DEMOGRAPHIC CONSEQUENCES OF ARTIFICIAL SELECTION AT THE LAP LOCUS IN VOLES (*MICROTUS TOWNSENDI*)

by

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ABSTRACT

A number of studies on small mammals have shown that changes in the frequency of alleles at polymorphic loci are correlated with population fluctuations. To determine whether this association between demography and genetics is causal, I altered gene frequencies in two field populations of *M. townsendi*. Using starch gel electrophoresis, I detected a leucine aminopeptidase (LAP) polymorphism in *M. townsendi*. The fast allele, LAP-F, was present in a control population at a frequency of about .35 from July 1971 to July 1973. By removing homozygous SS voles from one experimental population I maintained an LAP-F frequency of about .75. Removal of FF homozygotes from a second population resulted in an LAP-F frequency of about .25. I monitored demographic variables of the populations while the selection was being applied. The populations went through increasing and peak phases and then declined sharply during the spring of 1973. There were indications that different genotypes had an advantage in survival and reproduction during different phases of population density. The selection that maintained the polymorphism on the control area could be correlated with population density. However, the overall fitness of each experimental population was not affected by its genotypic composition at this locus.

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INTRODUCTION

Microtine rodents undergo periodic fluctuations in population density which are not directly related to known changes in the environment of the population (Chitty 1960; Krebs 1966; Krebs et al 1969). The absence of obvious extrinsic regulation of such populations has led Chitty (1967, 1969) to suggest that genetic changes are a necessary part of the conditions leading to numerical fluctuations. During the period of low numbers and population increase, so the story goes, certain genotypes are favored by selection. As density increases, an aggressive genotype gains the selective advantage through the elimination from the breeding population of those less able to withstand crowding. A decline in numbers will occur when the increasing selection for aggressive individuals has decreased the total population fitness with regard to forces other than intra-specific competition.

The above hypothesis assumes that the population contains genetic variation capable of responding to short-term selective pressures. Electrophoretic studies of proteins have revealed large amounts of apparently persistent allelic variation in natural populations (e.g., Lewontin and Hubby 1966; Selander et al 1971). Evidence that selection does maintain such variation and can be effective over short periods has been found (Yarbrough and Kojima 1967; Kojima and Tobari 1969). It is at least reasonable, then, to use electrophoretic variants as genetic markers when one is investigating the implications of

Chitty's hypothesis of population regulation through genetic change.

Several authors have monitored electrophoretic markers during detailed demographic studies on fluctuating populations. Semeonoff and Robertson (1968) found that the allele frequency of an esterase polymorphism changed during a population decline of Microtus agrestis. Canham (1969) reported that the relative fitnesses of the genotypes of a transferrin and of an albumin polymorphism were related to changes in density of Peromyscus maniculatus and Clethrionomys gapperi populations. Changes in allele frequencies at a transferrin locus (Tamarin and Krebs 1969) and at both transferrin and leucine aminopeptidase loci (Gaines and Krebs 1971) have been correlated with changes in density in Microtus pennsylvanicus and M. ochrogaster populations. The results of these studies are compatible with Chitty's hypothesis that the changes influencing numerical fluctuations are genetic. They are also consistent with the view that genetic changes have no causal relationship with population fluctuations, but are only a side-effect of the numerical changes (Charlesworth and Giesel 1972).

This thesis describes an attempt to discover the relationship between the allele frequency of an electrophoretic marker, leucine aminopeptidase (LAP), and the demography of a field population of Microtus townsendi. I chose to work with LAP because the genotypes could be accurately typed in the lab, but I had no reason to suspect that the particular polymorphism was maintained by the same forces that operated on the LAP

polymorphism studied by Gaines and Krebs (1971). On each of two experimental areas, I continuously selected for one allele of the LAP polymorphism by introducing voles homozygous for the chosen allele and removing voles homozygous for the alternate allele. Demographic variables were monitored while the selection was being applied. My object was to determine whether changing the allele frequency of the electrophoretic marker would be sufficient to change the demographic patterns between the populations. I made no attempt to distinguish between effects due to the individual alleles and those due to possible linkage complexes.

