THE EFFECTS OF SELECTION ON CAGE POPULATIONS OF *DROSOPHILA* OF THE *VIRILIS* SPECIES GROUP

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PREFACE

Two distinct approaches to evolutionary problems were crystallized rather early in the development of the evolutionary concept. The first concentrated on unravelling and describing the actual course which the evolutionary process has taken in the history of the earth. This is the historical process, phylogeny, the methods of which are mainly those of systematics, comparative morphology, comparative embryology and palentology. The second approach emphasized studies on the mechanisms that bring about evolution, causal rather than historical problems, phenomena that can be studied experimentally.

In the twentieth century the attention of biologists shifted toward the causal aspects of organic evolution, especially among geneticists and biologists in related disciplines. Since evolution is a change in the genetic composition of populations, the study of the mechanisms of evolution fall within the province of population genetics. Changes observed in populations may be of different orders of magnitude and importance.

The present paper discusses experiments in which two closely related species, *Drosophila novamexicana* and *Drosophila americana texana* were crossed in the laboratory. These species are not known to be sympatric and have been shown to produce some fertile hybrids under laboratory conditions. Populations derived from crosses involving these species were maintained in population cages.

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INTRODUCTION

It has become well established that distinct but related species of the virilis group of the genus _Drosophila_ can be successfully intercrossed and that the hybrids produced are more or less fertile. Penetrating analysis of the chromosome structure and relationships have been made by Patterson and Stone (1952). On the basis of genetic tests, the ten known forms of the virilis group were classified under four subgroups: (1) _virilis_ which probably is native in the eastern Palearctic and Oriental regions; (2) the closely related forms: _americana_ _americana_, _americana_ _texana_ and _novamexicana_; (3) the distantly related North American forms which include _montana_, _flavomontana_, _borealis_ and _lacicola_; and (4) _littoralis_ and _imerentesis_, both European forms. Two species were chosen for the present study: _Drosophila_ _novamexicana_ and _Drosophila_ _americana_ _texana_. On the basis of current knowledge, these forms are geographically isolated. The distribution area of _texana_ includes the states of Texas, Louisiana, Mississippi, Alabama, Florida, Georgia, Oklahoma, Arkanasas, Tennessee, North Carolina, and Virginia. _D_. _novamexicana_ has been collected at three different localities: south-eastern Arizona, southern New Mexico, and western Colorado.

Patterson and Stone (1952) suggested that as a result of hybridization and recombination of the hereditary materials of _novamexicana_ and _texana_ arose _D_. _americana_ _americana_. They claimed that the gene arrangements in the chromosomes of _D_. _americana_ _americana_ are combinations of the inversions present separately in _D_. _novamexicana_ and _D_. _americana_ _texana_. It may be noted that _D_. _americana_ _americana_ and _D_. _americana_ _texana_ are at present subspecies which interbreed in the zone of overlap of their geographic distribution (from Arkansas to Tennessee).

Laboratory models of hypothetical zones of geographic areas of overlapping populations of novamexicana and texana were initiated in November, 1961, with the following purpose in mind: to determine the results of competition and selection when the hybrids formed were allowed to remain in the population. It was hoped that inferences of the possible selection pressures in a natural population could be made from laboratory populations. The laboratory populations used in this study were initiated with gene arrangements that had a definite frequency in the gene pool of the population. These gene arrangements were characteristic of each population. As the populations were sampled repeatedly at given intervals, the relative frequencies of the chromosomes of different types were observed to change. These changes, apparently unconnected with man-induced modifications of nature, give an idea of the nature of evolutionary process.

REVIEW OF LITERATURE

In a number of species of *Drosophila* genetic control is now such that the artificial construction of various kinds of gene pools presents no particular difficulty. Classical methods for the experimental study of gene pools in the laboratory (L'Heritier and Teissier, 1937; Teissier, 1942; Wright and Dobzhansky, 1946; Reed and Reed, 1948; Merrill, 1953; Buzzati-Traverso, 1955; Carson, 1958) provide an opportunity for the application of selection and the methods thus devised afford some control of population size.

L'Heritier and Teissier (1937) followed the fate of various mutant genes which were introduced into populations of flies kept in large cages with controlled amounts of food. They found that rather than being eliminated, certain mutant genes tended to become balanced in the population at definite levels (see also Teissier 1942, 1943). Many other investigators worked with modifications of their methods and gave further evidences for the persistent genetic variability in laboratory populations (Kalmus, 1945; Reed and Reed, 1950; Ludvin, 1951; Kerr and Wright, 1954; Buzzati-Traverso, 1955; Merrill and Underhill, 1956; Carson, 1958; Hockman, 1961).

Dobzhansky and collaborators studied populations of *Drosophila pseudoobscura* using genetic variability of the chromosomal type found in various wild populations. From these studies it has been theorized that balanced polymorphism, both of the genetic and the chromosomal type, give adaptive value by helping to buffer the population against extremes of various environmental conditions. The superiority of the heterozygotes is sufficient to keep the polymorphic condition balanced in the population, even at the expenses of the inevitable production of certain homozygous individuals which will be less fit than the population as a whole (Dobzhansky, 1951; Dobzhansky and Wallace, 1953; Wallace, 1954).

Buzzati-Traverso (1955) dealing with the same problem has suggested that heterozygosity for groups of polygenes as well as for single genes may serve as the selective basis of increased adaptive value and that natural selection acting over a period of time may bring about visible or measurable changes in individual flies that parallel increased fitness of the organism to its environment. This increased fitness might also show up as an increase in the total biomass produced by certain populations in certain environments.

Studies using interspecific hybrids in laboratory populations have been done by Zimmering (1948), Merrill (1951), and Moore(1952). These studies were directed toward the role of selection between two competing different Mendelian populations and it was found that both species coexisted, with one of them being favored. Hybrids were not formed or were inviable or sterile. Koopman (1950) introduced Drosophila pseudoobscura and Drosophila persimilis, each marked by a mutant gene, into a population cage. In each generation he discarded the hybrids which were phenotypically normal, in order to test the increase in sexual isolation due to selection.

Birch (1961) bred together in a population cage two sibling species of the tephrited fruit fly of the genus Dacus. His purpose was to measure differences in adaptation of the two species to temperature and crowded conditions. He found that a difference of 3^{o} C. reversed the direction of selection between the two species and their hybrids, as did also the differences between "crowded" and "uncrowded" populations.

Bruneau (unpublished thesis) hybridized in population cages three related species of Drosophila of the virilis group. The populations remained polymorphic and showed adaptive superiority of the heterozygous chromosomes to either homozygous combination in almost all populations. In certain populations and for certain chromosomes homozygous combinations were found to be superior to the heterozygotes.

Using two related species of Drosophila of the mulleri subgroup Mettler (1957) introduced them into population cages. He tested the effects of competition and selection between the species and their interspecific hybrids. Of the three chromosomes followed for the effects of selection the second and third exhibited heterosis, the X chromosome homozygote of one species (D. mojavensis) proved superior in ability to compete.

LeFever (unpublished thesis) crossed two subspecies of flies: D. americana americana and D. americana texana in population cages. He followed the X and fifth chromosomes, and in all but one instance the heterozygous combination had a higher frequency than either of the homozygous chromosomes. He also considered the possibility of interaction between the sampled genotypes.

MATERIALS AND METHODS

A. Cage Populations.

The flies that served as material for the investigation were *Drosophila novamexicana* collected from Patagonia, Arizona (stock number 2358.6) and *Drosophila americana texana* collected from Jamestown, South Carolina (stock number 2320.2a). Each laboratory stock was derived from a single wild female fertilized in nature. Both stocks were kindly provided by the Genetics Foundation of the University of Texas.

Experimental populations derived from crosses involving *D. novamexicana* and *D. americana texana*, and their F_1 hybrids were maintained in population cages. Nine populations which were arranged into three groups were analyzed:

I. Cages 1 and 2 were reciprocal crosses. Cages 6 and 9 were experimental populations initiated with F_1 hybrid males and females to determine the effects in a population where the first generation consisted of various F_2 hybrids; here crosses, if any, were of necessity between hybrid forms.

II. Cages 4, 5, 7 and 8 were experimental populations of reciprocal crosses between F_1 hybrids and a non-hybrid in order to determine the effects on chromosome frequencies in a population where the F_1 hybrids were backcrossed.

III. Cage 3 consisted of a population where crosses were made using males and females of both species to determine if hybridization occurs when there was a choice of mate. This type of cross tested the effects of competition between species and hybrids, if hybridization occurred, or solely between the two species if hybridization did not take place.

The experimental populations were bred in population cages similar to those used by Wright and Dobzhansky (1946), which in turn were modifications of those devised by L'Heretier and Teissier (1933). The cages were wooden boxes with outside dimensions of 14 x 10 x 6 inches. The bottom of the cages had 15 circular openings, 2½ inches in diameter, closed by tightly fitted corks. On the corks were placed crystallizing dishes, 2 inches in diameter, filled with culture medium that consisted of a mixture of water, yeast, agar, molasses, karo syrup, crushed bananas and proprionic acid. The medium was diced to facilitate egg laying by the females. The top of the box had a glass window through which the flies and the conditions of the food cups could be observed. The lateral and back sides the cages had windows for ventilation, covered by wire and gauze netting to prevent the entry and escape of flies. It was found necessary to cover the two lateral sides with aluminum foil in order to prevent the loss of moisture from the cage. The opposite side had a metallic funnel closed by a cork, which served as an opening to moisten the food in the dishes. A weak yeast suspension, was injected into the cage through a glass tube, while the flies were breeding. This water-yeast suspension was added daily and provided extra nourishment for the larvae (Wright and Dobzhansky, 1946).

The flies were raised in regular culture bottles. Virgins from these were aged for six days and introduced into the population cages. An initial population of 200 females and 200 males with known chromosomal constitution was introduced into each of nine cages. The incidence of the chromosomal types in the populations was determined per cage, per generation. Samples were taken at 15 days from origin and then at 30 days intervals after the initial sampling. The sampling procedure was the following: A fresh food cup was inserted into the cage and removed 24 hours later. Bits of this food covered with eggs were placed in regular culture bottles. When the larvae were fully grown (about 8 days after the sample was taken) their salivary glands were stained and their chromosomal configuration determined by microscopic examination.

To make the sample as representative as possible, the monthly sample of 800 chromosomes was subdivided into 5 subsamples. That is, chips of food with eggs were taken on each of 5 successive days. This gave 5 groups of 160 chromosomes each. A sample may be considered as a fair measure of the status of the population of a cage at the time when it was taken.

The abreviations for the species involved in the study were:

T - Drosophila americana texana

N - Drosophila novamexicana

TN - F_1 hybrids, derived from Drosophila americana texana females and Drosophila novamexicana males.

NT - F_1 hybrids, derived from Drosophila novamexicana females and Drosophila americana texana males.

The crosses involved and the date started are summarized in the following table:

INITIAL EXPERIMENTAL POPULATIONS

Group	Cage No.	Started	Initial population	
I	1	November 25, 1961	T	♀
			N	♂
	2	December 1, 1961	N	♀
			T	♂
	6	April 10, 1962	TN	♀
			TN	♂
	9	July 10, 1962	NT	♀
			NT	♂
II	4	April 6, 1962	TN	♀
			N	♂
	5	April 9, 1962	N	♀
			TN	♂
	7	April 15, 1962	TN	♀
			T	♂
	8	April 15, 1962	T	♀
			TN	♂
III	3	April 5, 1962	T	♀
			N	♀
			T	♂
			N	♂

The crosses to obtain the F_1 hybrids TN and NT were done by mass matings in regular culture bottles, with 80 virgin females and males introduced in each bottle. The F_1 progeny were separated while virgins, aged for six days and then transferred to the population cage. This procedure was followed in all experimental populations initiated with F_1 hybrids, with the exception of cage 9. Due to the low number of F_1 hybrids recovered in regular culture bottles, the N ♀ and T ♂ cross was done in a population cage, by introducing 200 virgin N ♀♀ and 200 virgin T ♂♂. The flies were left to breed and 15 days later the food cups were removed. The entire content of each cup containing eggs was divided and placed in six regular culture bottles, where the F_1 progeny hatched and were collected. The F_1 hybrids were then transferred to a new population cage.

All cages were initiated by placing the desired flies in it and one dish full of food. New food was added every three days for the remainder of the investigation. The room temperature where the cages were kept was 23 ± 2° C.

B. Cytological Techniques.

The cytological examination of the salivary gland chromosomes furnished information regarding the kinds of gene arrangements present in the experimental populations. Such examination was made using temporary aceto-orcein mounts (one percent orcein in 45 percent acetic acid). This method is unrivalled as a time-saving device, and moreover fresh temporary mounts are frequently superior to even the best permanent preparations. Full-grown larvae were decapitated in normal physiological saline solution (0.67 gm NaCl/100 ml of H_2O). The salivary glands were placed in 1 N. HCL for one minute and then placed in aceto-orcein stain for 12 minutes. The glands were removed from the stain and placed on a slide in one drop of 45 percent acetic acid. The glands were covered with a coverslip and their chromosomes spread by pressing lightly on the coverslip with a needle. The preparation was then ringed with a mixture of resin, Canada balsam and lanolin.

In order to determine the gene arrangements of each species, the gene arrangement of *Drosophila virilis* was selected as standard. *D. virilis* has no inversion in either the homozygous or heterozygous condition. Therefore the F_1 hybrids of *D. virilis* and *D. novamexicana* and *D. virilis* and *D. americana texana* showed heterozygous inversions which could be recognized by the characteristic inversion loops. The chromosome maps of this standard gene arrangement as worked out by Hsu (1952) were utilized. The homozygous chromosome combinations for each species were determined by the banding pattern and each inversion was located and recognized by the sequence of the bands on each of the salivary chromosomes.

When *D. novamexicana* and *D. americana texana* were crossed to *D. virilis*, microscopic examination of the salivary gland chromosomes of the F_1 hybrids revealed the following gene arrangements:

Chromosome number	*D. virilis* and *D. novamexicana*		*D. virilis* and *D. americana texana*	
	Inversion	Chromosomal region	Inversion	Chromosomal region
X	overlapping a, b, c	L to N	overlapping a, b	N to Y
2	b		-	-
	overlapping a, c	K to U	a	K to U
3	a	N to Z	a	N to Z
4	a	L to W	-	-
5	b	A to D	-	-
	a	K to V	a	K to V

In the crosses between D. novamexicana and D. americana texana the X, second, fourth and fifth chromosomes were followed. The presence of the same inversion in the third chromosome of both species made the cytological distinction of these chromosomes impossible. The sixth chromosome was not analyzed due to its minute size.

C. Analysis of Results.

In a random mating population the frequency of any genotype at one locus is given by the binomial square rule. The frequency of genotypes for the loci simultaneously will be the appropriate term in the product of the two binomial expansions of the separate loci. Thus if the frequency of A is q_1 and that of B is q_2, the genotype frequencies at A locus are: q_1^2 AA, $2q_1\ (1-q_1)$ Aa and $(1-q_1)^2$ aa; while for the B locus, the frequencies are: q_2^2 BB, $2q_2\ (1-q_2)$ Bb and $(1-q_2)^2$ bb. For the combined genotypes the frequencies will be:

AABB	AaBB	aabb
$q_1^2\ q_2^2$	$2q_1\ (1-q_1)\ q_2^2$	$(1-q_1)^2\ (1-q_2)^2$

A new order of complexity is introduced when an attempt is made to study simultaneously two or more segregating systems in the same population, because of the probability that the evolutionary fates of the different components of a polymorphic system are not independent.
Such will be the case if there is interaction between the different loci in the determination of the fitness of various genotypes. For example, the fitness of individuals of the genetic constitution AA, may be greater than those of the constitution aa, if at the second locus these individuals are BB; but the fitness relationship may be reversed in the presence of bb at the second locus. If such is the case the loci A, a and B, b are not independent in their fates in the population.

White (1957) working with the grasshopper Moraba scurra presented statistical evidence which showed that the pericentric inversions carried on two different chromosome pairs in this species were not combined at random in the adult male individuals of certain natural populations. The deviations from random combinations were regarded as proof of genetic interaction between the two systems. This statistical analysis, as worked out by Griffing, tested the interaction effects by determining the deviations from proportionality to the marginal frequencies, in the case of each of the nine genotypes. The analysis involved the arrangement of the nine different karyotypes in a 3 x 3 matrix. To test whether the three chromosomal combinations were randomly combined with the other three chromosomal combinations, the expected frequency of each karyotype was determined from the marginal totals by multiplying each row total by each column total and then dividing by the total number of observations. The observed value minus the expected value gave the deviations. In a table of this kind the deviations in each row and each column necessarily sums to zero, and the table as a whole has four degrees of freedom, when the deviations from expectation are tested by the chi-square method. It involved the partitioning of the X^2 into four orthogonal components each associated with a single degree of freedom.

The data, thus take the form of a 3 x 3 matrix as illustrated:

		Chromosome 2			
		TT	TN	NN	Row Total
Chromosome 4	TT	n_{11}	n_{12}	n_{13}	$N_{1.}$
	TN	n_{21}	n_{22}	n_{23}	$N_{2.}$
	NN	n_{31}	n_{32}	n_{33}	$N_{3.}$
Column Total		$N_{.1}$	$N_{.2}$	$N_{.3}$	N

$$\text{Theoretical frequency}_{11} = \frac{N_{.1}\ (N_{1.})}{N}$$

$$\text{Deviation}_{11} = n_{11} - \frac{N_{.1}\ (N_{1.})}{N}$$

Three tables like the one illustrated above were done per experimental population, per analysis, utilizing: (a) chromosomes 2 and 4 (b) chromosomes 2 and 5 (c) chromosomes 4 and 5. The observed frequencies n_{11} ..... n_{33} were taken from the data, the theoretical frequencies and deviations were calculated by the method explained.

The null hypothesis considered (which is alternative to the random mating and no selection) was that the chromosome pairs in the population were independent systems. The test for interaction involved the $X^2_{(4)}$ partitionable into four orthogonal components based on linear and quadratic contrasts. Probability values were determined for each $X^2_{(4)}$ value to see whether or not the results supported the null hypothesis. Any $X^2_{(4)}$ value greater than 9.49 was considered significant and thus led to the rejection of the hypothesis.

RESULTS AND OBSERVATIONS

There was no common denominator in the nine experimental populations studied. Group I which included cages 1, 2, 6 and 9 were duplicates in regard to the initial composition of the population. Cages 1 and 2 were reciprocal crosses of *texana* and *novamexicana*. Cages 6 and 9 were reciprocal crosses in which the experimental populations were initiated with F_1 hybrid progeny. Group II included cages 4, 5, 7 and 8. They represented reciprocal crosses between the F_1 hybrid and the parental *texana* or *novamexicana*. Group III consisted of cage 3 where the population used as founders were males and females of both species.

Tables 1 to 27 summarize the results of the nine experiments. The information is arranged to show the percentage of homozygous and heterozygous second, fourth and fifth chromosomes. The X chromosome is treated separately since it obviously constituted material which behaved remarkably differently and was subjected to quite different selection pressures (Tables 29 to 31). Homozygous *texana* chromosomes are represented by TT, homozygous *novamexicana* chromosomes by NN, and the heterozygous condition by TN or NT. The chromosomal composition of the population is given in percentage. The distribution of the autosomal classes found in each larva analyzed is given (Tables 3, 6, 9, 12, 15, 18, 21, 24 and 27). In these tables homozygous *texana* is denoted by T, homozygous *novamexicana* by N, and the heterozygous condition by H.

The data are represented graphically in figures 1 to 18. The percentage of homozygous and heterozygous combinations of the chromosomes is shown for each population. The time ordinate is given in elapsed number of days.

The interaction effects, using White's (1957) method of analysis are shown on Tables 33 to 82.

Group I

Cage 1. (Tables 1, 2 and 3, Figures 1 and 10)

Cage 1 was begun on October 10, 1961. A few days later the cage was found to have a contamination of Drosophila melanogaster and was discontinued before samples were taken. It was set up again on November 25, 1961 with an initial population of 400 virgin flies of equal numbers of texana females and novamexicana males. After an initial tendency to oscillate the population size came into an equilibrium with the food supply.

The cross was obligatory producing only F_1 hybrids (H-H-H) in the first generation. The second generation showed a remarkable drop in frequency of the heterozygous combination. In the next generation the heterozygous chromosome combination built up and remained the chromosome combination recovered most frequently (except for the X chromosome). The frequencies of the homozygous chromosome combinations fluctuated, but the novamexicana homozygous chromosome had a higher frequency in almost all samples.

Table 2 shows that the equilibrium of the chromosome types was reached for the fifth chromosome.

In table 3 the distribution of the autosomal classes recovered in each analysis is presented. All 27 possible combination were present. No noticeable trend in change of class frequencies was observed.

The data are presented graphically in Figures 1 and 10.

Cage 2. (Tables 4, 5 and 6, Figures 2 and 11)

This cage was started with novamexicana females and texana males. The cross was obligatory producing only F_1 hybrids (H-H-H). The cage went poorly at the beginning, not may eggs being laid. The population size did not increase substantially until after approximately 75 days from origin (visual estimation).

The F_2 showed a remarkable drop in the frequency of the heterozygous chromosome combination and the selective advantage of the heterozygous combination was not shown for any of the chromosomes involved in the investigation. The homozygous novamexicana chromosome combination was highest in frequency in all samples and for all chromosomes followed. Table 4 shows such results.

Equilibrium of the chromosome types was not reached for any of the chromosomes. The total number of novamexicana was greater than 50 percent (See table 5).

The population remained chromosomally polymorphic with the homozygous texana and the heterozygous chromosome combination at low frequencies.

Almost all the 27 possible autosomal classes were present. There was a slight tendency toward an increase in frequencies of the N-N-N and the N-T-N classes with a decrease in the frequency of the T-T-T class and the H-H-H class (See table 6).

The data are presented graphically in Figures 2 and 11.

Cage 6. (Tables 7, 8 and 9, Figures 3 and 12)

Experiment six was started with male and female F_1 hybrids from the cross texana females x novamexicana males. The cage went well and a large number of larvae were produced in each generation. The population built up rapidly.

The heterozygous chromosome was more frequent in the first three analyses, but dropped in the 105-day analysis to 28 percent and remained at that frequency for the remainder of the experiment. The homozygous novamexicana combination increased in the 105-day analysis and remained more or less stable. In all instances the frequency of novamexicana chromosome combination was higher than that of texana.

The second chromosome heterozygotes were far more frequent than the two homozygous combination in all analyses, but in the 165-day analysis the homozygous novamexicana was more abundant.

The frequency of the heterozygous fourth chromosome fluctuated but in almost all instances was more abundant than either of the two homozygous combinations. The homozygous novamexicana chromosomes were more frequent than the homozygous texana combination in all samples.

The relative frequencies for the three zygotic combinations of the fifth chromosome were somewhat similar to those of the fourth chromosome. The heterozygous combination was always more frequent than either of the homozygotes. The texana chromosome arrangement was the lowest in frequency in each analysis (See table 7).

Table 8 shows that the novamexicana chromosome frequency always remained over 50 percent and thus higher than the texana chromosome frequency. Equilibrium of the chromosome types was reached only for the fourth chromosome.

Almost all the 27 possible autosomal classes were present. No trend toward selective advantage of a particular autosomal class was noticed.

The data are presented graphically in Figures 3 and 12.

Cage 9. (Tables 10, 11 and 12, Figures 4 and 13)

The founder stocks for this experimental population were male and female F_1 hybrids, obtained from the cross _novamexicana_ ♀ x _texana_ ♂. The cage went well, with a rapid increase in population size.

