain the data at one locus, namely the T locus, at which variability has been uncovered in nearly all populations studied (Anderson, 1964; Dunn, 1957a; Petras, 1967b), and for which suitable models have already been developed (e.g. Lewontin and Dunn, 1960). This model was then applied to alleles at another locus, namely the hemoglobin β locus, which is also polymorphic in most populations studied, to see how well the model would explain the data from natural populations and if necessary to determine how the model would need to be modified to be consistent with observations on natural populations.

II DESCRIPTION OF GENETIC SYSTEMS

A The T Locus

The t alleles are widespread in house mouse (Mus musculus) populations and so have been well characterized (Anderson, 1964; Anderson et al, 1964; Dunn, 1953; 1957a; 1957b; 1960; Dunn and Suckling, 1956; Dunn et al, 1958; 1960; Petras, 1967b). These alleles are located at the Brachyury locus (T locus) on linkage group IX (Allen, 1955). In a homozygous condition the t alleles result in lethality or male sterility, and so should be selected out of a population. The fitness of a heterozygous (+/t) mouse appears normal, although this has been questioned (Dunn et al, 1958). One unusual aspect of the t allele is that most of the fertilizing sperm produced by a +/t male are t bearing, that is there is a transmission ratio advantage favouring t alleles. Dunn (1960) found this advantage to range from 0.895 to 0.998, with a mean of around 0.952 in t alleles derived from natural populations. The t allele can be recognized in a heterozygous animal by mating the heterozygote with a mouse heterozygous for a third allele, the brachy (T) allele, at the T locus. Mice of the genotype T/+ have a short, blunt tail, and the T/T genotype is lethal.

When T/+ females are mated with +/t males the following genotypes and phenotypes are observed:

T/t	tailless
T/+	short, blunt tail
+/t	normal tail
+/+	normal tail

Therefore if the unknown male is +/+ then none of the T-bearing zygotes would have a t-allele so none should be tailless. However if the unknown male is +/t then at least one quarter of the offspring should be tailless, or one half of the T-bearing offspring should be tailless. By classifying seven T-bearing offspring for each male, the error of misclassification is less than 1%. The same approach can be used to classify females. Furthermore because several studies have shown that the transmission ratio in males heterozygous for a lethal t allele is high, in a few cases approaching 1.00 (Dunn, 1960; Petras, 1967b) the number of T-bearing offspring that must be typed can be reduced to two, and the error of misclassification still remains less than 1%.

Most of the information regarding the frequency of t alleles in natural populations has been due to the work of Dunn and his colleagues (Anderson, 1964; Anderson et al, 1964; Dunn, 1953, 1957a, 1957b, 1960; Dunn and Suckling, 1956; Dunn et al, 1958; 1960). At least one other study (Petras, 1967b) has reported frequencies of t alleles from populations where large sized samples were obtained. The results of these studies are shown in Table 1.

As background for the present study t allele frequency data were acquired for house mouse populations collected at

Table 1: Summary of the frequency of the more common alleles at each of two loci known to be polymorphic in mouse populations, studied from locations around the world.

SYSTEM	ALLELE STUDIED	FREQUENCY OF ALLELE	LOCALITY	REFERENCE
T LOCUS	t	0.16	Ann Arbor	Petras, 1967b
		0.119	Alberta	Anderson, 1964
		0.17	U.S.A.	Dunn et al, 1960
Hemoglobin	Hbb^s	0.88	Windsor	Petras et al, 1969
		0.69	Ann Arbor	Petras, 1967a
		0.50	Tennesse	Popp and St.Amand,1960
		0.61	Germany	Heincke and Wagner,1964
		0.407	Skokholm	Berry and Murphy, 1970
		0.55	Cen. California	Selander, Yang and Hunt, 1969
		0.44	S. California	"
		0.61	Arizona	"
		0.94	Minnesota	"
		0.91	Illinois	"
		0.80	Florida	"
		0.94	Jamaica	"
		0.54	Venezuela	"
		0.67	N. Denmark	Selander,Hunt and Yang, 1969
		0.84	S. Denmark	"
		0.85	Ontario,1970	Petras, unpublished
		0.767	Ontario, 1971	"
		0.740	Ontario, 1972	"
		0.760	Ontario, 1973	"
		0.770	Ontario, 1974	"

21 sites in southwestern Ontario (see Figure 8 for map of area). All available male mice were tested for the presence of t alleles. Animals were classified only as to whether or not each carried a t allele. No attempt was made to distinguish between lethal or sterile t alleles, or between various lethal t alleles, as has been done elsewhere (Anderson, 1964; Petras, 1967b). The results are shown in Table 2. Half the populations tested showed no evidence for the presence of t alleles. Unfortunately sample sizes were in some cases small. The frequency estimates range from zero to 0.273, with an overall frequency of 0.081.

The results of the breeding program give further evidence for the widespread distribution of the t allele polymorphism. The overall frequency of the pooled data is the lowest reported where total sample size is large (see Table 1). These results are, nevertheless, consistent with those of Anderson (1964), who also found a number of populations not polymorphic for t alleles. This occurrence of t-less populations could readily be accounted for by highly limited gene flow between crib populations, and consequently local extinctions of the t allele.

Table 2: Frequency estimates of *t* alleles in samples obtained from corn crib populations in southwestern Ontario.

LOCALITY	+/+	+/t	STERILE	FREQUENCY
Houle	86	17	14	0.083
Comartin	10	5	0	0.167
Damphousse	8	0	1	0.000
Brown	11	3	1	0.063
G. Belanger	6	2	0	0.125
C. Belanger	1	0	0	0.000
Belanger	7	1	0	0.063
Arner	5	6	0	0.273
Nussey	3	1	0	0.125
Baillargeon	5	0	0	0.000
Pinsonneault	15	0	0	0.000
Maitre North	6	2	0	0.125
Maitre South	29	3	0	0.045
Parkes	2	0	0	0.000
Gagner	5	0	0	0.000
Martin	5	0	0	0.000
Van K.	2	2	1	0.250
Bodner	1	0	0	0.000
Roy	4	1	1	0.100
Bondy	7	0	1	0.000
McKim	6	0	0	0.000
POOLED	224	43	19	0.081

B The Hemoglobin β (Hbb) Locus

Like the polymorphism at the T locus, the polymorphism at the locus controlling the β-chain of hemoglobin (Hbb-locus) is also widespread. Starch gel electrophoresis of erythrocytic lysates has revealed the existence of two common alleles, Hbb^s and Hbb^d (Heinecke and Wagner, 1964; Petras, 1967a; Popp and St. Amand, 1960) which result in three phenotypes under certain electrophoretic conditions (Petras and Martin, 1969). These alleles are located at a locus on linkage group I (Russell and Gerald, 1958).

Information on the allelic frequencies at the Hbb locus in mouse populations from various locations around the world are listed in Table 1.

Wild house mice were captured from corn cribs (see appendix II for method) during the summers of 1970 through 1974. Erythrocytic lysates were prepared using the technique of Biddle and Petras (1967); starch gel electrophoresis using the method of Petras and Martin (1969) was performed on all lysates; and frequency estimates for the allele giving the single pattern were calculated. These are summarized in Table 1. The Hbb locus was polymorphic in nearly all populations sampled.

Based on the data of the two polymorphic loci described estimates of the amount of heterozygosity were calculated (Table 3).

Table 3: Estimates of the amount of heterozygosity in natural populations based on data from two polymorphic loci.

SYSTEM	LOCATION	ALLELIC FREQUENCY	FREQUENCY VARIANCE	ESTIMATE OF HETEROZYGOSITY
T locus	S.Ontario, 1973	0.081	0.0982	0.162
	Ann Arbor	0.156	0.0099	0.312
	Alberta	0.119	0.0238	0.238
Hbb locus	S.Ontario, 1970	0.85	0.0125	0.276
	1971	0.77	0.0243	0.370
	1972	0.74	0.0233	0.368
	1973	0.76	0.0092	0.362
	1974	0.77	0.0134	0.335

III EVIDENCE FOR POPULATION STRUCTURING

Numerous studies of wild populations of the house mouse, Mus musculus, indicate that these populations are subdivided into endogamous breeding units or demes. This evidence comes from studies of biochemical polymorphisms and from ecological and behavioural studies of populations of Mus.

A Genetic Data

Studies on biochemical polymorphisms in house mouse populations have given mixed results. Petras (1967a) and Petras et al (1969) observed a deficiency of heterozygotes in several mouse populations, which they explain by inbreeding or population subdivision. Roderick et al (1971) observed no evidence for inbreeding as measured by a numerical deficiency of heterozygotes. However, sample sizes were small. Berry and Murphy (1970) felt that the effects of natural selection were overriding the effects of genetic drift to produce an excess of heterozygotes. Selander (1970) not only observed a heterogeneity in allelic frequencies among samples from farms in the same region and from barns on the same farm, but also spatial variation within a single barn. These he explained on the basis of tribal subdivision of populations and genetic drift.

B Ecological Data

Ecological studies have revealed restricted movements of mice. Brown (1953) found no movement of mice between fields and farm buildings, although he conceded that it did occur. Southern and Laurie (1946) caught mice in fields but these were restricted to hedgerows. These mice probably acted as immigrants when commensal habitats became available. Rowe et al (1963) studying the movements of mice around corn ricks, observed that most mice entered the rick within two months of its construction and few mice left the rick until four months later. Petras (1967a), while trapping mice in and around buildings, estimated that seventeen percent moved to buildings other than those in which they were first caught. These studies generally suggest that populations occupying different regions of a habitat are to a great extent isolated.

C Behavioural Data

Populations of wild house mice maintained in the laboratory have also provided information on population structuring and territorial behaviour. Crowcroft (1955) observed dominant males defending territories around nest boxes with one or more females. Anderson and Hill (1965) in studying territory formation in a laboratory cage, observed that aggressive encounters between mice were required before a territory boundary was recognized by mice. Reimer and Petras (1967) found that once a territory was established immigrants of either sex were not tolerated in the territory, and that females to some extent helped to defend the territory. Based on the above studies, deme size has been estimated to be five or less animals. This is especially true if, as Busser et al (1974) indicated, aggressive males make the greatest contribution to succeeding generations, and that while non-aggressive males may be tolerated by dominant animals, they make little contribution to reproduction in natural populations.

There are some indications that territoriality tends to break down under certain conditions. For instance, Davis (1958) suggests that house mice are territorial at low densities, but at high densities may associate into groups which have social rank. This does not alter the general picture significantly since subdivision still occurs.

IV STOCHASTIC MODEL AND THE t ALLELE

A Development and Description of the Stochastic Model

The computer model that is used in this study was based largely on a model developed by Lewontin and Dunn (1960) to explain findings at the T locus. A stochastic rather than a deterministic model was chosen because random events could then be included in the model. The first models of the t allele system were deterministic, however, and thus they merit description.

Prout (1953) described a system where balance was achieved between selection and transmission ratio. However, the model gave unrealistic results since the transmission ratio favoured the t allele in both sexes, an incorrect assumption. Bruck (1957) derived an expression for the equilibrium gene frequency for the case of a recessive lethal with abnormal transmission ratio in one sex only. In the model, if

m = proportion of t gametes in the effective sperm pool (= transmission ratio).

$\hat{p}$ = equilibrium frequency of t alleles among adults,

then

$$\hat{p} = \frac{1}{2} - \frac{\sqrt{m(1-m)}}{2m}$$

For a transmission ratio of 0.95, $\hat{p}$ is 0.385, which is a much higher value for the t allele frequency than is seen

in any well sampled populations of the house mouse (Anderson, 1964; Dunn et al, 1960; Petras, 1967b). A similar result for male sterile t alleles was derived by Dunn and Levene (1961), where $\hat{p}_s$, the equilibrium frequency for the sterile t allele is given by:

$$\hat{p}_s = 2m-1,$$

where m is the male transmission ratio. Again the frequency of male sterile t alleles is overestimated because the deterministic model assumes a population of infinite size and random mating. This is not the case in real populations. Petras (1967b) modified Bruck's model to include an inbreeding coefficient, which can be considered a measure of the Wahlund effect or of numerical deficiency of heterozygotes because of population subdivision. In the modified model, if $F = \frac{\sigma^2}{\bar{p}_i(1-\bar{p}_i)}$,

where F is the inbreeding coefficient, σ^2 the variance of gene frequencies in the subdivision and $\hat{p}_i$ the overall frequency of the t allele at equilibrium, then

$$\hat{p}_i = \frac{(4m-F-6Fm) \pm \sqrt{4Fm(F-8+Fm+10m) + 16m(1-m) + F^2}}{8m(1-F)}.$$

For a transmission ratio of 0.95 and an inbreeding coefficient of 0.18 the equilibrium value of the t allele frequency expected from the model is 0.18, which is in good agreement with empirical estimates (Anderson, 1964; Dunn et al, 1960; Petras, 1967b). The inbreeding coefficient estimate is based on data derived from studies of wild mouse populations sampled near Ann Arbor and typed for allelic variation at the Es-2

locus (Petras, 1967a). The good agreement between the observed and expected t allele frequencies suggests that population subdivision could be the mechanism for reducing the t allele frequency in natural populations.

Computer models which take into account population subdivision and random events have also been developed. The first to address the t allele problem was devised by Lewontin and Dunn (1960). This stochastic model used a Monte Carlo procedure to simulate the interactions between selection, transmission ratio abnormality, and restricted population size. The conclusion reached using this model was that geographical populations are composed of demes fixed for wild-type alleles and of demes with a high frequency of t alleles. The loss of the t allele in the former demes is due to random drift, and the rate of loss is sensitive to the magnitude of the transmission ratio so that only alleles with a high transmission advantage will remain in the population for any appreciable time. The original model dealt only with lethal t alleles, and has been extended (Lewontin, 1962) to include male sterile t alleles. These models did not consider the effects of interdemic migration. While ecological evidence suggests that migration between populations is low as already mentioned, its occurrence is not ruled out. Therefore, Levin et al (1969) described a system which was essentially the same as that of Lewontin and Dunn, but which included interdemic migration. Migrant genotypes came from what would be considered a floating population associated with each deme, that is a group —

of genotypes associated with the family unit, but which do not take part in reproduction within their parental unit. The results of the model indicate that even with a low level of migration (3 percent), the t allele frequency approached that of the unmodified deterministic model of Bruck (1957) when deme size was greater than four. One aspect of this model, however, the manner in which migrants moved from one deme to another, can be questioned since Reimer and Petras (1967) showed that once demes were established, interdemic migration was rare. For this reason a new stochastic model was devised modelled on populations of the house mouse sampled in southwestern Ontario.

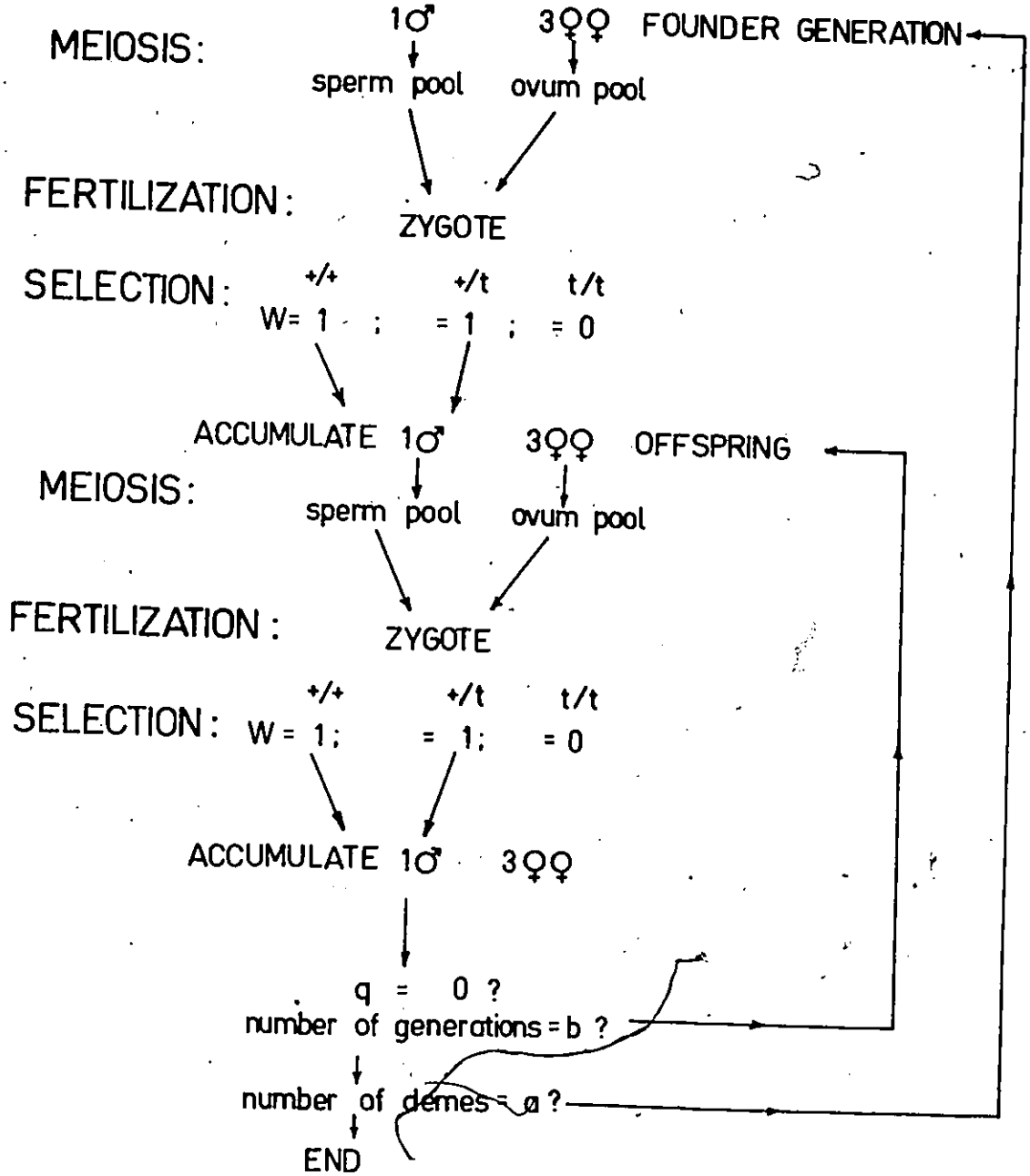
B The modified model

The scheme for the program is shown in Figure 1. Each individual is represented in the program by a two digit number, each digit representing one of two alleles at a single locus, that is +1, +1 represented +/+; +1, -1 represented +/t; and -1, -1 represented t/t genotypes. Each deme or breeding unit consisted of one male and three females. Throughout the study the genetically effective size of each deme was held constant and was the same for all demes.

At the outset, a number, 'q' representing the frequency of the t allele is designated and based on this number the genotypes of the four individuals of each deme are generated. To accomplish this a random number between one and one hundred inclusive is generated. If the random number

Figure 1: Flow chart scheme of the Monte Carlo program used in the t allele simulation

INPUT : q, initial t allele frequency
$W_{+/+} = 1$; $W_{+/t} = 1$; $W_{t/t} = 0$
m, male transmission ratio
a, number of demes per population
b, migration rate



generated is less than or equal to q, a -1 is chosen, otherwise a +1 is chosen. This same procedure is repeated twice for each individual (two alleles at one locus) or a total of eight times for a generation. After the genotype of each animal is determined, that genotype is tested for its fitness.

To test for fitness, a new random number is generated. If the random number is less than or equal to W, the fitness of the particular genotype, the individual survives and is stored in memory as an adult animal. If the random number is greater than W, the animal is declared unfit and is discarded.

Because the generation of alleles representing each individual is based on an initial allelic frequency, the exact genotypic composition of the first or founder generation of a deme does not have to be specified. Obviously several demes generated in the same way may have very different genotypic compositions. In the program, the number of demes or breeding units, 'a', can be varied; in most cases ten demes were studied. The genotypes of all individuals and the frequency of the t allele was printed for each founder generation.

The generation after the founder generation and all subsequent generations were based on the genotypes of the adults, and not on the t allele frequency. In this procedure, male gametes are generated from the one male adult, female gametes from the three adult females. In the case of the t allele, parents have either a +/+ or +/t genotype. If the male parent is +/+, the sperm is always +. However, if the male parent is +/t, then the male gamete can be either + or t. A random

number is generated, and if the number is equal to or less than m, the transmission ratio, then a t-bearing gamete is chosen (-1 in terms of the computer analogue). Otherwise, a wild type gamete is chosen. To choose a female gamete, a normal transmission ratio is assumed, and the six female gametes (from three adults) are pooled so each gamete has an equal chance of being chosen. A random number between one and six inclusive is generated and one of the six female gametes chosen on the basis of that number. One male and one female gamete are combined to produce each of one male and three female genotypes, each of which is subject to testing for fitness as already described. When four surviving adults have been produced, the genotypes of all four together with the t allele frequency are printed. The process of generating new genotypes, that is the cycle of producing adults from adults, continues until either fixation for the wild type allele occurs or until a set number of generations, 'b', has been reached.

In order to simulate a population of mice, more than one deme is produced. Groups of five, ten or twenty demes were considered. All founder generations formed were based on the same initial t allele frequency, and reproduced as described.

The computer model was made more complex by introducing interdemic migration. In order to simulate interdemic migration a pooling procedure was used. For example, suppose the population consisted of ten demes. To simulate a migration rate of one percent, once in every 100 generations the genotypes

of all ten demes would be pooled and an overall t allele frequency determined. Then based on the new overall frequency, ten new founder demes would be established as previously described. To simulate a ten percent migration rate, the pooling procedure would occur once every ten generations. In this way any rate of interdemic migration could be simulated.

Under these conditions, if a population is made up of ten demes, then the total population size is forty animals, with reproduction, migration and genetic drift occurring as described. Since this situation is analogous to a single population, a repetition of the simulation several times would represent several populations. In this study, each set of input parameters was processed five times which is analogous to five separate populations. No interpopulation migration was considered. Only interdemic migration (within a single population) is possible. The total size of the five population groups or metapopulation in the example of ten demes is 200 individuals. The unit of program between each migration was termed a cycle. For a metapopulation subject to a migration rate of five percent, this cycle represents 800 generations. A summary of the parameters used for the runs made with the t allele program is shown in Table 4.