METHODS

Study Area

The study area was on Westham Island in the Fraser River delta, 4 miles west of Ladner, B. C., and about twenty-five road miles from the University of British Columbia campus. Trapping was carried out from July 1971 to July 1973 at the Department of National Defense radio receiving station on the island. The ground was generally flat, with an old introduced pasture-mix vegetation. The land was protected from flooding by dikes and drainage ditches, but standing water covered some sections during the winter of both years.

Three sites were marked out with 100 stakes each, in a ten by ten pattern. Each stake was 25 feet from the next, and each grid covered 1.5 acres. The size and relative position of each grid are shown in Fig. 1. From November to March 1971-72, about 20% of grid G, about 30% of grid I, and about 40% of grid H were covered with standing water. About half these amounts was present on each grid through December and January 1972-73.

Trapping Schedule

Longworth live-traps were placed in *M. townsendi* runways near each stake on the grids. An attempt was made to have an excess of traps available to the voles at all times. Therefore, one or two traps, depending on the population density, were placed near each stake. Every second week, traps were set Monday afternoon and checked Tuesday morning and afternoon and Wednesday morning. The traps were locked open in place to serve as prebait stations between trapping periods. During hot weather, trapping was done only over the two nights to avoid mortality in the traps during the heat of the day. My trapping schedule was affected by various acts of God, such as a heavy rainfall during October 1971, which necessitated my sacrificing the third check that week, and acts of man, such as the mowing of the entire area in September 1971 and of the areas around the grids at other times. These emergencies affected all grids at the same time and I have not considered their consequences in this thesis.

A vole caught for the first time was bled from the suborbital sinus and given a numbered ear-tag. Tag number, location on the grid, and weight to the nearest gram were recorded for each animal caught during a trapping period. Breeding condition was assessed from testis position in the males and from vaginal perforation, nipple development, and pubic symphsis closure in the females. Litters in traps and noticeable pregnancies were recorded.

Electrophoresis

I used a horizontal starch gel electrophoretic method with Connaught starch (Connaught Medical Research Laboratories, Toronto, Canada) and the plasma protein buffer system of Selander (1969). The gel molds, trays, and slicing procedure were adapted from those described by Tsuyuki et al (1966). I applied the serum from the blood samples to the gel slots with filter paper inserts, subjected the gels to 150 v for 3 hr, and then incubated them for 2 hr in the staining solution of Brewer (1970) at pH 5.2.

The functional name leucine aminopeptidase has been applied to "various amino acid naphthylamidases" which reduce the substrate l-leucyl- -naphthyl amide (Smith et al 1965). Staining revealed the zones of LAP-activity shown in Fig. 2. A zone of slower mobility appeared to be monomorphic in all animals typed; the second zone was polymorphic, and the three staining patterns were labelled FF, FS, and SS. The polymorphism conformed to a two-allele autosomal inheritance model. A breeding colony was maintained to provide information on the genetic control of the polymorphism, but only 29 crosses were successful in the two years. However, the results of typing the 271 offspring for LAP showed no evidence against the assumed mode of inheritance (Table 1).

Based on these electrophoretically determined genotypes, a program of artificial selection was carried out in the field. Mice typed as SS on grid G were removed and released on grid H;

those typed as FF on grid H were removed and released on grid G (see Fig. 1). The selection was carried on throughout the study as new mice entered the population. Grid I was the control grid; all new mice were typed for LAP but none was removed or added.

Transfers

During the study, a total of 66 animals, representing 8.6% of the total catch on grid H, were typed as FF and removed. These animals were released on grid G, but only 19 (27%) of these 66 stayed on grid G until at least the next trapping period. These additional 19 represented 1.7% of the total of 1110 animals caught on grid G during the study. Of the 104 (9.3%) animals typed as SS on grid G and removed, 61 (59%) were caught at least one trapping period after release on grid H. These represented of 7.9% of the total of 765 animals caught on grid H. During both breeding and non-breeding seasons a greater proportion of the animals transferred to grid H took up residence than did those transferred to grid G (see Table 2).