The behavior of the chromosomes in each of the zygotic combinations was remarkably similar. The heterozygous combination was more abundant in all samples with only a limited degree of fluctuation. The homozygous _novamexicana_ and _texana_ combinations showed equilibrium for almost all chromosomes. (Table 10).

For the X chromosome the heterozygous combination was in all but one sample (15-day analysis) recovered in higher frequency. The homozygous chromosome types reached equilibrium at the 105-day analysis.

Table 11 shows the chromosome frequencies for Cage 9. _Novamexicana_ chromosome frequency was in almost all samples 50 percent or somewhat higher.

Only the H-H-H combination in the autosomal class was represented in the initial population. This class remained the most abundant, but almost all the other possible classes were present. There was a slight selection trend in favor of the double and triple heterozygous chromosomes. (See Table 12).

Graphic representation of the data is in Figures 4 and 13.

Group II

Groups II included four experimental populations which represented two reciprocal crosses between the F_1 hybrids and the parental _texana_ or _novamexicana_. In general, the heterozygous chromosome combination showed selective advantage. The frequency of the chromosomal combination in the X chromosome varied, depending on the parental stock used as founder for the population.

Cage 4. (Tables 13, 14 and 15, Figures 5 and 14)

This experimental population was started with F_1 hybrid females, derived from a cross between texana females and novamexicana males, crossed to the parental novamexicana males. The cage went well with the expected population increse and stabilization.

The fourth and fifth chromosome analysis showed a higher recovery of the heterozygous combination in the 135 and 165-day analysis, after showing fluctuation in frequency in the previous analysis. The homozygous texana combination was the lowest in frequency in all cases. The novamexicana homozygous combination showed a progressive decrease in frequency (exception: fourth chromosome, 75-day analysis).

For the second chromosome the homozygous texana combination was always lowest in frequency of recovery. The novamexicana chromosome combination predominated in two analyses, the heterozygous chromosome combination in the other four analyses (Table 13).

For the X chromosome the frequency of the three possible combinations was as follows: the texana homozygous chromosome combination was recovered less often, the novamexicana homozygous chromosome combination except in one analysis (the 135-day analysis) always showed a higher frequency (Table 13).

The cage was started with 25% texana chromosomes and 75% novamexicana chromosomes. In general there was an increase in the texana chromosome frequencies and in the 165-day analysis, it reached 42.22%. The abundance of the heterozygous chromosome combination was responsible for the increase in frequency of the texana chromosome (See Table 14).

Table 15 shows the distribution of the autosomal classes per sample. In the 15-day analysis all possible classes were present. Other analyses showed that there was a trend toward the recovery of classes which contained H and N chromosomes. Those classes with T chromosomes were the least frequent, throughout the experiment.

The detailed constitution of the population during its history is shown in Figure 5 and 14.

Cage 5. (Tables 16, 17 and 18, Figures 6 and 15)

The founder stock for the fifth experimental population consisted of novamexicana females, and F_1 hybrid males, obtained by crossing texana females with novamexicana males. The cage went well and after an initial oscillation in population size the population built up and no other fluctuations were noticed.

The population remained polymorphic throughout the experiment. In all analyses done and for all chromosomes the homozygous texana chromosome combination was the least abundant.

For the three autosomes involved in the study, the heterozygous chromosome combination showed the highest frequencies. The homozygous novamexicana chromosome combination generally decreased progressively in frequency. (See Table 16).

The frequencies of the novamexicana homozygous chromosome combination and the heterozygous chromosome combination showed fluctuations for the X chromosome. Heterosis cannot be said to have been established and selection trends were erratic (See Table 30).

As in the previous experimental population the texana chromosome type increased from its original 25% frequency until it almost equalled the novamexicana chromosome type. (See table 17).

The autosomal classes are shown in Table 18. The 15-day analysis showed distribution of all possible chromosome combinations. The other analyses showed slight trends favoring the triple and double heterozygous classes, as if the population were under a stabilizing selection pressure with the selective advantage for the heterozygous classes.

The data are graphically represented in Figures 6 and 15.

Cage 7. (Tables 19, 20 and 21, Figures 7 and 16)

The flies which served as material for this experimantal population were F_1 hybrid females, derived from a cross between *texana* females and *novamexicana* males, crossed to *texana* males. The cage went well, no reduction in population size was observed after the population density plateau was reached.

The 15 and 45-day analyses showed little difference in the frequencies of the homozygous *texana* chromosome combination and the heterozygous chromosome combination in the second chromosome. Successive analyses showed a marked reduction in the frequencies of the *texana* chromosome combination with an inverse increase of the heterozygous chromosome combination. Due to the experimental design the *novamexicana* homozygous chromosome combination did not appear in the 15-day analysis, but slowly increased in its frequency, reached a maximum in the 105-day analysis, after which its frequency slowly dropped.

The analysis of the fourth chromosome revealed a slow increase in frequency for the heterozygous chromosome, followed by a drop and then a progressive recovery. In the last three analyses the heterozygous chromosome combination was more abundant than either homozygous. The homozygous *texana* chromosome combination showed a progressive decrease in frequency. The frequencies of the homozygous *novamexicana* chromosome combination fluctuated. No equilibrium of the homozygous chromosome types was reached; texana always predominated (See Table 19).

In the fifth chromosome, of the three possible chromosome combinations, the heterozygous predominated in all but one of the analyses. The frequencies of the homozygous texana chromosome combination fluctuated, as did the homozygous novamexicana chromosome combination, although the later always remained less abundant (Table 19).

In general for the X chromosome the homozygous texana chromosome combination was recovered most abundantly.

Table 20 shows the chromosome frequencies for this experimental population. Although the frequencies of the novamexicana chromosomes fluctuated in almost all analyses they showed an increase from the original 25% frequency. Equilibrium of the chromosome types was only reached for the fifth chromosome.

Table 21 shows the distribution of the autosomal classes. The 15-day analysis showed formation of all possible classes. The following analysis showed a slight trend toward the formation of a cluster of classes around the heterozygous chromosome. Such a cluster somewhat bends toward the H-T-T and H-H-T combinations.

The data are presented diagramatically in Figures 7 and 16.

Cage 8. (Tables 22, 23 and 24, Figures 8 and 17)

The founder stock for this experimental population consisted of texana females and F_1 hybrid males derived from a cross between texana females and novamexicana males. The cage went well.

Analysis of the second chromosome frequency revealed the heterozygous combination to be more abundant or as frequent as the homozygous texana chromosome combination. The homozygous novamexicana combination was always less abundant and did not make its appearance until the 75-day analysis.

In the fourth chromosome either the heterozygous chromosome combination or the homozygous texana chromosome combination predominated. Novamexicana homozygous chromosomes did not appear until the 75-day analysis and remained at a low frequency.

Analysis of the fifth chromosome revealed that the heterozygous chromosome combination equalled or exceeded the frequencies of the homozygous texana chromosome. Novamexicana homozygous chromosomes gradually increased, but in all cases remained at low frequencies (Table 22).

In all analyses of the X chromosome, the texana homozygous chromosome was favored (Table 30).

In all automosomes followed, novamexicana chromosome frequencies increased above the original 25% frequency. For the X chromosome the novamexicana chromosome frequencies fluctuated (See Tables 23 and 28).

The data are represented diagramatically in Figures 8 and 17.

Table 24 shows the distribution of the autosomal classes. The 15-day analysis showed the distribution to be non-random, although all possible classes were present. In the following analysis, there was a slight trend indicating selective advantage of the triple hybrid class (H-H-H). This class was maintained in relative abundance. The classes of double hybrids (H-H-T, T-H-H, H-T-H) showed slighty favorable selection trends.

Group III

Cage 3. (Tables 25, 26 and 27, Figures 9 and 18)

Cage 3 consisted of an experimental population where crosses were made using males and females of both species. The cage went well.

Repeated sampling of the experimental population showed that the homozygous novamexicana chromosome combination was recovered more abundantly than either the homozygous texana chromosome or the heterozygous chromosome combination. The population remained polymorphic with fluctuations between the frequencies of the homozygous texana chromosomes and the heterozygous combination (Table 25).

The X chromosome showed nearly the same chromosome combination frequencies as did the autosomes, the homozygous novamexicana chromosomes being in all cases more abundant (Table 31).

Table 26 shows that the frequency of novamexicana chromosomes was higher than the original 50% and always higher than the texana chromosome frequency. Equilibrium of the chromosome types was only reached for the second chromosome after 165-days of selection.

The distribution of the autosomal classes is presented on Table 27. The N-N-N class was maintained quite well in the population. There was selection against the T-T-T class, but no other trends were noticed.

DISCUSSION

A. Cage Populations.

When a genetically variable gene pool faces a new environmental challenge, changes may be expected to occur. To understand such changes it would be ideal to know the details of the structure and interaction of the gene pool before and after the changes. Although such conditions can hardly be met in any study of natural populations, an approach at least can be made using experimental laboratory populations.

Experimental populations set up in population cages are not intended to be replicas of wild conditions. On the contrary the investigator arbitrarily controls, as far as possible, the intricate variables involved and aims to follow one of them. From population cage analysis much of the evidence for the adaptive function of Drosophila chromosomal polymorphism has been derived. Observation of changes in the relative frequencies of competing gene arrangements is usually said to be sufficient to determine the net adaptive value or fitness value of the competing karyotypes (Dobzhansky and Levene 1951). However, experimental populations once initiated evolve new genotypes. These genotypes may be novel in nature and might never have occurred in the wild population. The factors of the wild environment upon which the population's adaptation depends are virtually unknown. The investigator can never hope to even approximate the wild condition. The laboratory conditions are novel to the species, yet they are not so extreme that the species norm of reaction cannot permit both reasonable survival and adjustment of its gene pool. It is this adjustment which was studied in the work described.

The data described in the present paper utilized inversions, which served as markers in the analysis of the experimental populations. Inversions represent blocks of genes in particular sequences, so it was the gene sequences which actually served as the entities followed. By appropriate crosses various hybrids were formed with different combinations of the gene arrangements. Populations of hybrids and homozygous "species" developed different genetic systems under similar pressures of selection. The fitness of the different gene sequences was defined as to their relative contribution to the gene pool of the next generation, measurable in terms of their relative abundance. The carriers of the different gene sequences were demonstrated to have different selective values. The assumption was that the carrier of a particular gene arrangement might be better adapted than one with another sequence, and thus become more abundant in the population.

Group I

Cage 1, 2, 6, 9.

These experimental populations were duplicates in regard to the initial quantitative composition of the population. Cages 1 and 2 were reciprocal crosses with the obligatory formation of hybrids in the F_1. Cages 6 and 9 were reciprocal experimental populations initiated with F_1 hybrids.

There was no common denominator in the results obtained from experimental populations, but no chromosomal combination was eliminated. The events in the populations were determined by the degree to which the heterozygotes were superior to the homozygotes (heterosis), as well as whether the two homozygotes were equal in selective value or whether one of them was superior to the other.

Wide divergences in the outcome of what should have been replicate experiments were obtained. These divergencies were mainly of two kinds; (1) different equilibria of the chromosome types apparently reached or not reached by populations which were quantitatively of similar initial composition and (2) erratic selection trends, which made the same component of the population alternately increase and decrease in frequency. The changes in equilibrium value and in selection trends have been observed in Mendelian populations of mixed geographic origin and rarely in populations of geographically uniform origin (Dobzhansky and Pavlovsky, 1953). The explanation given to this complex phenomenon is that the gene complexes in the chromosomes with different gene arrangements from the same natural population have been coadapted by a long process of natural selection to produce fitness in heterozygotes. The results of Wallace (1955), Vetukhiv (1954) and Levine (1955) suggest that coadaptation involves the whole genotype.

One can hardly suppose that the gene complexes between two different species are coadapted by natural selection to produce superior fitness in artificial hybrids. A different explanation of the effect of heterozygosity seems to be necessitated by the data, unless one assumes that the formation of heterotic hybrids is indicative of common ancestry between the two species.

In artificial hybrid populations the combination of genes derived from different Mendelian populations, gives a great variety of genotypes, most of which may never have existed or survived in nature. New adaptively integrated genotypes are formed and may be different in different populations. Natural selection would tend to perpetuate the genotypes which possess high adaptive value under the experimental conditions.

Da Cunha and Dobzhansky (1954) have claimed that the amount of chromosomal polymorphism is a function, in species of *Drosophila*, of the number of ecological niches occupied by those species. This claim, so far seems to be supported by facts (Carson, 1955). *Novamexicana* is restricted in geographic distribution and therefore it is subjected to relatively consistant environmental fluctuations. Its gene sequences have been claimed to be of only one type; it is a chromosomically monomorphic species (Hsu, 1952). One would imagine the species to be adaptively specialized. On the other hand, *texana* has a wide geographic range and displays a high degree of chromosomal polymorphism (Hsu, 1952). When the two species were set up in a population cage the homozygous *novamexicana* chromosome combination significantly outproduces the homozygous *texana* chromosome combination. This is assumed to indicate that in the relatively constant niche provided by the population cages, the *novamexicana* homozygotes have superior selective value.

Group II

Cages 4, 5, 7, 8.

The experimental populations included in this group represented two reciprocal backcrosses of the F_1 hybrids to the parental homozygote, either *novamexicana* or *texana*. Cages 4 and 5 were duplicates in regard to the initial chromosomal composition. The results of the three autosomes followed were generally similar in that the heterozygotes showed heterosis. Nearly every sample of each cage had more heterozygotes than were to be expected according to the Hardy-Weinberg formula.

The three possible gene arrangements for each chromosome were present in all samples and balanced polymorphic equilibrium was reached for most of the autosomes. Selection trends were slightly erratic and if equilibrium of the chromosome types was reached it was not at similar percentage values.

Cage 7 and 8 were backcrosses and duplicates, in regard to the initial composition of the experimental population. The results were generally similar to those of Cages 4 and 5: the heterozygote in nearly all samples showed heterosis; the population remained chromosomally polymorphic. The selection trends were slightly erratic and if equilibrium of the chromosomes types was reached it was not around similar percentages values.

In all four experimental populations, the frequencies of the chromosome types lower in the initial populations generally showed a consistant increase. This increase can be accounted for by the fact that all cages showed heterosis.

The fate of the homozygous chromosome combinations was determined by the initial composition of the population. The homozygous chromosome started at a higher frequency (75 percent) remained in all cases more abundant than the homozygous chromosome started at 25 percent frequency. The chromosomal type initially at low frequency increased in frequency and was maintained in the population due to the selective advantage of the heterozygote.

Although the trends toward selection of a particular autosomal class were slight, this group of experimental populations seemed to show a slight selective advantage favoring the triple or double heterozygous autosomes. These were the chromosomal classes which were maintained quite well as the populations were repeatedly sampled (See

Tables 15, 18, 21, 24).

These results might show that the selective advantage of a particular class depends: (1) on the physical environment; (2) on the initial quantitative composition of the population; and (3) on the fact that a population as a whole is a harmoniously genotypic balanced system (Wright, 1952).

Without attempting an extended review of this complicated subject it might be worthwhile to mention a few of the interrelated facts.

It has long been known that the expression of a gene is subjected to the influence of genetic modifiers and that a gene changes its expression in different genetic backgrounds. Multifactorial inheritance has been recognized for several decades. Reeve and Robertson (1953) have shown that when a polygenic system is altered by selection so that the model phenotype is driven in a given direction, a conservative force tends to cause it to revert when selection is relaxed.

Dobzhansky and co-workers (1958) have shown that populations of several species of Drosophila are polymorphic in chromosomal structure and that this polymorphism is maintained because of the adaptive superiorities of the structural heterozygotes. Synthetic populations of structurally different chromosomes of diverse geographic origins or diverse gene pools may or may not develop adaptive advantages of the structural heterozygotes.

Waddington (1958) started with a wild type population and by means of artificial selection built up a polygenic system producing a phenotype indistinguishable from that characteristic of a given homozygous mutant. Working from an entirely different point of view, Mayr (1953) has pointed out that peripheral populations of many species of birds seem to be restricted in phenotypic variability as long as they are tied to the central population by interbreeding, but often display sudden and striking changes in phenotype when they become isolated from the gene pool of the whole species.

All these diverse observations point in the same direction. They emphasize that the genetic material of cross-fertilizing populations is not a fortuitous aggregate of particular units, but is an integrated whole in which the elements work in concert. Any change in the proportions of different genetic elements produced by selection requires compensatory changes in other elements to produce a newly integrated equilbrium.

Group III

Cage 3.

This cage consisted of an experimental population initially composed of males and females of both species, The outcome of the experiment did not deviate too much from what was expected. Cross fertility had been found between the different members of the virilis group (Patterson, 1947). In a mixed population where there is a choice of mates, one would expect a relative abundance of crosses to occur within the species. In general terms, the experiment becomes one of interspecific competition.

Studies of interspecific competition have led to certain theoretical and experimental conclusions. On the basis of theoretical equations, Volterra (1926) predicted that two types with identical needs and habits cannot survive in the same place if they compete for limited resources. Zimmering (1948) demonstrated experimentally the validity of the theory. Analysis of the instances in which both species survive has shown that they occupy slightly different niches (Crombie, 1947, and others).

An unforeseen exception to the rule was found in Drosophila in the survival of two types because of the superiority of inversion heterozygotes. The survival of more than one type maintains the genetic variability in the population.

In Cage 3 the novamexicana arrangement in each chromosome was higher in frequency in all samples. Under the relatively restricted environmental conditions which the population cage provided, the novamexicana chromosome arrangement outproduced the texana chromosome arrangement. However, the population remained polymorphic after 165-days of selection. Both species and their hybrids coexisted in the population. The heterozygous chromosome combinations were usually more frequent than the homozygous texana. The existence of the heterozygotes would tend to maintain the population polymorphic. Such polymorphism was not balanced due to the fact that there was no heterosis. One would expect marked fluctuations in the frequencies of the heterozygotes and the texana homozygotes, while the novamexicana homozygous combinations would tend to remain in a rather constant range of fluctuation.

B. The X Chromosome.

The outcome of the nine experimental populations showed that the X chromosome represented quite different genetic material and was subjected to quite different selection pressures.

Several extra difficulties were encountered while dealing with the X chromosome. The data are based only on the females from each analysis. This means that the number of X chromosomes analyzed was less than that for the autosomes. This number varied from sample to sample. The X chromosome of the males was followed, and it was found that the ratio between males and females was upset, the females always outproducing the males (See Table 32). Similar upsets in the sex ratio were found by Bruneau (unpublished thesis) and he suggested it may be due to the crowded conditions present in the cage, resulting in competition between the sexes.

Selection trends were highly erratic. Of the nine experimental populations, chromosomal equilibrium for the X was reached in Cages 1, 4, 5 and 9. In three of the experimental populations there was selective advantage for the homozygous novamexicana X chromosome (Cages 2, 4, 3). Only in Cage 9 did the heterozygous X chromosome combination show selective advantage. Cages 1, 5, and 6 fluctuated in selection trends favoring the homozygous or the heterozygous X chromosome combinations. In Cages 7 and 8 the homozygous texana X chromosome showed selective advantages (Tables 29, 30 and 31).

In general it can be said that the homozygous X chromosome combinations were favored.

The failure of the heterozygous X chromosome to be superior in all except one of the tests conditions may be due to the special need of the X chromosome for equal adaptedness in haploid and diploid conditions (Muller, 1950). In Muller's words:

> "A study of the expression of mutant genes which exist in two doses in the female and one in the male (those in the X chromosome) shows that the species genetic mechanisms have been evolved for compensating the effects in the two sexes much more nearly the same than it otherwise would be."

There might be a strong internal balace which may give the homozygous chromosome type superior adaptive value.

Another possible and perhaps more feasable explanation for the superiority of the homozygous X chromosome is that given by Haldane (1957). He claimed that alleles added to autosomal inversions must be cumulatively heterotic, while those added to segments of sex chromosomes that are genetically isolated from one another by suppression of crossing over, need not possess that property. Haldane's explanation is favored and it could serve as a working hypothesis for future investigations.

These species have previously been used in experimental population studies by Bruneau (unpublished thesis). The results are comparable to those reported here. Using the same type of experimental cages and methods of analysis, he hybridized the species *Drosophila virilis*, *D. novamexicana* and *D. a. texana*. The frequency of *virilis* chromosomes was predominant in crosses either with *texana* or *novamexicana*. In most cases the heterozygotes showed heterosis. Bruneau reported that, for any species, the reciprocal obligatory populations gave similar results and that little difference existed between these and the F_1 initiated populations. As already discussed, the results in the present investigation were not similar for the reciprocal crosses or for the F_1 initiated populations.

Mettler (1957) utilized experimental cages in a similar investigation using *Drosophila* of the mulleri subgroup: *D. arizonensis* and *D. mojavensis*. When reared together in population cages the population came to consist mostly of heterozygotes and the parental species were maintained in low frequencies. Cytological analysis showed that in most cases the second chromosome heterozygote and the third chromosome heterozygote exhibited heterosis. Only in one of the populations did the X chromosome heterozygote show heterosis, otherwise *mojavensis* homozygotes had a greater selective value. As discussed, the results in the present investigation were similar, the *novamexicana* X chromosome showing a greater selective value.

It has been suggested by Patterson and Stone (1952) that *D.*

americana americana arose as the result of hybridization and recombination of the hereditary materials of D. novamexicana and D. americana texana. The present investigation as well as those reported by Bruneau and Mettler showed that occasional crosses could produce heterotic combination. These heterotic combinations could have survived and continued to contribute genes from one species to another which might eventually have added extra variability leading to the formation of subspecies.

C. Statistical Considerations.

The organization of genotypes is undoubtedly a very complex phenomenon. To what extent and in what direction species respond to selection is usually explained in terms of genetic variability, but it seems obvious that this is only part of the answer.

In an effort to determine whether or not selection for one inversion system resulted in the incidental appearance of another, White's (1957) method of statistical analysis for "interaction effects" was done for each experimental population, chromosome pair (2 and 4, 2 and 5, 4 and 5), and population analysis (See tables 33 to 82). Chi-square values were calculated (with four degrees of freedom) and positive "interaction effects" were found to exist between the inversion systems of the chromosome pairs in almost all population analyses and for all experimental populations.

There are four possible explanations for the considerably consistent and interesting results. (1) The mating system of the populations may not have been at random, i.e. failure of some flies carrying a particular genotype to mate. (2) There may have been a negative correlation between the several components of the selective value of which only one, the relative frequency of a particular inversion system, was measured. (3) Selective values or some components of them may have been frequency-dependent. (4) The fates of the several components of an evolutionary system are not independent.

Assortative matings does not seem unlikely on a priori grounds, since we were dealing with artificial populations constructed from two different Mendelian populations. The assumption that the populations were panmictic, might not have been strictly true. Indeed, it is believed not to be true at all in experimental population 3, where both species were bred together with a choice of mates (tables 78 to 82). It should be noted that this was the only experimental population where "positive interaction effects" were obtained in all analyses and for all chromosome pairs. In the other experimental populations, for each chromosome pair statistically treated, at least one analysis gave "negative interaction effects". This might show that if there was departure from random mating, it might not have been significant, since there is no reason to assume that the mating patterns varied in each population from generation to generation. In spite of reservations, it is believed worthwhile to consider the other alternative which might also explain the results obtained.

The experimental design followed in the study did not provide for a method to study correlations between the several components of the selective value. Whether or not there was a positive effect of a deficient genotype on fecundity which would compensate for its negative effect on variability can only be dealt with theoretically.

It is believed that the differential mortality of the various genotypes occurred quite early in the life cycle. Patterson and Stone (1949) did hybridization studies involving novamexicana and texana, directed toward determining the fertility of the hybrids formed. Although these hybrids are not strictly comparable to the ones formed in a population cage experiment (the number of different genotypes formed in a cage experiment is exceedingly large and variable, and the fertility of all these possible genotypes has not been tested), the hypothesis that the differential survival of genotypes occurs among gametes, zygotes or larval stages is favored.