Table 4: Input parameter values for t allele simulation.[a]

NUMBER OF DEMES	MALE TRANSMISSION RATIO	PERCENT MIGRATION
10	0.90	1
10	0.90	4
10	0.90	5
10	0.90	10
20	0.90	1
20	0.90	3.3
20	0.90	5
20	0.90	10
5	0.95	1
5	0.95	5
5	0.95	10
10	0.95	1
10	0.95	4
10	0.95	5
10	0.95	10
20	0.95	1
20	0.95	3.3
20	0.95	5
20	0.95	10

$N_e = \frac{4N♀\ N♂}{N♀ + N♂} = 3.00$ = effective genetic size of all demes,

where $N♂$ is the number of males, $N♀$ is the number of females
female transmission ratio is assumed to be normal (0.50) .

C Simulation Results

The results of the simulation are presented in Table 5 and Figure 2. The tabulated results include the frequency and variance of the t allele at generations 3, 10 and 20 of each cycle up to the maximum of forty cycles, together with the proportion of demes fixed in the last generation of each cycle. In those demes which are not fixed the t allele occurs at various frequencies up to 0.50. For selected input parameters the frequency distribution across all demes in the metapopulation was drawn for every fifth cycle up to the maximum of forty cycles (Figure 2). The overall frequency (based on the last generation of each cycle) of the t allele, q, for the metapopulation is also shown. The shape of the distribution of unfixed demes is J-shaped, and the most frequent class is 0.50.

To summarize these data, the proportion of demes fixed for the wild-type allele by the end of cycle 40 was plotted as a function of the number of demes and of the migration rate when the male transmission ratio is 0.95 (see Figure 3). When the interdemic migration rate is 1 percent, all demes become fixed for the wild type allele by cycle 40. As the migration rate increases the proportion of fixed demes decreases.

If the number of demes in a population is 5, all demes become fixed for the wild type allele unless the migration rate is 10 percent. As the number of demes increases, the proportion of fixed demes decreases.

The family of curves in Figure 3 were drawn when the

Table 5a: Frequency and variance estimates, calculated for the t allele simulation.

t-allele	NUMBER OF DEMES	TRANSMISSION RATIO	MIGRATION RATE	PROPORTION OF FIXED DEMES
	10	0.90	0.01	

GENERATION	3		10		20		
CYCLE	$\bar{q}$	σ^2	$\bar{q}$	σ^2	$\bar{q}$	σ^2	
1	.397	.0262	.294	.0422	.229	.0551	0.50
2	.035	.0144	.032	.0129	.022	.0085	0.94
3	.000	.0000	.000	.0000	.000	.0000	1.00
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Table 5b: Frequency and variance estimates, calculated for the t allele simulation.

t-allele	NUMBER OF DEMES	TRANSMISSION RATIO	MIGRATION RATE	PROPORTION OF FIXED DEMES
	10	0.90	0.04	

GENERATION	3		10		20		
CYCLE	$\bar{q}$	σ^2	$\bar{q}$	σ^2	$\bar{q}$	σ^2	
1	.344	.0368	.289	.0483	.209	.0462	0.48
2	.256	.0482	.189	.0462	.150	.0437	0.62
3	.167	.0497	.159	.0486	.105	.0345	0.74
4	.085	.0300	.065	.0251	.057	.0244	0.88
5	.070	.0301	.055	.0213	.042	.0185	0.90
6	.017	.0055	.017	.0074	.015	.0060	0.96
7	.017	.0074	.015	.0060	.020	.0090	0.96
8	.012	.0038	.020	.0096	.015	.0053	0.96
9	.017	.0074	.010	.0049	.010	.0049	0.98
10	.015	.0060	.010	.0049	.007	.0027	0.98
11	.005	.0012	.007	.0027	.010	.0049	0.98
12	.000	.0000	.000	.0000	.000	.0000	1.00
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Table 5c: Frequency and variance estimates, calculated for the t allele simulation.

t-allele	NUMBER OF DEMES	TRANSMISSION RATIO	MIGRATION RATE	PROPORTION OF FIXED DEMES
	10	0.90	0.05	

GENERATION	3		10		20		
CYCLE	$\bar{q}$	σ^2	$\bar{q}$	σ^2	$\bar{q}$	σ^2	
1	.333	.0310	.192	.0368	.262	.0487	0.38
2	.321	.0394	.312	.0475	.224	.0523	0.48
3	.329	.0449	.269	.0527	.204	.0521	0.54
4	.237	.0544	.172	.0471	.130	.0436	0.70
5	.172	.0465	.127	.0383	.080	.0296	0.82
6	.130	.0405	.082	.0309	.072	.0280	0.84
7	.047	.0135	.030	.0121	.045	.0192	0.90
8	.067	.0256	.045	.0160	.045	.0184	0.90
9	.057	.0244	.047	.0204	.045	.0184	0.90
10	.062	.0244	.055	.0224	.050	.0225	0.90
11	.062	.0244	.045	.0192	.020	.0076	0.94
12	.020	.0076	.010	.0049	.002	.0002	0.98
13	.010	.0049	.000	.0000	.000	.0000	1.00
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Table 5d: Frequency and variance estimates, calculated for the t allele simulation.

t-allele	NUMBER OF DEMES	TRANSMISSION RATIO	MIGRATION RATE	PROPORTION OF FIXED DEMES
	10	0.90	0.10	

GENERATION	3		10		
CYCLE	$\bar{q}$	σ^2	$\bar{q}$	σ^2	
1	.385	.0237	.354	.0396	0.20
2	.348	.0338	.339	.0413	0.24
3	.271	.0409	.240	.0536	0.46
4	.304	.0463	.261	.0474	0.38
5	.304	.0433	.215	.0511	0.50
6	.254	.0530	.210	.0570	0.56
7	.279	.0547	.194	.0485	0.54
8	.282	.0466	.242	.0551	0.46
9	.254	.0524	.187	.0513	0.56
10	.202	.0491	.182	.0461	0.56
11	.227	.0571	.200	.0561	0.58
12	.222	.0524	.187	.0518	0.58
13	.195	.0531	.157	.0453	0.62
14	.177	.0461	.160	.0504	0.66
15	.197	.0486	.167	.0477	0.60
16	.204	.0507	.165	.0501	0.64
17	.215	.0524	.182	.0506	0.58
18	.182	.0480	.230	.0530	0.62
19	.210	.0546	.189	.0499	0.56
20	.194	.0468	.192	.0518	0.56
21	.201	.0459	.207	.0521	0.52
22	.194	.0468	.181	.0601	0.62
23	.199	.0517	.174	.0485	0.60
24	.194	.0481	.160	.0454	0.62
25	.189	.0493	.150	.0435	0.64
26	.171	.0447	.187	.0518	0.58
27	.205	.0541	.160	.0480	0.62
28	.212	.0494	.137	.0449	0.70
29	.172	.0491	.159	.0485	0.64
30	.176	.0466	.160	.0493	0.62
31	.204	.0522	.162	.0461	0.62
32	.207	.0527	.142	.0347	0.58
33	.137	.0413	.132	.0432	0.70
34	.157	.0466	.142	.0428	0.66
35	.139	.0358	.149	.0428	0.64
36	.182	.0538	.177	.0511	0.60
37	.152	.0424	.132	.0432	0.70
38	.192	.0493	.180	.0531	0.60
39	.199	.0504	.159	.0423	0.58
40	.194	.0504	.130	.0429	0.70

Table 5a: Frequency and variance estimates, calculated for the t allele simulation.

t-allele	NUMBER OF DEMES	TRANSMISSION RATIO	MIGRATION RATE	PROPORTION OF FIXED DEMES
	20	0.90	0.01	

GENERATION	3		10		20		
CYCLE	$\bar{q}$	σ^2	$\bar{q}$	σ^2	$\bar{q}$	σ^2	
1	.413	.0201	.333	.0397	.220	.0488	0.46
2	.039	.0168	.035	.0146	.029	.0118	0.93
3	.005	.0025	.000	.0000	.000	.0000	1.00
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Table 5f: Frequency and variance estimates, calculated for the t allele simulation.

t-allele	NUMBER OF DEMES	TRANSMISSION RATIO	MIGRATION RATE	PROPORTION OF FIXED DEMES
	20	0.90	0.03	

GENERATION	3		10		20		
CYCLE	$\bar{q}$	σ^2	$\bar{q}$	σ^2	$\bar{q}$	σ^2	
1	.390	.0275	.305	.0440	.249	.0498	0.41
2	.205	.0534	.163	.0461	.127	.0423	0.70
3	.136	.0403	.096	.0351	.063	.0224	0.84
4	.040	.0139	.031	.0135	.025	.0102	0.94
5	.017	.0068	.011	.0050	.009	.0037	0.98
6	.018	.0078	.018	.0078	.019	.0085	0.96
7	.017	.0068	.014	.0061	.011	.0039	0.98
8	.012	.0051	.020	.0096	.012	.0050	0.97
9	.010	.0032	.009	.0037	.008	.0030	0.98
10	.008	.0030	.005	.0024	.010	.0049	0.98
11	.000	.0000	.000	.0000	.000	.0000	1.00
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Table 5g: Frequency and variance estimates, calculated for the t allele simulation.

t-allele	NUMBER OF DEMES	TRANSMISSION RATIO	MIGRATION RATE	PROPORTION OF FIXED DEMES
	20	0.90	0.05	

GENERATION	3		10		20		
CYCLE	$\bar{q}$	σ^2	$\bar{q}$	σ^2	$\bar{q}$	σ^2	
1	.393	.0254	.322	.0406	.274	.0517	0.38
2	.304	.0429	.256	.0530	.201	.0519	0.54
3	.285	.0497	.215	.0469	.165	.0495	0.63
4	.193	.0518	.173	.0501	.110	.0364	0.73
5	.136	.0410	.127	.0436	.081	.0279	0.79
6	.084	.0311	.072	.0283	.045	.0178	0.89
7	.049	.0189	.037	.0153	.025	.0118	0.95
8	.020	.0080	.013	.0054	.003	.0006	0.99
9	.004	.0013	.005	.0024	.000	.0000	1.00
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Table 5h: Frequency and variance estimates, calculated for the t allele simulation.

t-allele	NUMBER OF DEMES	TRANSMISSION RATIO	MIGRATION RATE	PROPORTION OF FIXED DEMES
	20	0.90	0.10	

GENERATION	3		10		
CYCLE	$\bar{q}$	σ^2	$\bar{q}$	σ^2	
1	.350	.0334	.280	.0474	0.34
2	.295	.0485	.235	.0480	0.41
3	.259	.0516	.200	.0534	0.54
4	.220	.0518	.200	.0534	0.54
5	.230	.0477	.177	.0464	0.57
6	.192	.0505	.167	.0500	0.62
7	.209	.0520	.171	.0492	0.59
8	.254	.0536	.203	.0548	0.54
9	.233	.0497	.226	.0522	0.49
10	.204	.0440	.159	.0467	0.63
11	.173	.0517	.128	.0424	0.61
12	.188	.0494	.143	.0446	0.66
13	.165	.0479	.118	.0406	0.73
14	.151	.0469	.107	.0357	0.73
15	.117	.0343	.110	.0397	0.76
16	.139	.0439	.122	.0398	0.71
17	.166	.0468	.153	.0465	0.65
18	.177	.0494	.146	.0442	0.66
19	.180	.0493	.151	.0451	0.65
20	.174	.0486	.135	.0444	0.70
21	.218	.0525	.183	.0494	0.56
22	.248	.0523	.191	.0496	0.55
23	.234	.0512	.190	.0503	0.55
24	.222	.0493	.190	.0503	0.56
25	.227	.0506	.191	.0522	0.57
26	.223	.0540	.167	.0445	0.58
27	.224	.0550	.166	.0489	0.61
28	.167	.0477	.141	.0428	0.65
29	.186	.0482	.160	.0483	0.63
30	.212	.0517	.165	.0485	0.63
31	.160	.0433	.142	.0448	0.67
32	.169	.0481	.128	.0409	0.69
33	.146	.0452	.122	.0405	0.71
34	.153	.0454	.129	.0444	0.72
35	.149	.0426	.118	.0364	0.70
36	.170	.0503	.123	.0381	0.69
37	.169	.0487	.143	.0455	0.68
38	.158	.0445	.128	.0419	0.70
39	.144	.0413	.126	.0422	0.71
40	.147	.0460	.121	.0399	0.72

Table 5i: Frequency and variance estimates, calculated for the t allele simulation.

t-allele	NUMBER OF DEMES	TRANSMISSION RATIO	MIGRATION RATE	PROPORTION OF FIXED DEMES
	5	0.95	0.01	

GENERATION	3		10		20		
CYCLE	$\bar{q}$	σ^2	$\bar{q}$	σ^2	$\bar{q}$	σ^2	
1	.395	.0372	.350	.0487	.230	.0536	0.36
2	.115	.0398	.130	.0441	.115	.0422	0.76
3	.069	.0222	.090	.0329	.090	.0344	0.80
4	.070	.0276	.055	.0224	.055	.0224	0.88
5	.005	.0005	.000	.0000	.000	.0000	1.00
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Table 5j: Frequency and variance estimates, calculated for the t allele simulation.

t-allele	NUMBER OF DEMES	TRANSMISSION RATIO	MIGRATION RATE	PROPORTION OF FIXED DEMES
	5	0.95	0.05	

GENERATION	3		10		20		
CYCLE	$\bar{q}$	σ^2	$\bar{q}$	σ^2	$\bar{q}$	σ^2	
1	.374	.0377	.305	.0550	.279	.0515	0.36
2	.360	.0441	.344	.0478	.299	.0499	0.32
3	.380	.0406	.339	.0444	.274	.0475	0.32
4	.304	.0478	.269	.0506	.235	.0603	0.52
5	.279	.0541	.199	.0552	.159	.0465	0.64
6	.245	.0580	.194	.0511	.189	.0512	0.52
7	.215	.0569	.200	.0562	.195	.0575	0.60
8	.249	.0523	.254	.0542	.220	.0616	0.56
9	.215	.0593	.210	.0570	.195	.0575	0.60
10	.219	.0538	.214	.0529	.204	.0508	0.52
11	.230	.0532	.200	.0600	.180	.0576	0.64
12	.194	.0499	.210	.0570	.174	.0435	0.56
13	.225	.0573	.190	.0550	.175	.0549	0.64
14	.210	.0570	.180	.0526	.109	.0350	0.72
15	.110	.0389	.095	.0364	.060	.0264	0.88
16	.055	.0224	.060	.0264	.045	.0185	0.88
17	.055	.0224	.060	.0264	.040	.0184	0.92
18	.065	.0237	.050	.0184	.020	.0096	0.96
19	.030	.0116	.035	.0142	.040	.0184	0.92
20	.050	.0200	.055	.0224	.040	.0184	0.92
21	.095	.0364	.065	.0237	.070	.0261	0.84
22	.100	.0400	.090	.0329	.080	.0336	0.84
23	.070	.0263	.055	.0224	.055	.0224	0.88
24	.055	.0224	.060	.0264	.025	.0073	0.92
25	.055	.0224	.060	.0264	.045	.0185	0.88
26	.000	.0000	.000	.0000	.000	.0000	1.00
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Table 5k: Frequency and variance estimates, calculated for the t allele simulation.

t-allele	NUMBER OF DEMES	TRANSMISSION RATIO	MIGRATION RATE	PROPORTION OF FIXED DEMES
	5	0.95	0.10	

GENERATION	3		10		
CYCLE	$\bar{q}$	σ^2	$\bar{q}$	σ^2	
1	.424	.0263	.374	.0413	0.20
2	.439	.0153	.445	.0151	0.04
3	.414	.0211	.434	.0190	0.08
4	.444	.0117	.419	.0261	0.12
5	.464	.0107	.460	.0122	0.04
6	.424	.0239	.395	.0396	0.20
7	.394	.0333	.379	.0381	0.20
8	.389	.0294	.364	.0373	0.20
9	.374	.0377	.309	.0474	0.32
10	.370	.0443	.320	.0513	0.32
11	.420	.0336	.344	.0454	0.24
12	.389	.0335	.344	.0415	0.24
13	.434	.0228	.399	.0263	0.12
14	.448	.0381	.399	.0325	0.16
15	.438	.0116	.394	.0333	0.16
16	.428	.0153	.424	.0201	0.08
17	.408	.0197	.329	.0449	0.24
18	.354	.0459	.334	.0408	0.24
19	.384	.0350	.374	.0413	0.20
20	.374	.0375	.330	.0287	0.32
21	.340	.0494	.315	.0563	0.36
22	.300	.0512	.304	.0537	0.36
23	.400	.0363	.324	.0487	0.28
24	.369	.0344	.354	.0459	0.24
25	.364	.0349	.380	.0393	0.20
26	.414	.0272	.324	.0511	0.32
27	.329	.0486	.290	.0520	0.36
28	.319	.0476	.304	.0513	0.32
29	.374	.0413	.334	.0421	0.24
30	.329	.0460	.310	.0550	0.36
31	.274	.0536	.260	.0560	0.44
32	.335	.0533	.304	.0537	0.36
33	.300	.0536	.264	.0541	0.40
34	.235	.0603	.230	.0582	0.52
35	.249	.0523	.255	.0605	0.48
36	.279	.0502	.274	.0562	0.40
37	.289	.0494	.220	.0528	0.48
38	.294	.0548	.290	.0570	0.40
39	.294	.0498	.284	.0555	0.40
40	.364	.0436	.330	.0523	0.32

Table 51: Frequency and variance estimates, calculated for the t allele simulation.

t-allele	NUMBER OF DEMES	TRANSMISSION RATIO	MIGRATION RATE	PROPORTION OF FIXED DEMES
	10	0.95	0.01	

GENERATION	3		10		20		
CYCLE	$\bar{q}$	σ^2	$\bar{q}$	σ^2	$\bar{q}$	σ^2	
1	.394	.0347	.369	.0394	.295	.0567	0.36
2	.200	.0561	.205	.0592	.160	.0525	0.64
3	.070	.0269	.067	.0249	.047	.0205	0.90
4	.047	.0205	.032	.0129	.030	.0141	0.94
5	.015	.0060	.017	.0074	.017	.0074	0.96
6	.000	.0000	.000	.0000	.000	.0000	1.00
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Table 5m: Frequency and variance estimates, calculated for the t allele simulation.

t-allele	NUMBER OF DEMES	TRANSMISSION RATIO	MIGRATION RATE	PROPORTION OF FIXED DEMES
	10	0.95	0.04	

GENERATION	3		10		20		
CYCLE	$\bar{q}$	σ^2	$\bar{q}$	σ^2	$\bar{q}$	σ^2	
1	.406	.0238	.387	.0333	.301	.0445	0.26
2	.362	.0389	.332	.0504	.287	.0545	0.38
3	.342	.0468	.317	.0513	.269	.0564	0.42
4	.284	.0525	.254	.0555	.230	.0582	0.50
5	.214	.0518	.215	.0574	.197	.0556	0.58
6	.254	.0530	.245	.0574	.230	.0589	0.52
7	.257	.0577	.257	.0615	.215	.0593	0.56
8	.239	.0517	.219	.0545	.195	.0550	0.58
9	.232	.0524	.204	.0534	.170	.0529	0.64
10	.235	.0585	.220	.0577	.192	.0524	0.58
11	.284	.0524	.229	.0532	.229	.0564	0.50
12	.257	.0583	.242	.0564	.214	.0536	0.52
13	.232	.0524	.212	.0557	.177	.0544	0.62
14	.244	.0556	.242	.0571	.224	.0561	0.52
15	.269	.0520	.277	.0545	.220	.0572	0.52
16	.269	.0532	.259	.0567	.250	.0588	0.46
17	.232	.0529	.182	.0525	.180	.0537	0.62
18	.235	.0585	.164	.0482	.147	.0510	0.70
19	.157	.0499	.157	.0530	.152	.0500	0.68
20	.237	.0563	.179	.0518	.165	.0521	0.64
21	.159	.0487	.172	.0556	.152	.0500	0.68
22	.179	.0518	.172	.0543	.160	.0505	0.66
23	.195	.0556	.190	.0538	.187	.0544	0.60
24	.182	.0550	.175	.0524	.134	.0422	0.68
25	.170	.0485	.172	.0518	.150	.0486	0.68
26	.112	.0394	.087	.0332	.057	.0205	0.84
27	.062	.0264	.055	.0225	.047	.0193	0.88
28	.057	.0225	.057	.0244	.035	.0143	0.92
29	.037	.0144	.047	.0205	.047	.0205	0.90
30	.025	.0106	.030	.0141	.030	.0141	0.94
31	.010	.0049	.010	.0049	.010	.0049	0.98
32	.017	.0074	.020	.0096	.020	.0096	0.96
33	.015	.0060	.020	.0096	.012	.0038	0.96
34	.000	.0000	.000	.0000	.000	.0000	1.00
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Table 5 n: Frequency and variance estimates, calculated for the t allele simulation.