For the presentation of results and the discussion that follows I will refer to breeding seasons defined by the percentages of voles in breeding condition on the grids. During the study five periods of breeding performance could be distinguished as follows:

Summer 1971	July 1 to Nov. 1 1971	breeding
Winter 1971-72	Nov. 15, 71 to Feb. 7, 72	non-breeding
Summer 1972	Feb. 21 to Sept 18 1972	breeding
Winter 1972-73	Oct. 2, 72 to Feb. 5, 73	non-breeding
Summer 1973	Feb. 18 to July 23, 73	breeding

Most tables will be presented with the data grouped over these breeding seasons and the graphs of density and allele frequency will be shown with the non-breeding seasons shaded.

Sources of Error

A discussion of the genotypic and demographic differences between the grids must first cover the possible sources of error introduced by the experiment.

Mortality directly attributable to the experiment appeared to be low with the trapping program employed. The totals of animals found dead in traps not properly prebaited, accidently killed during handling, and found dead of unknown causes were 43 (4%) out of 1110 on grid G, 36 (5%) of 765 on grid H, and 35 (4%) of 959 on the control grid I. I found no evidence that this mortality was non-random with respect to sex or genotype. Within this study, I had no satisfactory method of establishing the effect that bleeding had on the survival of the individual voles. Of the total of 2,834 animals caught, 2,774 (98%) were bled, and the majority of these were bled at the time of first

capture. I assume for the purposes of this discussion that the effects of bleeding were the same over both sexes and all genotypes.

As discussed by Krebs (1966) and Hilborn (1974), the trapping procedure was designed to enumerate all animals present in the trappable population to avoid the necessity of one's assuming random sampling when estimating population parameters. An index of trappability was calculated to determine the efficiency of this enumeration. I estimated the trappability of M. townsendi by comparing the actual number caught during one trapping period with the minimum number known to be alive at that trapping. The minimum number known to be alive contains those previously tagged mice that are missed during the trapping period but caught at some later trapping. Between 81% and 98% of all animals in the trappable population present on a grid were caught during each trapping period. I found no difference between the trappabilities of males and females during any time of year on any grid, nor were there any differences between grids. During the late winter on all grids, trappability was uniformly good, but during the summer trappability was lower probably owing to the altered trapping program mentioned above. These data are presented in Table 3, summarized by time of year and grid.

Very small voles were rarely caught in Longworth traps, but this would affect my analysis only if the probability of capture was different between grids or genotypes. I considered mean body weight at the time of first capture as an index of relative

trappability (Table 4). I compared the different genotypes on the control grid with a Kruskal-Wallis one-way ANOVA (Siegel 1956). I found no significant differences in mean body weight at the time of first capture between individuals of different genotypes. Mean body weight at first capture was lower for the males during summer 1971 than during the summers of 1972 or 1973, and was lower for females than for males at all times. I concluded from these data that the individuals of the different genotypes were entering the trapped population at comparable sizes, and assumed that they were equally susceptible to trapping throughout life.

RESULTS

I attempted to discover whether or not a difference in allele frequencies would lead to a change in demographic processes. An answer to this question could be obtained only if the population did indeed show the phenomenon of interest, numerical fluctuation, and if I was successful in altering the LAP allele frequency.

Population Density

The minimum numbers of males and females known to be alive are graphed for each grid (Figures 3, 4, and 5). Grid H had a consistently lower density than that on either grid G or grid I, but the three populations underwent similar numerical changes. Densities on grid G and grid I were similar, and the low frequency of LAP-F on grid I was not associated with a low density of *M. townsendi*. I concluded that the low density of the grid H population was not associated with the LAP composition of the population. Numbers dropped on grid H during the autumn of 1971, when standing water reduced the available grid area. On all grids, vole density increased throughout the winter of 1971-72, dropped slightly in the early spring of 1972, and increased throughout the summer. After a short decline in the fall of 1972, densities reached their highest on all grids during December 1972. The populations declined until May 1973, then increased until the end of the study. The mean weekly rates

of population increase (Table 5) reflect these patterns. The direction of density change between trapping periods (+,0,-) was compared between the grids. Density changed in the same direction on all three grids between 34 of 50 trapping periods for males and between 38 of 50 periods for females. Large fluctuations in density occurred on each grid during the study, but all grids changed with similar rates at the same times.

Variability among study sites is traditionally dealt with through replication of control and experimental areas, but in this study I had no replicates. The control differed from grid G in allele frequency (see below) and from grid H in *M. townsendi* population density. The frequency of LAP-F was low on both grid I and grid H, and in spite of the artificial selection against LAP-F on grid H, was similar on the two grids during the study. Peak densities maintained on grids I and G were about 200 voles, but on grid H were about 130 voles. Grids I and G were less subject to winter flooding than grid H, and reduction of available habitat is the simplest explanation for the lower density.