The frequency-dependent selective values as considered mathematically by Levene (1953) is unlikely to account for the high selective value of different genotypes under similar experimental conditions. Where different genotypes are adapted to alternative ecological niches, a particular favored genotype will tend to increase in frequency. Environmental conditions are not claimed to have been stable in this study, but all the experimental populations were treated alike. This explanation is very complex, since it involves factors unknown to the investigator and there seems to have been no obvious ecological differences among the experimental populations. Spiess (1957) has demonstrated that some of the selective values of the inversions in D. persimilis were frequency-dependent in certain population experiments.

A fourth possible explanation for the results obtained is that the fates of the different components of an evolutionary system are not independent. The estimates of variability from the binomial square proportions showed that there is a "positive interaction effect" between the chromosome arrangements in determining genotypic fitness. It should be emphasized that the genetic material of cross-fertilizing populations is not a fortuitous aggregate of particular units, but is an integrated whole in which the elements work in concert. Any change in proportions of different genetic elements produced by selection, requires compensatory changes in other elements to produce a newly-integrated quilibrium.

An important concept in the dynamics of a population have been given by Lerner (1954). It is claimed that the gentic composition of a population is homeostatic; that is, the genetic composition of a population can adjust to assure its survival. This adjustment involves the property of the population to resist sudden changes in its genetic composition. Such resistance may often be adaptive, since too rapid response to selection force might easily trap the population and cause its extinction. Compensatory mechanisms are developed by the genotypes. One such compensatory mechanism might have been the simultaneous increase or decrease in frequency of two different inversion systems, by means of which a population could have produced a newly integrated genetic equilibrium. Genetic homoestatic mechanisms might have been the possible cause for the "positive interaction effects" obtained in the population cage experiments. The "positive interaction effects" might lead to the stability of genotypes. This stability, although anti-evolutionary in one sense, is essential to evolution, for if genotypes do not have some continuity in time, it is impossible for natural selection to act in any directed fashion. It is interesting to notice that for most experimental populations positive interaction effects were not obtained until the second or third population analysis.

Serious objections to the statistical model utilized have been raised by Wallace (1958). He has pointed out that one cannot legitimately calculate the expected number of homozygotes and heterozygotes in a population on the basis of the binomial square rule, without assuming that the gemetic frequencies have remained constant from the beginning of the generation sampled. This important point is relevant in <u>Drosophila</u>

populations, since the initial zygotic frequencies can be transformed by selection into virtually any other set of frequencies.

Whether the statistical method utilized is entirely reliable or not no doubt will be discovered eventually, and more refined methods for the study of the evolutionary dynamics and dynamic gentic systems will be developed.

SUMMARY AND CONCLUSIONS

1. Populations derived from crosses involving two closely-related species, _Drosophila americana texana_ and _Drosophila novamexicana_ were maintained in population cages.

2. These species are not known to be sympatric but have been shown to produce fertile hybrids in the laboratory.

3. The performance of nine experimental populations and the fate of the chromosomes carried by them was followed.

4. The nine populations were initiated as follows:

I.

1. _texana_ females x _novamexicana_ males and the reciprocal cross.
2. F_1 hybrids from the cross of _texana_ females and _novamexicana_ males.
3. F_1 hybrids from the cross of _novamexicana_ females and _texana_ males.

II.

1. F_1 hybrids derived from the cross of _texana_ females and _novamexicana_ males crossed to the parental _novamexicana_ male and the reciprocal cross.
2. F_1 hybrids derived from the cross of _texana_ females and _novamexicana_ males crossed to the parental _texana_ males and the reciprocal cross.

III.

1. Males and females of both species.

5. The populations were analyzed cytologically at regular intervals to determine the effects of selection between the species and their interspecific hybrids.

6. Cytological analysis of the chromosomes was possible since the species differed by inversions in the X, second, fourth and fifth chromosomes.

7. Many but by no means all the heterozygous chromosomes combinations contributed to increase fitness of the genotypes. In certain populations and certain cages, homozygous novamexicana chromosomes were shown to be superior to the heterozygous chromosomes.

8. Novamexicana chromosome type was generally more frequent than the texana.

9. Populations subjected to the same selective forces evolved in separate ways showing the complexity of the process and the different path which evolution may take in spite of quantitative similar composition of the population and similar selective forces.

10. It is concluded that the fates of the different components of an evolutionary system are not independent as shown by statistical analyses.

11. A discussion is presented giving the relationships of this study to others of similar and related nature.

SUGGESTIONS FOR FURTHER STUDY

1. Since an upset in the sex ratio has been repeatedly observed, it would be desirable to determine whether it is due to the crowded conditions and competition in the population cages (Bruneau, 1956) or whether hybridization has a direct effect in upseting the mechanism of sex ration.

2. The release of tremendous variability due to recombination is obvious in hybridization studies. Further work is needed in the study of the release of genetic variability due to crossing over. This species provide excellent material for cytological work in crossingover, especially the second chromosome which differs by double inversions.

3. Further studies are needed to show whether or not related species with a restricted geographic range and a wide geographic range, shows selective advantages for the chromosomes of the species of restricted geographic range in cage populations.

4. Detailed analyses of the behavior of the X chromosome in cage populations is desirable. Such studies could clarify many interesting points.

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APPENDIX A

TABLE 1

Frequencies of homozygous and heterozygous chromosome combinations, Cage 1

Sample No.		0	1	2	3	4	5	6
Days from Origin		0	15	45	75	105	135	165
Chromosome Combination								
	TT	50.00	0.00	30.48	10.75	13.13	17.17	11.11
2	TN	0.00	100.00	24.08	61.29	68.88	51.11	56.66
	NN	50.00	0.00	41.46	27.95	17.17	31.11	32.22
	TT	50.00	0.00	34.14	29.03	17.17	16.16	24.44
4	TN	0.00	100.00	15.85	45.16	52.22	45.55	52.22
	NN	50.00	0.00	50.00	25.80	25.80	37.77	23.33
	TT	50.00	0.00	40.24	22.58	27.77	15.15	14.14
5	TN	0.00	100.00	18.29	48.38	52.22	53.33	56.66
	NN	50.00	0.00	41.46	29.03	20.66	31.11	28.88

TABLE 2

Chromosomal frequencies, Cage 1

Sample No.		0	1	2	3	4	5	6
Days from Origin		0	15	45	75	105	135	165
Chromosome	Species							
2	T	50.00	50.00	45.12	41.39	47.77	43.33	39.44
	N	50.00	50.00	54.88	58.61	52.22	56.66	60.55
4	T	50.00	50.00	42.07	51.61	43.8	39.44	50.55
	N	50.00	50.00	57.93	48.39	56.1	60.55	50.44
5	T	50.00	50.00	47.92	46.77	53.8	42.22	42.77
	N	50.00	50.00	52.08	53.23	46.1	57.77	57.22

TABLE 3

Distribution of chromosomal classes, Cage 1

Days from Origin	2	T	T	T	T	T	T	T	T	T	H	H	H	H	H	H	H	H	H	N	N	N	N	N	N	N	N	N
	4	T	T	T	H	H	H	N	N	N	T	T	T	H	H	H	N	N	N	T	T	T	H	H	H	N	N	N
	5	T	H	N	T	H	N	T	H	N	T	H	N	T	H	N	T	H	N	T	H	N	T	H	N	T	H	N
0		50																										50
15															100													
45		8	1	2	2	1		2	2	6	1	5	1	5	1	1	3	2	7	4		8	5	1		5	2	9
75		1			1	4		1	1	2	5	3	3	3	25	6	2	7	3	4	2	7		3	4	3		3
105		2	1	2		1	1	1		4	7		1	3	33	2	5	6	5	2		1	3	3	1	2	1	3
135			1	5	2	2	1	1	1	4	1	2	2	2	23		1	6	2	1	2	1	1	5		3	4	7
165			1	2		5	1		2	1	3	5	1		31	3	3	1	5	2	2	5	2	5	1	2	2	5

TABLE 4

Frequencies of homozygous and heterozygous chromosome combinations, Cage 2

Sample No.		0	1	2	3	4	5	6
Days from Origin		0	15	45	75	105	135	165
Chromosome Combination								
	TT	50.00	0.00	41.86	36.61	24.71	17.52	8.88
2	TN	0.00	100.00	6.91	6.66	20.22	26.80	20.00
	NN	50.00	0.00	51.16	55.51	55.05	55.67	71.11
	TT	50.00	0.00	47.67	35.51	25.84	34.02	28.88
4	TN	0.00	100.00	1.67	6.66	20.22	17.52	18.88
	NN	50.00	0.00	51.16	57.71	53.93	48.45	52.22
	TT	50.00	0.00	44.18	45.51	26.96	20.61	16.16
5	TN	0.00	100.00	5.81	8.89	19.10	25.77	18.18
	NN	50.00	0.00	50.00	45.51	53.93	53.60	64.44

TABLE 5

Chromosomal frequencies, Cage 2

Sample No.		0	1	2	3	4	5	6
Days from Origin		0	15	45	75	105	135	165
Chromosome	Species							
2	T	50.00	50.00	45.34	40.00	34.83	30.93	18.88
	N	50.00	50.00	54.66	60.00	65.16	68.06	81.11
4	T	50.00	50.00	48.25	38.88	35.95	42.78	38.33
	N	50.00	50.00	51.75	61.11	64.04	57.21	61.66
5	T	50.00	50.00	47.09	50.00	36.51	33.50	26.11
	N	50.00	50.00	52.91	50.00	64.4	66.40	73.88

TABLE 6

Distribution of chromosomal classes, Cage 2

Days from	2	T	T	T	T	T	T	T	T	T	H	H	H	H	H	H	H	H	H	N	N	N	N	N	N	N	N	N
Origin	4	T	T	T	H	H	H	N	N	N	T	T	T	H	H	H	N	N	N	T	T	T	H	H	H	N	N	N
	5	T	H	N	T	H	N	T	H	N	T	H	N	T	H	N	T	H	N	T	H	N	T	H	N	T	H	N
0		50																										50
15															100													
45		8	2	10	1			8		6	1	1	1				1		2	7	1	10	1			13	1	12
75		2	1	7	1		2	11	2	6			1				1	1		12	1	9		1	2	9	2	19
105		5		1			3	1	3	7		1	2		4	1	3	2	3	3		10	4	4	2	9	1	20
135		2	2				2	5	2	3	1	4	3	2	4	2	1	5	3	4	2	14	3	2	3	4	4	20
165		1	1	2				1		4			2		9	2	1	5	2	3		15	2	4	1	6		29

TABLE 7

Frequencies of heterozygous and homozygous chromosome combinations, Cage 6

Sample No. Days from Origin		0 0	1 15	2 45	3 75	4 105	5 135	6 165
Chromosome Combination								
	TT	0.00	17.52	20.21	17.89	12.22	10.46	7.86
2	TN	100.00	60.82	56.38	60.67	64.44	60.46	41.57
	NN	0.00	21.64	23.40	21.34	23.33	29.06	50.56
	TT	0.00	10.30	18.08	19.10	18.88	13.95	8.98
4	TN	100.00	67.01	60.63	48.31	40.00	48.83	56.47
	NN	0.00	22.68	21.27	32.58	41.00	37.20	34.83
	TT	0.00	9.28	18.08	14.60	18.88	23.25	13.48
5	TN	100.00	62.88	61.70	48.31	48.88	46.51	48.31
	NN	0.00	27.83	20.21	37.07	32.22	30.23	38.20

TABLE 8

Chromosomal frequencies, Cage 6

Sample No. Days from Origin		0 0	1 15	2 45	3 75	4 105	5 135	6 165
Chromosome	Species							
2	T	50.00	47.94	48.40	48.31	44.44	40.69	28.65
	N	50.00	52.06	51.59	51.69	55.55	59.30	71.34
4	T	50.00	43.81	48.40	43.25	38.88	38.37	37.07
	N	50.00	56.18	51.59	56.75	61.11	61.62	62.92
5	T	50.00	40.72	48.93	38.76	43.33	46.51	37.64
	N	50.00	59.27	51.06	61.23	56.66	53.48	62.35

TABLE 9

Distribution of chromosomal classes, Cage 6

Days from	2	T	T	T	T	T	T	T	T	T	H	H	H	H	H	H	H	H	H	N	N	N	N	N	N	N	N	N
Origin	4	T	T	T	H	H	H	N	N	N	T	T	T	H	H	H	N	N	N	T	T	T	H	H	H	N	N	N
	5	T	H	N	T	H	N	T	H	N	T	H	N	T	H	N	T	H	N	T	H	N	T	H	N	T	H	N
0															100													
15		1	1	2	2	6		1	3	1		1	3	2	35	10		4	4		1	1	1	7	3	1	4	3
45		4	2	1	2	6	2		1	1	3	3		2	33	5	2	3	3	1	2	2		7	2	2	1	4
75		2	1	3		2	1	2	3	2		3	5	2	30	4	2	1	7	1		1		3	2	3	2	6
105		2		1		2		2	4		2	4	4	3	18	7	5	7	8	1	1	2	1	3	2	1	5	5
135					2	2	1		3			3	4	4	13	9	6	11	3	1	2	1	5	3	5	2	4	2
165		1	1			1	1		1	2		1	1	2	21	5		4	3	2		2	3	13	4	4	1	16

TABLE 10

Frequencies of homoxygous and heterozygous chromosome combinations, Cage 9

Sample No.		0	1	2	3	4	5	6
Days from Origin		0	15	45	75	105	135	165
Chromosome Combination								
	TT	0.00	12.35	20.21	15.55	13.33	10.98	
2	TN	100.00	59.55	55.31	66.66	72.22	69.23	
	NN	0.00	28.08	24.46	17.77	14.44	19.78	
	TT	0.00	16.85	18.08	16.66	16.66	15.38	
4	TN	100.00	58.42	60.63	66.66	64.44	67.03	
	NN	0.00	24.71	21.27	16.66	18.88	17.58	
	TT	0.00	12.35	19.14	16.66	16.66	13.18	
5	TN	100.00	70.75	69.14	70.00	67.77	69.23	
	NN	0.00	16.85	11.70	13.33	15.55	17.58	

TABLE 11

Chromosomal frequencies, Cage 9

Sample No.		0	1	2	3	4	4	6
Days from Origin		0	15	45	75	105	135	165
Chromosome	Species							
2	T	50.00	42.13	47.87	48.88	49.44	45.60	
	N	50.00	57.86	52.12	51.11	50.55	54.40	
4	T	50.00	46.06	48.40	50.00	48.88	48.90	
	N	50.00	53.93	51.59	50.00	51.11	51.10	
5	T	50.00	47.75	53.72	51.66	50.55	47.80	
	N	50.00	52.25	46.27	48.33	49.44	52.20	

TABLE 12

Distribution of chromosomal classes, Cage 9

Days from Origin	2	T	T	T	T	T	T	T	T	T	H	H	H	H	H	H	H	H	H	N	N	N	N	N	N	N	N	N
	4	T	T	T	H	H	H	N	N	N	T	T	T	H	H	H	N	N	N	T	T	T	H	H	H	N	N	N
	5	T	H	N	T	H	N	T	H	N	T	H	N	T	H	N	T	H	N	T	H	N	T	H	N	T	H	N
0															100													
15		2	2		2	4			1		1	5		2	30	3	1	8	3	1		3	1	8	3	1	4	4
45		2	2	1	2	9		2			2	1	1	3	34	3	3	5		3	4	1		6		1	3	5
75		4	1		1	4		1	1	3	2	4	1	4	44	2		1	2	2	1			6		1	1	4
105			2			8			2		4	2	4	5	30	7		10	2	1	2	1	1	6	1	1	1	
135		1	2			5			2		4	2	2	3	32	10	1	8	2		1		3	7	3		2	

TABLE 13

Frequencies of heterozygous and homozygous chromosome combinations, Cage 4

Sample No.		0	1	2	3	4	5	6
Days from Origin		0	15	45	75	105	135	165
Chromosome	Combination							
	TT	0.00	0.00	4.81	10.11	7.86	8.23	10.00
2	TN	50.00	51.04	43.37	42.69	50.56	58.82	47.77
	NN	0.00	48.95	51.80	47.19	40.33	32.94	42.22
	TT	0.00	0.00	7.23	15.73	17.94	9.41	12.22
4	TN	50.00	50.00	45.78	26.96	32.58	52.94	60.00
	NN	0.00	50.00	46.98	57.30	49.43	37.64	27.77
	TT	0.00	0.00	7.23	20.22	12.35	11.76	11.11
5	TN	50.00	47.91	40.96	37.07	47.19	51.76	57.77
	NN	0.00	52.08	51.80	42.69	40.44	36.47	31.11

TABLE 14

Chromosomal frequencies, Cage 4

Sample No.		0	1	2	3	4	5	6
Days from Origin		0	15	45	75	105	135	165
Chromosome	Species							
2	T	25.00	25.52	26.50	31.46	33.14	37.64	33.88
	N	75.00	74.47	73.50	68.53	66.85	62.35	66.11
4	T	25.00	25.00	43.10	29.21	34.26	35.88	42.22
	N	75.00	75.00	56.9	70.78	65.73	64.11	57.77
5	T	25.00	23.96	27.71	38.76	35.95	37.64	40.00
	N	75.00	76.04	72.28	61.23	64.04	62.35	60.00

TABLE 15

Distribution of chromosomal classes, Cage 4

Days from	2	T	T	T	T	T	T	T	T	T	H	H	H	H	H	H	H	H	H	N	N	N	N	N	N	N	N	N
Origin	4	T	T	T	H	H	H	N	N	N	T	T	T	H	H	H	N	N	N	T	T	T	H	H	H	N	N	N
	5	T	H	N	T	H	N	T	H	N	T	H	N	T	H	N	T	H	N	T	H	N	T	H	N	T	H	N
0															50													50
15															19	9		9	12					10	11		8	18
45						2		1		1					21	5		6	3	1		5	3	4	7		3	21
75		2	1		1				1	2		2	2	1	15	6	1	8	4	2	1	3		1	1	10	4	21
105				2		1			2	2		2	6	4	19		2	5	7	1	2	1	1	3	2	3	9	15
135		1				2	2	1		1		4		4	23	6	1	7	5		1	2	1	5	2	2	2	13
165		5	1			3						2		4	29	5		3	1	1		1		6	6		8	15

TABLE 16

Frequencies of heterozygous and homozygous chromosome combinations, Cage 5

Sample No.		0	1	2	3	4	5	6
Days from Origin		0	15	45	75	105	135	165
Chromosome	Combination							
	TT	0.00	0.00	21.34	13.82	13.68	15.38	18.07
2	TN	50.00	51.06	55.05	62.76	62.10	54.94	59.03
	NN	50.00	48.93	23.59	23.40	24.21	29.67	22.89
	TT	0.00	0.00	7.86	12.76	13.68	19.78	8.43
4	TN	50.00	52.12	64.04	45.74	60.00	54.94	53.01
	NN	50.00	47.87	28.08	41.48	27.36	25.27	38.55
	TT	0.00	0.00	1.12	7.44	7.36	9.89	12.04
5	TN	50.00	50.00	59.55	44.68	71.57	62.63	69.87
	NN	50.00	50.00	39.32	47.87	21.05	27.47	18.07

TABLE 17

Chromosomal frequencies, Cage 5

Sample No.		0	1	2	3	4	5	6
Days from Origin		0	15	45	75	105	135	165
Chromosome	Species							
2	T	25.00	25.53	48.87	45.21	44.73	42.85	47.59
	N	75.00	74.46	51.12	54.78	55.26	57.15	52.40
4	T	25.00	26.06	39.88	35.63	42.63	47.25	34.93
	N	75.00	73.93	60.11	64.36	57.36	52.74	65.06
5	T	25.00	25.00	30.89	29.78	43.15	41.20	46.98
	N	75.00	75.00	69.10	70.21	56.84	58.80	53.01

TABLE 18

Distribution of chromosomal classes, Cage 5

Days from	2	T	T	T	T	T	T	T	T	T	H	H	H	H	H	H	H	H	H	N	N	N	N	N	N	N	N	N
Origin	4	T	T	T	H	H	H	N	N	N	T	T	T	H	H	H	N	N	N	T	T	T	H	H	H	N	N	N
	5	T	H	N	T	H	N	T	H	N	T	H	N	T	H	N	T	H	N	T	H	N	T	H	N	T	H	N
0															50													50
15															15	9		11	9					12	14		9	15
45			2	1		7	3	1	2	3		1	1		39	5			4			2		2	2		1	13
75		1	2	1		2		1	3	3	1	1	4	3	24	15		7	5			2	1		2		3	13
105			3	1		7	1		1			6	1	3	34	4	1	6	4			1		7	1	3	3	8
135		3	2	2		7						3	2		30	5		6	4	2	2	2	1	5	2	3	2	8
165		1	2			3		4	2	3	1	3		1	29	2		9	4				1	6	2	2	4	4

TABLE 19

Frequencies of homozygous and heterozygous chromosome combinations, Cage 7

Sample No.		0	1	2	3	4	5	6
Days from Origin		0	15	45	75	105	135	165
Chromosome	Combination							
	TT	50.00	50.51	49.45	27.77	18.88	21.11	34.78
2	TN	50.00	49.48	48.35	62.22	70.00	68.88	57.60
	NN	0.00	0.00	2.19	10.00	11.11	10.00	7.60
	TT	50.00	48.45	48.35	41.11	35.55	34.44	29.34
4	TN	50.00	51.54	49.45	35.55	57.77	55.55	58.59
	NN	0.00	0.00	2.19	23.33	6.66	10.00	11.95
	TT	50.00	59.79	36.26	38.88	27.77	33.33	27.17
5	TN	50.00	40.20	61.53	48.88	65.55	61.11	69.56
	NN	0.00	0.00	2.19	12.22	6.66	5.55	3.29

TABLE 20

Chromosomal frequencies, Cage 7

Sample No.		0	1	2	3	4	5	6
Days from Origin		0	15	45	75	105	135	165
Chromosome	Species							
2	T	75.00	75.25	73.6	58.88	53.88	55.55	63.58
	N	25.00	24.74	26.3	41.11	46.11	44.44	36.41
4	T	75.00	54.22	53.0	58.88	64.44	62.22	58.69
	N	25.00	25.77	27.0	41.11	35.55	37.77	41.30
5	T	75.00	79.89	67.77	63.33	60.55	63.88	61.95
	N	25.00	20.10	32.22	36.66	39.44	36.11	38.04

TABLE 21

Distribution of chromosomal classes, Cage 7

Days from	2	T	T	T	T	T	T	T	T	T	H	H	H	H	H	H	H	H	H	N	N	N	N	N	N	N	N	N
Origin	4	T	T	T	H	H	H	N	N	N	T	T	T	H	H	H	N	N	N	T	T	T	H	H	H	N	N	N
	5	T	H	N	T	H	N	T	H	N	T	H	N	T	H	N	T	H	N	T	H	N	T	H	N	T	H	N
0		50													50													
15		17	12		12	11					13	6		13	12													
45		13	4			1			4	3	11	8	1	13	11	1	3	4	4	2		1		4		1		1
75		5	3	1	2	4			2	1	9	9		6	33	2	2	1		2	2	1	1	3	1			
105		5	4	1	2	4			1	1	9	9		5	34	2	2	1		2	2	1		3	1	1		
135		8	3		2	4		2		1	6	13		6	34	1	1			1	1			1	1	2	1	2
165		10	8	1	4	7			1	1	4	4		4	37		1	3						1	1	2	3	