t-allele	NUMBER OF DEMES	TRANSMISSION RATIO	MIGRATION RATE	PROPORTION OF FIXED DEMES
	10	0.95	0.05	

GENERATION	3		10		20		
CYCLE	$\bar{q}$	σ^2	$\bar{q}$	σ^2	$\bar{q}$	σ^2	
1	.372	.0366	.372	.0410	.324	.0486	0.30
2	.369	.0407	.314	.0494	.264	.0528	0.40
3	.352	.0473	.337	.0451	.277	.0569	0.42
4	.322	.0482	.297	.0530	.249	.0539	0.44
5	.232	.0531	.242	.0556	.229	.0563	0.50
6	.325	.0518	.249	.0512	.267	.0593	0.44
7	.312	.0545	.277	.0506	.250	.0593	0.48
8	.314	.0476	.277	.0531	.250	.0586	0.48
9	.234	.0522	.197	.0536	.182	.0531	0.60
10	.262	.0531	.275	.0606	.220	.0559	0.52
11	.324	.0549	.287	.0544	.250	.0586	0.48
12	.337	.0470	.317	.0520	.277	.0557	0.40
13	354	.0420	.312	.0538	.272	.0559	0.42
14	.292	.0504	.309	.0512	.269	.0539	0.40
15	.274	.0542	.262	.0582	.250	.0606	0.48
16	.257	.0515	.237	.0582	.190	.0557	0.60
17	.225	.0580	.199	.0529	.172	.0503	0.62
18	.187	.0545	.192	.0562	.157	.0490	0.66
19	.177	.0544	.140	.0440	.135	.0473	0.72
20	.152	.0462	.162	.0520	.120	.0404	0.72
21	.182	.0550	.147	.0510	.132	.0457	0.72
22	.130	.0441	.095	.0372	.087	.0318	0.82
23	.087	.0331	.090	.0369	.077	.0317	0.84
24	.115	.0410	.110	.0377	.100	.0400	0.80
25	.140	.0440	.125	.0449	.115	.0430	0.76
26	.127	.0445	.132	.0464	.117	.0420	0.74
27	.203	.0413	.110	.0429	.095	.0364	0.80
28	.162	.0514	.150	.0485	.127	.0440	0.72
29	.162	.0519	.160	.0504	.155	.0490	0.66
30	.150	.0485	.132	.0464	.125	.0449	0.74
31	.150	.0505	.152	.0500	.142	.0447	0.68
32	.228	.0508	.152	.0475	.145	.0475	0.68
33	.155	.0522	.150	.0473	.125	.0449	0.74
34	.165	.0533	.130	.0436	.125	.0449	0.74
35	.167	.0528	.132	.0464	.132	.0464	0.72
36	.140	.0484	.120	.0436	.107	.0412	0.78
37	.170	.0521	.154	.0475	.137	.0488	0.72
38	.165	.0508	.157	.0490	.140	.0439	0.68
39	.225	.0504	.140	.0427	.132	.0432	0.70
40	.154	.0475	.160	.0504	.150	.0485	0.68

Table 5o: Frequency and variance estimates, calculated for the t allele simulation.

t-allele	NUMBER OF DEMES	TRANSMISSION RATIO	MIGRATION RATE	PROPORTION OF FIXED DEMES
	10	0.95	0.10	

GENERATION	3		10		
CYCLE	$\bar{q}$	σ^2	$\bar{q}$	σ^2	
1	.396	.0268	.369	.0363	0.18
2	.396	.0389	.357	.0462	0.26
3	.382	.0360	.364	.0386	0.20
4	.414	.0297	.369	.0350	0.18
5	.386	.0309	.344	.0467	0.24
6	.402	.0315	.379	.0381	0.20
7	.384	.0331	.350	.0450	0.24
8	.309	.0459	.314	.0494	0.32
9	.327	.0486	.285	.0537	0.38
10	.242	.0514	.285	.0594	0.42
11	.312	.0546	.274	.0549	0.40
12	.287	.0515	.280	.0572	0.40
13	.287	.0570	.275	.0568	0.42
14	.299	.0499	.280	.0541	0.38
15	.327	.0481	.312	.0501	0.32
16	.307	.0526	.297	.0543	0.36
17	.332	.0472	.302	.0550	0.36
18	.331	.0459	.297	.0499	0.32
19	.334	.0446	.307	.0513	0.34
20	.315	.0520	.315	.0564	0.36
21	.317	.0508	.282	.0536	0.38
22	.299	.0513	.297	.0555	0.38
23	.324	.0455	.289	.0534	0.36
24	.339	.0444	.282	.0542	0.38
25	.367	.0402	.339	.0475	0.28
26	.324	.0437	.292	.0566	0.38
27	.306	.0476	.317	.0520	0.32
28	.335	.0490	.319	.0500	0.32
29	.304	.0519	.279	.0534	0.38
30	.254	.0499	.239	.0554	0.48
31	.304	.0481	.300	.0562	0.38
32	.327	.0494	.304	.0500	0.34
33	.307	.0551	.250	.0562	0.46
34	.262	.0564	.262	.0570	0.44
35	.257	.0564	.222	.0550	0.52
36	.267	.0574	.227	.0547	0.50
37	.279	.0534	.252	.0577	0.46
38	.242	.0584	.217	.0534	0.52
39	.252	.0547	.237	.0582	0.50
40	.291	.0491	.242	.0552	0.46

Table 5p: Frequency and variance estimates, calculated for the t allele simulation.

t-allele	NUMBER OF DEMES	TRANSMISSION RATIO	MIGRATION RATE	PROPORTION OF FIXED DEMES
	20	0.95	0.01	

GENERATION	3		10		20		
CYCLE	$\bar{q}$	σ^2	$\bar{q}$	σ^2	$\bar{q}$	σ^2	
1	.427	.0190	.396	.0323	.339	.0425	0.24
2	.163	.0511	.144	.0475	.127	.0427	0.71
3	.031	.0132	.032	.0142	.028	.0124	0.94
4	.005	.0025	.005	.0025	.005	.0025	0.99
5	.000	.0000	.000	.0000	.000	.0000	1.00
6							
7							
8							
9							
10							
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39							
40							

Table 5q: Frequency and variance estimates, calculated for the t allele simulation.

t-allele	NUMBER OF DEMES	TRANSMISSION RATIO	MIGRATION RATE	PROPORTION OF FIXED DEMES
	20	0.95	0.03	

GENERATION	3		10		20		
CYCLE	$\bar{q}$	σ^2	$\bar{q}$	σ^2	$\bar{q}$	σ^2	
1	.414	.0270	.340	.0406	.304	.0532	0.35
2	.293	.0479	.274	.0540	.251	.0556	0.46
3	.289	.0499	.280	.0565	.247	.0564	0.47
4	.309	.0479	.286	.0550	.238	.0555	0.48
5	.239	.0551	.229	.0584	.168	.0509	0.62
6	.182	.0516	.153	.0489	.135	.0467	0.71
7	.167	.0494	.167	.0531	.153	.0489	0.66
8	.211	.0561	.181	.0528	.157	.0485	0.65
9	.182	.0494	.143	.0458	.134	.0456	0.71
10	.177	.0472	.134	.0447	.114	.0425	0.76
11	.082	.0315	.076	.0292	.070	.0212	0.84
12	.086	.0332	.066	.0272	.054	.0235	0.89
13	.061	.0248	.069	.0291	.057	.0244	0.88
14	.059	.0238	.059	.0254	.049	.0199	0.89
15	.072	.0275	.072	.0287	.067	.0282	0.86
16	.067	.0269	.066	.0276	.046	.0195	0.90
17	.066	.0272	.056	.0235	.055	.0245	0.89
18	.064	.0273	.049	.0209	.043	.0188	0.91
19	.030	.0131	.029	.0130	.022	.0097	0.95
20	.039	.0164	.044	.0195	.034	.0152	0.93
21	.067	.0266	.071	.0291	.057	.0244	0.88
22	.052	.0225	.044	.0185	.040	.0164	0.91
23	.055	.0235	.050	.0213	.047	.0205	0.90
24	.030	.0125	.034	.0152	.034	.0152	0.93
25	.051	.0219	.047	.0192	.037	.0163	0.92
26	.019	.0066	.029	.0130	.030	.0141	0.94
27	.034	.0152	.034	.0152	.028	.0124	0.94
28	.030	.0125	.035	.0163	.030	.0141	0.94
29	.055	.0219	.059	.0244	.055	.0225	0.88
30	.055	.0229	.049	.0215	.045	.0204	0.91
31	.047	.0205	.052	.0225	.050	.0225	0.90
32	.051	.0215	.044	.0189	.042	.0184	0.91
33	.062	.0254	.049	.0195	.039	.0164	0.91
34	.042	.0165	.035	.0163	.039	.0164	0.93
35	.024	.0088	.019	.0085	.019	.0085	0.96
36	.024	.0108	.019	.0085	.014	.0062	0.97
37	.015	.0073	.014	.0062	.010	.0033	0.97
38	.010	.0049	.010	.0049	.005	.0025	0.99
39	.015	.0073	.010	.0049	.010	.0049	0.98
40	.009	.0038	.000	.0000	.000	.0000	1.00

Table 5r: Frequency and variance estimates, calculated for the t allele simulation.

t-allele	NUMBER OF DEMES	TRANSMISSION RATIO	MIGRATION RATE	PROPORTION OF FIXED DEMES
	20	0.95	0.05	

GENERATION	3		10		20		
CYCLE	$\bar{q}$	σ^2	$\bar{q}$	σ^2	$\bar{q}$	σ^2	
1	.384	.0344	.340	.0466	.307	.0545	0.35
2	.324	.0468	.287	.0551	.246	.0576	0.47
3	.282	.0539	.248	.0541	.223	.0546	0.51
4	.291	.0566	.263	.0539	.253	.0566	0.46
5	.292	.0522	.292	.0534	.276	.0572	0.42
6	.324	.0485	.292	.0541	.256	.0566	0.45
7	.262	.0532	.259	.0566	.248	.0569	0.47
8	.292	.0535	.262	.0538	.237	.0557	0.47
9	.253	.0522	.268	.0548	.222	.0583	0.52
10	.254	.0549	.242	.0555	.228	.0580	0.52
11	.282	.0536	.237	.0543	.187	.0542	0.59
12	.217	.0548	.209	.0584	.166	.0483	0.62
13	.185	.0531	.177	.0545	.132	.0455	0.71
14	.169	.0488	.163	.0507	.155	.0506	0.67
15	.203	.0539	.186	.0538	.165	.0518	0.64
16	.181	.0519	.162	.0562	.147	.0491	0.68
17	.177	.0483	.182	.0528	.161	.0492	0.65
18	.226	.0558	.216	.0554	.197	.0547	0.56
19	.223	.0548	.228	.0571	.190	.0541	0.59
20	.225	.0569	.209	.0539	.187	.0564	0.61
21	.197	.0556	.188	.0541	.170	.0525	0.64
22	.222	.0564	.190	.0554	.171	.0536	0.64
23	.195	.0544	.181	.0493	.182	.0560	0.62
24	.217	.0560	.194	.0573	.161	.0532	0.67
25	.208	.0558	.176	.0492	.175	.0520	0.62
26	.221	.0546	.216	.0593	.199	.0568	0.58
27	.216	.0555	.190	.0544	.157	.0508	0.65
28	.229	.0587	.214	.0555	.179	.0505	0.60
29	.226	.0564	.221	.0542	.197	.0534	0.56
30	.212	.0551	.188	.0548	.165	.0508	0.64
31	.158	.0501	.154	.0509	.132	.0477	0.73
32	.199	.0530	.194	.0530	.164	.0508	0.64
33	.197	.0527	.183	.0541	.163	.0497	0.64
34	.226	.0550	.226	.0576	.186	.0560	0.61
35	.240	.0589	.200	.0556	.175	.0517	0.62
36	.180	.0503	.177	.0521	.147	.0494	0.69
37	.187	.0526	.179	.0537	.167	.0515	0.64
38	.189	.0532	.173	.0526	.142	.0484	0.70
39	.178	.0515	.165	.0524	.145	.0476	0.68
40	.211	.0551	.182	.0551	.170	.0509	0.63

Table 5s: Frequency and variance estimates, calculated for the t allele simulation.

t-allele	NUMBER OF DEMES	TRANSMISSION RATIO	MIGRATION RATE	PROPORTION OF FIXED DEMES
	20	0.95	0.10	

GENERATION	3		10		
CYCLE	$\bar{q}$	σ^2	$\bar{q}$	σ^2	
1	.399	.0298	.390	.0364	0.18
2	.402	.0309	.378	.0377	0.19
3	.425	.0236	.391	.0353	0.17
4	.411	.0280	.405	.0332	0.15
5	.425	.0239	.392	.0332	0.16
6	.411	.0308	.356	.0454	0.25
7	.412	.0268	.343	.0432	0.25
8	.401	.0330	.353	.0450	0.25
9	.391	.0337	.352	.0405	0.21
10	.349	.0463	.344	.0466	0.27
11	.400	.0481	.359	.0405	0.20
12	.405	.0256	.399	.0313	0.15
13	.388	.0308	.370	.0386	0.20
14	.402	.0286	.381	.0365	0.17
15	.393	.0349	.367	.0396	0.21
16	.414	.0242	.384	.0337	0.17
17	.413	.0241	.391	.0380	0.19
18	.409	.0258	.368	.0383	0.19
19	.402	.0309	.362	.0449	0.24
20	.366	.0395	.347	.0464	0.26
21	.405	.0289	.380	.0397	0.20
22	.405	.0274	.359	.0404	0.21
23	.394	.0316	.345	.0428	0.24
24	.394	.0325	.378	.0383	0.19
25	.408	.0288	.337	.0477	0.27
26	.381	.0386	.349	.0454	0.24
27	.402	.0299	.392	.0366	0.18
28	.412	.0249	.408	.0304	0.13
29	.412	.0255	.384	.0331	0.16
30	.436	.0175	.386	.0357	0.17
31	.437	.0197	.422	.0253	0.11
32	.421	.0183	.403	.0316	0.14
33	.432	.0206	.359	.0414	0.22
34	.388	.0348	.352	.0452	0.24
35	.385	.0384	.324	.0487	0.30
36	.380	.0349	.320	.0510	0.32
37	.389	.0306	.366	.0410	0.21
38	.366	.0369	.330	.0435	0.26
39	.381	.0368	.341	.0488	0.27
40	.409	.0287	.367	.0441	0.23

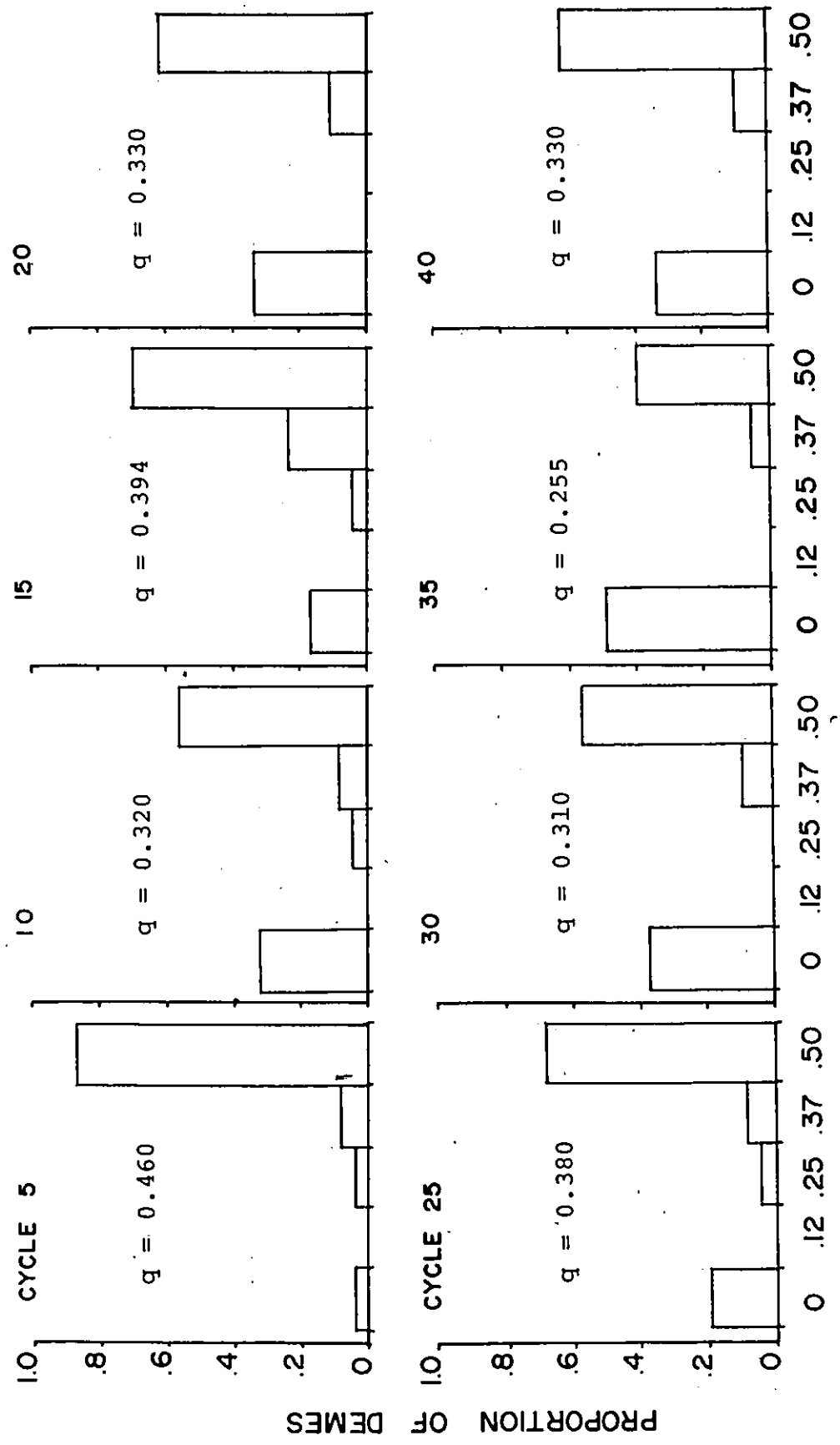


Figure 2a: Frequency distributions of the t allele when m = 0.95, migration rate = 10 percent, and population size = 5 demes.

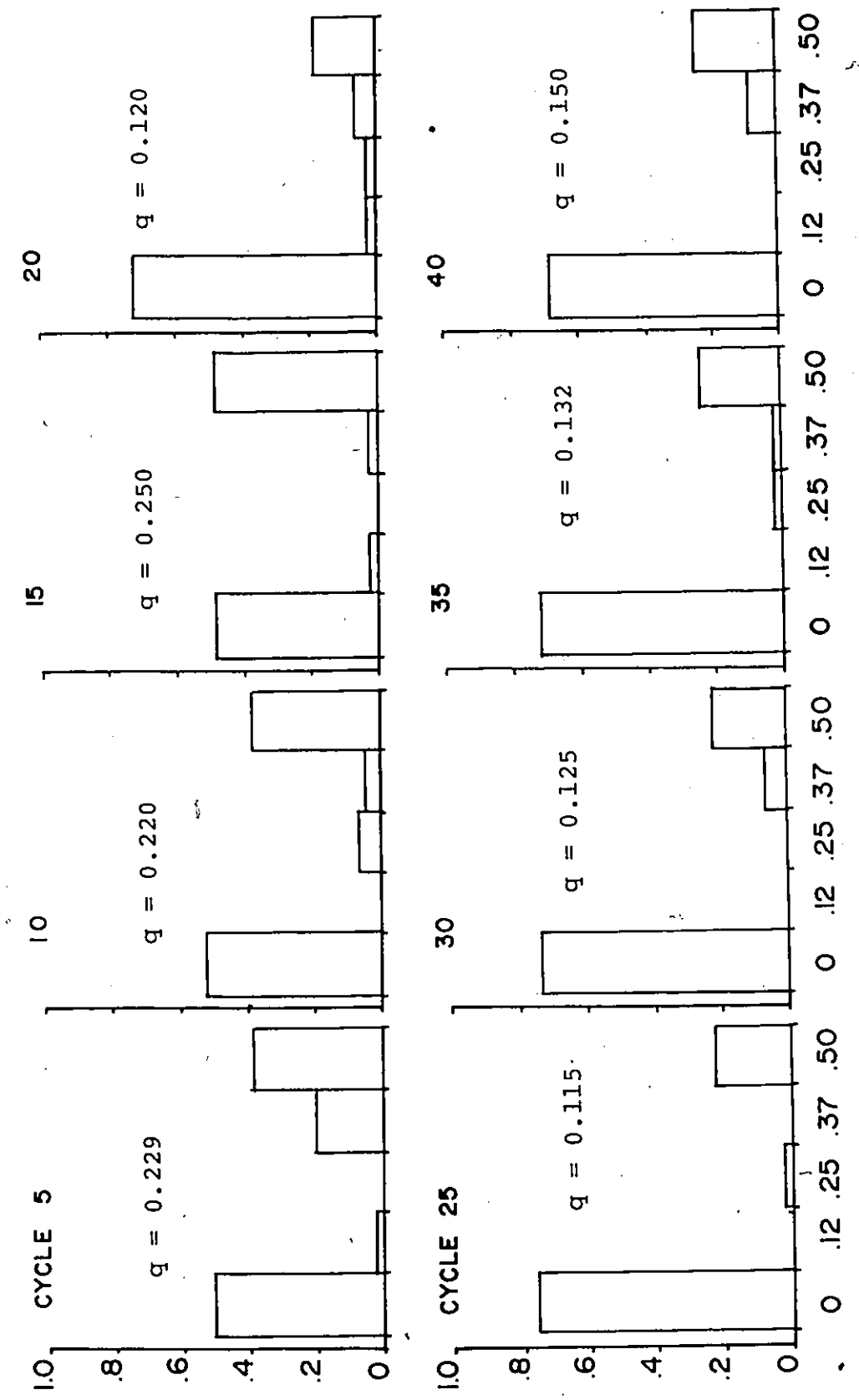


Figure 2b: Frequency distributions of the t allele when m = 0.95, migration rate = 5 percent, and population size = 10 demes.