Allele Frequency

I found no significant LAP-F frequency differences between the sexes on any grid. A Kruskal-Wallis one-way ANOVA gave significant allele frequency differences between the three grids for all periods. The graphs of allele frequency, (Figures 6, 7, and 8) illustrate that the difference between the experimental

grids G and H was sustained from the middle of the first breeding period until the end of the study. The mean bi-weekly changes in LAP-F frequency are shown in Table 6. Allele frequency was changing on all grids between July 1971 and September 1971 before I began the experimental selection, and some allele frequency difference was already established between the experimental grids. The mean bi-weekly change in allele frequency from the time the experiment began in September 1971 until the end of the study was greater on both experimental grids (+.37% on grid G and -.32% on grid H) than on the control (+.03%). The experimental technique was apparently successful since allele frequencies changed on the experimental grids by about the same amounts and in directions consistent with the selection applied.

Allele Frequency and Density

Having established that there was indeed an allele frequency separation between the two experimental areas, I then tested for an association of allele frequency with density.

The results of a correlation of density and allele frequency for each season are shown in Table 7. For males, during summer 1972 on grid H, winter 1972-73 on grid I, and summer 1973 on grids G and I, there were significant positive associations. Negative correlations were found on both G and H during summer 1973. For males over the entire study, there was a significant positive correlation between allele frequency and

density on grid I and a significant negative correlation on grid H.

For females, significant positive correlations of density with allele frequency were found during winter 1971-72 on grids I and H, summer 1972 on grid G and summer 1973 on grid I. During summer 1972, significant negative correlations were found on grids I and H. Over the entire study, the density of females on grid G was significantly positively correlated with the allele frequency and on grid H was significantly negatively correlated with allele frequency.

These correlations contain little information on the experimental grids since I cannot remove the effect of transfers. Density of voles increased during most of the study on all grids, while LAP-F frequency dropped on grid H and rose on grids I and G. I would expect the overall positive correlation of density and allele frequency on grid G, since the experimental selection for LAP-F was continued over the study. The opportunity for selection increased when numbers increased, and selection resulted in a higher frequency of LAP-F. On grid H the opposite selection was carried out, and by similar reasoning the negative correlation of LAP-F frequency and density could be expected. I interpret the significant associations of allele frequencies and densities on the experimental grids to be only an expression of the experimental selection. The strongest correlation occurred on the control grid when numbers were dropping in late winter 1972-73, and indicated that LAP-S had a selective advantage at that time. However, the evidence for an

association between numbers and allele frequencies is slight, and must be substantiated with individual demographic information.

Demography and Genotypes

If the genotypes of the LAP polymorphism have different selective advantages depending on the population changes, then one should be able to discover this from demographic information. I considered minimum two-week survival rates, reproductive performance, and body weights of males in order to discover any such relationship.

I wished to separate genetic effects on demography from area effects. The logical method was to consider the demographic information available for each genotype on each grid. However, all SS homozygotes were removed from grid G as they entered the population. Any estimates of demographic variables for that genotype on grid G were based on a small sample of the new animals in the population, and could not be considered representative. A similar bias existed on grid H, where FF homozygotes were removed. On the control grid I, all three genotypes could be considered for comparisons of demographic variables. Therefore, I followed a standard procedure in my analysis. When testing for effects due to grids I compared the heterozygotes between all three grids, the FF homozygotes between grid G and grid I, and the SS homozygotes between grid H and grid I. When looking for genetic effects I compared the

genotypes within each grid: FF homozygotes, heterozygotes, and SS homozygotes on grid I; FF homozygotes with heterozygotes on grid G; and SS homozygotes with heterozygotes on grid H.