TABLE 22

Frequencies of homozygous and heterozygous chromosome combinations, Cage 8

Sample No.		0	1	2	3	4	5	6
Days from Origin		0	15	45	75	105	135	165
Chromosome	Combination							
	TT	50.00	48.45	38.82	44.94	41.11	32.96	31.11
2	TN	50.00	51.54	61.17	44.94	41.11	57.14	58.88
	NN	0.00	0.00	0.00	10.11	17.77	9.89	10.00
	TT	50.00	51.54	42.35	48.31	44.44	26.37	28.88
4	TN	50.00	48.45	57.64	42.69	43.33	62.63	62.22
	NN	0.00	0.00	0.00	8.98	12.12	10.98	8.88
	TT	50.00	38.14	40.00	48.31	46.66	30.76	28.88
5	TN	50.00	61.85	52.82	50.56	46.66	62.63	60.00
	NN	0.00	0.00	1.18	1.12	6.66	6.59	11.11

TABLE 23

Chromosomal frequencies, Cage 8

Sample No.		0	1	2	3	4	5	6
Days from Origin		0	15	45	75	105	135	165
Chromosome	Species							
2	T	75.00	74.22	69.41	67.14	61.66	61.53	60.55
	N	25.00	25.77	38.58	32.85	38.33	38.46	39.44
4	T	75.00	75.77	71.17	69.62	66.11	57.69	60.00
	N	25.00	24.22	28.82	30.37	33.88	42.30	40.00
5	T	75.00	69.07	69.41	73.59	70.00	62.08	58.88
	N	25.00	30.92	30.58	26.40	30.00	37.91	41.11

TABLE 24

Distribution of chromosomal classes, Cage 8

Days from Origin	2 4 5	T T T	T T H	T T N	T H T	T H H	T H N	T N T	T N H	T N N	H T T	H T H	H T N	H H T	H H H	H H N	H N T	H N H	H N N	N T T	N T H	N T N	N H T	N H H	N H N	N N T	N N H	N N N
0		50													50													
15		20	17		4	6					3	10		9	28													
45		17	6		5	5					7	5		6	33				1									
75		16	9		7	4		4			7	7		1	24			1		3	1	1	1	1		2		
105		12	7	1	7	11		1	1		10	8		7	15			1		3			3	2				
135		9	5		3	12		2			2	4		7	31	1	3	1	3	2		2		3			1	
165		9	5	1	1	7	1	2	2		2	8		11	32					2	1			1	1			4

TABLE 25

Frequencies of homozygous and heterozygous chromosome combinations, Cage 3

Sample No. Days from Origin		0 0	1 15	2 45	3 75	4 105	5 135	6 165
Chromosome	Combination							
	TT	50.00	34.05	26.43	20.65	3.06	8.88	6.97
2	TN	0.00	19.58	13.79	18.47	30.61	22.22	26.74
	NN	50.00	45.36	59.77	68.86	66.32	68.88	66.27
	TT	50.00	34.05	35.63	40.21	19.38	23.33	17.44
4	TN	0.00	19.58	13.79	14.13	28.57	24.44	26.74
	NN	50.00	45.36	50.57	45.65	52.04	52.22	55.81
	TT	50.00	34.05	25.28	31.52	16.32	26.66	17.44
5	TN	0.00	19.58	18.39	19.56	28.57	25.55	23.55
	NN	50.00	45.36	56.32	48.91	55.10	47.77	50.00

TABLE 26

Chromosomal frequencies, Cage 3

Sample No. Days from Origin		0 0	1 15	2 45	3 75	4 105	5 135	6 165
Chromosome	Species							
2	T	50.00	44.85	33.33	29.89	18.36	20.00	20.34
	N	50.00	55.15	66.66	70.10	81.63	80.00	79.65
4	T	50.00	44.85	42.52	47.28	33.67	35.55	30.81
	N	50.00	55.15	57.47	52.71	66.32	64.44	69.18
5	T	50.00	44.85	34.48	41.30	30.61	39.44	33.72
	N	50.00	55.15	65.51	58.69	69.38	60.55	66.27

TABLE 27

Distribution of chromosomal classes, Cage 3

Days from	2	T	T	T	T	T	T	T	T	T	H	H	H	H	H	H	H	H	H	N	N	N	N	N	N	N	N	N
Origin	4	T	T	T	H	H	H	N	N	N	T	T	T	H	H	H	N	N	N	T	T	T	H	H	H	N	N	N
	5	T	H	N	T	H	N	T	H	N	T	H	N	T	H	N	T	H	N	T	H	N	T	H	N	T	H	N
0		50																										50
15		34													19													44
45		9	2	2	1	1	1	1		3	4	2			6	1		1	1	6		9		1	1	4	2	29
75		10	2	1				4	1	1	1	5	1	1	6	3				8	3	7		2	1	4		31
105		1				1	1					2	2	2	15	3		6		3		12	1	2	2	9	1	35
135		4			1	1			1		2	1			13	1		2	1	10		6		2	3	6	2	34
165		1			1				1		4	1	2		10	1		7	2	6		5	1	5	4	5	3	27

APPENDIX B

TABLE 28

X chromosomal frequencies, for the nine experimental populations

Sample No.			0	1	2	3	4	5	6
Days from Origin			0	15	45	75	105	135	165
Group	Cage	Species							
I	1	T	50.00	50.00	60.00	50.00	42.64	48.75	49.33
		N	50.00	50.00	40.00	50.00	57.35	51.25	50.66
	2	T	50.00	50.00	51.04	47.11	49.28	46.79	31.01
		N	50.00	50.00	48.95	52.88	50.71	53.20	68.98
	6	T	50.00	39.87	46.15	41.09	29.57	31.16	34.93
		N	50.00	60.12	53.84	58.90	70.42	68.83	65.06
	9	T	50.00	40.25	45.12	47.40	48.68	50.00	
		N	50.00	59.75	54.87	52.60	51.31	50.00	
II	4	T	25.00	18.75	32.87	41.55	27.33	40.00	38.60
		N	75.00	81.25	67.12	58.44	72.66	60.00	61.40
	5	T	25.00	18.49	31.09	22.60	33.92	43.12	42.36
		N	75.00	81.50	68.91	77.39	66.07	56.87	57.63
	7	T	75.00	80.02	71.87	75.31	63.69	64.37	70.51
		N	25.00	19.97	28.12	24.68	36.30	35.62	29.48
	8	T	75.00	83.50	87.10	80.37	77.61	68.75	74.05
		N	25.00	16.50	12.90	19.62	23.38	31.25	25.94
III	3	T	50.00	37.79	36.84	49.31	34.37	30.86	33.56
		N	50.00	62.20	63.15	50.68	65.62	69.13	66.43

TABLE 29

Frequencies of homozygous and heterozygous combinations of the X chromosome, experimental populations of Group I

Sample No.		0	1	2	3	4	5	6
Days from Origin		0	15	45	75	105	135	165
Cage	Combination							
1	TT	50.00	0.00	53.33	28.12	11.76	23.75	30.66
	TN	0.00	100.00	13.33	43.75	61.76	50.00	37.33
	NN	0.00	0.00	33.33	28.12	26.74	26.25	32.00
2	TT	0.00	0.00	47.91	40.38	42.85	33.33	42.92
	TN	0.00	100.00	6.25	13.46	12.85	26.92	11.39
	NN	50.00	0.00	45.83	46.15	42.28	39.74	45.29
6	TT	0.00	15.18	25.64	17.80	15.49	16.88	20.54
	TN	50.00	49.36	41.02	46.57	28.16	28.57	28.76
	NN	0.00	35.89	33.33	35.61	56.33	54.54	50.68
9	TT	0.00	24.64	17.07	27.27	25.00	23.68	
	TN	50.00	31.16	59.09	40.25	47.36	52.63	
	NN	0.00	44.15	26.82	32.46	27.63	23.68	

TABLE 30

Frequencies of homozygous and heterozygous combinations of the X chromosome, experimental populations of Group II

Sample No.		0	1	2	3	4	5	6
Days from Origin		0	15	45	75	105	135	165
Cage	Combination							
4	TT	0.00	0.00	16.43	28.57	13.13	14.16	18.98
	TN	50.00	37.50	32.87	25.97	28.00	50.66	39.24
	NN	0.00	62.50	50.68	45.45	58.66	34.66	41.77
5	TT	0.00	0.00	8.53	8.26	14.28	17.50	20.83
	TN	0.00	36.98	45.12	28.76	38.28	51.25	43.05
	NN	50.00	63.01	46.34	63.01	46.47	31.25	36.11
7	TT	0.00	60.52	50.00	59.49	45.20	40.00	51.28
	TN	50.00	39.47	43.75	31.64	36.98	48.75	39.46
	NN	0.00	0.00	6.25	8.86	17.80	11.25	10.25
8	TT	50.00	67.18	74.32	68.08	61.84	53.75	56.96
	TN	0.00	32.81	25.67	26.58	31.57	30.00	34.17
	NN	0.00	0.00	0.00	6.32	6.57	16.25	8.86

TABLE 31

Frequencies of homozygous and heterozygous combinations of the X chromosome, experimental population of Group III

Sample No.		0	1	2	3	4	5	6
Days from Origin		0	15	45	75	105	135	165
Cage	Combination							
3	TT	50.00	26.74	31.57	42.46	23.75	22.22	21.91
	TN	0.00	22.09	10.52	13.69	21.25	17.28	23.28
	NN	50.00	51.16	57.89	43.83	55.00	60.49	54.79

APPENDIX C

TABLE 32

Counts of males and females per analysis, per cage

Sample No. Days from Origin			1 15	2 45	3 75	4 105	5 135	6 165
Group	Cage							
I	1	♂		37	29	22	10	15
		♀		45	64	68	80	75
	2	♂		38	38	19	19	11
		♀		48	52	70	78	79
	6	♂	18	16	16	19	9	16
		♀	79	78	73	71	77	73
	9	♂	12	12	13	14	15	
		♀	77	82	77	76	76	
II	4	♂	16	10	12	14	10	11
		♀	80	73	77	75	75	79
	5	♂	21	7	21	11	11	11
		♀	73	82	73	84	80	72
	7	♂	21	11	11	17	10	14
		♀	76	80	79	75	80	78
	8	♂	33	11	10	14	11	11
		♀	64	74	79	76	79	79
III	3	♂	11	11	19	18	9	13
		♀	86	76	73	80	81	73

APPENDIX D

TABLE 33

Composition of experimental population 1, 45 day analysis, with deviations from proportionality to marginal frequencies

		Chromosome 4			
		TT	TN	NN	Totals
Chromosome 2	TT	8(-.536)	3(-.963)	14(1.500)	25
	TN	7(-.512)	4(.513)	11(.000)	22
	NN	13(1.049)	6(.452)	16(-1.500)	35
	Totals	28	13	41	82

$X^2_{(4)}$ = .6535 P(.98-.95)

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 2	TT	12(1.635)	4(-.573)	9(-1.060)	25
	TN	7(-2.951)	8(3.61)	9(-.658)	24
	NN	15(1.318)	3(-3.036)	15(1.72)	33
	Totals	34	15	33	82

$X^2_{(4)}$ = 6.6365 P(.20-.10)

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 4	TT	11(-1.878)	6(.147)	15(1.732)	32
	TN	9(3.769)	3(.622)	1(-4.390)	13
	NN	13(-1.890)	6(-.760)	18(2.659)	37
	Totals	33	15	34	82

$X^2_{(4)}$ = 5.2007 P(.30-.20)

TABLE 34

Composition of experimental population 1, 75 day analysis, with deviations from proportionality to marginal frequencies

		Chromosome 4			
		TT	TN	NN	Totals
Chromosome 2	TT	1(-1.903)	5(.484)	4(1.42)	10
	TN	12(-4.548)	32(6.259)	13(-1.709)	57
	NN	14(6.452)	5(-6.869)	7(.291)	26
	Totals	27	42	24	93

$X^2_{(4)} = 13.8510$ $P < .01$

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 2	TT	3(.420)	5(.377)	2(-.795)	10
	TN	12(-2.967)	33(6.183)	13(-3.215)	58
	NN	9(2.549)	5(-6.559)	11(4.011)	25
	Totals	24	43	26	93

$X^2_{(4)} = 9.9639$ $P(.05-.02)$

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 4	TT	10(4.194)	6(-7.064)	11(2.871)	27
	TN	3(-6.247)	32(11.194)	8(-4.946)	43
	NN	7(2.054)	7(-4.290)	9(2.076)	23
	Totals	20	45	28	93

$X^2_{(4)} = 23.0943$ $P < .01$

TABLE 35

Composition of experimental population 1, 105 day analysis, with deviations from proportionality to marginal frequencies

		Chromosome 4			
		TT	TN	NN	Totals
Chromosome 2	TT	5(2.867)	2(-4.266)	5(1.400)	12
	TN	8(-2.844)	38(6.123)	15(-3.300)	61
	NN	3(.022)	7(-1.877)	7(1.900)	17
	Totals	16	47	27	90

$X^2_{(4)}$ = 10.0323 P(.05-.02)

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 2	TT	3(-.063)	3(-3.533)	6(3.600)	12
	TN	13(-3.100)	41(6.700)	9(-3.600)	63
	NN	7(3.167)	5(-3.166)	3(.000)	15
	Totals	23	49	18	90

$X^2_{(4)}$ = 14.0903 $P < .01$

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 4	TT	12(7.40)	1(-8.600)	5(1.200)	18
	TN	4(-7.711)	38(13.467)	4(-5.711)	46
	NN	7(.356)	9(-4.866)	10(4.512)	26
	Totals	23	48	19	90

$X^2_{(4)}$ = 29.4667 $P < .01$

TABLE 36

Composition of experimental population 1, 135 day analysis, with deviations from proportionality to marginal frequencies

		Chromosome 4			
		TT	TN	NN	Totals
Chromosome 2	TT	5(2.334)	5(-1.577)	6(-.755)	16
	TN	5(-3.166)	28(7.856)	16(-4.689)	49
	NN	5(.834)	4(-6.277)	16(5.445)	25
	Totals	15	37	38	90

$X^2_{(4)}$ = 14.6691 $P < .01$

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 2	TT	4(1.667)	3(-5.166)	8(3.500)	15
	TN	4(-3.466)	34(7.867)	10(-4.400)	48
	NN	6(1.800)	12(-2.722)	9(.900)	27
	Totals	14	49	27	90

$X^2_{(4)}$ = 13.8779 $P < .01$

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 4	TT	3(.667)	4(-4.166)	8(3.500)	15
	TN	6(-.222)	29(7.223)	5(-7.000)	40
	NN	5(-.444)	16(-3.055)	14(2.900)	35
	Totals	14	49	27	90

$X^2_{(4)}$ = 12.8085 P(.02-.01)

TABLE 37

Composition of experimental population 1, 165 day analysis, with deviations from proportionality to marginal frequencies

		Chromosome 4			
		TT	TN	NN	Totals
Chromosome 2	TT	2(-.222)	4(-1.222)	4(1.445)	10
	TN	8(-2.888)	30(4.412)	11(-1.522)	49
	NN	10(3.112)	13(-3.188)	8(.078)	31
	Totals	20	47	23	90

$X^2_{(4)}$ = 4.8717 P(.50-.30)

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 2	TT	0(-1.444)	6(.334)	4(1.112)	10
	TN	7(-.366)	35(6.100)	9(-5.733)	51
	NN	6(1.812)	10(-6.433)	13(4.623)	29
	Totals	13	51	26	90

$X^2_{(4)}$ = 11.2819 P(.05-.02)

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 4	TT	5(2.067)	8(-4.222)	9(2.156)	22
	TN	3(-3.266)	36(9.889)	8(-6.622)	47
	NN	4(1.200)	6(-5.666)	11(4.467)	21
	Totals	12	50	28	90

$X^2_{(4)}$ = 18.3576 $P < .01$

TABLE 38

Composition of experimental population 2, 45 day analysis, with deviations from proportionality to marginal frequencies

			Chromosome 4		
		TT	TN	NN	Totals
Chromosome 2	TT	19(3.535)	0(-.813	16(-2.750)	35
	TN	2(-.651)	1(.860)	3(-.209)	6
	NN	17(-2.883)	1(-.046)	27(2.931)	45
	Totals	38	2	46	86

$X^2_{(4)}$ = 3.9074 P(.50-.30)

			Chromosome 5		
		TT	TN	NN	Totals
Chromosome 2	TT	16(-.325)	2(-.093)	18(.303)	36
	TN	2(-.511)	1(.652)	3(.070)	6
	NN	31(1.047)	2(-.558)	21(-.488)	44
	Totals	39	5	42	86

$X^2_{(4)}$ = 1.5308 P(.90-.80)

			Chromosome 5		
		TT	TN	NN	Totals
Chromosome 4	TT	16(-4.023)	2(.570)	23(3.454)	41
	TN	2(1.024)	0(-.069)	0(-.953)	2
	NN	24(3.000)	1(-.500)	18(-2.500)	43
	Totals	42	3	41	86

$X^2_{(4)}$ = 4.2127 P(.50-.30)

TABLE 39

Composition of experimental population 2, 75 day analysis, with deviations from proportionality to marginal frequencies

		Chromosome 4			
		TT	TN	NN	Totals
Chromosome 2	TT	10(-2.329)	3(.825)	20(1.506)	33
	TN	1(-1.241)	1(.605)	4(.638)	6
	NN	23(3.572)	2(-1.428)	27(-2.142)	52
	Totals	34	6	51	91

$X^2_{(4)} = 3.9871$ P(.50-.30)

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 2	TT	14(-.065)	2(-1.164)	16(1.231)	32
	TN	2(-.637)	2(1.407)	2(-.769)	6
	NN	24(.704)	5(-.241)	24(-.461)	53
	Totals	40	9	42	91

$X^2_{(4)} = 1.5674$ P(.90-.80)

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 4	TT	15(1.033)	1(-2.065)	15(1.033)	31
	TN	1(-2.153)	3(2.308)	3(-.153)	7
	NN	25(1.121)	5(-.241)	23(-.879)	53
	Totals	41	9	41	91

$X^2_{(4)} = 10.4709$ P(.05-.02)

TABLE 40

Composition of experimental population 2, 105 day analysis, with deviations from proportionality to marginal frequencies

		Chromosome 4			
		TT	TN	NN	Totals
Chromosome 2	TT	6(.102)	4(-.011)	11(-.089)	21
	TN	3(-2.056)	7(3.562)	8(-1.505)	18
	NN	16(1.956)	6(-3.550)	28(1.596)	50
	Totals	25	17	47	89

$X^2_{(4)} = 6.4354$ P(.20-.10)

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 2	TT	7(1.338)	3(-.775)	11(-.561)	21
	TN	3(-2.123)	9(5.585)	7(-3.460)	19
	NN	14(.787)	4(-4.808)	31(4.023)	49
	Totals	24	16	49	89

$X^2_{(4)} = 6.6814$ P(.20-.10)

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 4	TT	9(3.057)	1(-3.393)	13(.338)	23
	TN	1(-3.393)	10(6.753)	6(-3.359)	17
	NN	13(.338)	6(-3.359)	30(3.023)	49
	Totals	23	17	49	89

$X^2_{(4)} = 23.6259$ $P < .01$

TABLE 41

Composition of experimental population 2, 135 day analysis, with deviations from proportionality to marginal frequencies

		Chromosome 4			
		TT	TN	NN	Totals
Chromosome 2	TT	4(-1.278)	2(-.969)	10(2.248)	16
	TN	8(-.557)	9(4.172)	9(-3.597)	26
	NN	20(1.856)	7(-3.206)	28(1.351)	55
	Totals	32	18	47	97

$X^2_{(4)} = 7.2140$ P(.20-.10)

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 2	TT	5(1.846)	4(-.381)	8(-1.463)	17
	TN	4(-.824)	13(6.299)	9(-5.474)	26
	NN	9(-1.020)	8(-5.917)	37(6.939)	54
	Totals	18	25	54	97

$X^2_{(4)} = 13.5618$ $P < .01$

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 4	TT	7(.196)	8(-.505)	18(.310)	33
	TN	4(.495)	6(1.619)	7(-2.113)	17
	NN	9(-.690)	11(-1.113)	27(1.805)	47
	Totals	20	25	52	97

$X^2_{(4)} = 1.4797$ P(.90-.80)

TABLE 42

Composition of experimental population 2, 165 day analysis, with deviations from proportionality to marginal frequencies

		Chromosome 4			
		TT	TN	NN	Totals
Chromosome 2	TT	3(.689)	0(-1.511)	5(.823)	8
	TN	1(-4.200)	11(7.600)	6(-3.400)	18
	NN	22(3.512)	6(-6.088)	36(2.578)	64
	Totals	26	17	47	90

$X^2_{(4)} = 27.4396$ $P < .01$

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 2	TT	2(.667)	0(-1.511)	6(.845)	8
	TN	2(-1.000)	12(8.600)	4(-7.600)	18
	NN	11(.334)	5(-7.088)	48(6.756)	64
	Totals	15	17	58	90

$X^2_{(4)} = 37.3230$ $P < .01$

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 4	TT	5(.556)	1(-4.000)	19(3.445)	25
	TN	2(-1.022)	14(10.600)	1(-9.577)	17
	NN	9(.467)	3(-6.600)	36(6.134)	48
	Totals	16	18	56	90

$X^2_{(4)} = 51.9195$ $P < .01$

TABLE 43

Composition of experimental population 6, 15 day analysis, with deviations from proportionality to marginal frequencies

		Chromosome 4			
		TT	TN	NN	Totals
Chromosome 2	TT	4(2.248)	8(-3.391)	5(1.145)	17
	TN	3(-3.082)	47(7.464)	9(-4.381)	59
	NN	3(.836)	10(-4.072)	8(3.238)	21
	Totals	10	65	22	97

$X^2_{(4)} = 12.3412$ P(.02-.01)

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 2	TT	4(2.423)	9(-1.515)	4(-.907)	17
	TN	3(-2.474)	39(2.506)	17(-.030)	59
	NN	2(.052)	12(-.886)	7(.939)	21
	Totals	9	60	28	97

$X^2_{(4)} = 5.6063$ P(.30-.20)

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 4	TT	1(.073)	3(-3.185)	6(3.114)	10
	TN	6(-.030)	46(5.794)	13(-5.762)	65
	NN	2(-.041)	11(-2.608)	9(2.650)	22
	Totals	9	60	28	97

$X^2_{(4)} = 9.2166$ P(.10-.05)

TABLE 44

Composition of experimental population 6, 45 day analysis, with deviations from proportionality to marginal frequencies

		Chromosome 4			
		TT	TN	NN	Totals
Chromosome 2	TT	7(3.776)	8(-3.521)	4(-.244)	19
	TN	4(-5.021)	39(6.862)	10(-1.840)	53
	NN	5(1.256)	10(-3.340)	7(2.086)	22
	Totals	16	57	21	94

$X^2_{(4)} = 12.2173$ P(.02-.01)

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 2	TT	7(3.766)	9(-2.723)	3(-1.042)	19
	TN	6(-3.021)	38(5.341)	9(-2.276)	53
	NN	3(-.744)	11(-2.574)	8(3.320)	22
	Totals	16	58	20	94

$X^2_{(4)} = 10.6243$ P(.05-.02)

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 4	TT	5(2.607)	9(-1.851)	3(-.436)	17
	TN	4(-5.095)	46(9.618)	7(-4.521)	57
	NN	6(2.809)	5(-7.775)	9(4.962)	20
	Totals	15	60	19	94

$X^2_{(4)} = 26.5587$ $P < .01$

TABLE 45

Composition of experimental population 6, 75 day analysis, with deviations from proportionality to marginal frequencies