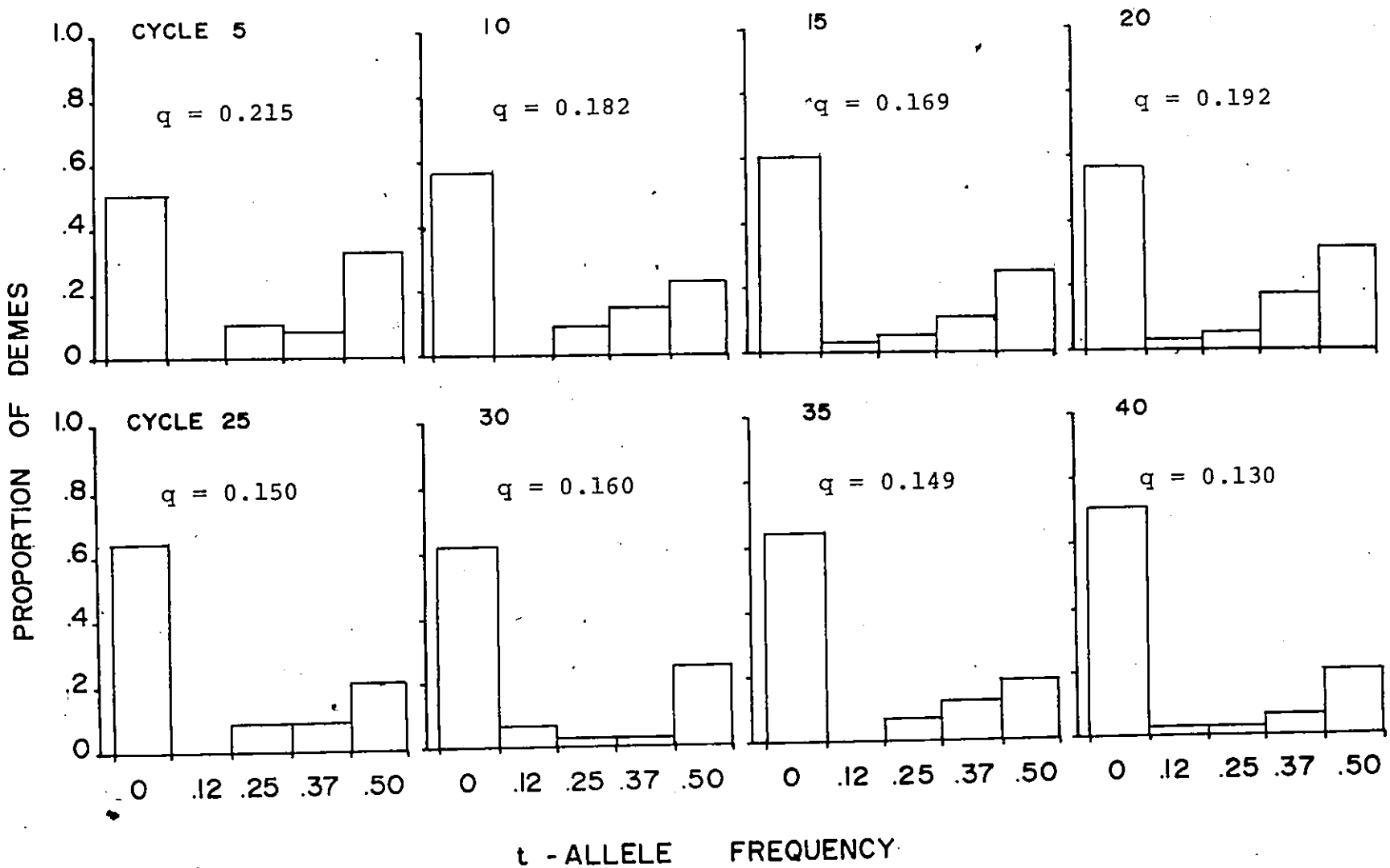


Figure 2c: Frequency distributions of the t allele when m = 0.90, migration rate = 10 percent, and population size = 10 demes.

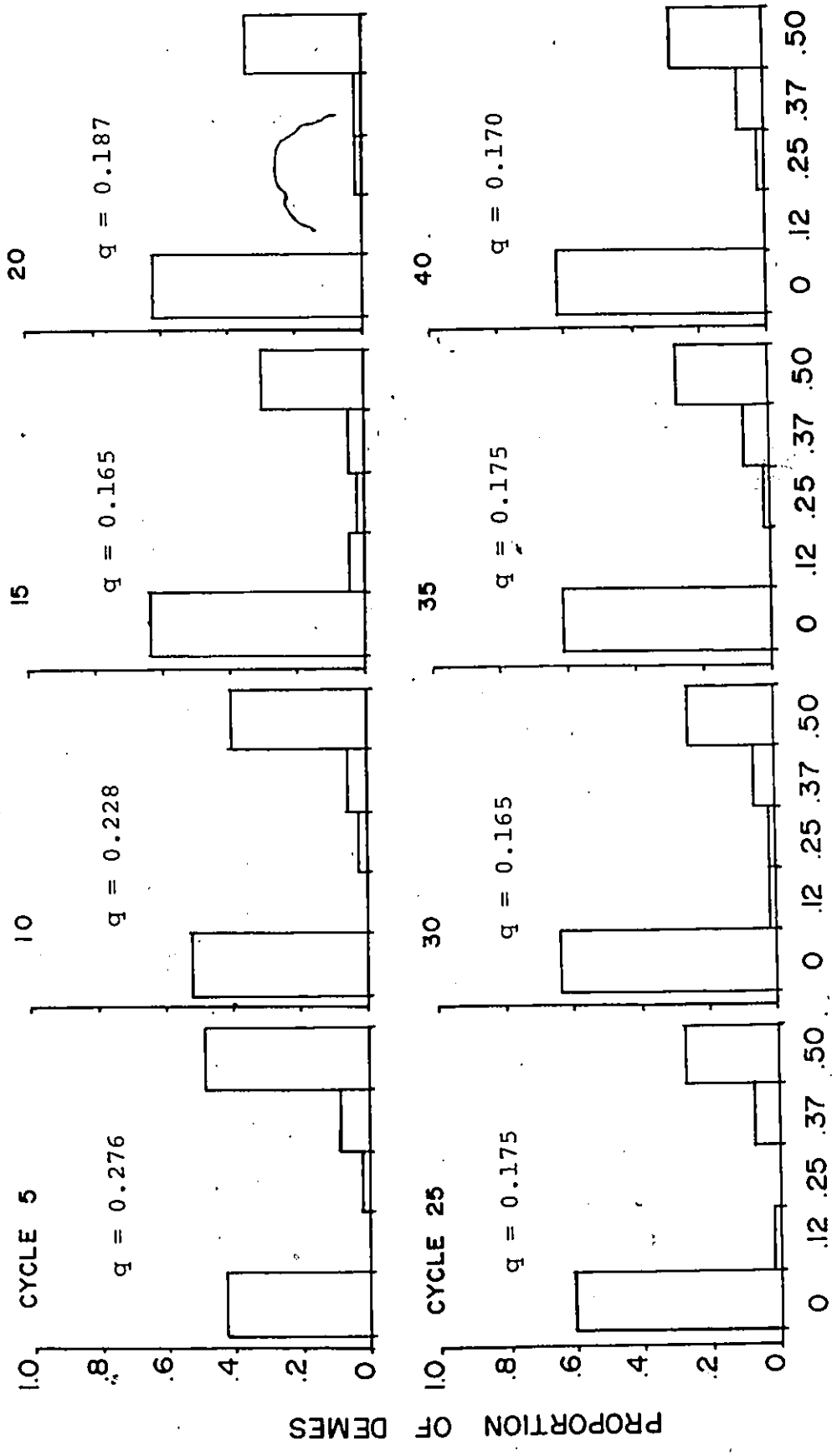


Figure 2d: Frequency distributions of the t allele when m = 0.95, migration rate = 5 percent, and population size = 20 demes.

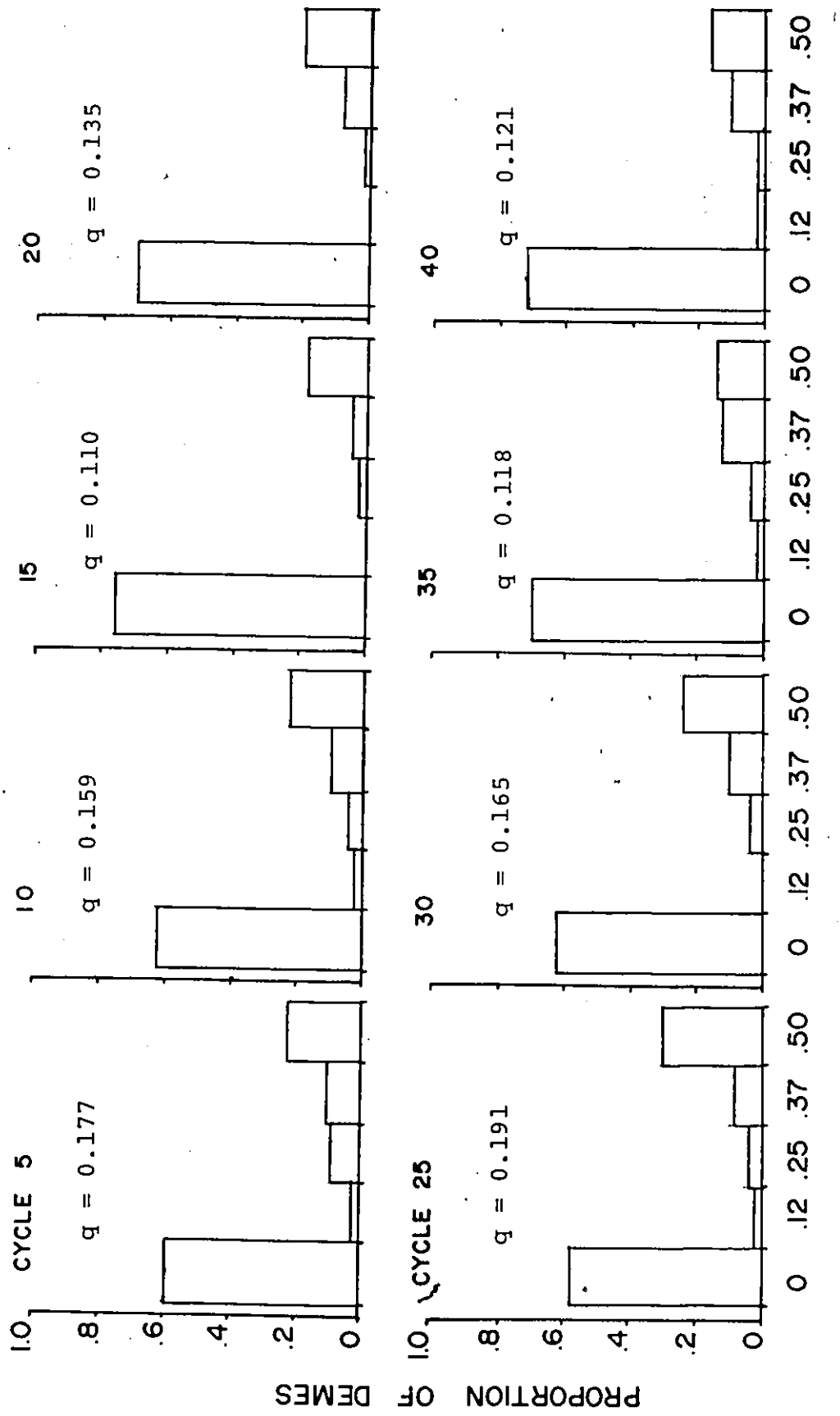
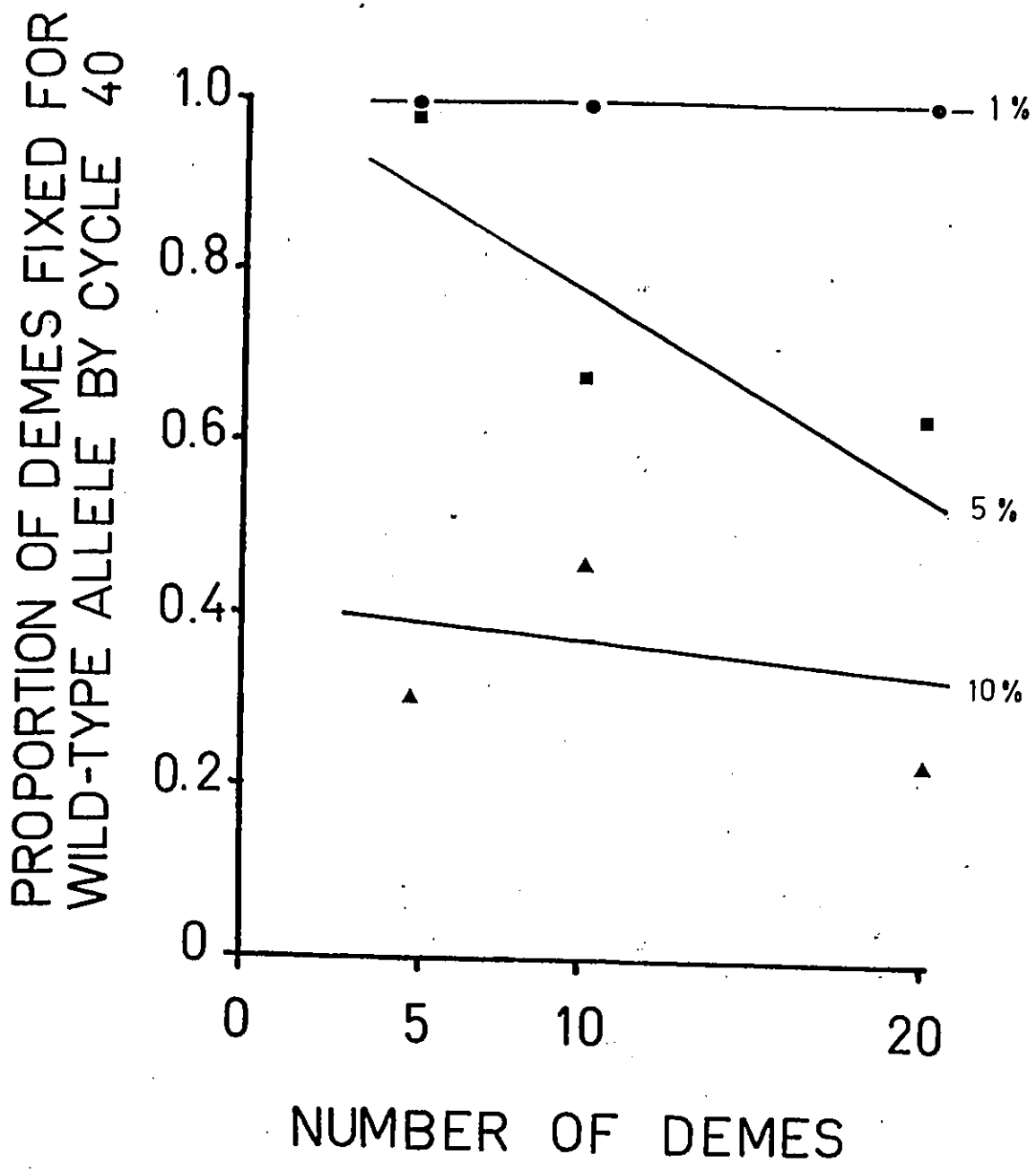


Figure 2e: Frequency distributions of the t allele when m = 0.90, migration rate = 10 percent, and population size = 20 demes.

Figure 3: Proportion of demes fixed for the wild-type allele by cycle 40 of the t allele simulation, as a function of number of demes and migration rate; male transmission ratio is 0.95.


PROPORTION OF DEMES FIXED FOR WILD-TYPE ALLELE BY CYCLE 40
1.0
0.8
0.6
0.4
0.2
0
1%
5%
10%
0
5
10
20
NUMBER OF DEMES

male transmission ratio was 0.95. Lowering the ratio to 0.90 causes the proportion of demes fixed to increase or the family of curves to be raised up. Then unless the interdemic migration rate is 10 percent, all demes become fixed for the wild-type allele by cycle 40.

To facilitate comparison between empirical and simulated results, the amount of heterozygosity based on the computer simulation was calculated when m was 0.95 migration rate was 5 percent and population size was 10 demes (see Table 6). The reasons for these particular values of m, migration rate and population size are discussed next.

Table 6: The amount of heterozygosity, based on the computer simulation of the t allele when m = 0.95, migration rate = 5 percent, and population size = 10 demes.

CYCLE	AVERAGE H FOR ALL RUNS	AVERAGE H PER RUN				
	R_t	R_1	R_2	R_3	R_4	R_5
1	0.73	0.69	0.57	0.75	0.78	0.80
5	0.48	0.48	0.10	0.38	0.56	0.87
10	0.50	0.79	0.38	0.19	0.41	0.73
15	0.52	0.78	0.86	0.00	0.65	0.31
20	0.28	0.48	0.20	0.00	0.31	0.44
25	0.27	0.62	0.00	0.00	0.00	0.71
30	0.24	0.90	0.00	0.00	0.00	0.32
35	0.29	0.70	0.00	0.00	0.00	0.78
40	0.31	0.74	0.00	0.00	0.00	0.82
OVERALL AVERAGE	0.40	0.69	0.23	0.15	0.30	0.64

D Criteria for stability

A simulation was considered stable if the values of the t allele frequency and level of heterozygosity were the same order of magnitude as empirical estimates and did not change significantly over the last 15 cycles. Clearly about 5 percent migration is required to maintain the t allele in the metapopulation where 10 and 20 demes are involved. However, for a 5 deme system at least 10 percent migration was necessary to maintain the t allele and this then resulted in a t allele frequency which approached or passed that of Bruck's deterministic model (Bruck, 1957). Therefore, a five deme population size was rejected for further use as not being sufficiently complex to buffer losses of the t-allele resulting from genetic drift.

For ten deme populations, the transmission ratio had to be 0.95 to prevent fixation for the wild-type allele. This value agrees well with empirical estimates of the transmission ratio (Dunn, 1953; 1957a; 1960).

The choices to be made then are between 5 and 10 percent migration, and 10 and 20 demes. The t-allele frequency at 10 percent migration in both 10 and 20 deme metapopulations is higher than empirical estimates (Table 1). Likewise 5 percent migration in a 20 deme system results in a t-allele frequency that is slightly higher than that observed in natural populations. As a result, the combination of variables which best described the t-allele system is a transmission ratio of 0.95, 5 percent migration and 10 demes.

E Discussion

The computer model can explain the maintenance of the polymorphism at the T locus when a transmission ratio of 0.95, a 5 percent interdemic migration rate and a population size of 10 demes are assumed. Values of frequency and heterozygosity agree well with empirical values from natural populations (Tables 1 and 3). Furthermore, the frequency variance values are of the same order of magnitude as in natural populations (Table 3). Like the natural populations (Table 2) many demes of the model are fixed for the wild-type allele. Levels of heterozygosity at the T locus vary from 16 to 31 percent in natural populations and from 15 to 69 percent in the simulated populations. The wider range of heterozygosity in the simulation may be attributed to the contribution to drift of the small and constant effective population size. Changes in the input parameters could of course also reduce the upper limit of heterozygosity, but this would likewise affect the frequency and variance values.

V APPLICATION OF THE MODEL TO THE Hbb LOCUS

The basic program which was developed to explain allelic frequencies at the T locus was applied to data involving the Hbb locus. Since the T locus is no longer being considered, transmission ratios both sexes are normal (0.50). The production of male and female offspring from a parental generation proceeded in the same manner as in the t allele model, with one male and three females being produced each generation in each deme. The migration rate was 5 percent in most runs made, and the pooling procedure used to simulate migration as in the t allele model. At the Hbb locus there are two common alleles. The fitness of these alleles and of the genotypes is not known. The specific goal of the application of the model is to see if the model developed for the t allele can explain the frequency, frequency variance and heterozygosity observed at the Hbb locus in natural populations, and if not what types of changes are required. The simplest explanation is that the observed frequencies and frequency variances (see Table 3) are a result of gene flow between populations, and no selection is involved. More complex explanations could involve selection of a specific magnitude against the homozygotes. A summary of the input parameters used in this simulation is given in Table 7.

If the fitness of all three genotypes is 1.0, then the

Table 7: Input parameter values for the non-lethal allele simulation.[a]

NUMBER OF DEMES	PERCENT MIGRATION	FITNESS		
		W_1	W_2	W_3
10	5	1.000	1.000	1.000
10	10	1.000	1.000	1.000
10	5	0.900	1.000	0.900
10	5	0.800	1.000	0.800
10	5	0.700	1.000	0.700
10	5	0.500	1.000	0.500
10	5	0.925	1.000	0.825
10	5	0.850	1.000	0.650
10	5	0.700	1.000	0.300
20	5	0.700	1.000	0.300
10	5	0.700	1.000	0.600
10	5	0.700	1.000	0.550
10	5	0.700	1.000	0.500
10	5	0.400	1.000	0.200

a $N_e = \frac{4N♀N♂}{N♀+N♂} = 3.00$ = effective genetic size of all demes;

transmission ratios in both sexes are 0.50 .
$N♀$ = number of females, $N♂$ = number of males.

system is analogous to a neutral allele system. The results of this simulation are given in Table 8a and Figure 4a. Both alleles remain in the metapopulation, however all demes eventually became fixed for one or the other allele. Because there is no migration between populations, this type of fixation cannot change, and the metapopulation would continue stable indefinitely. To ensure that the fixation observed was not due simply to insufficient migration, the simulation was repeated using 10 percent migration. These results are given in Table 8b. Again both alleles remain in the metapopulation, but all populations fixed for one or the other allele. These results suggest, therefore, that a non-lethal polymorphism cannot be maintained by equilibrium between genetic drift and interdemic migration.

The non-lethal program was modified to introduce genotypic selection against homozygotes. Fisher (1922) first showed that, assuming a Hardy-Weinberg equilibrium and constant genotypic fitnesses, an equilibrium gene frequency of 0.50 could be achieved if the fitnesses of both homozygotes were equal and less than that of the heterozygote; any values of homozygote fitnesses will give this result as long as they are equal and less than the heterozygote fitness. The results of varying genotypic fitnesses are shown in Tables 8c, 8d, 8e and 8f, and Figure 4b. Unless both homozygote fitnesses were reduced from 1.0 to 0.7, fixation for one or the other allele still occurred in all populations. While this gives an indication of the selective force necessary to maintain a

Table 8a: Frequency and variance estimates, calculated for the non-lethal allele simulation.

NON-LETHAL ALLELE 1.00/1.00/1.00	NUMBER OF DEMES	TRANSMISSION RATIO	MIGRATION RATE	PROPORTION OF FIXED DEMES
	10	0.50	0.05	

GENERATION	3		10		20		
CYCLE	$\bar{q}$	σ^2	$\bar{q}$	σ^2	$\bar{q}$	σ^2	
1	.529	.1037	.582	.1915	.592	.2368	0.98
2	.566	.1608	.580	.2156	.565	.2420	0.98
3	.536	.1758	.527	.2219	.500	.2500	1.00
4	.507	.2074	.522	.2266	.530	.2416	0.96
5	.514	.2164	.500	.2456	.500	.2500	1.00
6	.544	.2093	.550	.2425	.542	.2461	0.98
7	.575	.2052	.577	.2300	.580	.2436	1.00
8	.574	.1883	.587	.2309	.600	.2400	1.00
9	.599	.1653	.612	.2071	.612	.2327	0.98
10	.632	.1816	.632	.2109	.662	.2215	0.98
11	.647	.1986	.635	.2213	.640	.2304	1.00
12	.615	.2096	.645	.2221	.657	.2230	0.98
13	.666	.1889	.637	.2140	.657	.2230	0.98
14	.642	.2134	.612	.2327	.620	.2356	1.00
15	.637	.2183	.607	.2338	.620	.2356	1.00
16	.630	.2181	.660	.2244	.660	.2240	1.00
17	.630	.2164	.622	.2253	.620	.2356	1.00
18	.625	.2197	.680	.2176	.620	.2356	1.00
19	.615	.2263	.635	.2280	.640	.2304	1.00
20	.650	.2115	.647	.2161	.620	.2356	1.00
21	.605	.2352	.600	.2400	.600	.2400	1.00
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Table 8b: Frequency and variance estimates, calculated for the non-lethal allele simulation.