Survival and Genotype

In order to investigate the genetic component of survival, I compared the average minimum survival rates for genctypes on each grid (Tables 8, 9, and 10) by means of a chi-square contingency test. Transferred animals were not included in the calculation of survival rates on the experimental grids. On control grid I during summer 1973 for males and summer 1973 for females, significant differences were found between survival of the three genotypes FF, SS, and FS. On the experimental grids only the males showed significant differences among genotypes. On grid G during summer 1971 the survival of the FF homozygotes was significantly higher than that of the heterozygotes. On grid H during summer 1971, the survival of the SS homozygote males was significantly higher than that of the heterozygotes. The differences in male survival between genotypes on both experimental grids during summer 1971 are not paralleled by differences between these genotypes on the control grid during the period. Nor is the relatively low survival of heterozygote males on grid I reflected on the experimental grids during summer 1973.

Average minimum survival rates were compared between grids (Figures 9 and 10) for individual genotypes. During summer 1971

survival rates of heterozygotes on grid I were significantly better for both males and females than those of the heterozygotes on either experimental grid. Survival of the SS homozygotes on grid I was significantly better than that on grid H for both males and females during summer 1971. For males during summer 1973 survival rates of the SS homozygotes on grid H and the FF homozygotes on grid G were significantly lower than those of the corresponding homozygotes on the control grid. The differences in survival rates between grids were more consistent than those between genotypes.

Breeding Condition and Genotype

I used the position of the testis as an index of breeding condition in male *M. townsendi.* Only adult males, those weighing more than 44 g, were considered since the sample sizes of juveniles and subadults were small. Tables 11, 12, and 13 show the percentages of adult males with scrotal testes. On grid I during the summer of 1971 there were significantly fewer SS males in breeding condition than either FS or FF males. On grid G during summer of 1973 there were significantly fewer FS males breeding than FF males. On grid H during the winter of 1972 there were fewer SS males in breeding condition than FS males.

Between the grids, during the winter of 1972-73 there was a significantly higher percentage of FS males in breeding condition on grid H. There was a higher percentage of FS males in breeding condition on grid H than on either grid G or grid I

over the entire study. For FF homozygotes during the winter of 1971-72 there was a higher percentage in breeding condition on grid G than on grid I. During the summer of 1971 grid H had a higher percentage of SS males breeding than did grid I.

The size of the nipples is considered the most useful field index of breeding condition in M. townsendi (Tamarin and Krebs 1967). Lactating females have medium or large nipples. Chi-square tests for differences between genotypes in numbers of females lactating (Tables 14, 15, and 16) revealed significant differences on grid I during the summer of 1971, grid G during the summer of 1972, and on grid G over the entire study. Tests for differences between grids revealed significantly fewer breeding FS females on grid H than on the other grids during summer 1971.

Although significant differences between genctypes and between grids showed up in the percentages of voles in breeding condition, these differences followed no obvious pattern. Only on grid I during summer 1971 did both males and females have the same relationship (FF>FS>SS) for percentages of each genotype in breeding condition. During that period the LAP-F frequency increased on grid I, but I found no such relationship between breeding and allele frequency change during any other period of the study.

The most noticeable pattern in breeding performance was the difference between the years of the study. Breeding was maintained at a low level on all grids throughout the winter of 1971-1972, but had stopped by the end of September 1972.

However, the percentages of voles in breeding condition were not different between summers. No differences were apparent between the grids in the obvious year-to-year variation of length of breeding seasons.

Body Weights and Growth Rates

The distribution of male body weights changed on each grid during the study (Figures 11, 12, and 13). The change was most noticeable on grid I, where the average weight of males went from about 50 g during summer 1971 and winter 1971-72, to about 60 g during summer 1972, then down to about 45 g in winter 1972-73 and back up to about 56 g in summer 1973 (see Tables 17, 18, and 19). On the two experimental grids the average weights were not as high as on the control during summer 1972, but did drop to about 46 g during winter 1972-73.' except fcr summer 1972, the changes in body weight distribution were consistent between all three grids throughout the study.

Instantaneous relative growth rates, adjusted to a standard 35 g vole by regression, were calculated for males (see Krebs et al 1969). The mean growth rates for each period and genotype are shown in Tables 20, 21, and 22. During all three summers on grid I, growth rates were lowest for the FF homozygotes. Grcwth rates for the heterozygotes were lower than those for the SS homozygote during all three summers on grid H and during the summers of 1971 and 1972 on grid I. On grid G, the growth rate of FF homozygotes was higher than that of the heterozygotes in

summer 1971, but lower during summer 1973. Growth rates were not consistently different between grids for any genotype.