		Chromosome 4			
		TT	TN	NN	Totals
Chromosome 2	TT	6(3.472)	3(-4.247)	6(1.153)	15
	TN	8(-2.314)	35(8.392)	11(-6.595)	54
	NN	3(-.820)	5(-4.662)	12(5.484)	20
	Totals	17	43	29	89

$X^2_{(4)} = 22.6533$ P<.01

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 2	TT	4(1.484)	6(-1.730)	6(.248)	16
	TN	5(-3.494)	32(5.911)	17(-2.415)	54
	NN	5(2,012)	5(-4.179)	9(2.158)	19
	Totals	14	43	32	89

$X^2_{(4)} = 8.2775$ P(.10-.05)

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 4	TT	3(.517)	5(-3.404)	9(2.888)	17
	TN	3(-3.280)	33(11.742)	7(-8.460)	43
	NN	7(2.765)	6(-8.337)	16(5.574)	29
	Totals	13	44	32	89

$X^2_{(4)} = 25.3121$ P<.01

TABLE 46

Composition of experimental population 6, 105 day analysis, with deviations from proportionality to marginal frequencies

		Chromosome 4			
		TT	TN	NN	Totals
Chromosome 2	TT	3(.923)	3(-1.522)	5(.600)	11
	TN	10(-.766)	27(3.567)	20(-2.800)	57
	NN	4(-.155)	7(-2.044)	11(2.200)	22
	Totals	17	37	36	90

$X^2_{(4)}$ = 2.9628 P(.70-.50)

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 2	TT	4(1.923)	6(.623)	1(-2.544)	11
	TN	9(-1.766)	29(1.134)	19(.634)	57
	NN	4(-.155)	9(-1.755)	9(1.912)	22
	Totals	17	44	29	90

$X^2_{(4)}$ = 4.8440 P(.50-.30)

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 4	TT	5(1.789)	5(-3.311)	7(1.523)	17
	TN	5(-1.611)	21(3.889)	9(-2.277)	35
	NN	7(-.177)	18(-.577)	13(.756)	38
	Totals	17	44	29	90

$X^2_{(4)}$ = 3.1704 P(.70-.50)

TABLE 47

Composition of experimental population 6, 135 day analysis, with deviations from proportionality to marginal frequencies

		Chromosome 4			
		TT	TN	NN	Totals
Chromosome 2	TT	0(-1.116)	6(1.907)	2(-.790)	8
	TN	8(.326)	26(-2.139)	21(1.814)	55
	NN	4(.791)	12(.233)	7(-1.023)	23
	Totals	12	44	30	86

$X^2_{(4)} = 2.9056$ P(.70-.50)

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 2	TT	2(.140)	5(1.187)	1(-1.325)	8
	TN	11(-2.023)	29(2.303)	16(-.279)	56
	NN	7(1.884)	7(-3.488)	8(1.605)	22
	Totals	20	41	25	86

$X^2_{(4)} = 3.6089$ P(.50-.30)

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 4	TT	1(-1.651)	6(.280)	5(1.373)	12
	TN	10(-.162)	20(-1.930)	16(2.094)	46
	NN	8(1.818)	15(1.652)	5(-3.465)	28
	Totals	19	41	26	86

$X^2_{(4)} = 4.0524$ P(.50-.30)

TABLE 48

Composition of experimental population 6, 165 day analysis, with deviations from proportionality to marginal frequencies

		Chromosome 4			
		TT	TN	NN	Totals
Chromosome 2	TT	2(1.371)	2(-1.932)	3(.562)	7
	TN	2(-1.415)	28(6.652)	8(-5.235)	38
	NN	4(.045)	20(-4.719)	20(4.675)	44
	Totals	8	50	31	89

$X^2_{(4)} = 11.1238$ P(.05-.02)

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 2	TT	1(.057)	3(-.382)	3(.326)	7
	TN	2(-2.988)	26(8.124)	9(-5.134)	37
	NN	9(2.933)	14(-7.741)	22(4.809)	45
	Totals	12	43	34	89

$X^2_{(4)} = 12.9521$ P(.05-.02)

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 4	TT	3(1.922)	2(-1.865)	3(-.056)	8
	TN	5(-1.741)	35(10.843)	10(-9.101)	50
	NN	4(-.179)	6(-8.977)	21(9.158)	31
	Totals	12	43	34	89

$X^2_{(4)} = 26.4428$ $P < .01$

TABLE 49

Composition of experimental population 9, 15 day analysis, with deviations from proportionality to marginal frequencies

		Chromosome 4			
		TT	TN	NN	Totals
Chromosome 2	TT	4(2.023)	6(-.303)	1(-1.719)	11
	TN	7(-2.707)	35(4.057)	12(-1.348)	54
	NN	5(.686)	10(-3.752)	9(3.068)	24
	Totals	16	51	22	89

$X^2_{(4)} = 7.3133$ P(.20-.10)

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 2	TT	4(2.765)	6(-.966)	0(-1.797)	10
	TN	4(-2.674)	44(6.383)	6(-3.707)	54
	NN	3(-.089)	12(-5.415)	10(5.507)	25
	Totals	11	62	16	89

$X^2_{(4)} = 19.2198$ $P<.01$

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 4	TT	4(2.113)	7(-2.752)	3(.641)	14
	TN	6(-1.146)	42(5.079)	5(-3.932)	53
	NN	2(-.966)	13(-2.325)	7(3.293)	22
	Totals	12	62	15	89

$X^2_{(4)} = 9.5223$ P(.05-.02)

TABLE 50

Composition of experimental population 9, 45 day analysis, with deviations from proportionality to marginal frequencies

		Chromosome 4			
		TT	TN	NN	Totals
Chromosome 2	TT	5(2.171)	7(-1.340)	2(-.829)	14
	TN	4(-7.925)	45(9.852)	10(-1.925)	59
	NN	10(5.756)	4(-8.510)	7(2.756)	21
	Totals	19	56	19	94

$X^{2}_{(4)} = 25.8404$ $P < .01$

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 2	TT	6(1.745)	12(-1.404)	2(-.340)	20
	TN	9(-2.063)	39(4.149)	4(-2.085)	52
	NN	5(.320)	12(-2.744)	5(2.426)	22
	Totals	20	63	11	94

$X^{2}_{(4)} = 6.6440$ P(.05-.02)

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 4	TT	7(2.788)	7(-4.489)	4(1.703)	18
	TN	8(-5.106)	42(6.256)	6(-1.148)	56
	NN	7(2.320)	11(-1.765)	2(-.553)	20
	Totals	22	60	12	94

$X^{2}_{(4)} = 9.6440$ P(.05-.02)

TABLE 51

Composition of experimental population 9, 75 day analysis, with deviations from proportionality to marginal frequencies

		Chromosome 4			
		TT	TN	NN	Totals
Chromosome 2	TT	5(2.500)	5(-5.000)	5(2.500)	15
	TN	7(-2.833)	49(9.667)	3(-6.833)	59
	NN	3(.334)	6(-4.666)	7(4.334)	16
	Totals	15	60	15	90

$X^{2}_{(4)} = 24.5919$ $P < .01$

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 2	TT	6(2.800)	3(-9.000)	9(6.200)	18
	TN	5(-5.311)	50(11.334)	3(-6.022)	58
	NN	5(2.512)	7(-2.333)	2(-.177)	14
	Totals	16	60	14	90

$X^{2}_{(4)} = 36.1393$ $P < .01$

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 4	TT	8(3.567)	7(-7.000)	6(3.434)	21
	TN	7(-4.822)	47(9.667)	2(-4.844)	56
	NN	4(1.256)	6(-2.666)	3(1.412)	13
	Totals	19	60	11	90

$X^{2}_{(4)} = 21.5106$ $P < .01$

TABLE 52

Composition of experimental population 9, 105 day analysis, with deviations from proportionality to marginal frequencies

		Chromosome 4			
		TT	TN	NN	Totals
Chromosome 2	TT	12(5.667)	6(-5.611)	1(.055)	19
	TN	15(-6.000)	46(7.500)	2(-1.500)	63
	NN	3(.334)	3(-1.888)	2(1.556)	8
	Totals	30	55	5	90

$X^2_{(4)} = 17.8272$ $P < .01$

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 2	TT	3(-.063)	3(-3.533)	6(3.600)	12
	TN	13(-3.100)	41(6.700)	9(-3.600)	63
	NN	7(3.167)	5(-3.166)	3(.000)	15
	Totals	23	49	18	90

$X^2_{(4)} = 14.0903$ $P < .01$

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 4	TT	5(2.867)	2(-4.266)	5(1.400)	12
	TN	8(-2.844)	38(6.123)	15(-3.300)	61
	NN	3(.022)	7(-1.877)	7(1.900)	17
	Totals	16	47	27	90

$X^2_{(4)} = 10.0232$ $P(.05-.02)$

TABLE 53

Composition of experimental population 9, 135 day analysis, with deviations from proportionality to marginal frequencies

		Chromosome 4			
		TT	TN	NN	Totals
Chromosome 2	TT	8(2.256)	6(-4.011)	3(1.867)	17
	TN	18(3.700)	42(4.900)	3(-1.200)	63
	NN	5(1.556)	5(-.888)	0(-.666)	10
	Totals	31	53	6	90

$X^2_{(4)} = 8.6341$ P(.01-.05)

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 2	TT	14(5.945)	14(-4.888)	1(-.933)	29
	TN	8(-6.722)	42(7.256)	3(-.533)	53
	NN	3(.778)	3(-2.244)	2(1.467)	8
	Totals	25	59	6	90

$X^2_{(4)} = 16.0171$ $P < .01$

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 4	TT	3(.667)	4(-4.166)	8(3.500)	15
	TN	6(-.222)	29(7.223)	5(-7.000)	40
	NN	5(-.444)	16(-3.055)	14(2.900)	35
	Totals	14	49	27	90

$X^2_{(4)} = 12.8085$ P(.02-.01)

TABLE 54

Composition of experimental population 4, 15 day analysis, with deviations from proportionality to marginal frequencies

		Chromosome 4			
		TT	TN	NN	Totals
Chromosome 2	TT				
	TN		28(2.480)	22(-2.479)	50
	NN		21(-2.479)	25(2.480)	46
	Totals		49	47	96

$X^2_{(4)} = 1.0268$ P(.95-.90)

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 2	TT				
	TN		29(4.500)	20(-4.500)	49
	NN		19(-4.500)	28(4.500)	47
	Totals		48	48	96

$X^2_{(4)} = 3.3764$ P(.50-.30)

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 4	TT				
	TN		30(5.500)	18(-5.500)	48
	NN		19(-5.500)	29(5.500)	48
	Totals		49	47	96

$X^2_{(4)} = 5.0496$ P(.30-.20)

TABLE 55

Composition of experimental population 4, 45 day analysis, with deviations from proportionality to marginal frequencies

		Chromosome 4			
		TT	TN	NN	Totals
Chromosome 2	TT	0(-.361)	2(-.891)	4(1.254)	6
	TN	1(-1.228)	24(6.169)	12(-4.939)	37
	NN	4(1.591)	14(-5.277)	22(3.687)	40
	Totals	5	40	38	83

$X^2_{(4)} = 8.7152$ P(.10-.05)

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 2	TT	1(-.292)	2(.362)	1(-1.072)	4
	TN	1(1.602)	24(9.254)	11(-7.650)	36
	NN	4(-.892)	8(-9.614)	31(8.723)	43
	Totals	6	34	43	83

$X^2_{(4)} = 14.5566$ $P < .01$

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 4	TT	1(-.433)	0(-2.457)	5(1.892)	6
	TN	4(1.109)	24(7.615)	12(-8.722)	40
	NN	1(-1.674)	10(-5.156)	26(6.832)	37
	Totals	6	34	43	83

$X^2_{(4)} = 15.9137$ $P < .01$

TABLE 56

Composition of experimental population 4, 75 day analysis, with deviations from proportionality to marginal frequencies

		Chromosome 4			
		TT	TN	NN	Totals
Chromosome 2	TT	3(1.742)	1(-1.157)	4(-.584)	8
	TN	4(-2.134)	21(10.484)	14(-8.348)	39
	NN	7(.394)	2(-9.525)	33(8.933)	42
	Totals	14	24	51	89

$X^2_{(4)} = 28.6825$ $P < .01$

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 2	TT	3(1.383)	3(-.056)	2(-1.325)	8
	TN	3(-4.685)	25(10.484)	10(-5.797)	38
	NN	12(3.304)	6(-10.426)	25(7.124)	43
	Totals	18	34	37	89

$X^2_{(4)} = 24.9790$ $P < .01$

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 4	TT	4(1.484)	4(-1.348)	6(-.134)	14
	TN	1(-3.314)	17(7.832)	6(-4.516)	24
	NN	11(1.832)	13(-6.483)	27(4.652)	51
	Totals	16	34	39	89

$X^2_{(4)} = 15.8786$ $P < .01$

TABLE 57

Composition of experimental population 4, 105 day analysis, with deviations from proportionality to marginal frequencies

		Chromosome 4			
		TT	TN	NN	Totals
Chromosome 2	TT	2(.821)	1(-1.359)	4(.540)	7
	TN	6(-1.584)	24(8.832)	15(-7.247)	45
	NN	7(.765)	5(-7.471)	25(6.708)	37
	Totals	15	30	44	89

$X^2_{(4)} = 16.2766$ $P < .01$

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 2	TT	0(-.943)	3(-.146)	4(1.090)	7
	TN	7(.798)	25(4.326)	14(-5.123)	46
	NN	5(.147)	12(-4.179)	19(4.034)	36
	Totals	12	40	37	89

$X^2_{(4)} = 5.9218$ P(.20-.10)

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 4	TT	1(-1.57)	4(-3.191)	11(4.349)	16
	TN	5(1.090)	20(6.967)	4(-8.056)	29
	NN	6(.680)	16(-3.775)	22(3.708)	44
	Totals	12	40	37	89

$X^2_{(4)} = 15.8414$ $P < .01$

TABLE 58

Composition of experimental population 4, 135 day analysis, with deviations from proportionality to marginal frequencies

		Chromosome 4			
		TT	TN	NN	Totals
Chromosome 2	TT	1(.342)	4(-.235)	3(-.105)	8
	TN	3(-.952)	32(6.589)	13(-5.635)	48
	NN	3(.612)	9(-6.352)	17(5.742)	29
	Totals	5	45	33	85

$X^2_{(4)} = 9.5545$ P(.05-.02)

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 2	TT	2(1.177)	2(-1.623)	3(.448)	7
	TN	5(-.882)	34(8.118)	11(-7.235)	50
	NN	3(-.294)	8(-6.494)	17(6.789)	28
	Totals	10	44	31	85

$X^2_{(4)} = 15.4873$ $P < .01$

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 4	TT	1(.059)	5(.859)	2(-.917)	8
	TN	3(-2.058)	30(7.742)	10(-5.682)	43
	NN	6(2.000)	9(-8.600)	19(6.600)	34
	Totals	10	44	31	85

$X^2_{(4)} = 14.7738$ $P < .01$

TABLE 59

Composition of experimental population 4, 165 day analysis, with deviations from proportionality to marginal frequencies

		Chromosome 4			
		TT	TN	NN	Totals
Chromosome 2	TT	5(4.000)	4(-1.500)	0(-2.500)	9
	TN	3(-1.777)	36(9.723)	4(-7.944)	43
	NN	2(-2.222)	15(-8.222)	21(10.445)	38
	Totals	10	55	25	90

$X^2_{(4)} = 42.8675$ $P < .01$

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 2	TT	6(3.900)	4(-1.000)	0(-2.900)	9
	TN	4(-1.133)	33(9.667)	5(-8.533)	42
	NN	2(-2.766)	13(-8.666)	24(11.434)	39
	Totals	11	50	29	90

$X^2_{(4)} = 42.0333$ $P < .01$

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 4	TT	7(5.412)	5(-2.366)	1(-3.044)	13
	TN	4(-2.477)	38(7.967)	11(-5.448)	53
	NN	0(-2.933)	8(-5.600)	16(8.534)	24
	Totals	11	51	28	90

$X^2_{(4)} = 41.7047$ $P < .01$

TABLE 60

Composition of experimental population 5, 15 day analysis, with deviations from proportionality to marginal frequencies

		Chromosome 4			
		TT	TN	NN	Totals
Chromosome 2	TT				
	TN		22(-1.404)	22(1.405)	44
	NN		28(1.405)	22(-1.404)	50
	Totals		50	44	94

$X^2_{(4)}$ = .3504 P(.50-.30)

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 2	TT				
	TN		25(2.022)	20(-2.021)	45
	NN		23(-2.021)	26(2.022)	49
	Totals		48	46	94

$X^2_{(4)}$ = .6970 P(.98-.95)

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 4	TT				
	TN		26(1.500)	23(-1.500)	49
	NN		21(-1.500)	24(1.500)	45
	Totals		47	47	94

$X^2_{(4)}$ = .3836 P(.99-.98)

TABLE 61

Composition of experimental population 5, 45 day analysis, with deviations from proportionality to marginal frequencies

		Chromosome 4			
		TT	TN	NN	Totals
Chromosome 2	TT	3(1.293)	9(-3.955)	7(1.663)	19
	TN	2(-2.404)	42(11.169)	5(-8.764)	49
	NN	3(1.113)	5(-8.213)	13(7.102)	21
	Totals	8	56	25	89

$X^2_{(4)} = 28.0599$ $P < .01$

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 2	TT	1(.574)	11(-.528)	7(-.044)	19
	TN	0(-1.101)	40(10.270)	9(-9.842)	49
	NN	1(.529)	3(-9.741)	17(9.214)	21
	Totals	2	54	33	89

$X^2_{(4)} = 29.5478$ $P < .01$

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 4	TT	0(-.0786)	3(-1.168)	4(1.248)	7
	TN	0(-.629)	46(12.652)	10(-12.022)	56
	NN	1(.708)	4(-11.483)	21(10.776)	26
	Totals	1	53	35	89

$X^2_{(4)} = 43.3946$ $P < .01$

TABLE 62

Composition of experimental population 5, 75 day analysis, with deviations from proportionality to marginal frequencies

		Chromosome 4			
		TT	TN	NN	Totals
Chromosome 2	TT	5(3.468)	2(-4.255)	7(1.043)	14
	TN	5(-2.184)	35(9.979)	16(-7.829)	56
	NN	2(-1.063)	5(-5.723)	17(6.783)	24
	Totals	12	42	40	94

$X^2_{(4)} = 19.0077$ $P<.01$

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 2	TT	2(1.032)	7(1.192)	4(-2.223)	13
	TN	4(-.393)	31(4.639)	24(-4.244)	59
	NN	1(-.638)	4(-5.829)	14(6.469)	22
	Totals	7	42	45	94

$X^2_{(4)} = 11.3069$ $P(.05-.02)$

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 4	TT	2(1.181)	2(-2.914)	7(1.735)	11
	TN	4(.724)	27(7.341)	13(-8.063)	44
	NN	1(-1.904)	13(-4.425)	25(6.330)	39
	Totals	7	42	45	94

$X^2_{(4)} = 14.5082$ $P<.01$

TABLE 63

Composition of experimental population 5, 105 day analysis, with deviations from proportionality to marginal frequencies

		Chromosome 4			
		TT	TN	NN	Totals
Chromosome 2	TT	4(2.495)	8(.064)	1(-2.557)	13
	TN	6(-.813)	42(5.979)	11(-5.147)	59
	NN	1(-1.663)	8(-6,042)	14(7.706)	23
	Totals	11	58	26	95

$X^2_{(4)} = 21.3640$ $P<.01$

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 2	TT	0(-.957)	11(1.558)	2(-.600)	13
	TN	4(-.347)	47(4.148)	8(-3.800)	59
	NN	3(1,306)	11(-5.705)	9(4.400)	23
	Totals	7	69	19	95

$X^2_{(4)} = 10.1700$ $P(.05-.02)$

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 4	TT	0(-1.031)	11(.979)	3(.053)	14
	TN	3(-1,126)	47(6.916)	6(-5.789)	56
	NN	4(2.158)	10(-7,894)	11(5.737)	25
	Totals	7	68	20	95

$X^2_{(4)} = 17.7345$ $P<.01$

TABLE 64

Composition of experimental population 5, 135 day analysis, with deviations from proportionality to marginal frequencies

			Chromosome 4		
		TT	TN	NN	Totals
Chromosome 2	TT	6(3.385)	8(.154)	0(-3.538)	14
	TN	5(-4.340)	35(6.979)	10(-2.637)	50
	NN	6(.957)	8(-7.131)	13(6.176)	27
	Totals	17	51	23	91

$X^2_{(4)} = 21.3696$ $P < .01$

			Chromosome 5		
		TT	TN	NN	Totals
Chromosome 2	TT	4(2.572)	8(-.142)	1(-2.428)	13
	TN	0(-5.604)	40(8.055)	11(-2.450)	51
	NN	6(3.033)	9(-7.912)	12(4.880)	27
	Totals	10	57	24	91

$X^2_{(4)} = 24.5820$ $P < .01$

			Chromosome 5		
		TT	TN	NN	Totals
Chromosome 4	TT	5(3.121)	8(-3.901)	6(.781)	19
	TN	1(-3.846)	42(11.308)	6(-7.461)	49
	NN	3(.726)	7(-7.406)	13(6.682)	23
	Totals	9	57	25	91

$X^2_{(4)} = 29.0389$ $P < .01$

TABLE 65

Composition of experimental population 5, 165 day analysis, with deviations from proportionality to marginal frequencies

		Chromosome 4			
		TT	TN	NN	Totals
Chromosome 2	TT	3(1.735)	3(-4.951)	9(3.217)	15
	TN	4(-.132)	32(6.386)	13(-5.891)	49
	NN	0(-1.602)	9(-1.072)	10(2.675)	19
	Totals	7	44	32	83

$X^2_{(4)} = 12.9459$ P(.02-.01)

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 2	TT	5(3.193)	7(-3.481)	3(.290)	15
	TN	2(-3.903)	41(6.760)	6(-2.855)	49
	NN	3(.711)	10(-3.277)	6(2.567)	19
	Totals	10	58	15	83

$X^2_{(4)} = 14.5982$ $P<.01$

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 4	TT	2(1.037)	5(-.590)	1(-.445)	8
	TN	2(-3.301)	39(8.254)	3(-4.951)	44
	NN	6(2.266)	14(-7.662)	11(5.398)	31
	Totals	10	58	15	83

$X^2_{(4)} = 17.9566$ $P<.01$

TABLE 66

Composition of experimental population 7, 15 day analysis, with deviations from proportionality to marginal frequencies

		Chromosome 4			
		TT	TN	NN	Totals
Chromosome 2	TT	28(3.709)	25(-3.708)		53
	TN	16(-3.708)	27(3.709)		43
	NN				
	Totals	44	52		96

$X^2_{(4)} = 2.3101$ P(.70-.50)

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 2	TT	29(-1.208)	21(1.209)		50
	TN	29(1.209)	17(-1.208)		46
	NN				
	Totals	58	38		96

$X^2_{(4)} = 2.5470$ P(.70-.50)

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 4	TT	32(4.584)	15(-4.583)		47
	TN	24(-5.583)	25(4.584)		49
	NN				
	Totals	56	40		96

$X^2_{(4)} = 3.6029$ P(.50-.30)

TABLE 67

Composition of experimental population 7, 45 day analysis, with deviations from proportionality to marginal frequencies

		Chromosome 4			
		TT	TN	NN	Totals
Chromosome 2	TT	36(14.734)	9(-13.747)	0(-.989)	45
	TN	7(-13.791)	35(12.759)	2(1.033)	44
	NN	0(-.945)	2(.990)	0(-.0439)	2
	Totals	43	46	2	91