NON-LETHAL ALLELE 1·00/1·00/1·00	NUMBER OF DEMES	TRANSMISSION RATIO	MIGRATION RATE	PROPORTION OF FIXED DEMES
	10	0.50	0.10	

GENERATION	3		10		
CYCLE	$\bar{q}$	σ^2	$\bar{q}$	σ^2	
1	.501	.1187	.520	.2172	0.82
2	.538	.1420	.564	.2165	0.86
3	.548	.1162	.557	.2212	0.84
4	.506	.1283	.457	.2071	0.80
5	.491	.1182	.481	.2044	0.72
6	.521	.1116	.672	.1695	0.74
7	.719	.0968	.640	.2005	0.84
8	.606	.1200	.625	.2045	0.84
9	.609	.1431	.610	.2250	0.92
10	.669	.2112	.660	.2064	0.92
11	.732	.1457	.750	.1750	0.94
12	.754	.1427	.725	.1724	0.86
13	.745	.1606	.755	.1712	0.94
14	.762	.1689	.760	.1824	1.00
15	.787	.1583	.790	.1609	0.98
16	.780	.1591	.790	.1609	0.98
17	.772	.1687	.775	.1706	0.98
18	.765	.1629	.770	.1721	0.98
19	.770	.1665	.777	.1708	0.98
20	.790	.1609	.780	.1716	1.00
21	.772	.1711	.780	.1716	1.00
22	.787	.1589	.785	.1650	0.98
23	.777	.1708	.792	.1598	0.98
24	.755	.1600	.760	.1824	1.00
25	.755	.1607	.767	.1700	0.96
26	.747	.1779	.720	.2016	1.00
27	.745	.1661	.732	.1913	0.98
28	.725	.1720	.737	.1840	0.96
29	.734	.1734	.707	.1892	0.92
30	.709	.1692	.690	.1958	0.92
31	.697	.1846	.700	.1975	0.94
32	.697	.1902	.700	.2100	1.00
33	.692	.1759	.697	.1959	0.92
34	.717	.1662	.737	.1814	0.94
35	.717	.1800	.720	.2016	1.00
36	.737	.1577	.767	.1738	0.98
37	.772	.1561	.780	.1623	0.96
38	.800	.1600	.800	.1600	1.00
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Table 8c: Frequency and variance estimates, calculated for the non-lethal allele simulation.

NON-LETHAL ALLELE	NUMBER OF DEMES	TRANSMISSION RATIO	MIGRATION RATE	PROPORTION OF FIXED DEMES
·900/1·00/·900	10	0.50	0.05	

GENERATION	3		10		20		
CYCLE	$\bar{q}$	σ^2	$\bar{q}$	σ^2	$\bar{q}$	σ^2	
1	.448	.1106	.460	.2096	.467	.2443	0.98
2	.537	.0887	.472	.1888	.475	.2349	0.94
3	.548	.0857	.512	.1841	.517	.2338	0.92
4	.516	.1351	.544	.1874	.592	.2143	0.86
5	.568	.1121	.635	.1874	.620	.2356	1.00
6	.593	.1260	.615	.2186	.602	.2374	0.98
7	.635	.1058	.667	.1739	.622	.2160	0.92
8	.566	.1415	.517	.2075	.515	.2410	0.96
9	.474	.1802	.452	.2149	.452	.2336	0.94
10	.442	.1793	.462	.2221	.475	.2370	0.94
11	.494	.1708	.462	.2113	.467	.2443	0.98
12	.452	.1692	.467	.2164	.472	.2421	0.96
13	.459	.1888	.515	.2341	.520	.2496	1.00
14	.539	.1954	.507	.2252	.492	.2420	0.96
15	.474	.2103	.457	.2367	.440	.2464	1.00
16	.445	.2270	.477	.2472	.460	.2484	1.00
17	.467	.2174	.442	.2333	.442	.2383	0.96
18	.420	.2318	.415	.2359	.405	.2372	0.98
19	.420	.2330	.420	.2436	.420	.2436	1.00
20	.422	.2325	.425	.2406	.420	.2436	1.00
21	.472	.2325	.497	.2477	.500	.2500	1.00
22	.482	.2212	.482	.2476	.480	.2496	1.00
23	.477	.2160	.530	.2334	.530	.2441	0.98
24	.510	.2161	.485	.2385	.480	.2496	1.00
25	.460	.2166	.482	.2387	.482	.2437	0.96
26	.482	.2145	.455	.2367	.490	.2449	0.98
27	.487	.2253	.480	.2389	.482	.2476	0.98
28	.482	.2202	.485	.2335	.475	.2456	0.98
29	.440	.2320	.432	.2370	.420	.2436	1.00
30	.447	.2288	.430	.2371	.420	.2436	1.00
31	.412	.2339	.412	.2339	.432	.2394	0.96
32	.420	.2361	.420	.2436	.420	.2436	1.00
33	.427	.2307	.417	.2373	.420	.2436	1.00
34	.410	.2351	.410	.2369	.420	.2436	1.00
35	.422	.2306	.427	.2326	.422	.2419	0.98
36	.410	.2369	.417	.2409	.420	.2436	1.00
37	.410	.2339	.402	.2384	.400	.2400	1.00
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Table 8d: Frequency and variance estimates, calculated for the non-lethal allele simulation.

NON-LETHAL ALLELE	NUMBER OF DEMES	TRANSMISSION RATIO	MIGRATION RATE	PROPORTION OF FIXED DEMES
.800/1.00/.800	10	0.50	0.05	

GENERATION	3		10		20		
CYCLE	$\bar{q}$	σ^2	$\bar{q}$	σ^2	$\bar{q}$	σ^2	
1	.548	.0916	.634	.1452	.657	.1850	0.82
2	.583	.0930	.634	.1503	.587	.2233	0.90
3	.523	.0919	.492	.1756	.505	.2244	0.86
4	.510	.0927	.512	.1788	.489	.2081	0.82
5	.411	.1017	.396	.1525	.432	.2163	0.86
6	.464	.1323	.459	.1830	.455	.2298	0.90
7	.444	.1823	.420	.2154	.425	.2406	0.98
8	.369	.1386	.394	.1893	.395	.2182	0.90
9	.440	.1397	.462	.1865	.492	.2277	0.88
10	.470	.1059	.494	.1552	.535	.2238	0.88
11	.479	.1283	.497	.1716	.485	.2342	0.92
12	.428	.1353	.419	.1793	.452	.2149	0.86
13	.361	.1082	.397	.1885	.377	.2090	0.88
14	.376	.1100	.304	.1587	.267	.1643	0.86
15	.331	.1250	.294	.1528	.275	.1756	0.88
16	.226	.0697	.262	.1328	.252	.1702	0.90
17	.259	.1083	.249	.1309	.220	.1558	0.92
18	.221	.0804	.259	.1339	.277	.1694	0.84
19	.226	.1010	.242	.1400	.237	.1524	0.88
20	.189	.0936	.199	.1153	.202	.1373	0.88
21	.217	.1063	.247	.1538	.220	.1641	0.96
22	.252	.1187	.255	.1694	.252	.1765	0.94
23	.277	.1551	.282	.1817	.290	.1964	0.94
24	.272	.1371	.290	.1884	.260	.1924	1.00
25	.187	.0928	.192	.1280	.225	.1673	0.96
26	.239	.1061	.245	.1654	.230	.1700	0.96
27	.219	.1181	.190	.1274	.187	.1438	0.96
28	.207	.1032	.202	.1362	.190	.1382	0.92
29	.184	.0753	.169	.1026	.180	.1476	1.00
30	.134	.0655	.145	.1412	.065	.0475	0.94
31	.109	.0632	.070	.0481	.072	.0611	0.98
32	.072	.0261	.077	.0596	.065	.0570	0.98
33	.100	.0496	.065	.0463	.100	.0900	1.00
34	.102	.0456	.092	.0463	.072	.0587	0.96
35	.050	.0192	.055	.0399	.050	.0425	0.98
36	.025	.0087	.022	.0122	.007	.0027	1.00
37	.000	.0000	.000	.0000	.000	.0000	1.00
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Table 8e: Frequency and variance estimates, calculated for the non-lethal allele simulation.

NON-LETHAL ALLELE	NUMBER OF DEMES	TRANSMISSION RATIO	MIGRATION RATE	PROPORTION OF FIXED DEMES
.700/1.00/.700	10	0.50	0.05	

GENERATION	3		10		20		
CYCLE	$\bar{q}$	σ^2	$\bar{q}$	σ^2	$\bar{q}$	σ^2	
1	.540	.0890	.556	.1794	.502	.2322	0.90
2	.522	.0899	.539	.1637	.522	.2167	0.82
3	.548	.0980	.507	.1798	.517	.2132	0.84
4	.501	.1134	.512	.1654	.560	.2189	0.86
5	.478	.1127	.471	.1569	.485	.2191	0.86
6	.463	.1116	.464	,1695	.484	.1948	0.74
7	.486	[illegible]	.459	.1804	.525	.2131	0.82
8	.543	.1307	.514	.2003	.492	.2333	0.90
9	.431	.1126	.439	.1639	.422	.2043	0.80
10	.503	.1339	.470	.1865	.532	.2280	0.90
11	.446	.1450	.464	.2221	.430	.2401	0.98
12	.384	.1586	.422	.2012	.400	.2194	0.90
13	.401	.1556	.357	.1982	.387	.2301	0.96
14	.424	.1925	.492	.2246	.502	.2403	0.96
15	.517	.2057	.522	.2261	.505	.2387	0.94
16	.501	.1842	.484	.2129	.465	.2350	0.94
17	.444	.1894	.449	.2253	.440	.2370	0.96
18	.427	.1963	.437	.2190	.462	.2352	0.94
19	.467	.1806	.444	.2050	.411	.2190	0.88
20	.405	.2020	.442	.2350	.457	.2459	0.98
21	.481	.1680	.467	.2074	.515	.2310	0.92
22	.469	.1601	.462	.2112	.475	.2299	0.90
23	.414	.1525	.450	.1975	.440	.2370	0.96
24	.476	.1479	.484	.1973	.517	.2175	0.86
25	.506	.1611	.499	.2139	.510	.2316	0.90
26	.471	.1471	,464	.2063	.500	.2400	0.96
27	.476	.1488	.492	.1952	.502	.2366	0.94
28	.551	.1451	.475	.1882	.492	.2248	0.86
29	.461	.1657	.444	.2025	.425	.2287	0.90
30	.342	.1479	.362	.1813	.405	.2152	0.88
31	.414	.1542	.452	.1991	.437	.2132	0.86
32	.429	.1656	.462	.2082	.517	.2294	0.90
33	.544	.1436	.504	.1933	.465	.2273	0.90
34	.402	.1584	.472	.2071	.495	.2318	0.92
35	.491	.1536	.499	.1987	.477	.2211	0.86
36	.428	.1490	.452	.1875	.490	.2354	0.92
37	.521	.1498	.524	.1913	.537	,2245	0.88
38	.544	.1494	.585	.1915	.545	.2249	0.90
39	.484	.1728	.454	.2273	.460	.2484	1.00
40	.506	.1473	.420	.1962	.450	.2318	0.92

Table 8f: Frequency and variance estimates, calculated for the non-lethal allele simulation.

NON-LETHAL ALLELE	NUMBER OF DEMES	TRANSMISSION RATIO	MIGRATION RATE	PROPORTION OF FIXED DEMES
.500/1.00/.500	10	0.50	0.05	

GENERATION	3		10		20		
CYCLE	$\bar{q}$	σ^2	$\bar{q}$	σ^2	$\bar{q}$	σ^2	
1	.560	.0689	.574	.1128	.611	.1460	0.58
2	.570	.0527	.606	.0819	.473	.1455	0.56
3	.505	.0815	.511	.1268	.502	.1629	0.60
4	.468	.0633	.468	.1222	.539	.1621	0.56
5	.521	.0492	.513	.0942	.501	.1441	0.48
6	.575	.0480	.568	.0806	.557	.1603	0.58
7	.573	.0682	.639	.0981	.661	,1120	0.50
8	.585	.0809	.644	.0962	.642	.1641	0.70
9	.568	.0718	.569	.1109	.559	.1629	0.62
10	.581	.0572	.611	.1061	.623	.1323	0.52
11	.593	.0551	.543	.1140	.527	.1647	0.62
12	.546	.0531	.563	.0929	.511	.1577	0.58
13	.528	.0397	.523	.1086	.602	.1630	0.66
14	.631	.0567	.611	.1126	.571	.1334	0.50
15	.551	.0509	.546	.1087	.549	.1602	0.56
16	.563	.0546	.568	.1074	.599	.1719	0.66
17	.557	.0584	.483	.0848	.491	.1298	0.46
18	.470	.0716	.514	.1155	.546	.1461	0.52
19	.543	.0536	.498	.0936	.494	.1368	0.48
20	.488	.0590	.486	.0896	.446	.1538	0.58
21	.515	.0462	.541	.0948	.539	.1561	0.56
22	.508	.0649	.554	.1080	.604	.1546	0.60
23	.528	.0645	.553	.0916	.544	.1643	0.60
24	.562	.0657	.621	.1087	.697	.1327	0.62
25	.656	.0666	.574	.1340	.564	.1845	0.72
26	.613	.0715	.646	.1223	.644	.1518	0.64
27	.620	.0730	.526	.1148	.527	.1683	0.64
28	.496	.0892	.556	.1504	.509	.1857	0.70
29	.566	.0953	.596	.1325	.552	.1801	0.68
30	.588	.0657	.594	.1010	.512	.1366	0.70
31	.507	.0568	.541	.1086	.484	.1554	0.52
32	.493	.0714	.481	.1248	.511	.1576	0.56
33	.548	.0583	.491	.1187	.462	.1638	0.60
34	.463	.0743	.531	.1237	.594	.1718	0.68
35	.586	.0687	.588	.0954	.556	.1565	0.56
36	.505	.0702	.553	.0981	.526	.1516	0.54
37	.561	.0678	.556	.1309	.534	.1533	0.56
38	.526	.0929	.528	.1382	.524	.1713	0.62
39	.493	.0923	.521	.1219	.524	.1533	0.56
40	.546	.0440	.546	.0801	.521	.1296	0.42

Table 8g: Frequency and variance estimates, calculated for the non-lethal allele simulation.

NON-LETHAL ALLELE	NUMBER OF DEMES	TRANSMISSION RATIO	MIGRATION RATE	PROPORTION OF FIXED DEMES
.700/1.00/.300	10	0.50	0.05	

GENERATION	3		10		20		
CYCLE	$\bar{q}$	σ^2	$\bar{q}$	σ^2	$\bar{q}$	σ^2	
1	.393	.0414	.221	.0635	.107	.0416	0.74
2	.081	.0206	.047	.0154	.111	.0120	0.98
3	.072	.0317	.067	.0399	.057	.0262	0.90
4	.052	.0178	.052	.0230	.015	.0060	0.96
5	.032	.0129	.020	.0096	.010	.0029	0.96
6	.032	.0154	.030	.0221	.047	.0367	0.96
7	.060	.0293	.037	.0188	.007	.0027	0.98
8	.005	.0012	.005	.0012	.012	.0075	0.98
9	.012	.0026	.015	.0053	.007	.0027	0.98
10	.000	.0000	.000	.0000	.000	.0000	1.00
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Table 8h: Frequency and variance estimates, calculated for the non-lethal allele simulation.

NON-LETHAL ALLELE	NUMBER OF DEMES	TRANSMISSION RATIO	MIGRATION RATE	PROPORTION OF FIXED DEMES
.700/1.00/.300	20	0.50	0.05	

GENERATION	3		10		20		
CYCLE	$\bar{q}$	σ^2	$\bar{q}$	σ^2	$\bar{q}$	σ^2	
1	.414	.0560	.259	.0912	.165	.0860	0.75
2	.161	.0441	.117	.0493	.090	.0485	0.84
3	.124	.0430	.086	.0321	.040	.0185	0.90
4	.040	.0136	.034	.0126	.014	.0049	0.96
5	.020	.0098	.011	.0050	.009	.0038	0.98
6	.015	.0063	.016	.0067	.010	.0037	0.97
7	.004	.0014	.000	.0000	.000	.0000	1.00
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Table 8i: Frequency and variance estimates, calculated for the non-lethal allele simulation.

NON-LETHAL ALLELE	NUMBER OF DEMES	TRANSMISSION RATIO	MIGRATION RATE	PROPORTION OF FIXED DEMES
.925/1.00/.825	10	0.50	0.05	

GENERATION	3		10		20		
CYCLE	$\bar{q}$	σ^2	$\bar{q}$	σ^2	$\bar{q}$	σ^2	
1	.535	.0761	.481	.1724	.452	.2343	0.94
2	.417	.0885	.444	.1706	.442	.2239	0.90
3	.460	.1001	.479	.2032	.417	.2335	0.96
4	.433	.0890	.357	.1760	.380	.2225	0.94
5	.441	.1135	.422	.2025	.407	.2330	0.96
6	.388	.1053	.409	.1869	.397	.2298	0.96
7	.403	.1028	.359	.1607	.375	.2161	0.90
8	.366	.0885	.294	.1510	.300	.2100	1.00
9	.251	.1230	.205	.1467	.185	.1470	0.98
10	.197	.0860	.195	.1392	.180	.1381	0.96
11	.204	.0946	.212	.1581	.230	.1721	0.98
12	.204	.1069	.170	.1223	.180	.1476	1.00
13	.164	.0672	.160	.0993	.157	.1242	0.96
14	.177	.0856	.112	.0836	.115	.0980	0.98
15	.080	.0341	.082	.0672	.090	.0769	0.98
16	.044	.0195	.027	.0107	.005	.0012	1.00
17	.005	.0012	.000	.0000	.000	.0000	1.00
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Table 8j: Frequency and variance estimates, calculated for the non-lethal allele simulation.

NON-LETHAL ALLELE	NUMBER OF DEMES	TRANSMISSION RATIO	MIGRATION RATE	PROPORTION OF FIXED DEMES
.850/1.00/.650	10	0.50	0.05	

GENERATION	3		10		20		
CYCLE	$\bar{q}$	σ^2	$\bar{q}$	σ^2	$\bar{q}$	σ^2	
1	.455	.0692	.439	.1624	.312	.1952	0.90
2	.234	.0691	.215	.1199	.200	.1405	0.92
3	.221	.0655	.219	.1180	.197	.1178	0.80
4	.167	.0750	.137	.0704	.100	.0730	0.92
5	.097	.0261	.077	.0391	.020	.0196	1.00
6	.000	.0000	.000	.0000	.000	.0000	1.00
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Table 8k: Frequency and variance estimates, calculated for the non-lethal allele simulation.

NON-LETHAL ALLELE	NUMBER OF DEMES	TRANSMISSION RATIO	MIGRATION RATE	PROPORTION OF FIXED DEMES
.700/1.00/.600	10	0.50	0.05	

GENERATION	3		10		20		
CYCLE	$\bar{q}$	σ^2	$\bar{q}$	σ^2	$\bar{q}$	σ^2	
1	.425	.0053	.398	.0990	.374	.1811	0.72
2	.400	.0854	.379	.1441	.322	.1800	0.82
3	.363	.0944	.379	.1504	.324	.1761	0.80
4	.371	.0801	.326	.1377	.289	.1681	0.80
5	.281	.0833	.244	.1291	.315	.1398	0.90
6	.331	.0576	.301	.1321	.285	.1657	0.82
7	.333	.0780	.306	.1398	.355	.1964	0.86
8	.413	.1116	.374	.1610	.377	.1795	0.74
9	.304	.0729	.264	.1122	.292	.1671	0.82
10	.277	.0820	.237	.1160	.210	.1281	0.84
11	.216	.0703	.199	.1142	.210	.1369	0.86
12	.211	.0653	.235	.1285	.270	.1656	0.82
13	.263	.0765	.214	.0965	.172	,1068	0.84
14	.174	.0551	.162	.0853	.168	.1118	0.84
15	.184	.0597	.194	.1116	.177	.1275	0.88
16	.174	.0647	.169	.0764	.170	.1145	0.92
17	.186	.0688	.217	.1219	.197	.1500	0.88
18	.219	.0804	.247	.1268	.235	.1510	0.96
19	.334	.1366	.377	.1273	.389	.1996	0.86
20	.359	.1566	.344	.1800	.312	.1964	0.82
21	.334	.1321	.284	.1593	.267	.1118	0.92
22	.251	.0809	.247	.1326	.222	.1524	0.90
23	.224	.0631	.244	.1321	.212	.1470	0.90
24	.226	.0880	.182	.0993	.172	.1343	0.90
25	.171	.0582	.137	.0760	.150	.1067	0.96
26	.157	.0538	.162	.0693	.145	.0950	0.90
27	.137	.0560	.149	.0777	.137	.1018	0.86
28	.139	.0633	.135	.0727	.100	.0673	0.90
29	.085	.0412	.087	.0476	.102	.0822	0.88
30	.154	.0815	.149	.0951	.127	.0995	0.96
31	.159	.0715	.132	.0818	.100	.0781	0.94
32	.097	.0520	.095	.0701	.092	.0768	0.96
33	.114	.0742	.127	.0908	.120	.0961	0.96
34	.112	.0615	.107	.0672	.112	.0876	0.94
35	.105	.0612	.122	.0893	.125	.1006	0.96
36	.107	.0583	.120	.0886	.117	.0940	0.96
37	.090	.0366	.087	.0593	.090	.0744	0.96
38	.084	.0343	.100	.0517	.092	.0572	0.88
39	.065	.0231	.109	.0629	.100	.0781	0.94
40	.095	.0470	.112	.0768	.102	.0773	0.92

Table 81: Frequency and variance estimates, calculated for the non-lethal allele simulation.