LAP and Demography

My experiment was based on correlative evidence from other species that allele frequencies of electrophoretic polymorphisms are related to demography. I will now summarize the evidence from my control grid for such a relationship between LAP and population processes in *M. townsendi*. During the study there was a positive correlation between numbers and LAP-F allele frequency, although this was significant only for the males. This association was most evident during spring 1972 and spring 1973 when numbers were dropping, and there was selection in favor of the LAP-S allele. During summer 1973 a steep decline in numbers (-3.5% per week) was followed by a rapid increase (1.6% per week). Male heterozygotes survived very poorly during both phases, both male and female FF homozygotes showed an enhanced survival during the increase, and SS homozygotes a decreased survival (Table 8). During summer 1971, when numbers were increasing there were fewer SS homozygotes in breeding condition in both males and females, and a corresponding rise in LAP-F frequency was evident. So there was some evidence that the different genotypes of LAP had variable fitnesses associated with demographic events on the control grid during my study.

DISCUSSION

The overall conclusion must be that the altered allele frequencies on the experimental grids did not produce any consistent effects on demography. Any differences between the genotypes on the control grid were in general not reflected in demographic differences between the experimental grids. The changes in LAP-F frequency had no discernable effect on the changes in numbers on grid G and grid H. There was an obvious pattern of changes between years in numbers, breeding condition, and body weights of voles on all grids and no grid deviated particularly from this pattern. The significant differences that I found between genotypes and grids for demographic variables did not affect the overall pattern of change between years.

Owing to possible interference with reproduction and social structure, the transferring of animals throughout the study may have been a major error in experimental design. One might postulate that the introduction of alien M. townsendi onto the experimental grids produced some social disturbance in the populations. Davis and Christian (1956) claimed that the introduction of animals into expanding populations of rats would stop the increase, and introductions into stationary populations would result in declines. On grid H in this study, introductions formed 7.9% of the total population, and this level of disturbance may have been a factor in keeping population densities low. Introductions to grid G formed only 1.7% of the total population, and densities were certainly no different from

those on the control grid. In general, few were transferred during any one trapping period, and whatever social effects were produced by the strange voles would presumably have dissipated by the next trapping. Terman (1962) reported that the introduction of alien Peromyscus would inhibit homing behavior in residents for only the first two days after introduction.

The population that the voles were released into appeared to have an effect on recruitment of the transfers. Orr (1966) found that removing residents before releasing alien Peromyscus resulted in 40% recruitment of the new mice. In this study, 27% of the mice transferred to grid G stayed until the next trapping period, and 59% of those transferred to grid H stayed until at least the next trapping period. The relatively high population density on grid G was probably responsible for the poor recruitment of the transfers. The voles transferred to grid H were suddenly exposed to a less crowded area and this change in their environment might account for the relatively high rate of recruitment.

Experimental attempts at testing Chitty's hypothesis have involved the cropping of adult residents from populations of microtines (Krebs 1966, Smyth 1968). Their experiments were undertaken expressly to have an effect on the social processes in the populations. While the cropping of animals was done on a much larger scale by those authors, I did not consider the possibilities of social disruption through the removal of residents in this experiment. A more informative design would be to alter the allele frequencies only at the beginning of the

study rather than to continue the selection process throughout. As well as minimizing the social disturbance, such an experiment would retain all genotypes on the grids. One could therefore compare directly between grids using total values for demographic variables. The return to original allele frequencies, if it occurred, could indicate specific selection pressures on the polymorphism.

A number of authors have shown that the allele frequency of an electrophoretic marker can determine the fitness of an individual in a population. Yarbrough and Kojima (1967) found the selective advantage among the genotypes of an Esterase 6 locus in Drosophila melanogaster cage populations to depend upon the frequency of the alleles in the population. Kojima and Tobari (1969) found that either homozygote of an alcohol dehydrogenase locus in Drosophila melanogaster had an enhanced viability if present at a low frequency, but had reduced viability if present in a high frequency. There were indications in M. townsendi that different genotypes had the relative advantage at different periods, but such differences apparently had little effect on the demographic events of the populations.