$X^2_{(4)} = 43.2129$ $P < .01$

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 2	TT	24(8.407)	19(-7.461)	0(-.945)	43
	TN	8(-8.681)	36(7.693)	2(.990)	46
	NN	1(.275)	1(-.230)	0(-.0439)	2
	Totals	33	56	2	91

$X^2_{(4)} = 19.7016$ $P < .01$

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 4	TT	28(12.044)	15(-11.659)	1(.033)	44
	TN	5(-11.318)	40(12.308)	0(-.989)	45
	NN	0(-.725)	1(-.230)	1(.956)	2
	Totals	33	56	2	91

$X^2_{(4)} = 32.3499$ $P < .01$

TABLE 68

Composition of experimental population 7, 75 day analysis, with deviations from proportionality to marginal frequencies

		Chromosome 4			
		TT	TN	NN	Totals
Chromosome 2	TT	16(5.723)	2(-7.166)	7(1.445)	25
	TN	18(-5.022)	27(6.467)	11(-1.444)	56
	NN	3(-.700)	4(.700)	2(.000)	9
	Totals	37	33	20	90

$X^2_{(4)}$ = 15.9670 $P < .01$

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 2	TT	10(1.056)	10(-1.244)	3(.189)	23
	TN	22(-.555)	30(1.645)	6(-1.088)	58
	NN	3(-.500)	4(-.400)	2(.900)	9
	Totals	35	44	11	90

$X^2_{(4)}$ = 1.5135 P(.90-.80)

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 4	TT	24(8.834)	13(-6.066)	2(-1.788)	39
	TN	7(-5.055)	23(7.845)	1(-3.766)	31
	NN	4(-3.777)	8(-1.777)	8(5.556)	20
	Totals	35	44	11	90

$X^2_{(4)}$ = 31.2471 $P < .01$

TABLE 69

Composition of experimental population 7, 105 day analysis, with deviations from proportionality to marginal frequencies

		Chromosome 4			
		TT	TN	NN	Totals
Chromosome 2	TT	8(2.256)	6(-4.011)	3(1.867)	17
	TN	18(-3.700)	42(4.900)	3(-1.200)	63
	NN	5(1.556)	5(-.888)	0(-.666)	10
	Totals	31	53	6	90

$X^2_{(4)} = 8.6771$ P(.10-.05)

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 2	TT	6(1.278)	9(-2.144)	2(.867)	17
	TN	16(-1.501)	45(3.700)	2(-2.200)	63
	NN	3(.223)	5(-1.555)	2(1.334)	10
	Totals	25	59	6	90

$X^2_{(4)} = 6.0924$ P(.20-.10)

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 4	TT	14(5.945)	14(-4.888)	1(-.933)	29
	TN	8(-6.722)	42(7.265)	3(-.533)	53
	NN	3(.778)	3(-2.244)	2(1.467)	8
	Totals	25	59	6	90

$X^2_{(4)} = 16.0182$ $P < .01$

TABLE 70

Composition of experimental population 7, 135 day analysis, with deviations from proportionality to marginal frequencies

		Chromosome 4			
		TT	TN	NN	Totals
Chromosome 2	TT	10(4.000)	5(-5.200)	3(1.200)	18
	TN	18(-3.000)	44(8.300)	1(-5.300)	63
	NN	2(-1.000)	2(-3.100)	5(4.100)	9
	Totals	30	51	9	90

$X^2_{(4)} = 33.8296$ $P < .01$

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 2	TT	12(5.667)	6(-5.611)	1(-.055)	19
	TN	15(-6.000)	46(7.500)	2(-1.500)	63
	NN	3(.334)	3(-1.888)	2(1.556)	8
	Totals	30	55	5	90

$X^2_{(4)} = 17.8272$ $P < .01$

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 4	TT	15(4.323)	16(-2.944)	0(-1.377)	31
	TN	11(-6.222)	38(7.445)	1(-1.222)	50
	NN	5(1.900)	1(-4.500)	3(2.600)	9
	Totals	31	55	4	90

$X^2_{(4)} = 31.3917$ $P < .01$

TABLE 71

Composition of experimental population 7, 165 day analysis, with deviations from proportionality to marginal frequencies

		Chromosome 4			
		TT	TN	NN	Totals
Chromosome 2	TT	19(9.609)	11(-7.782)	2(-1.826)	32
	TN	8(-7.554)	41(9.892)	4(-2.336)	53
	NN	0(-2.054)	2(-2.108)	5(4.164)	7
	Totals	27	54	11	92

$X^2_{(4)} = 45.4266$ $P < .01$

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 2	TT	14(4.674)	17(-5.597)	2(.924)	33
	TN	9(-5.695)	43(7.392)	0(-1.695)	52
	NN	3(1.022)	3(-1.793)	1(.772)	7
	Totals	26	63	3	92

$X^2_{(4)} = 14.8734$ $P < .01$

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 4	TT	14(6.392)	13(-6.478)	1(.087)	28
	TN	8(-7.673)	45(7.435)	1(-.760)	54
	NN	3(.283)	6(-.956)	1(.674)	10
	Totals	25	64	3	92

$X^2_{(4)} = 14.7822$ $P < .01$

TABLE 72

Composition of experimental population 8, 15 day analysis, with deviations from proportionality to marginal frequencies

		Chromosome 4			
		TT	TN	NN	Totals
Chromosome 2	TT	37(13.258)	10(-13.257)		47
	TN	12(-13.257)	38(13.258)		50
	NN				
	Totals	49	48		97

$X^2_{(4)} = 29.0232$ $P<.01$

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 2	TT	25(7.186)	23(-7.185)		48
	TN	11(-7.185)	38(7.186)		49
	NN				
	Totals	36	61		97

$X^2_{(4)} = 9.4558$ P(.10-.05)

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 4	TT	23(4.444)	27(-4.443)		50
	TN	13(-4.443)	34(4.444)		47
	NN				
	Totals	36	61		97

$X^2_{(4)} = 3.4945$ P(.50-.30)

TABLE 73

Composition of experimental populations 8, 45 day analysis, with deviations from proportionality to marginal frequencies

		Chromosome 4			
		TT	TN	NN	Totals
Chromosome 2	TT	24(10.024)	9(-9.635)	0(-.338)	33
	TN	12(-10.023)	39(9.636)	1(.339)	52
	NN	0(.000)	0(.000)	0(.000)	0
	Totals	36	48	1	85

$X^2_{(4)} = 20.3723 \; P < .01$

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 2	TT	21(8.200)	11(-7.447)	0(-.752)	32
	TN	13(-8.200)	38(7.448)	2(.753)	53
	NN	0(.000)	0(.000)	0(.000)	0
	Totals	34	49	2	85

$X^2_{(4)} = 14.4529 \; P < .01$

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 4	TT	24(9.589)	11(-9.176)	0(-.411)	35
	TN	11(-8.764)	37(9.330)	0(-.564)	48
	NN	0(-.823)	1(-.152)	1(.977)	2
	Totals	35	49	1	85

$X^2_{(4)} = 49.2314 \; P < .01$

TABLE 74

Composition of experimental population 8, 75 day analysis, with deviations from proportionality to marginal frequencies

		Chromosome 4			
		TT	TN	NN	Totals
Chromosome 2	TT	24(5.596)	11(-6.089)	4(.497)	39
	TN	13(-6.348)	26(8.034)	2(-1.685)	41
	NN	5(.753)	2(-1.943)	2(1.192)	9
	Totals	42	39	8	89

$X^2_{(4)} = 11.6529$ P(.05-.02)

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 2	TT	27(7.675)	13(-7.224)	0(-.449)	40
	TN	10(-9.325)	30(9.776)	0(-.449)	40
	NN	6(1.652)	2(-2.550)	1(.899)	9
	Totals	43	45	1	89

$X^2_{(4)} = 25.8095$ $P<.01$

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 4	TT	26(5.708)	16(-6.224)	1(.517)	43
	TN	10(-7.932)	28(8.360)	0(-.426)	38
	NN	6(2.225)	2(-2.134)	0(-.089)	8
	Totals	42	46	1	89

$X^2_{(4)} = 13.9111$ $P<.01$

TABLE 75

Composition of experimental population 8, 105 day analysis, with deviations from proportionality to marginal frequencies

		Chromosome 4			
		TT	TN	NN	Totals
Chromosome 2	TT	20(2.689)	16(-3.844)	2(1.156)	38
	TN	18(-2.044)	26(3.023)	0(-.977)	44
	NN	3(-.644)	5(.823)	0(-.177)	8
	Totals	41	47	2	90

$X^2_{(4)}$ = 3.4512 P(.50-.30)

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 2	TT	20(1.423)	18(-1.422)	0(.000)	38
	TN	17(-4.511)	27(4.512)	0(.000)	44
	NN	7(3.089)	1(-3.088)	0(.000)	8
	Totals	44	46	0	90

$X^2_{(4)}$ = 6.8366 P(.20-.10)

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 4	TT	26(6.067)	13(-6.066)	0(.000)	39
	TN	17(-6.511)	29(6.512)	0(.000)	46
	NN	3(.445)	2(-.444)	0(.000)	5
	Totals	46	44	0	90

$X^2_{(4)}$ = 7.6233 P(.20-.10)

TABLE 76

Composition of experimental population 8, 135 day analysis, with deviations from proportionality to marginal frequencies

		Chromosome 4			
		TT	TN	NN	Totals
Chromosome 2	TT	14(5.825)	15(-4.417)	2(-1.406)	31
	TN	6(-7.714)	39) 6.429)	7(1.286)	52
	NN	4(1.891)	3(-2.010)	1(.121)	8
	Totals	24	57	10	91

$X^2_{(4)} = 14.1552$ $P<.01$

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 2	TT	15(5.462)	16(-3.076)	0(-2.384)	31
	TN	11(-4.692)	35(3.616)	5(1.077)	51
	NN	2(-.769)	5(-.538)	2(1.308)	9
	Totals	28	56	7	91

$X^2_{(4)} = 11.3311$ P(.05-.02)

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 4	TT	13(5.616)	9(-6.032)	2(.418)	24
	TN	10(-7.538)	46(9.900)	1(-2.758)	57
	NN	5(1.924)	2(-4.263)	3(2.341)	10
	Totals	28	57	6	91

$X^2_{(4)} = 27.2019$ $P<.01$

TABLE 77

Composition of experimental population 8, 165 day analysis, with deviations from proportionality to marginal frequencies

		Chromosome 4			
		TT	TN	NN	Totals
Chromosome 2	TT	14(5.567)	10(-7.422)	4(1.823)	28
	TN	9(-6.900)	44(11.023)	0(-4.122)	53
	NN	4(1.300)	2(-3.600)	3(2.300)	9
	Totals	27	56	7	90

$X^2_{(4)} = 30.2047$ $P < .01$

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 2	TT	12(3.900)	12(-4.500)	3(.600)	27
	TN	13(-3.200)	41(8.000)	0(-4.800)	54
	NN	2(-.700)	2(-3.500)	5(4.200)	9
	Totals	27	55	8	90

$X^2_{(4)} = 35.0848$ $P < .01$

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 4	TT	13(5.200)	12(-3.833)	1(-1.311)	26
	TN	12(-5.100)	42(7.167)	3(-2.066)	57
	NN	2(-.100)	1(-3.227)	4(3.378)	7
	Totals	27	55	8	90

$X^2_{(4)} = 28.7591$ $P < .01$

TABLE 78

Composition of experimental population 3, 45 day analysis, with deviations from proportionality to marginal frequencies

		Chromosome 4			
		TT	TN	NN	Totals
Chromosome 2	TT	13(4.805)	3(-.172)	7(-4.632)	23
	TN	3(-1.275)	7(5.345)	2(-4.068)	12
	NN	15(-3.528)	2(-5.172)	35(8.702)	52
	Totals	31	12	44	87

$X^2_{(4)} = 32.3214$ $P < .01$

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 2	TT	10(4.437)	3(-.793)	9(-3.643)	22
	TN	2(-1.793)	9(6.414)	4(-4.620)	15
	NN	10(-2.643)	3(-5.643)	37(8.265)	50
	Totals	22	15	50	87

$X^2_{(4)} = 30.6266$ $P < .01$

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 4	TT	16(8.161)	4(-1.344)	11(-6.816)	31
	TN	1(-2.034)	8(5.932)	3(-3.896)	12
	NN	5(-6.264)	3(-4.586)	36(10.713)	44
	Totals	22	15	50	87

$X^2_{(4)} = 42.8154$ $P < .01$

TABLE 79

Composition of experimental population 3, 75 day analysis, with deviations from proportionality to marginal frequencies

		Chromosome 4			
		TT	TN	NN	Totals
Chromosome 2	TT	13(3.609)	0(-2.478)	6(-3.086)	19
	TN	7(.740)	9(6.914)	0(-7.652)	16
	NN	16(-6.304)	3(-4.434)	38(10.740)	57
	Totals	36	12	44	92

$X^2_{(4)} = 32.3424$ $P < .01$

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 2	TT	14(8.011)	3(-.717)	2(-7.293)	19
	TN	3(-2.358)	10(6.283)	4(-4.315)	17
	NN	12(-5.652)	5(-5.956)	39(11.609)	56
	Totals	29	18	45	92

$X^2_{(4)} = 38.4422$ $P < .01$

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 4	TT	18(6.337)	10(2.761)	9(-9.097)	37
	TN	2(-2.097)	7(4.457)	4(-2.358)	13
	NN	9(-4.239)	1(-7.217)	32(11.457)	42
	Totals	29	18	45	92

$X^2_{(4)} = 32.9136$ $P < .01$

TABLE 80

Composition of experimental population 3, 105 day analysis, with deviations from proportionality to marginal frequencies

		Chromosome 4			
		TT	TN	NN	Totals
Chromosome 2	TT	1(.419)	2(1.143)	0(-1.561)	3
	TN	4(-1.816)	20(11.429)	6(-9.612)	30
	NN	14(1.398)	6(-12.571)	45(11.174)	65
	Totals	19	28	51	89

$X^2_{(4)} = 37.4707$ $P < .01$

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 2	TT	1(.511)	1(.143)	1(-.653)	3
	TN	2(-2.897)	23(14.429)	5(-11.533)	30
	NN	13(2.388)	4(-14.571)	48(12.184)	65
	Totals	16	28	54	98

$X^2_{(4)} = 50.9797$ $P < .01$

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 4	TT	4(.898)	2(-3.428)	13(2.531)	19
	TN	4(-.571)	18(10.000)	6(-9.428)	28
	NN	8(-.326)	8(-6.571)	35(6.898)	51
	Totals	16	28	54	98

$X^2_{(4)} = 26.6802$ $P < .01$

TABLE 81

Composition of experimental population 3, 135 day analysis, with deviations from proportionality to marginal frequencies

		Chromosome 4			
		TT	TN	NN	Totals
Chromosome 2	TT	5(3.045)	2(.045)	1(-3.088)	8
	TN	3(-1.888)	14(9.112)	3(-7.222)	20
	NN	14(-1.155)	6(-9.155)	42(10.312)	62
	Totals	22	22	46	90

$X^{2}_{(4)} = 34.6871$ P<.01

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 2	TT	5(2.867)	2(-.044)	1(-2.822)	8
	TN	2(-3.066)	15(10.145)	2(-7.077)	19
	NN	17(.200)	6(-10.100)	40(9.900)	63
	Totals	24	23	43	90

$X^{2}_{(4)} = 44.1044$ P<.01

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 4	TT	16(10.400)	1(-4.366)	4(-6.033)	21
	TN	1(-4.866)	17(11.378)	4(-6.511)	22
	NN	7(-5.533)	5(-7.011)	35(12.545)	47
	Totals	24	23	43	90

$X^{2}_{(4)} = 53.8545$ P<.01

TABLE 82

Composition of experimental population 3, 165 day analysis, with deviations from proportionality to marginal frequencies

		Chromosome 4			
		TT	TN	NN	Totals
Chromosome 2	TT	1(.070)	0(-1.279)	4(1.210)	5
	TN	2(-2.279)	12(6.117)	9(-3.837)	23
	NN	13(2.210)	10(-4.837)	35(2.628)	58
	Totals	16	22	48	86

$X^2_{(4)} = 12.7723$ $P<.01$

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 2	TT	2(.886)	1(-.883)	3(.000)	6
	TN	1(-3.279)	18(10.780)	4(-7.500)	23
	NN	13(2.396)	8(-9.895)	36(7.500)	57
	Totals	16	27	43	86

$X^2_{(4)} = 32.5422$ $P<.01$

		Chromosome 5			
		TT	TN	NN	Totals
Chromosome 4	TT	7(4.384)	3(-2.058)	5(-2.325)	15
	TN	3(-1.011)	15(7.245)	5(-6.232)	23
	NN	5(-3.372)	11(-5.186)	32(8.559)	48
	Totals	15	29	42	86

$X^2_{(4)} = 25.5541$ $P<.01$

APPENDIX E

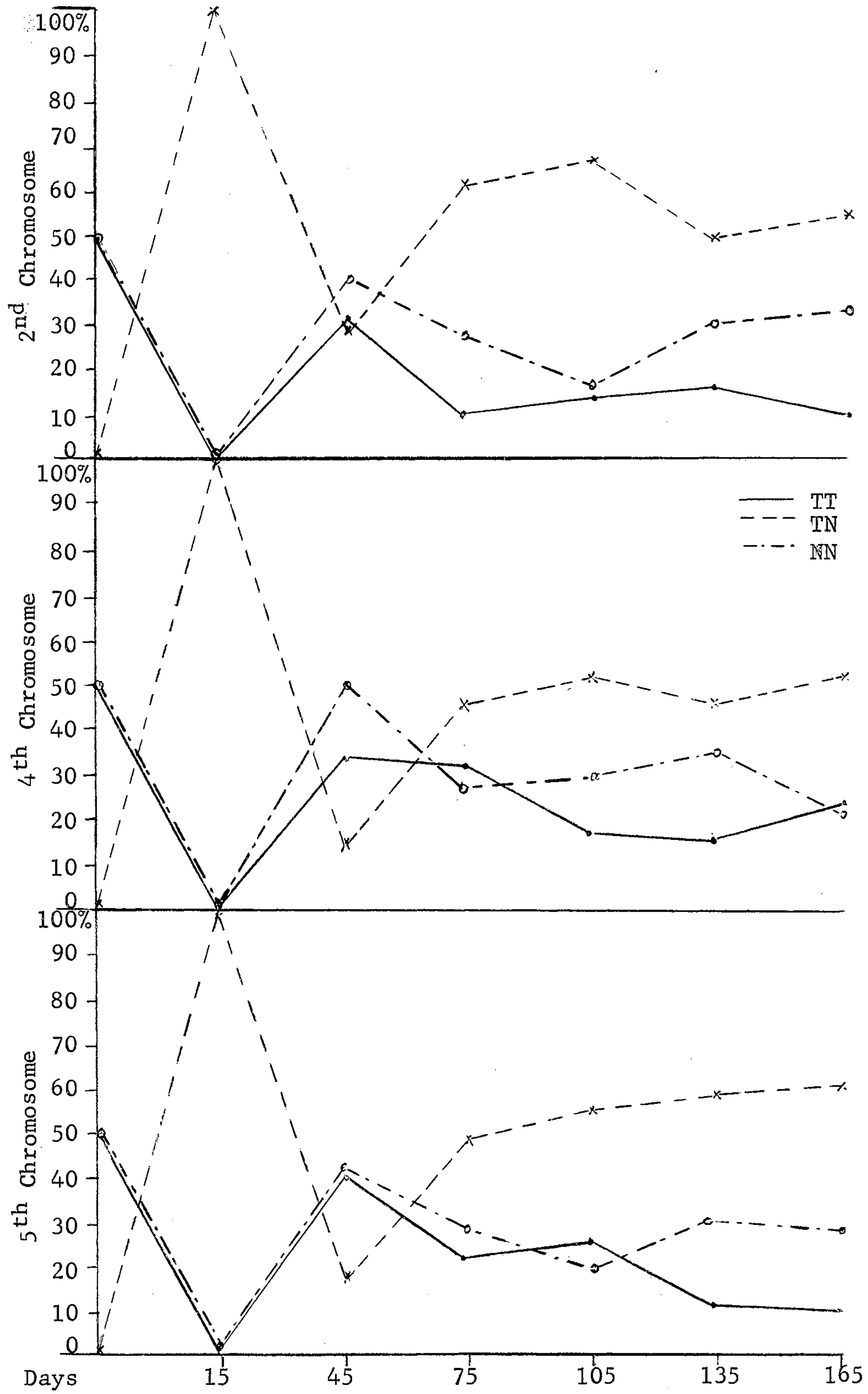

Fig. 1. Cage 1. Started with texana females and novamexicana males. The percentage of homozygous and heterozygous combinations of the three autosomes.

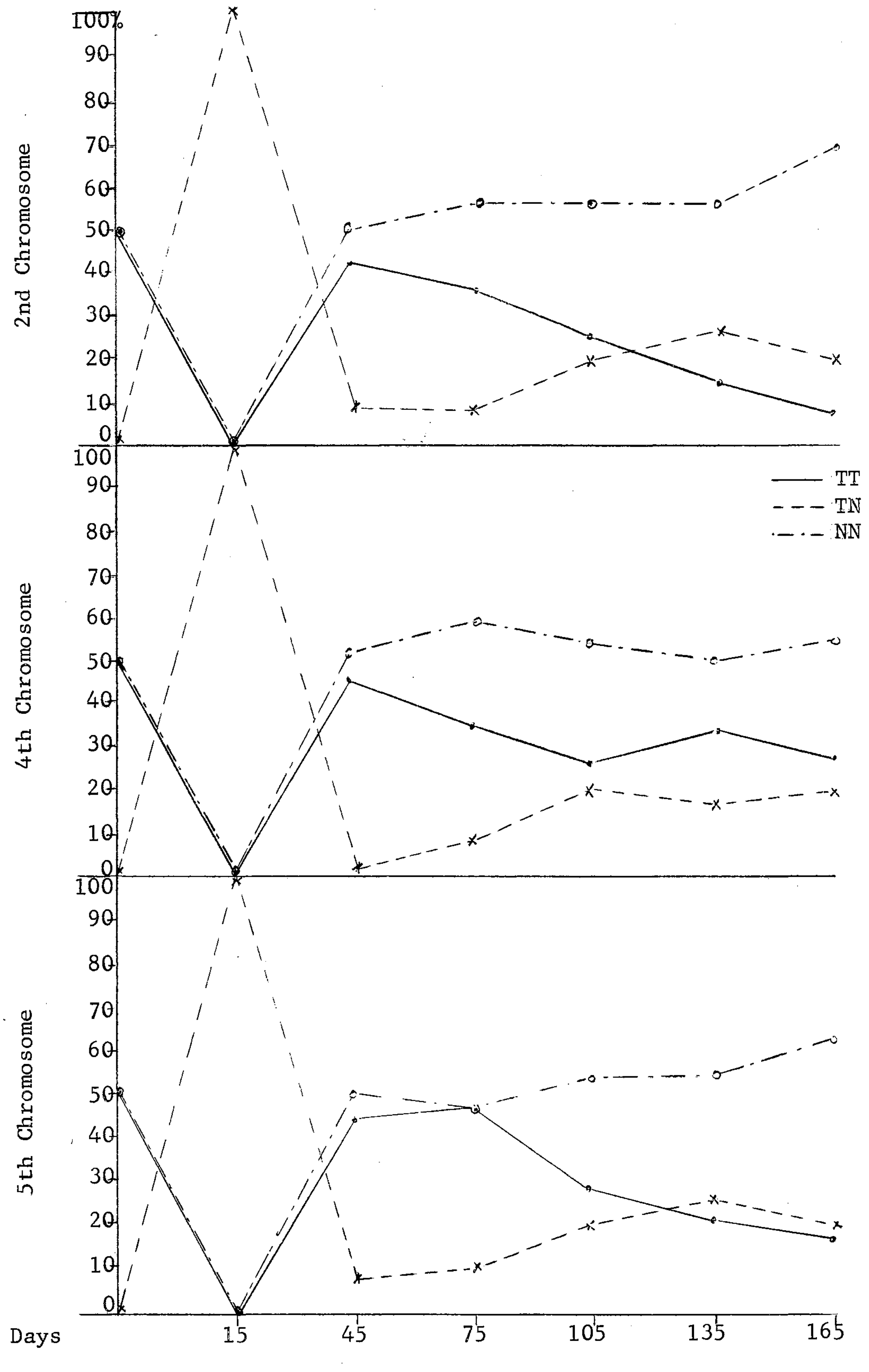

Fig. 2. Cage 2. Started with novamexicana females and texana males. The percentage of homozygous and heterozygous combinations of the three autosomes.