NON-LETHAL ALLELE	NUMBER OF DEMES	TRANSMISSION RATIO	MIGRATION RATE	PROPORTION OF FIXED DEMES
.700/1.00/.550	10	0.50	0.05	

GENERATION	3		10		20		
CYCLE	$\bar{q}$	σ^2	$\bar{q}$	σ^2	$\bar{q}$	σ^2	
1	.511	.0954	.526	.1641	.557	.1859	0.74
2	.498	.0859	.531	.1427	.477	.1873	0.70
3	.456	.0994	.439	.1693	.432	.2120	0.82
4	.384	.0934	.416	.1421	.344	.1875	0.80
5	.328	.0897	.292	.1310	.347	.1788	0.78
6	.329	.0715	.259	.0990	.287	.1676	0.82
7	.355	.0732	.394	.1241	.349	.1612	0.70
8	.311	.0679	.261	.1104	.282	.1520	0.76
9	.316	.0901	.276	.1310	.282	.1591	0.80
10	.280	.0811	.239	.1213	.190	.1262	0.88
11	.221	.0680	.264	.1226	.230	.1307	0.78
12	.249	.0797	.224	.0932	.217	.1392	0.86
13	.239	.0744	.204	.0906	.175	.1187	0.88
14	.212	.0796	.244	.1314	.257	.1645	0.88
15	.244	.0738	.174	.0889	.162	.1048	0.84
16	.159	.0583	.157	.0873	.165	.1096	0.86
17	.206	.0675	.194	.0790	.132	.0727	0.80
18	.119	.0453	.142	.0838	.125	.0903	0.92
19	.134	.0431	.142	.0859	.185	.1287	0.90
20	.184	.0642	.222	.1185	.227	.1553	0.90
21	.258	.0706	.284	.1400	.215	.1418	0.88
22	.254	.0703	.209	.0962	.157	.0891	0.78
23	.157	.0570	.162	.0829	.132	.0939	0.90
24	.136	.0427	.159	.0744	.137	.0924	0.86
25	.176	.0677	.152	.1026	.157	.1242	0.96
26	.159	.0466	.169	.0977	.165	.1245	0.92
27	.192	.0792	.154	.0974	.177	.1318	0.92
28	.169	.0518	.121	.0416	.167	.1089	0.86
29	.204	.0716	.145	.0789	.157	.1023	0.86
30	.201	.0644	.149	.0695	.129	.0695	0.78
31	.139	.0537	.209	.1317	.182	.1407	0.96
32	.234	.1043	.200	.1111	.202	.1459	0.92
33	.144	.0536	.102	.0518	.095	.0822	0.98
34	.099	.0346	.122	.0695	.127	.0859	0.88
35	.104	.0331	.070	.0324	.040	.0145	0.88
36	.045	.0152	.055	.0287	.020	.0063	0.94
37	.012	.0038	.005	.0012	.020	.0196	1.00
38	.015	.0060	.010	.0024	.040	.0384	1.00
39	.030	.0108	.027	.0149	.035	.0300	0.98
40	.022	.0085	.050	.0805	.005	.0012	0.98

Table 8m: Frequency and variance estimates, calculated for the non-lethal allele simulation.

NON-LETHAL ALLELE	NUMBER OF DEMES	TRANSMISSION RATIO	MIGRATION RATE	PROPORTION OF FIXED DEMES
.700/1.00/.500	10	0.50	0.05	

GENERATION	3		10		20		
CYCLE	$\bar{q}$	σ^2	$\bar{q}$	σ^2	$\bar{q}$	σ^2	
1	.496	.0509	.461	.1412	.399	.1788	0.70
2	.373	.0687	.254	.0885	.207	.1170	0.78
3	.221	.0640	.184	.0804	.170	.0859	0.76
4	.134	.0451	.119	.0582	.080	.0526	0.90
5	.122	.0405	.129	.0632	.125	.0956	0.94
6	.126	.0417	.112	.0590	.090	.0612	0.90
7	.104	.0342	.110	.0664	.107	.0679	0.88
8	.107	.0366	.087	.0361	.080	.0446	0.86
9	.087	.0341	.052	.0267	.030	.0241	0.98
10	.044	.0121	.025	.0075	.040	.0254	0.96
11	.042	.0133	.015	.0060	.030	.0241	0.98
12	.047	.0230	.045	.0259	.040	.0251	0.94
13	.020	.0064	.017	.0074	.007	.0027	0.98
14	.017	.0049	.002	.0003	.020	.0196	0.50
15	.022	.0065	.025	.0106	.030	.0241	0.98
16	.052	.0193	.040	.0181	.047	.0234	0.90
17	.062	.0235	.079	.0474	.052	.0267	0.88
18	.052	.0224	.052	.0305	.020	.0196	1.00
19	.017	.0055	.032	.0171	.000	.0000	1.00
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Table 8n: Frequency and variance estimates, calculated for the non-lethal allele simulation.

NON-LETHAL ALLELE	NUMBER OF DEMES	TRANSMISSION RATIO	MIGRATION RATE	PROPORTION OF FIXED DEMES
.400/1.00/.200	10	0.50	0.05	

GENERATION	3		10		20		
CYCLE	$\bar{q}$	σ^2	$\bar{q}$	σ^2	$\bar{q}$	σ^2	
1	.433	.0141	.395	.0435	.336	.0748	0.32
2	.413	.0365	.348	.0375	.343	.0352	0.16
3	.370	.0370	.333	.0359	.308	.0509	0.30
4	.367	.0422	.369	.0422	.343	.0518	0.24
5	.370	.0395	.366	.0406	.348	.0540	0.26
6	.373	.0568	.384	.0730	.363	.0778	0.34
7	.395	.0378	.351	.0491	.313	.1578	0.30
8	.348	.0481	.326	.0610	.279	.0668	0.42
9	.328	.0452	.283	.0415	.259	.0618	0.40
10	.301	.0589	.261	.0597	.201	.0483	0.46
11	.271	.0545	.234	.0450	.194	.0461	0.50
12	.323	.0471	.264	.0588	.241	.0653	0.48
13	.271	.0453	.267	.0697	.264	.0556	0.40
14	.361	.0456	.296	.0550	.271	.0697	0.44
15	.309	.0382	.291	.0471	.281	.0665	0.38
16	.365	.0324	.353	.0456	.224	.0504	0.30
17	.395	.0359	.348	.0608	.259	.0578	0.40
18	.348	.0391	.323	.0435	.289	.0532	0.32
19	.378	.0464	.323	.0435	.256	.0497	0.38
20	.363	.0366	.348	.0351	.371	.0629	0.26
21	.401	.0333	.346	.0375	.360	.0437	0.18
22	.388	.0479	.370	.0550	.381	.0732	0.28
23	.383	.0492	.344	.0477	.296	.0556	0.30
24	.268	.0462	.246	.0607	.204	.0521	0.50
25	.289	.0419	.291	.0556	.258	.0604	0.42
26	.378	.0386	.334	.0584	.306	.0664	0.32
27	.398	.0316	.354	.0437	.316	.0523	0.24
28	.359	.0384	.346	.0425	.349	.0604	0.28
29	.385	.0350	.358	.0477	.305	.0437	0.24
30	.373	.0393	.306	.0485	.291	.0551	0.36
31	.333	.0389	.375	.0575	.363	.0691	0.30
32	.432	.0400	.366	.0359	.343	.0494	0.22
33	.361	.0314	.371	.0601	.319	.0598	0.32
34	.401	.0363	.346	.0474	.296	.0624	0.34
35	.375	.0328	.358	.0395	.346	.0524	0.24
36	.365	.0373	.354	.0444	.316	.0591	0.30
37	.370	.0458	.323	.0508	.271	.0476	0.36
38	.339	.0418	.323	.0533	.254	.0546	0.42
39	.336	.0519	.314	.0605	.239	.0622	0.44
40	.368	.0529	.298	.0559	.301	.0584	0.32

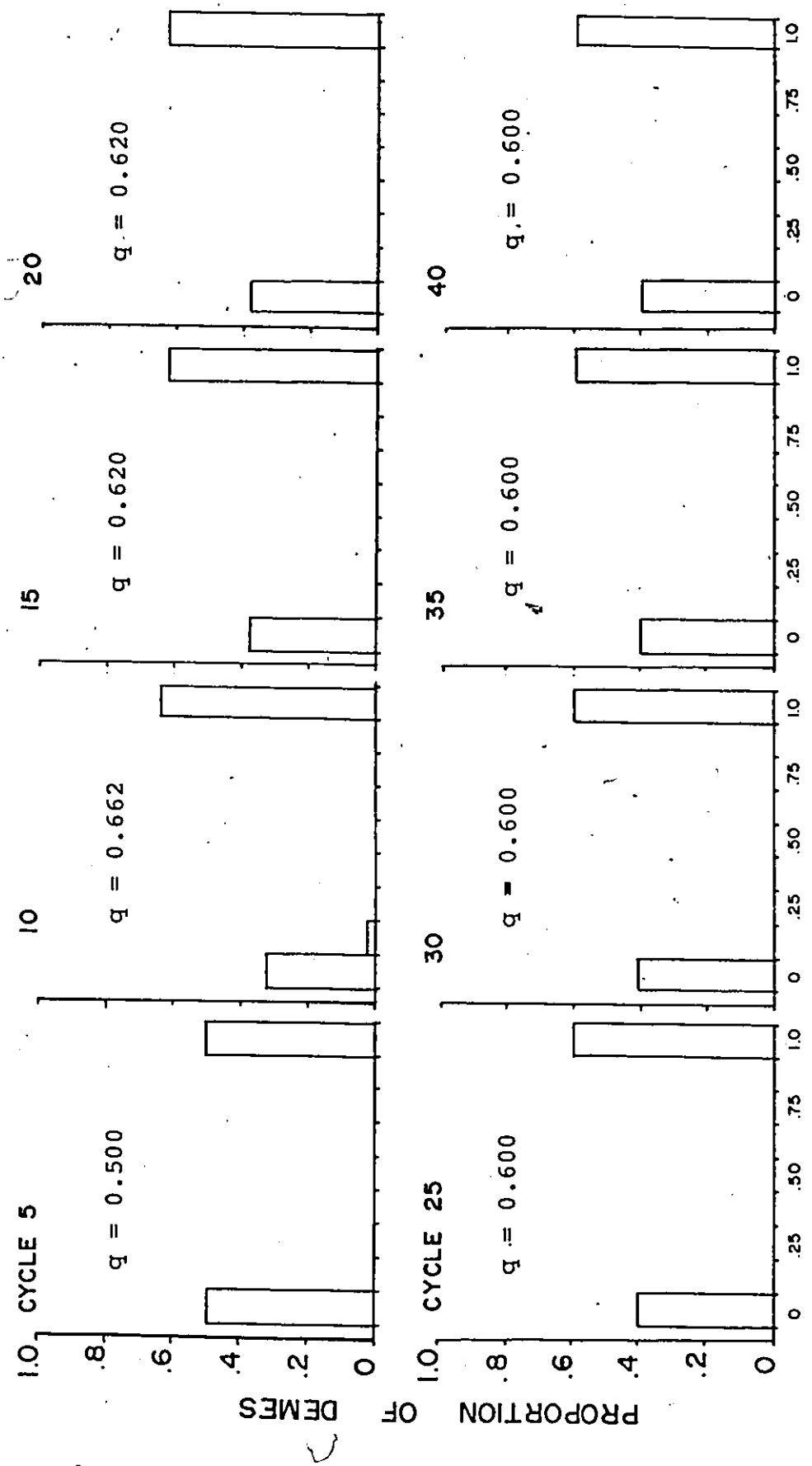


Figure 4a: Frequency distributions of the non-lethal allele when genotypic fitnesses are 1.0, 1.0, and 1.0 .

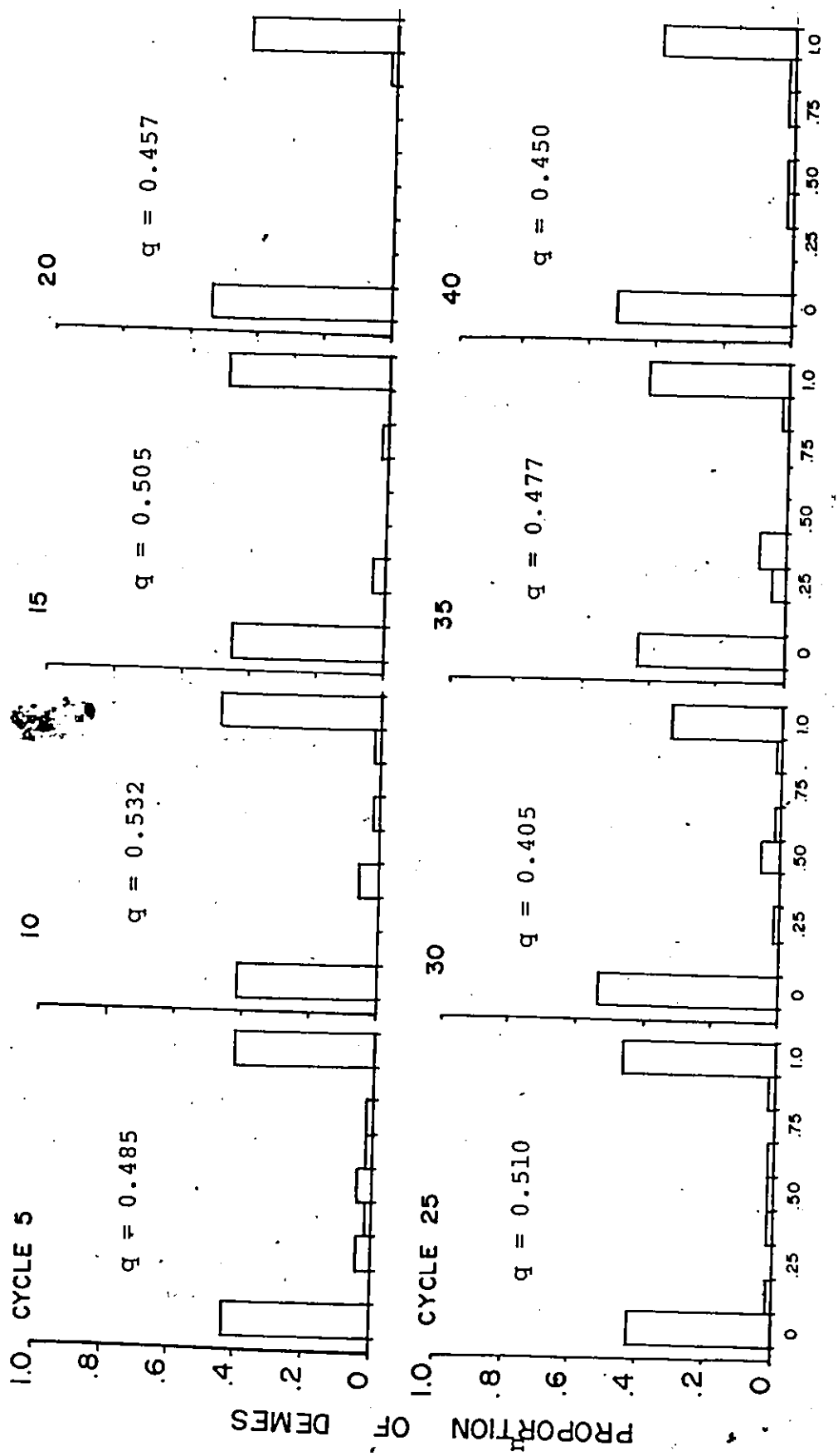


Figure 4b: Frequency distributions of the non-lethal allele when genotypic fitnesses are 0.7, 1.0 and 0.7 .

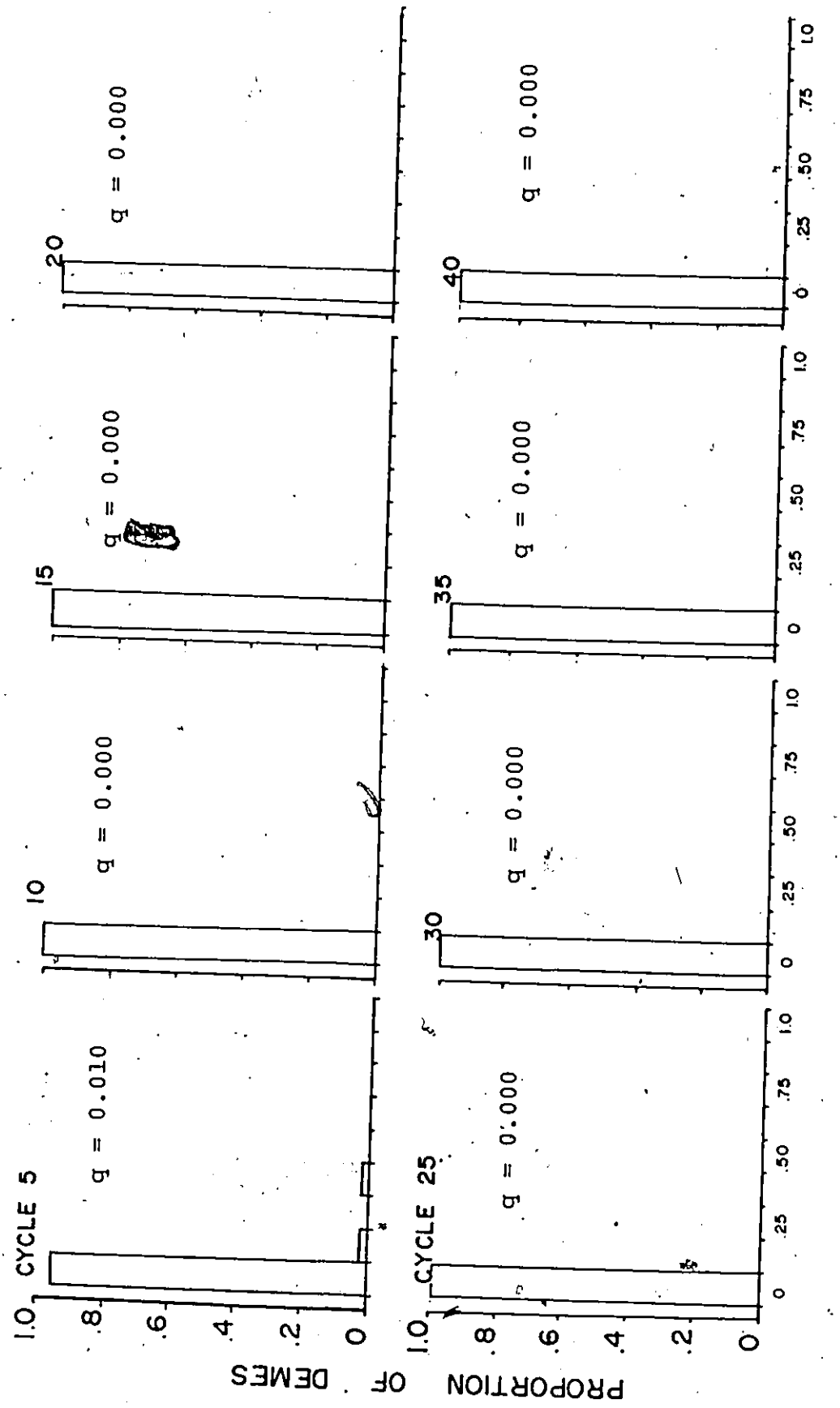


Figure 4c: Frequency distributions of the non-lethal allele when genotypic fitnesses are 0.7, 1.0 and 0.3 .

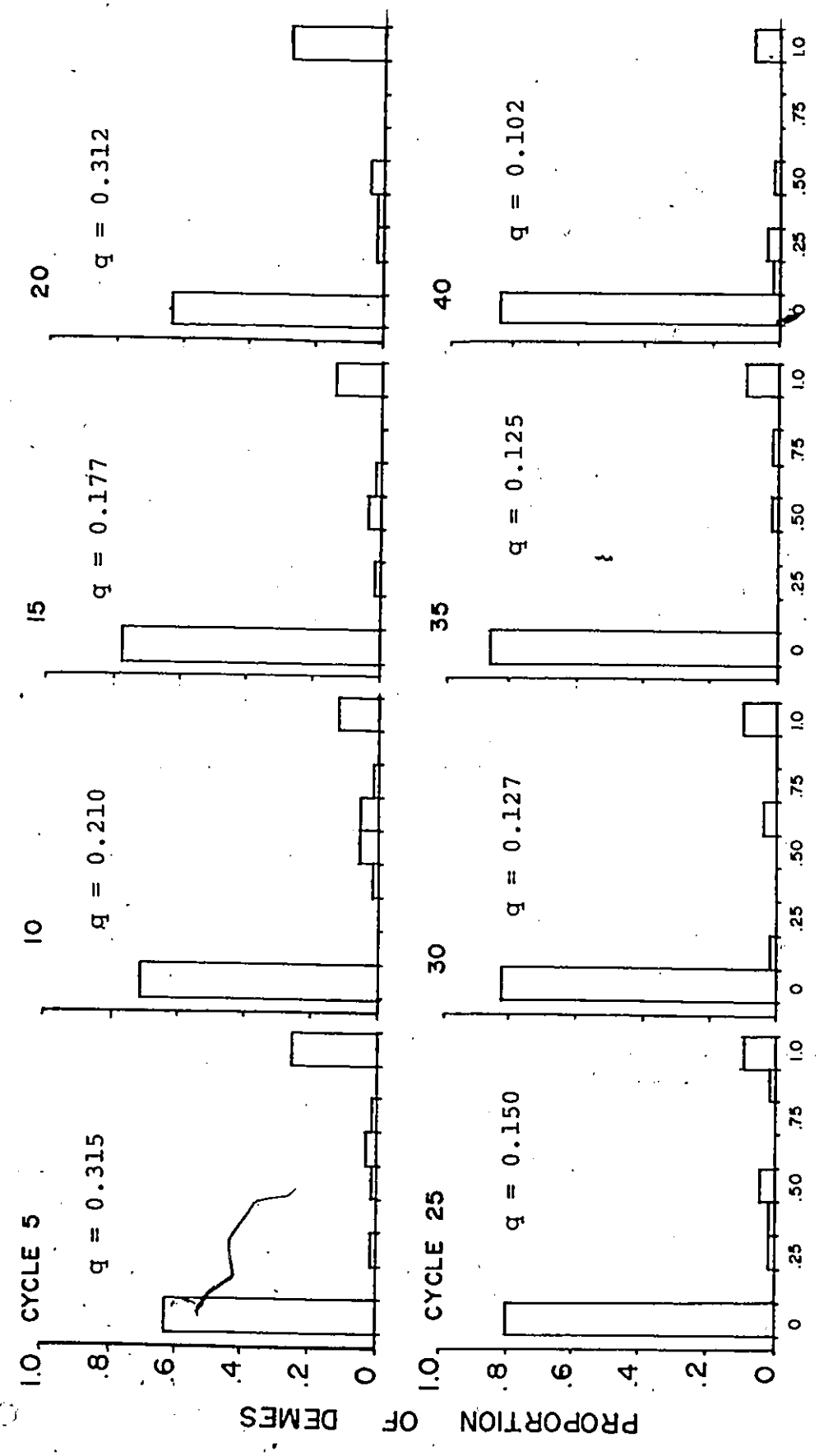


Figure 4d: Frequency distributions of the non-lethal allele when genotypic fitnesses are 0.7, 1.0 and 0.6 .