When I began this experiment, I had no evidence that the leucine aminopeptidase polymorphism influenced demography. Other studies have shown that the allele frequencies of electrophoretic markers chosen essentiallly at random are correlated with demographic events. Redfield (1972), from a study on colonizing blue grouse, found that both age of habitat and the density of the population were correlated with the

frequency of the heterozygotes of an Ng locus. Tamarin and Krebs (1969) found that a definable 'increase' genotype existed in both Microtus ochrogaster and Microtus pennsylvanicus. This transferrin genotype was selected for during increasing and peak periods of density, and selected against during the decline. These 'increase' and 'decline' genotypes were again defined by Gaines (1970) for transferrin and leucine aminopeptidase. The above studies indicated that a selective advantage can be detected for a particular electrophoretic genotype although the biochemical basis for the advantage is not known. However, in an experimental analysis of the relative fitnesses of transferrin genotypes in Microtus ochrogaster, Gaines et al (1971) found no significant effect of transferrin genotype on rate of population increase, percentage of lactating adults, recruitment index, or survival rate of voles in fenced enclosures. The results of my study indicate that the allele frequency of leucine aminopeptidase in the M. townsendi population had no effect on the population processes during the experiment. Therefore, any associations of allele frequency and numbers were probably an effect of numbers on the polymorphism rather than the converse. The differences I found between genotypes for survival, reproduction, and growth rates indicate that the allele frequency changes on the control grid were due to the selection which maintains the polymorphism.

Apparently, selection does act on the various genotypes of electrophoretic markers, yet these genotypes do not have an absolute fitness. Sved, Reed, and Bodmer (1966) were the first to suggest that great numbers of genetic polymorphisms in a

population would tend to obscure the optimal genotype. With some hundreds of independently segregating loci, there would be thousands of individuals in a population with essentially the same fitness. King (1967) makes the point that the loss of fitness sufficient to maintain a polymorphism need not significantly reduce the fitness of a population. Therefore changes in allele frequency at such loci during numerical fluctuations would be determined by the degree of favorability of the environment, and the polymorphism itself would have no effect on the demographic processes of the population.

My work with LAP was essentially a 'shot-in-the-dark' approach, although it was a logical next step in investigating the correlations of allele frequency with demography. In the light of this study, an explanation that allele frequency change causes demographic change cannot be accepted. However, this does not necessarily indicate a general relationship since LAP may have been a bad choice of marker. LAP was chosen for the same reason that other polymorphisms have been studied: the facility of typing it in the lab. Therefore, the studies to date which have invoked electrophoretic polymorphisms as markers for demographic change contain no information on genetic influences on demography. An effort must be made to determine the genetical basis of population processes, such as aggression, which are thought to be directly involved in numerical fluctuations, before the hypothesis that genetic change influences numerical fluctuations in microtines can be evaluated.

Table 1. LAP types for colony crosses of *M. townsendi* tested for chi-square goodness of fit.

LAP Cross:	No. of Litters:	No. of Offspring:			p
		SS	FS	FF	
SS x SS	2	40	0	0	
SS x FS	11	53	51	0	>.98
SS x FF	3	0	15	0	
FS x FS	6	11	15	10	>.50
FS x FF	5	0	20	22	>.90
FF x FF	2	0	0	34	

Table 2. Number of transferred *M. townsendi* remaining on the experimental grids until at least the next trapping session. Total number transferred in parentheses.

	To Grid G		To Grid H	
	Males	Females	Males	Females
Summer 1971	0 (5)	1 (3)	8 (9)	4 (8)
Winter 1971-72	6 (9)	3 (4)	6 (11)	9 (10)
Summer 1972	3 (16)	3 (9)	6 (16)	7 (13)
Winter 1972-73	0 (2)	2 (10)	12 (17)	5 (13)
Summer 1973	0 (4)	1 (4)	1 (3)	3 (3)
Totals	10 (30)	9 (36)	33 (56)	28 (47)

Table 3. Percentage maximum trappability of tagged M. townsendi grouped by time of year. The minimum number known to be alive in parentheses.