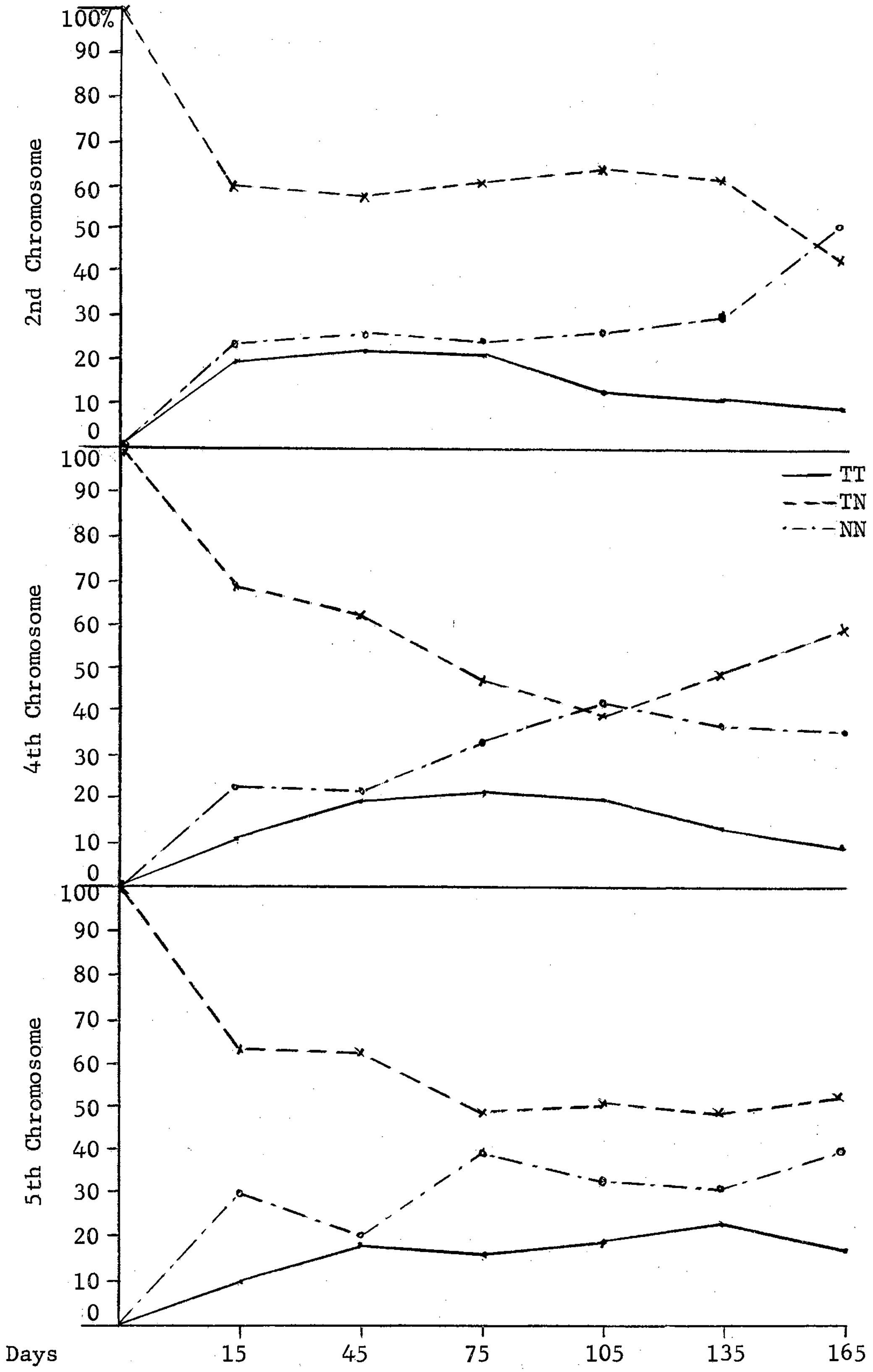

Fig. 3. Cage 6. Started with hybrid (<u>texana</u> x <u>novamexicana</u>) females and males. The percentage of homozygous and heterozygous chromosome combinations of the three autosomes.

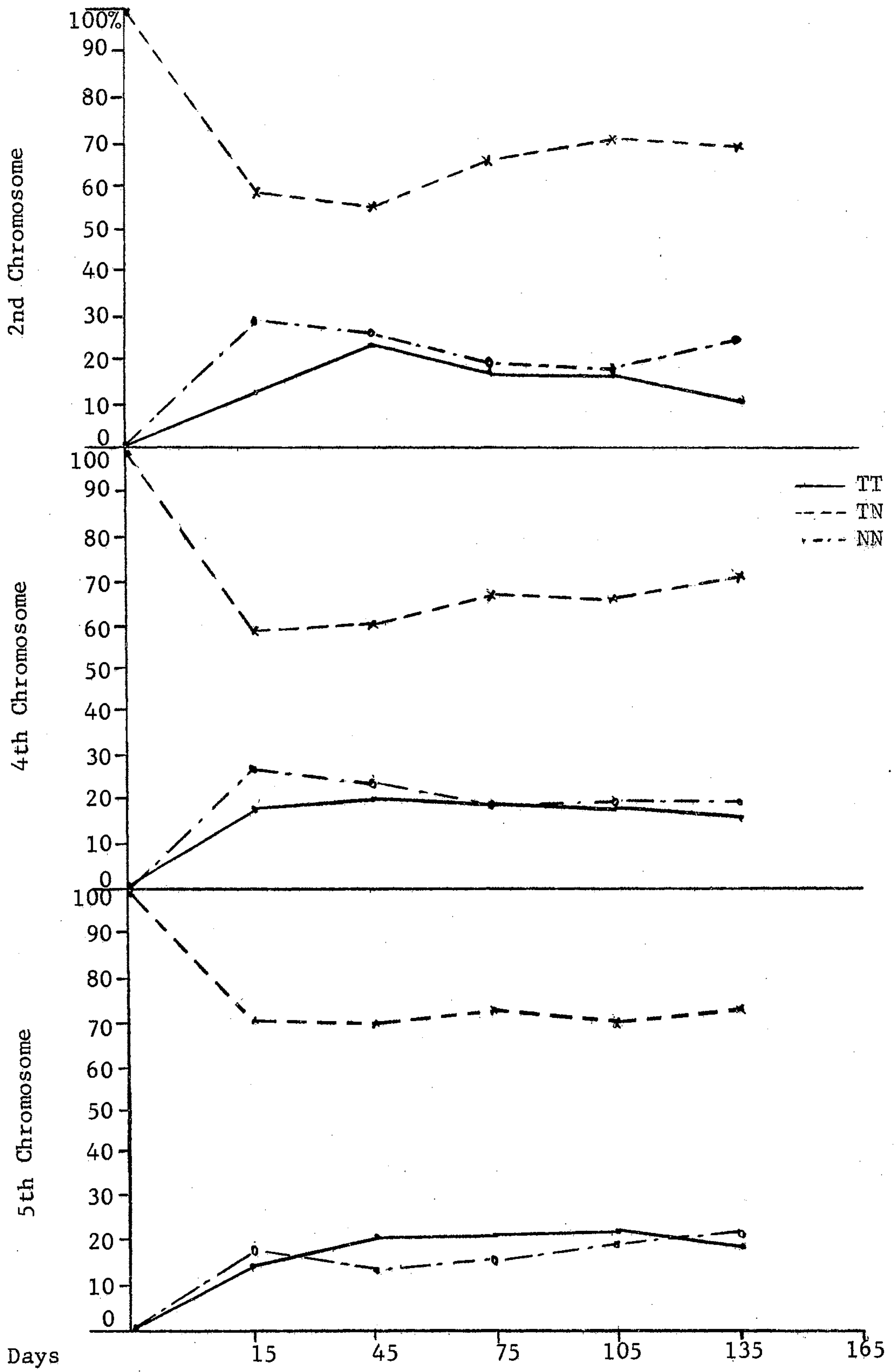

Fig. 4. Cage 9. Started with hybrid (<u>novamexicana</u> x <u>texana</u>) females and males. The percentage of homozygous and heterozygous chromosome combinations of the three autosomes.

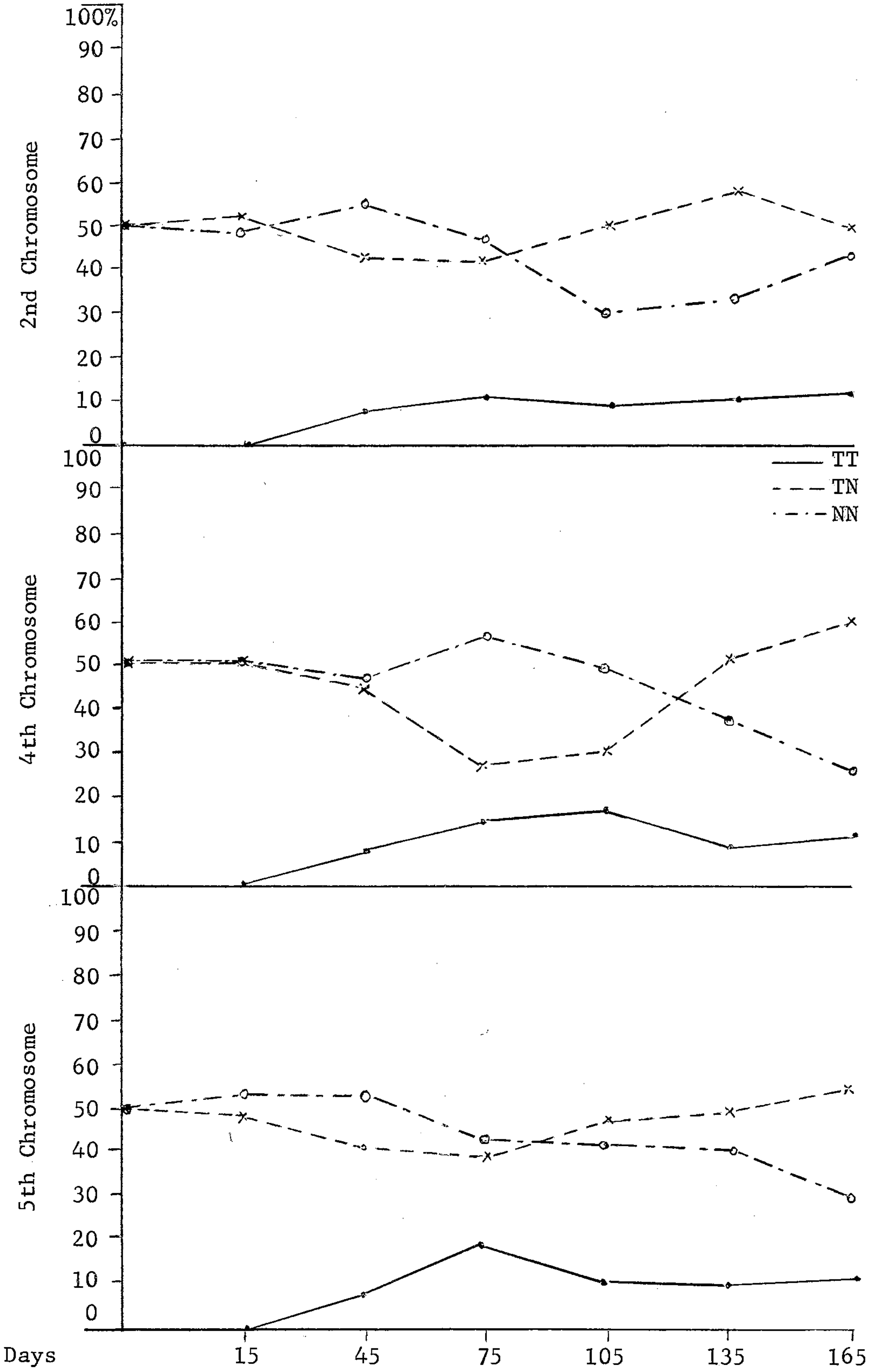

Fig. 5. Cage 4. Started with hybrid (<u>texana</u> x <u>novamexicana</u>) females and <u>novamexicana</u> males. The percentage of homozygous and heterozygous chromosome combinations of the three autosomes.

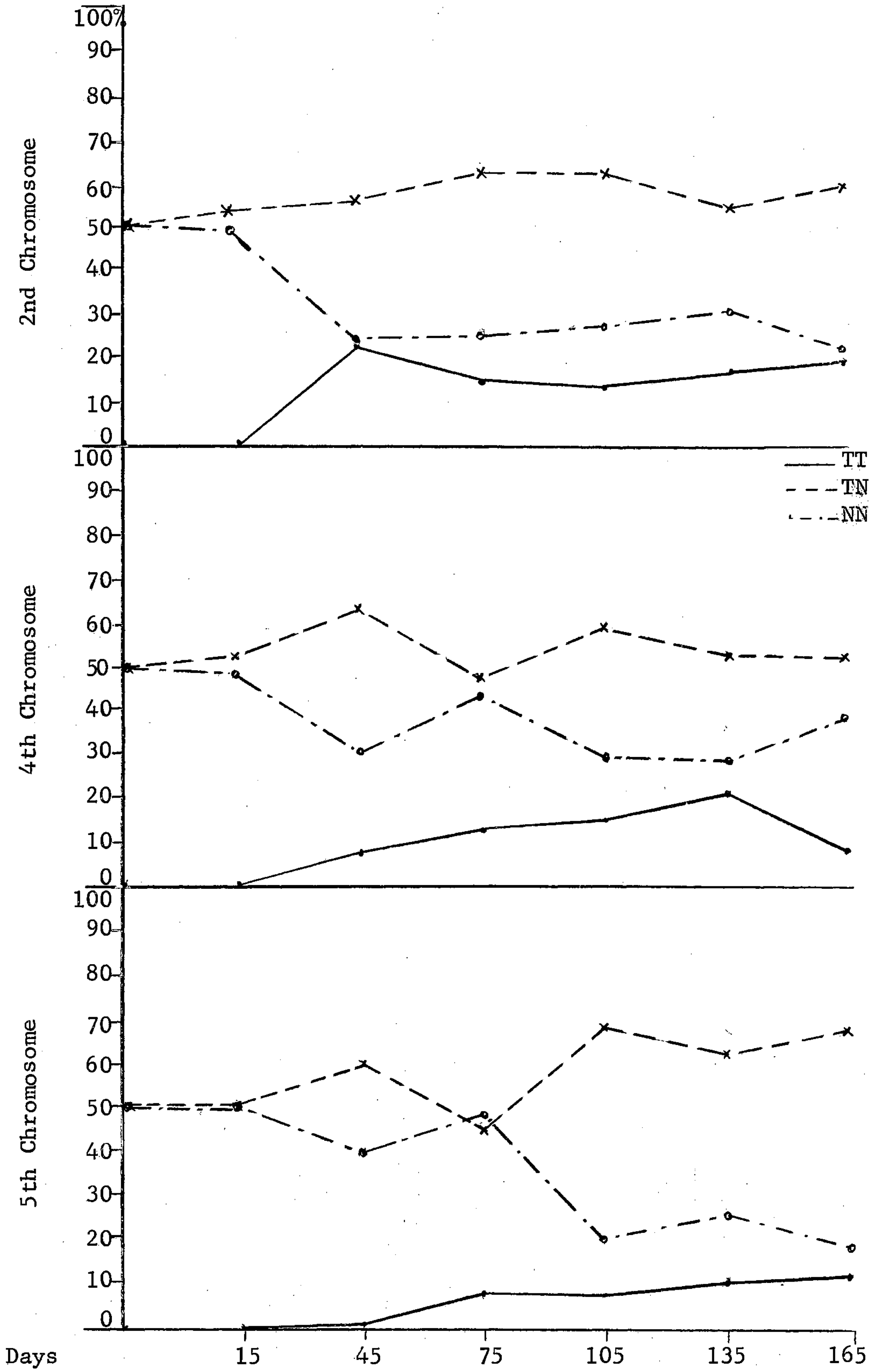

Fig. 6. Cage 5. Started with novamexicana females and hybrid (texana x novamexicana) males. The percentage of homozygous and heterozygous chromosome combinations of the three autosomes.

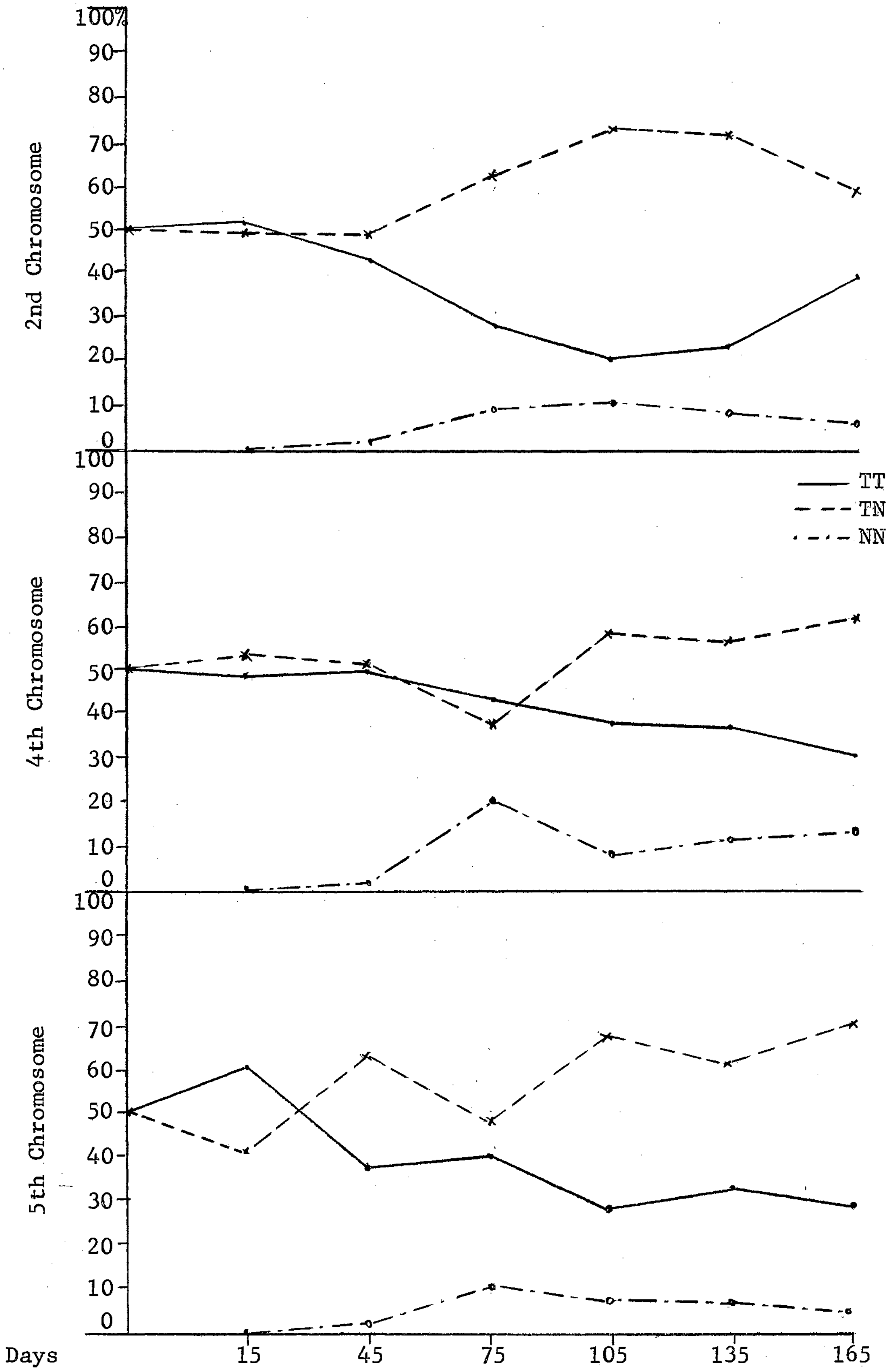

Fig. 7. Cage 7. Started with hybrid (<u>texana</u> x <u>novamexican</u>) females and <u>texana</u> males. The percentage of homozygous and heterozygous combinations of the three autosomes.

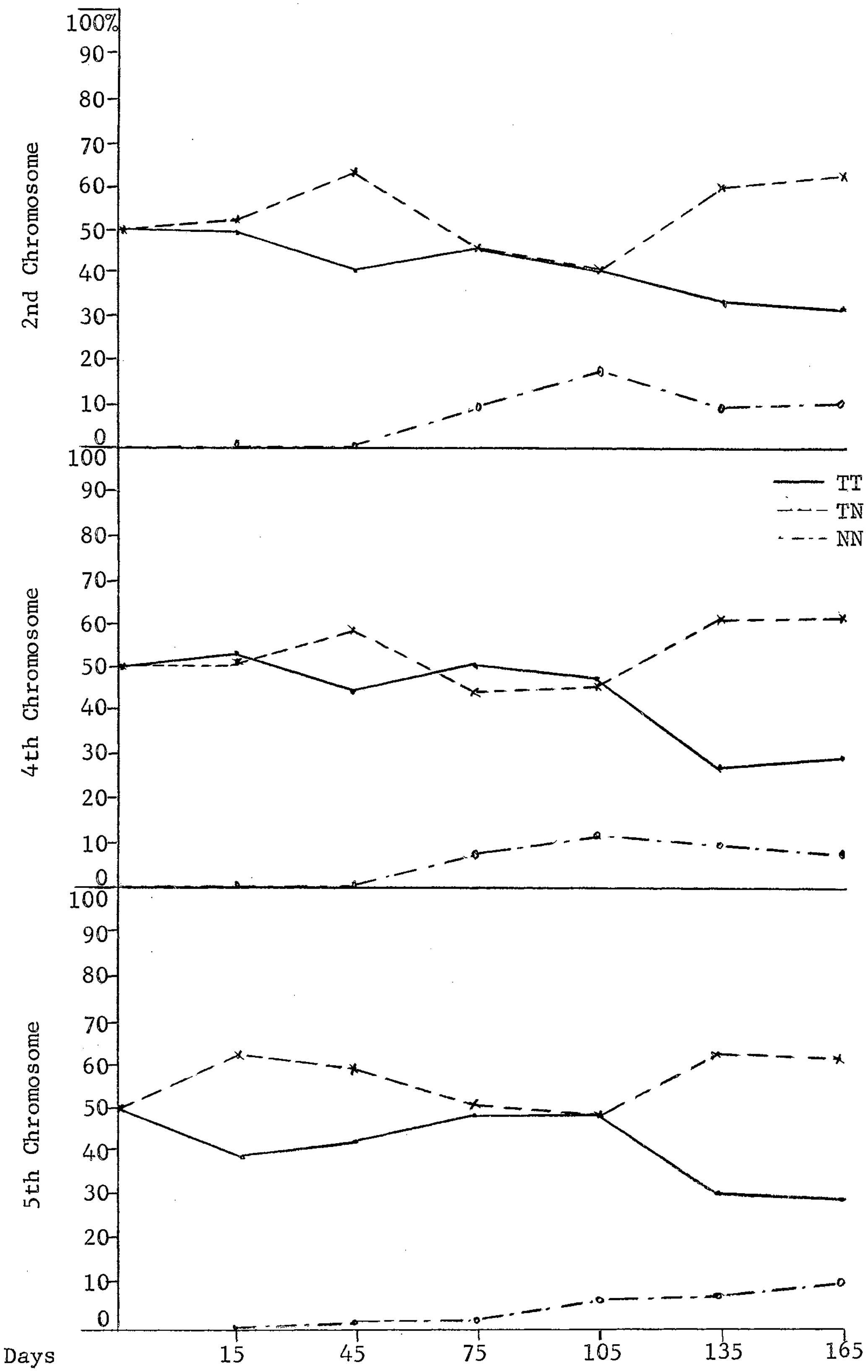

Fig. 8. Cage 8. Started with texana females and hybrid (texana x novamexicana) males. The percentage of homozygous and heterozygous combinations of the three autosomes.