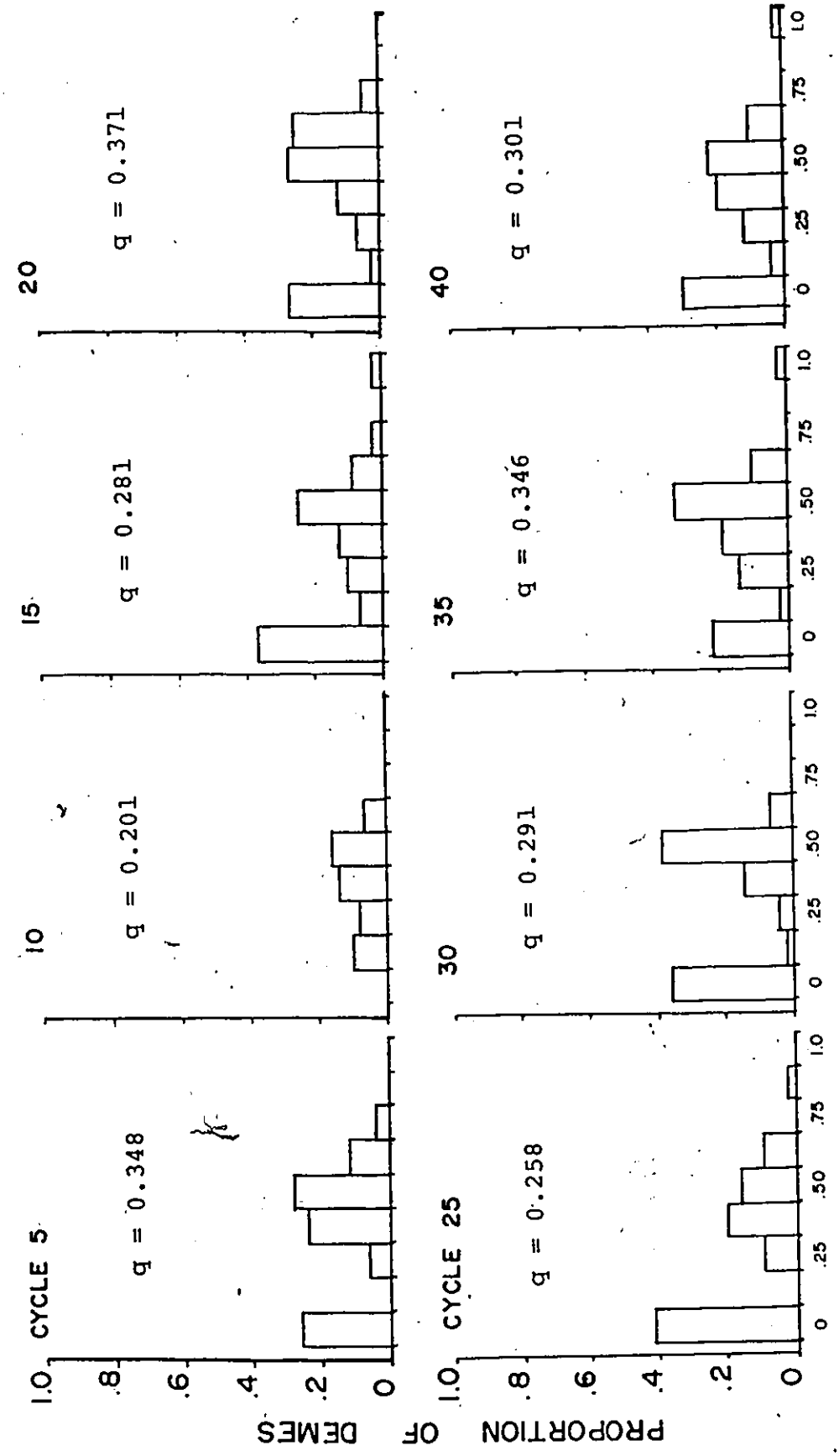


Figure 4e: Frequency distributions of the non-lethal allele when genotypic fitnesses are 0.4, 1.0 and 0.2 .

polymorphism, the allelic frequency and amount of heterozygosity observed at the Hbb-locus were not achieved.

To achieve an allelic frequency of 0.7 for the more common allele the fitnesses of the homozygotes were changed to 0.7 and 0.3; Fisher (1922) has shown that any values of fitness in the same ratio will give an equilibrium gene frequency of 0.7 if the population otherwise meets Hardy-Weinberg requirements. These results are shown in Tables 8g, 8h, 8i and 8j; and Figure 4c. Fixation for the more favoured allele occurred rapidly. Reducing selection against the homozygotes in the same ratio did not affect the outcome and the allele whose homozygote had greater fitness quickly became fixed in all demes.

To check that the number of demes used in the simulation was not affecting the results, the simulation using fitness values of 0.7 and 0.3 was repeated for 20 demes (Table 8h); again fixation for the more favoured allele occurred quickly in all demes of the metapopulation. Therefore Fisher's findings that particular ratios of homozygote fitnesses should result in an equilibrium frequency situation does not hold true in small breeding units where genetic drift is occurring.

Since when both homozygote fitness values were 0.7, a polymorphism was achieved a simulation in which homozygote fitness values of 0.7 and 0.6 were used was run. The simulations were repeated but with differences between the fitness values increased. These results are given in Tables

8k, 8l, and 8m, and Figure 4d. A polymorphism was maintained when fitness values were 0.7 and 0.6, but the frequency of the more favoured allele was approximately 0.9. Furthermore, the proportion of fixed demes was high (0.92) and so the amount of heterozygosity was extremely low which is not the case for the Hbb locus in natural populations. Increasing the difference between the homozygote fitness further increased the values of allelic frequency and lowered the heterozygosity until fixation for the more favoured allele occurred when fitness values were 0.7 and 0.5 (Table 8m). Although a polymorphism was again produced, the allelic frequency and amount of heterozygosity were not similar to those of the Hbb locus data.

Since a great disparity between the simulated results and observed values was always observed when the fitness of the more common homozygote was around 0.7, a trial and error approach was taken to see if appropriate values of empirical data could not be reached. This resulted in a simulation in which homozygote fitness values of 0.4 and 0.2 were used. The results are shown in Table 8n and Figure 4e. The frequency of the less common allele was approximately 0.3, with a range of between 0.38 to 0.19, over the forty cycles of the run. The frequency variance was of the same order of magnitude as the empirical data (Table 3). The value of heterozygosity is high, however (Table 9), approximately twice that observed in natural populations (Table 3). This however, can be decreased by just slight changes in the fitness values of the two homozygotes.

Table 9: Estimates of herterozygosity, based on the computer simulation(genotypic fitness values used are 0.4, 1.0, 0.2) for the non-lethal allele.

	AVERAGE H FOR ALL RUNS	AVERAGE H PER RUN				
CYCLE	R_t	R_1	R_2	R_3	R_4	R_5
1	0.63	0.62	0.56	0.75	0.58	0.63
5	0.62	0.75	0.63	0.56	0.59	0.56
10	0.45	0.31	0.48	0.53	0.71	0.21
15	0.52	0.62	0.51	0.57	0.52	0.40
20	0.61	0.71	0.70	0.37	0.65	0.64
25	0.48	0.42	0.56	0.45	0.57	0.39
30	0.55	0.50	0.60	0.40	0.72	0.52
35	0.63	0.74	0.64	0.67	0.50	0.60
40	0.53	0.59	0.34	0.53	0.58	0.61
OVERALL AVERAGE	0.56	0.59	0.56	0.54	0.60	0.57

VI DISCUSSION

There are two general theories to explain the genetic variation observed in natural populations. The balance theory emphasizes that aspect of natural selection, namely heterosis, which can preserve or even increase variation. On the contrary, the neoclassical theory asserts that when natural selection occurs it is almost always purifying, and that there is a class of redundant or neutral mutations which is not sensitive to adaptation and natural selection. This latter class is what is observed when the tool of electrophoresis is applied. The ubiquity and stability of electrophoretically detectable genetic variation is accounted for by mutation and gene flow between populations. The neoclassical theory can explain well the polymorphisms in the large populations ($>10^4$). However, most populations are not on the order of 10^4 or 10^5 individuals, and so it is of interest to know whether mutation and gene flow alone can account for the variation in small populations or if some other evolutionary force must be considered. Furthermore, the precise size of the breeding unit in natural populations, and the exact rate of gene flow between the units are not known. Estimates of these factors have been made, but these are based on allelic frequency data, and by measuring physical movements of animals in natural habitats.

Evidence for structuring of the house mouse in a natural environment has been found in the analysis of allelic frequency data derived from studies of some biochemical polymorphisms which are known to exist in natural populations of Mus (Petras, 1967a; Petras et al, 1969; Selander, 1970). Territorial behaviour studies have shown that populations of mice maintained under laboratory conditions are subdivided, and that both males and females can participate in the maintenance of territorial boundaries (Crowcroft, 1965; Anderson and Hill, 1965; Reimer and Petras, 1967). A behavioural mechanism which may help to determine territorial boundaries is marking with urine (Desjardins et al, 1973; Ralls, 1970). Phermones in the urine of male mice have been implicated in aggressive behaviour between male mice (Mugford and Nowell, 1970).

Stochastic models of population structure have been developed and used to explain allele frequency data observed in natural populations for a polymorphism at the T locus. These models are of interest because random events together with the characteristics of the t alleles may be included in the model (Lewontin and Dunn, 1960; Lewontin, 1962; Levin et al, 1969). Critical to the success of these models was the size of the breeding unit; a small deme size, on the order of 10 individuals, was required before the effects of genetic drift became important.

Estimates of allelic frequency and inbreeding coefficient were used by Petras (1967a) to estimate the effective genetic size of the mouse populations. Using two extreme models of

population structure, Wright's Island Model (Wright, 1943) and Isolated By Distance (Wright, 1951), the size of the panmictic unit was estimated to vary between 6 and 80, and 8 and 20 individuals respectively. Petras (unpublished) has estimated that perhaps no more than 10 or 12 animals make up the founder population in corn crib populations. This conclusion was supported by Hawkeswood (1975) in a study of mouse population dynamics in which population numbers could be closely followed. The evidence all indicates that the effective genetic size of these populations is low.

The model was designed to simulate migration in a manner different from previous simulations. Levin et al (1969) had migrants being chosen from a floating population associated with each deme, but which made no genetic contribution to it. Various studies have indicated that such a situation does occur in natural populations (Crowcroft, 1955; Davis, 1958; Reimer and Petras, 1967; Mackintosh, 1970). Young males reaching maturity can either replace older dominant males (Reimer and Petras, 1967) or establish their own territory (Mackintosh, 1970).

Migration between demes appears to be a rare event, as has already been discussed. Since the present model is based on data obtained from mice inhabiting corn cribs, and since no evidence is available at present to suggest that breeding units remain intact after a crib is emptied an annual pooling of all mice in a crib has been assumed. The probability of mortality at the time of habitat destruction is high and as a

result only a very few animals reinhabit the corn cribs when the new crop is stored. In the development of the model, an attempt was made to simulate interdemic migration through the pooling of surviving individuals. This was followed, in the model, by a re-establishment of population structure, which occurs in the natural populations when the crib habitat is restored (Hawkeswood, 1975). Perhaps genetically effective migration is lower than expected from habitat stability because the migration rate that shows the closest correspondence to the t allele data was 5 percent, that is pooling once in twenty generations. In considering the natural populations this rate seems low. Since the crib habitat is destroyed on an annual basis, there is time for only about three generations between poolings. However, a migration ratio higher than 10 percent results in a t allele frequency that exceeds those of natural populations and in fact approaches values predicted by Bruck's deterministic model (Bruck, 1957). Therefore only a 5 percent migration rate gives a frequency level consistent with those of natural populations. A possible explanation for this dilemma is that the deme structure may not be totally broken down when the crib is emptied. If a few individuals of a deme remain together, the genetically effective migration rate could turn out to be zero for that cycle if these individuals migrate back into the crib together and form a new deme.

Furthermore, knowledge about the fitness of the heterozygote itself is practically non-existent for natural environments. As Dunn et al (1958) concluded, the evolutionary

forces affecting the T locus "must be sought in the conditions under which the wild populations live, especially the population structure in respect to size of breeding units, intensity of inbreeding, and similar factors."

There are two aspects of the model, namely, constant population size and the genetically effective migration rate, which appear to be oversimplifications of the problem.

The computer model does not make provision for population expansion. This is not a serious shortcoming, since the genetically effective size of a population starting from a small group of founders and expanding, is the harmonic mean of the number of individuals per generation. The formula is

$$\frac{1}{H_x} = \frac{1}{N} \Sigma(1/X_i) \quad \text{(Crow and Kimura, 1970)}$$

where H_x is the harmonic mean,

N is the number of generations,

X_i is the number of individuals per generation.

Consider for example one pair of mice which, acting as the founder generation, produce three generations of offspring. Suppose the population size in each of four generations is 2, 8, 32 and 128. This would occur if each mating gave six offspring per litter with an equal ratio of males and females and all animals survive. The effective size of this population would be the harmonic mean,

$$H_x = \frac{1}{(\frac{0.664}{4})} \approx 6$$

Therefore effective size of three used in the model is not an unrealistic estimate, since not all mice in each generation will survive, nor will all animals survive over all generations.

An examination of the migration as used in the present model shows that it differs slightly from that of Levin et al (1969); however this rate is not the genetically effective rate. It is a measure of the frequency of the pooling operation. A true measure of genetically effective migration must take into account the source of the individuals involved. If a deme remained intact throughout the pooling procedure subsequently re-entering the crib as a unit, the effective migration rate for the deme would be zero. One, two or three migrants entering a deme would give effective migration rates of 0.25, 0.50 and 0.75 respectively. These migration rates weighted by the probability that each occurs multiplied by the pooling migration rate would give the genetically effective rate of migration. Table 10 summarizes the genetically effective migration rates for the different values used in the model.

The model of Lewontin and Dunn (1960) gave results very similar to the present model in terms of rates of fixation. Persistence of the t allele in a large population was not studied since interdemic migration was not required to maintain the t allele when the breeding unit consisted of 20 or more individuals. Levin et al (1969) concluded that with 3 percent migration random drift would only have an important effect on

Table 10: Genetically effective rates of migration calculated for different population sizes and pooling rates.

NUMBER OF DEMES	POOLING RATE (PERCENT)	GENETICALLY EFFECTIVE MIGRATION RATE (PERCENT)
5	1	0.60
	5	3.00
	10	6.00
10	1	0.67
	5	3.37
	10	6.74
20	1	0.71
	5	3.56
	10	7.12

t allele frequencies if the breeding units had a genetically effective size of less than four. In the present model, the drift effect is always important, since the genetically effective size was three.

Using the model developed for the t allele, an examination of a second genetic system, the Hbb locus, was carried out since a model which is consistent with the t allele data should also be consistent with Hbb data. Under the conditions of the model neutral alleles will not remain polymorphic. Furthermore slight selective pressure appears ineffective in maintaining a polymorphism. Only when selective pressures were strong was a stable polymorphism established.

The above conclusion is not surprising. Using the method of Kimura and Crow (1964) the average homozygosity and effective number of alleles in a randomly mating population can be calculated. For an effective size of three, and assuming a mutation rate of 10^{-5}, average heterozygosity is 0.99988, and the effective number of alleles in the population is 1.00012. Therefore almost no heterozygosity is expected in a population with such a low effective size.

Therefore, mutation and gene flow cannot by themselves account for the allelic frequencies observed at the Hbb locus. In order to explain the empirical data strong selective forces must counteract the effects of genetic drift.

Summary

1) An examination of house mice (Mus musculus) collected from corn cribs in southwestern Ontario revealed further evidence for the widespread distribution of a polymorphism at the T locus. The overall frequency of the t alleles at this locus was 0.081.

2) These same mice were examined for a polymorphism at the hemoglobin β (Hbb) locus. The overall frequency of the more common allele, Hbb^S, at this locus is 0.70 .

3) Ecologic data was reviewed, and suggests that house mouse populations are structured, with little gene flow between breeding units.

4) A stochastic model was developed to account for the polymorphism at the T locus.

5) The model, consisting of a number of breeding units or demes of one male and three females, a male transmission ratio of 0.95, and an interdemic migration rate of 5 percent explains well the empirical data at the T locus.

6) Varying the number of demes per population had no significant effects on the t allele frequency.

7) The model was applied to the Hbb locus to see how well the model could explain the data from natural populations.

8) The observed frequencies and frequency variances at the Hbb locus could not be accounted for only by gene flow between populations.

9) Strong selective pressures were required to establish a

stable polymorphism with the same frequency and frequency variance in the model as are observed at the Hbb locus in natural populations.

APPENDIX I

A Introduction

In describing the t allele model, it has generally been assumed that the only factors involved in maintaining the t allele at a relatively low frequency were the abnormal transmission ratio which tends to increase the t allele frequency, and genetic drift and selection against homozygotes (t/t) which tends to reduce the t allele frequency. However, since there should be a reason why the t allele has survived in the house mouse, from an evolutionary viewpoint another factor should be operating on the t allele, a factor such as a higher fitness of the heterozygous male as compared to the wild type homozygote. Under laboratory conditions, Dunn et al (1958) have in fact reported that males heterozygous for the t allele possess a net reproductive advantage, and so, therefore, should be more fit than males homozygous for the wild-type allele.

Such studies are not readily possible under natural conditions; however behavioural patterns have received some attention (De Fries et al, 1966; Levine et al, 1965).

One aspect of behaviour that has been well documented is marking behaviour (Desjardins et al, 1973; Mugford and Nowell, 1970; Ralls, 1971). Mammals are known to mark with urine or secretions from scent glands in any situation where they are both intolerant of and dominant to other members of the same species. They mark where they are likely to attack

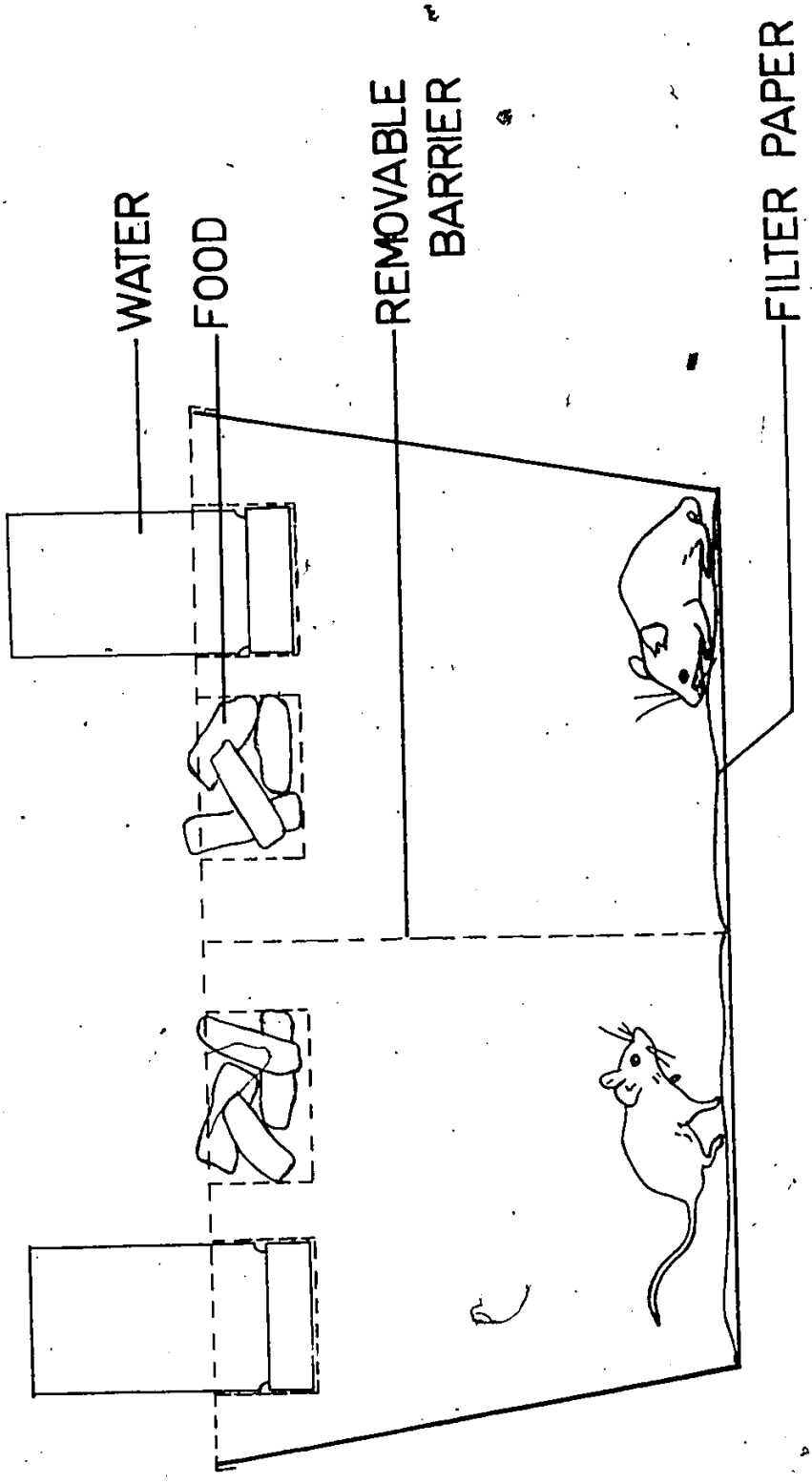
another member of the same species and win (Ralls, 1971). Desjardins et al (1973), observed that male mice isolated at weaning profusely marked when housed in the presence of another male. Further, socially dominant males all but completely suppressed subordinant males housed in the same cage even though separated by a screen barrier.

A modification of the procedure used by Desjardins et al (1973) was used to test the hypothesis that males heterozygous for the t allele were more aggressive than males homozygous for the wild type allele.

B Experimental Procedure

Mice were placed in clean cages lined with filter paper for twenty-four hours. The number of fecal pellets at the end of this period was used as an index of the inate level of excitability. Two groups of mice were tested, t-bearing and non-t-bearing males. Marking patterns of the individually housed mice were also observed. After 24 hours, the mice were housed in large cages divided into two compartments by a wire mesh barrier (Figure 5). Unlimited food and water were supplied to all mice, and cages were again lined with filter paper. The schedule of activities through which the mice progressed is shown below.

Figure 5: Cage setup used in observing fighting behaviour in wild mice; barrier can be removed allowing physical contact between mice.


WATER
FOOD
REMOVABLE BARRIER
FILTER PAPER

DAY	BEHAVIOUR PARAMETERS MEASURED
1	Mice housed separately; urine patterns observed.
2-5	Barrier removed for 30 minutes per day; Attack latency; Frequency of attacks Presence/absence of blood on filter paper; Day on which definite dominant/subordinant urine pattern first occurred.

Two groupings of mice were observed. First, males homozygous for wild type alleles at the T locus were paired with similar homozygous males, and second, males homozygous for wild type allele at the T locus were paired with males heterozygous for the t allele. At the end of testing the relative success of t-bearing males was noted.

C Results

The results of the aggressive behaviour tests are shown in Table 11 and Figure 6. Significant differences between the groups appeared only on the first two days of confrontation. Fight latency was less in pairings in which a t-bearing male was included on days one and two of the procedure. Fighting frequency was higher in the group including the t-bearer only on day one. Fight intensity as revealed by the presence of blood on the filter paper was higher in the t-bearing group, however, again only on day one of the procedure. No other significant differences in behaviour were observed.

The patterns of urine marking showed definite evidence of dominance. Typical examples of patterns observed are shown in Figure 6. Isolated animals marked the entire cage,

Table 11: Analysis of fighting behaviour.

BEHAVIOUR	t-BEARING GROUP (MEAN SCORE)	WILD TYPE GROUP (MEAN SCORE)	SIGNIFICANCE
Fecal pellet count	98.20	95.54	N.S.
Fight latency:			
Day 1	1.71	6.25	t' = 2.317
2	1.18	8.50	t = 2.521
3	2.53	3.33	N.S.
4	5.25	2.63	N.S.
Fight frequency:			
Day 1	6.00	3.00	t = 2.040
2	4.67	3.87	N.S.
3	2.60	3.29	N.S.
4	1.85	2.31	N.S.
Days until dominance appears	2.46	2.50	N.S.
Fight intensity (presence of blood)	1.27 (19)	0.533 (8)	t = 2.323
Genotype of dominant male	8 +/+; 5 +/t		N.S.
Age of dominant male	11 younger/ 9 older than partner		N.S.

Figure 6: Urine patterns of wild mice:

(left) urine pattern of an isolated mouse

(centre) patterns of two male housed together, but with no physical contact

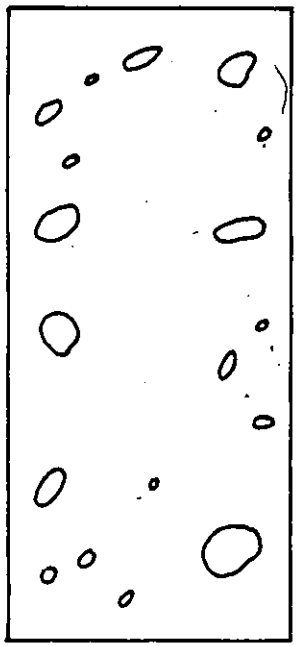
(right) patterns of two mice housed together after 4 days of contact

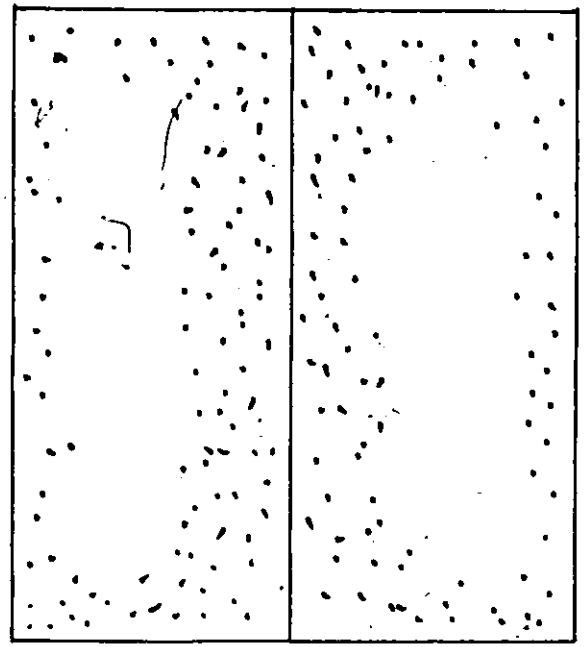
ISOLATED

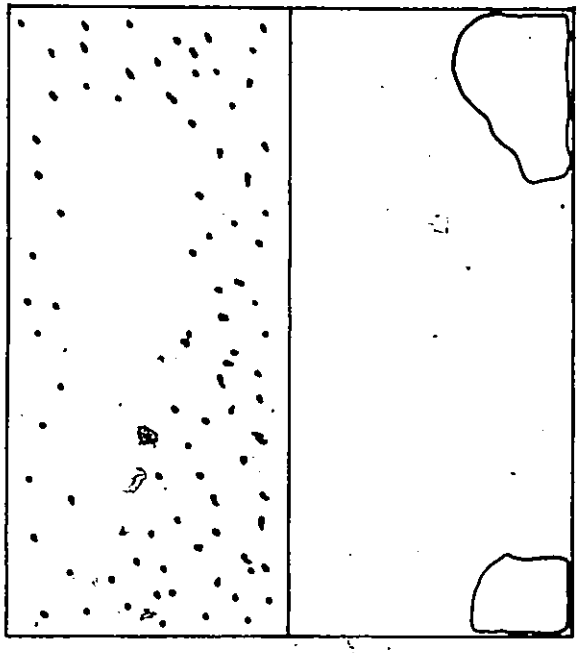
PAIRED

BARRIER IN

BARRIER OUT







placing the majority of marks near the cage edges. Marks varied in size from small spots to pools. Paired animals changed their marking behaviour. While kept separated, both animals marked profusely with many small spots placed around the edge of the cage, but with a majority placed along the wire mesh barrier separating the animals. After the barrier had been removed and one animal had become dominant, the urine pattern of the subordinate changed. While the dominant male continued to mark profusely especially along the barrier, the subordinate marked only in the corners farthest away from the barrier; the marks were confined to one or two very large pools. The subordinate did not continue to mark along the barrier separating the two males.

D Discussion

In the computer model presented in Chapter III, the fitness of the t-bearing male heterozygote was considered equal to that of the wild type homozygote. There is at least preliminary evidence that males heterozygous for lethal t alleles are selectively superior to males homozygous for the wild type allele (Dunn et al, 1958). There is no evidence of heterozygote inferiority in either males or females, although not enough data has been analyzed to make a definitive conclusion. The behaviour associated with the t allele tends to support the idea of heterozygote advantage. Reimer and Petras (1967) observed that fighting frequency between male mice increased during the first two days of territory establish-

ment, after which the frequency decreased, and social order appeared to have been established. This same behaviour appears in the analysis of fighting behaviour. In this case, levels of fighting in pairs involving a t-bearing male occurred sooner and were more vigorous on the first two days of the fighting schedule. By the third day the two groups were behaving similarly. If the first two days are most important in determining which animals control territory, become dominant and contribute genetically to the next generation, then the t-bearing male may have the advantage of being a better, more aggressive fighter.

The evidence is circumstantial in that the more aggressive behaviour associated with the t-bearing males may be due to other causes. For instance, it is known that olfactory stimuli are important in causing the release of aggressive behaviour (Ropartz, 1968), and differences in phermones between male and female mice can cause different aggressive responses (Mugford and Nowell, 1970). Also, the social experience of young mice can effect the way in which they behave as adults (Kahn, 1954; 1961; Luberman, 1963). The evidence from the present study is preliminary and merits further investigation.

APPENDIX II

TRAPPING METHODS

The house mouse, Mus musculus, is a ubiquitous rodent occurring in a wide range of habitats and consequently populations from a variety of environmental situations have been well studied.

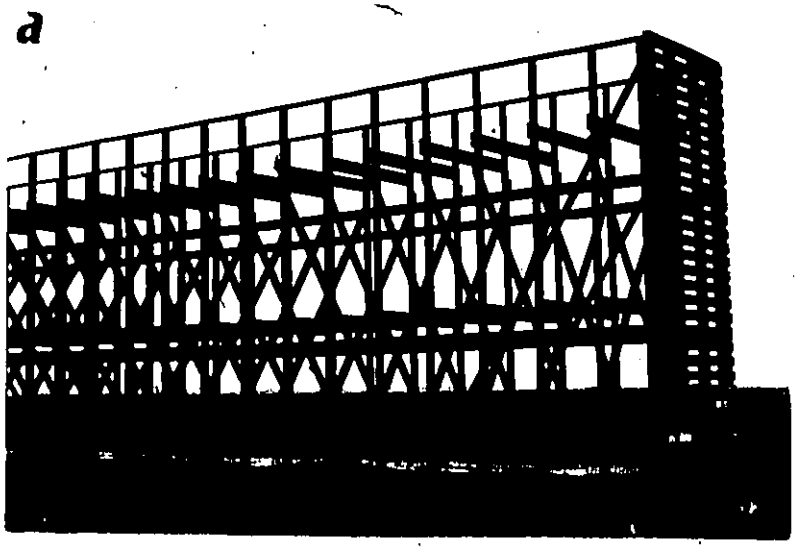
The commensal habitat studied here is one associated with the growing of corn (Zea mays) in Essex and Kent counties in southwestern Ontario. Corn, a major crop in this area, is used primarily in animal feed, cereal production, and the distilling industry and so prior to marketing is air dried over winter in structures or cribs specifically designed for this purpose (Figure 7). These corn cribs are distributed throughout the two counties involved. The geographic relationship of farms with corn cribs included in this study are shown in Figure 8 and an example of the distances between corn cribs and other buildings on a single farm are shown in Figure 9.

Many of the better constructed corn cribs have a base of concrete extending above and below ground as much as twenty-five centimeters. On this base is erected a wooden frame which is covered with a wire mesh or wooden slats. Air passes freely through the structure enhancing drying of the corn. The corn is picked in late fall (November) and is stored in the cribs until the following spring or Summer (May-September). The specific time at which the corn is removed from a crib varies from farm to farm and is to a considerable degree dependent on the grain market. The emptying of a crib is a fairly rapid process usually taking about a day and at the

Figure 7a: View of an empty corn crib, illustrating construction style.

Figure 7b: View of a corn crib similar to Figure 1a, but full of corn.

a



b

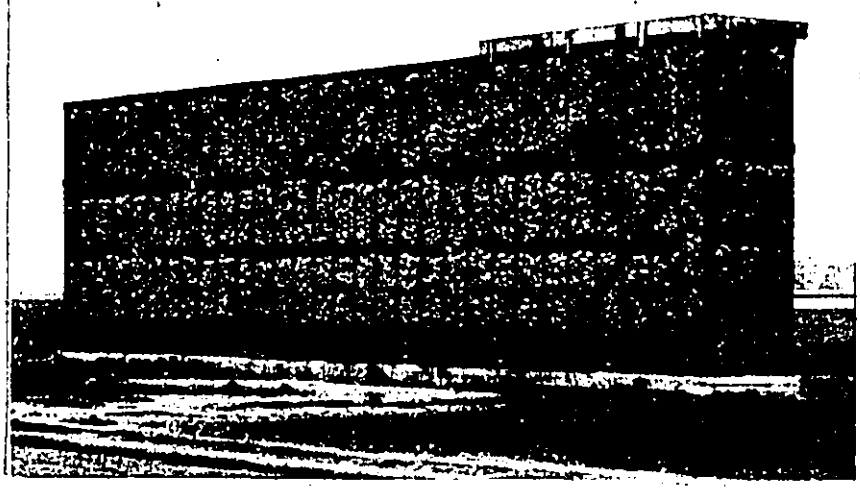


FIGURE 8: Map of trapping sites. Open circles represent approximate locations of populations sampled.

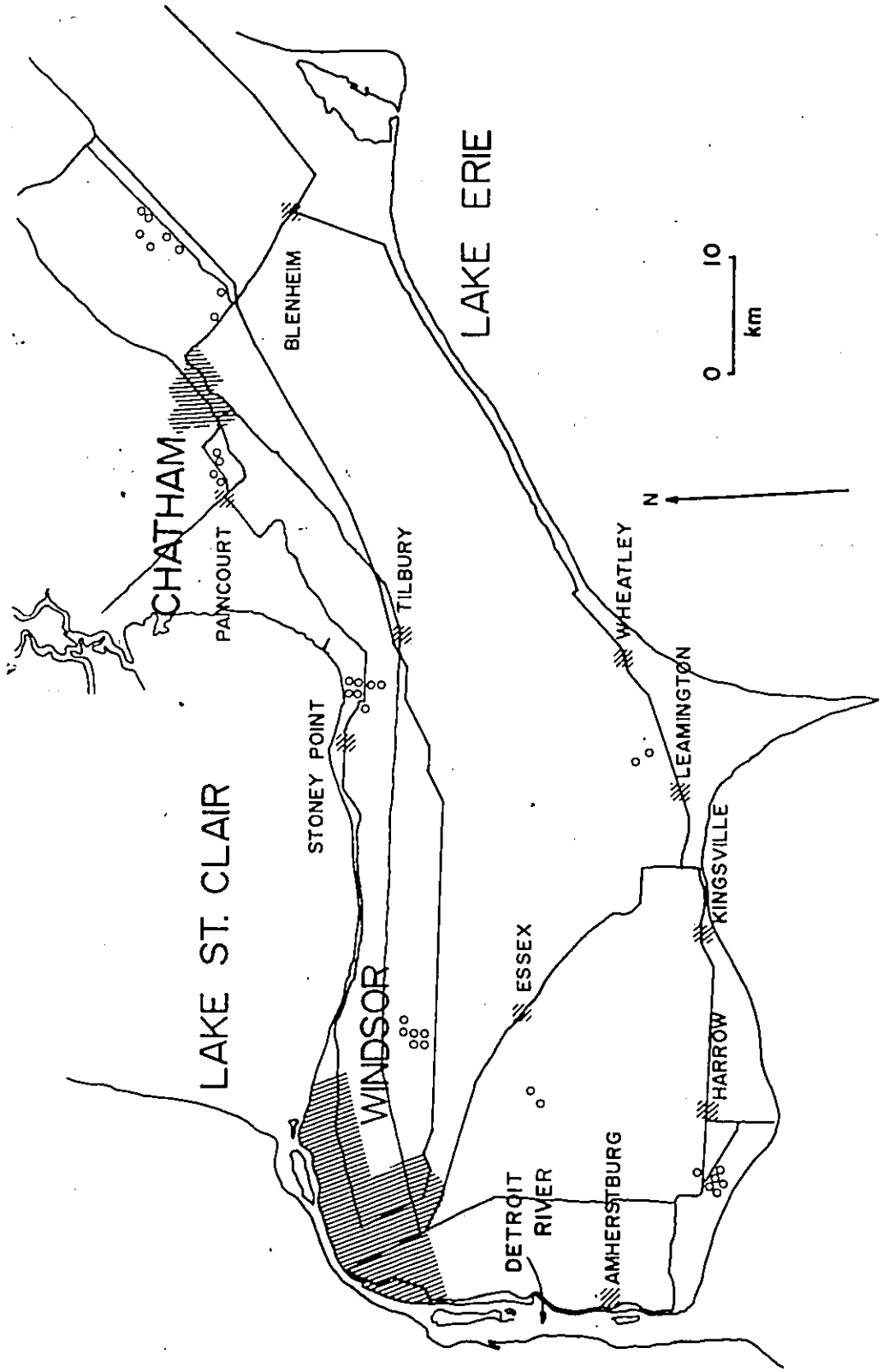
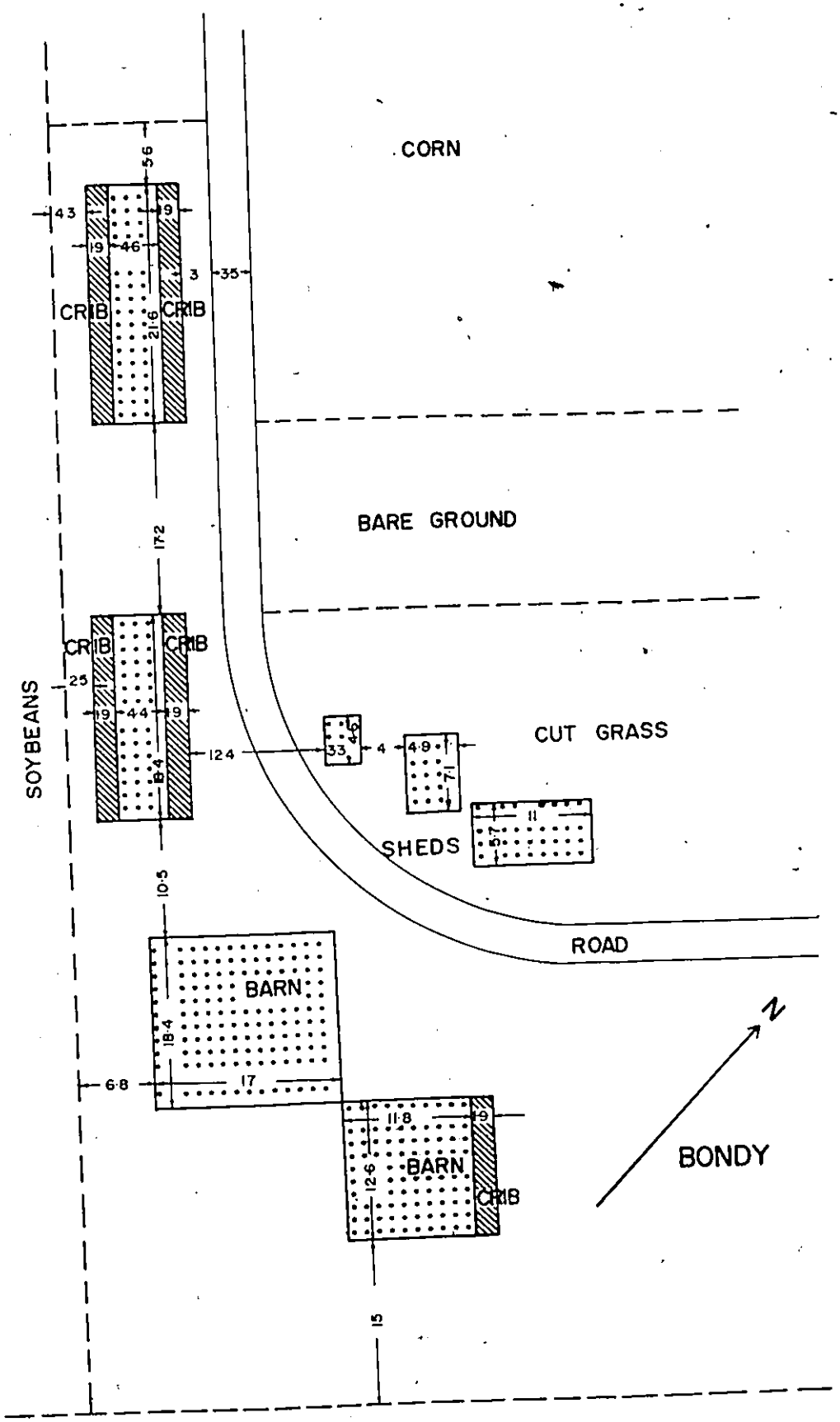

LAKE ERIE
LAKE ST. CLAIR
CHATHAM
BLENHEIM
PAINCOURT
TILBURY
STONEY POINT
WINDSOR
WHEATLEY
LEAMINGTON
KINGSVILLE
ESSEX
HARROW
AMHERSTBURG
DETROIT RIVER
N
0
10
km

FIGURE 9: Map of a typical farm, showing relative distances between cribs and other farm buildings.


CORN
BARE GROUND
CUT GRASS
SHEDS
ROAD
SOYBEANS
BONDY
N
CRIB
CRIB
CRIB
CRIB
BARN
BARN
CRIB
56
43
9
19
46
3
35
21·6
17·2
25
9
44
19
8·4
12·4
33
4·6
4
4·9
7·1
5·7
11
10·5
18·4
6·8
17
11·8
9
12·6
15

slowest no more than three days.

Collections of mice were made at 35 farms located throughout the study area (Figure 8). The mice were caught from May to September in both 1973 and 1974. The collections were made at the time when all the corn was being removed from a crib. Only populations obtained from corn cribs with concrete bases in a good state of repair, that is having no holes or cracks into which mice could escape, are included. Ground cover immediately around the corn crib usually was kept cut by the farmer. In the cases where this was not so, the ground cover was removed to reduce the number of escapees. In a few cases, cultivated ground ran right up to the base of the crib. This did not interfere with trapping.

To ensure efficient trapping a hardware cloth (screen) barrier was set up one meter from the base of the crib. Sherman live-traps were set up at ground level along the base of the corn crib and along the barrier. The removal of the corn forced all small mammals out of the crib. Mice fleeing from the corn were either allowed to run freely into traps or caught by hand and placed in an empty trap. Each population was sampled only once per season, with as many members of the population being captured as possible. No attempt was made to capture mice from any other farm buildings or the surrounding fields.

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