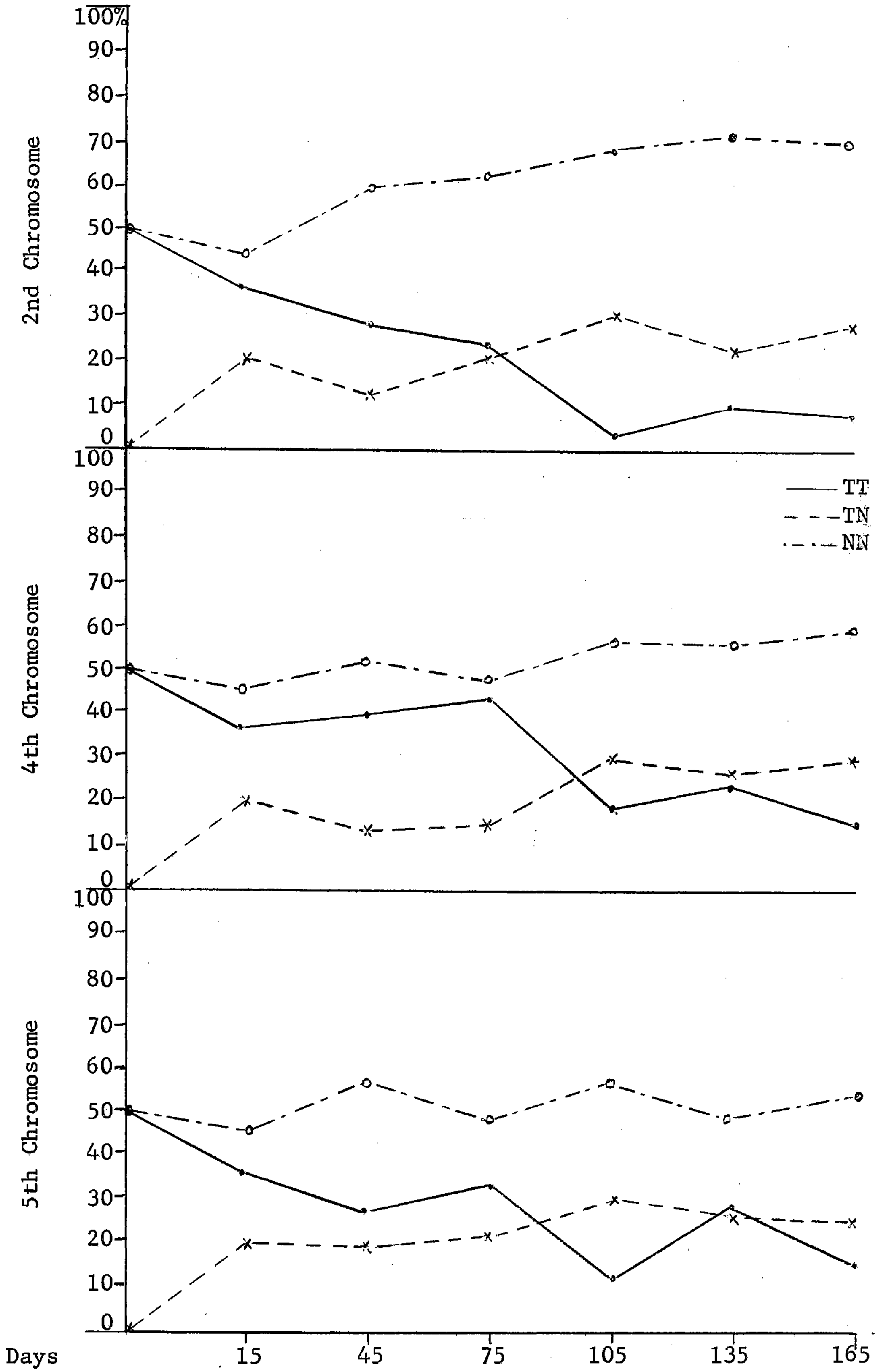

Fig. 9. Cage 3. Females and males of both species. The percentage of homozygous and heterozygous combinations of the three autosomes.

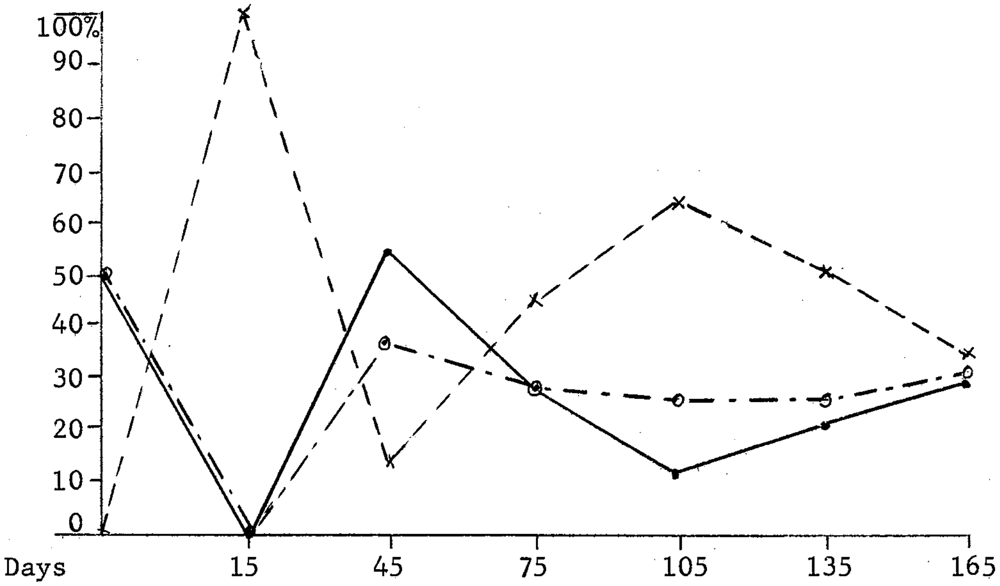

Fig. 10. Cage 1. Started with texana females and novamexicana males. The percentage of homozygous and heterozygous combinations of the X chromosome.

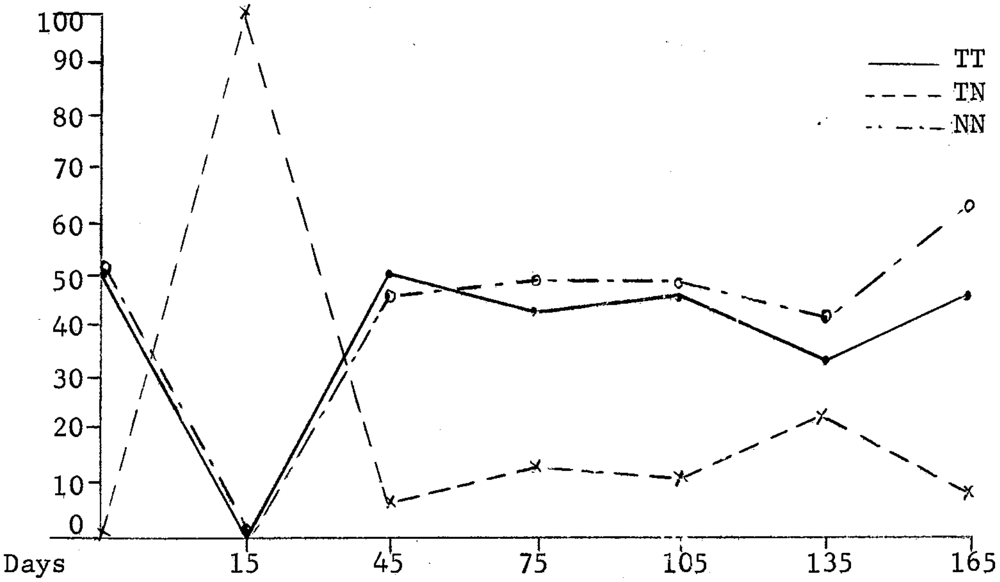

Fig. 11. Cage 2. Started with novamexicana females and texana males. The percentage of homozygous and heterozygous combinations of the X chromosome.

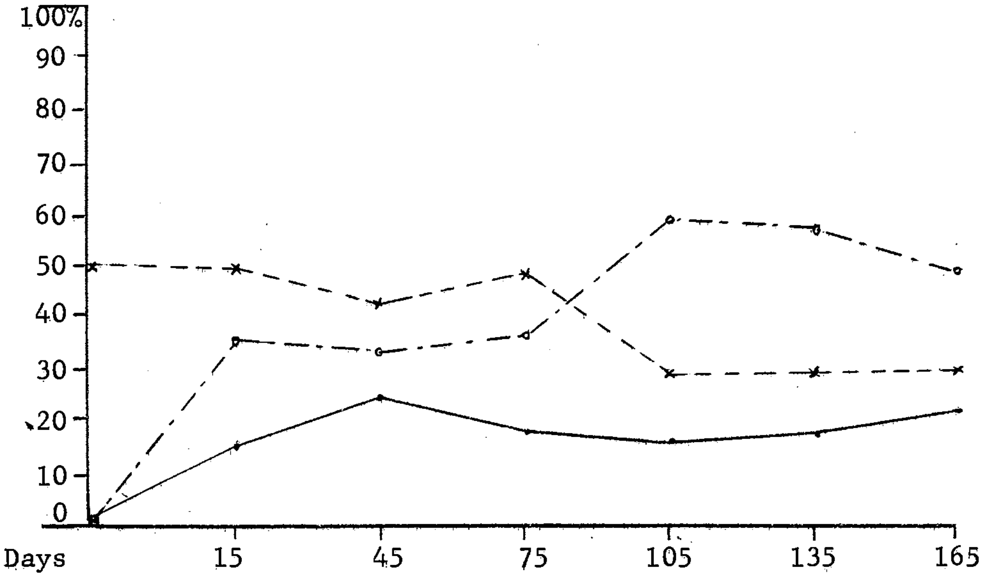

Fig. 12. Cage 6. Started with hybrids (texana x novamexicana) females and males. The percentage of homozygous and heterozygous chromosome combinations of the X chromosome.

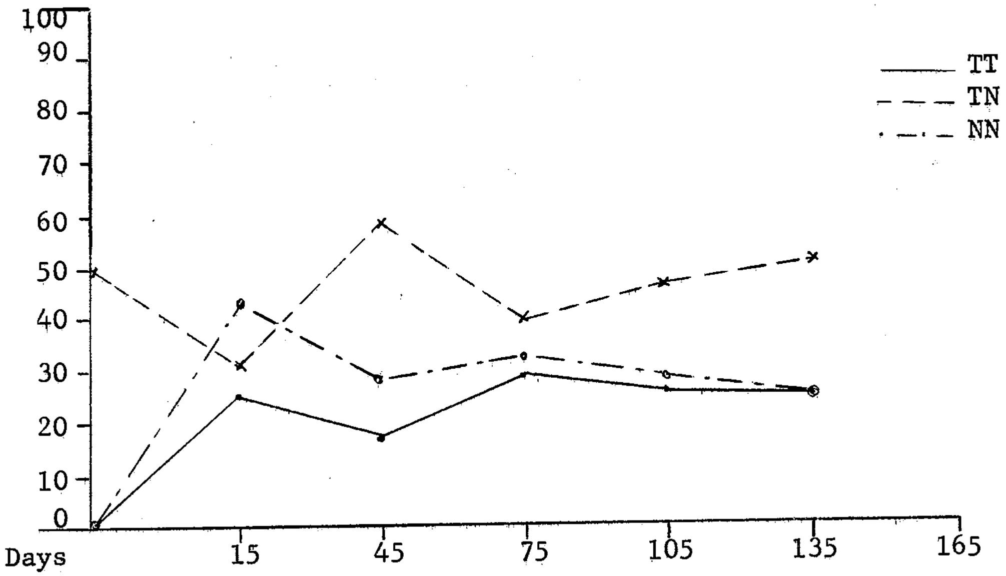

Fig. 13. Cage 9. Started with hybrid (texana x novamexicana) females and males. The percentage of homozygous and heterozygous chromosome combinations of the X chromosome.

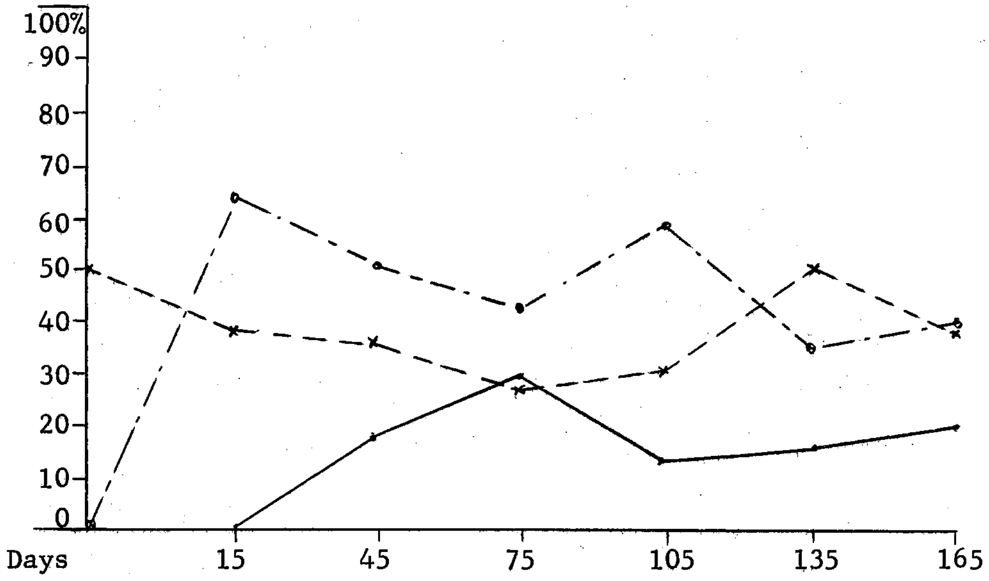

Fig. 14. Cage 4. Started with hybrid (*texana* x *novamexicana* females and *novamexicana* males. The percentage of homozygous and heterozygous chromosome combinations of the X chromosome.

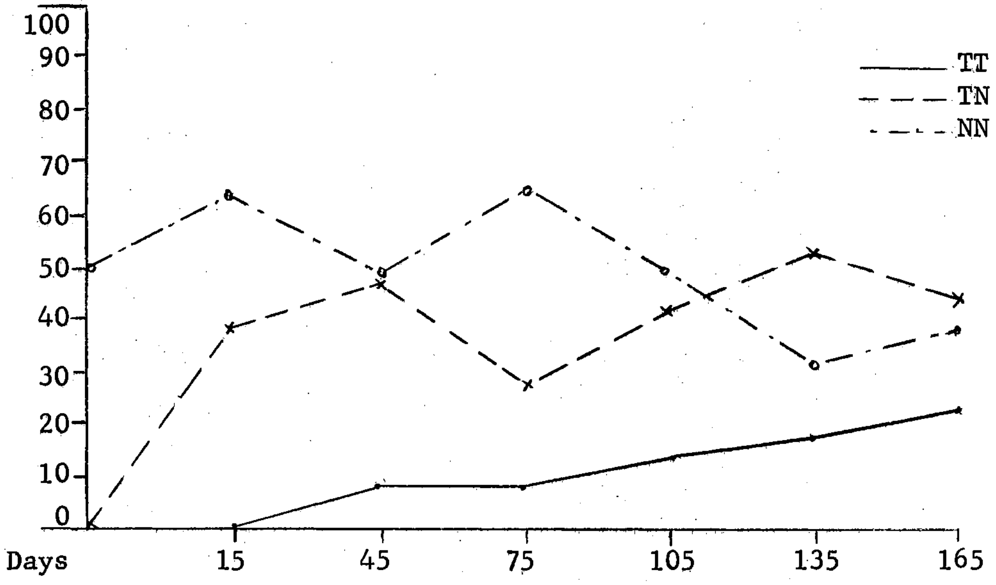

Fig. 15. Cage 5. Started with *novamexicana* females and hybrid (*texana* x *novamexicana*) males. The percentage of homozygous and heterozygous combinations of the X chromosome.

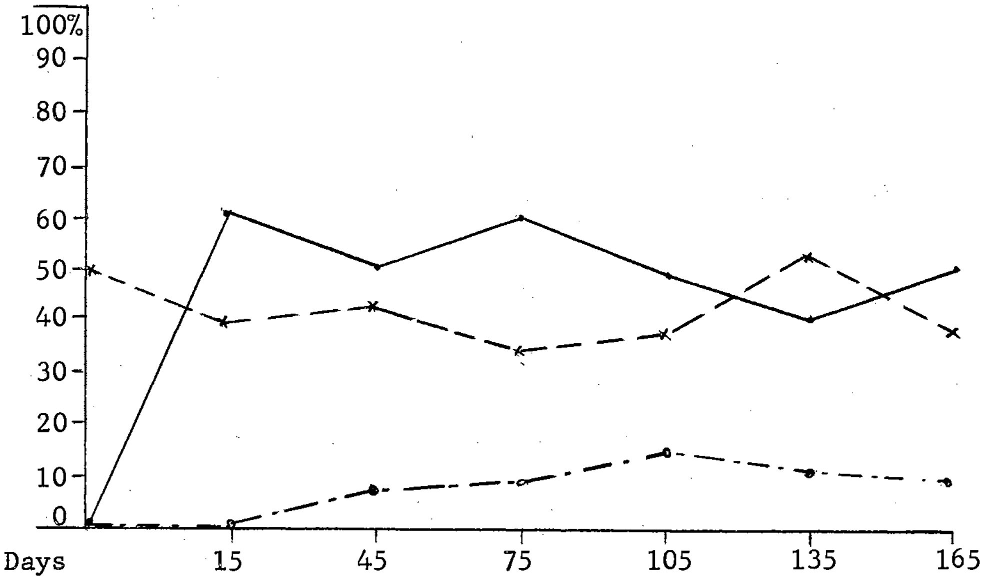

Fig. 16. Cage 7. Started with hybrid (<u>texana</u> x <u>novamexicana</u>) females and <u>texana</u> males. The percentage of homozygous and heterozygous combinations of the X chromosome.

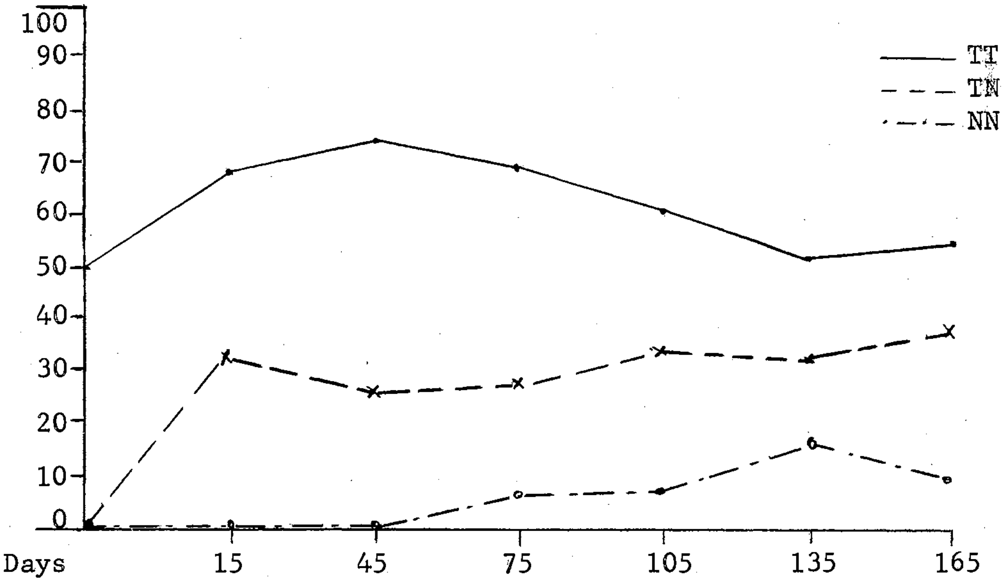

Fig. 17. Cage 8. Started with <u>texana</u> females and hybrid (<u>texana</u> x <u>novamexicana</u>) males. The percentage of homozygous and heterozygous combinations of the X chromosome.

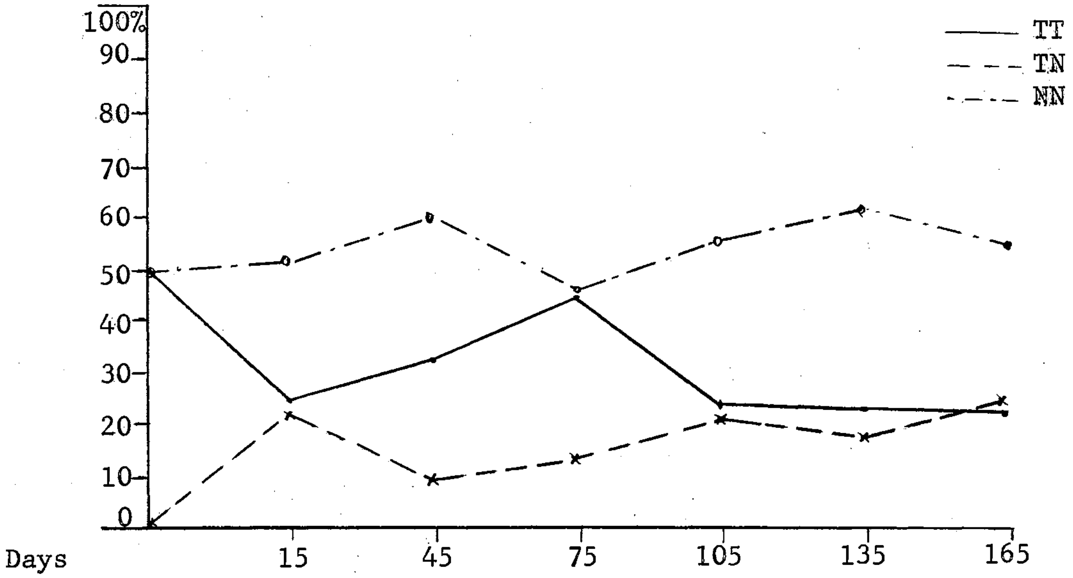

Fig. 18. Cage 3. Females and males of both species. The percentage of homozygous and heterozygous combinations of the X chromosome.

VITA

Doris E. Colón

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Doctor of Philosophy

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