	Grid G		Grid H		Grid I	
	Males	Females	Males	Females	Males	Females
July-Sept 1971	91	88	88	96	100	97
	(54)	(118)	(42)	(68)	(24)	(34)
Oct 71-Jan 72	82	84	93	86	85	98
	(325)	(430)	(194)	(212)	(456)	(508)
Feb-May 1972	94	90	96	91	94	92
	(322)	(509)	(249)	(369)	(408)	(727)
June-Sept 1972	85	83	91	84	87	81
	(511)	(630)	(310)	(430)	(415)	(702)
Oct 72-Jan 73	83	91	90	88	89	86
	(883)	(908)	(497)	(512)	(618)	(1007)
Feb-May 1973	96	95	92	95	92	93
	(375)	(454)	(180)	(283)	(224)	(460)
Jun-July 1973	89	91	93	90	91	89
	(164)	(222)	(94)	(144)	(118)	(173)
Average	87	89	92	90	91	92

Table 4. Mean body weight at the time of first capture of *M. townsendi* on the control grid I. Number of voles in parentheses.

		Males	Females
Summer 1971	FF	46.00 ± 4.94 (7)	40.50 ± 6.07 (6)
	FS	43.31 ± 2.47 (26)	38.93 ± 2.15 (29)
	SS	47.94 ± 3.80 (17)	41.14 ± 2.87 (21)
Winter 71-72	FF	37.80 ± 5.05 (5)	38.27 ± 2.11 (11)
	FS	42.48 ± 1.84 (42)	35.24 ± 1.00 (46)
	SS	42.05 ± 2.53 (22)	33.04 ± 1.59 (26)
Summer 1972	FF	57.69 ± 1.95 (13)	41.06 ± 2.77 (17)
	FS	51.15 ± 1.42 (72)	40.28 ± 1.68 (57)
	SS	45.45 ± 1.57 (64)	40.22 ± 1.44 (68)
Winter 72-73	FF	39.67 ± 3.31 (18)	34.06 ± 2.15 (17)
	FS	41.96 ± 1.57 (52)	37.12 ± 1.07 (77)
	SS	39.79 ± 1.71 (43)	38.72 ± 1.73 (39)
Summer 1973	FF	51.00 ± 4.52 (8)	43.00 ± 6.03 (3)
	FS	44.15 ± 2.36 (26)	38.00 ± 2.20 (26)
	SS	43.52 ± 2.71 (25)	35.83 ± 2.07 (29)

Table 5. Instantaneous rates of population increase for M. townsendi on all grids expressed as percent per week.

		Grid G	Grid H	Grid I
Summer 1971		3.5	3.0	9.6
Winter 71-72		3.2	3.2	1.5
Summer 1972		1.6	0.8	-0.6
Winter 71-72		1.2	0.2	0.6
Summer 1973 *	(a)	-3.6	-2.8	-3.5
	(b)	2.4	3.1	1.6

* Voles were breeding during summer 1973, but a decline in numbers on all grids was pronounced enough to warrant my separating the period into "decline" and "increase" phases given in (a) and (b).

Table 6. Percent bi-weekly change in LAP-F frequency for *M. townsendi*.

		Grid G	Grid H	Grid I
Summer 1971		2.24	-3.82	1.67
Winter 71-72		1.20	-0.11	0.78
Summer 1972		0.09	0.24	-0.10
Winter 72-73		-0.05	-0.67	0.09
Summer 1973	(a)	1.35	1.06	1.63
	(b)	0.03	-0.46	0.05
Average*		0.53	-0.83	0.16
Average**		0.37	-0.32	0.03

* From July 1971 to July 1973

** From September 1971, when experiment began, to end.

Table 7. Correlation of density and LAP-F frequency in *M. townsendi*. Number of sampling periods in parentheses.

		Grid G		Grid H		Grid I	
		N	r	N	r	N	r
Summer 1971	Males	(8)	.15	(8)	-.18	(6)	.58
	Females	(8)	.37	(8)	-.59	(7)	.42
Winter 71-72	Males	(7)	.23	(7)	-.42	(7)	.58
	Females	(7)	.46	(7)	.79*	(7)	.89**
Summer 1972	Males	(16)	-.43	(16)	.51*	(16)	-.21
	Females	(16)	.80**	(16)	-.57*	(16)	-.53*
Winter 71-72	Males	(10)	-.39	(10)	.00	(10)	.82**
	Females	(10)	.23	(10)	-.13	(10)	.25
Summer 1973	Males	(12)	-.58*	(12)	-.59*	(12)	.60
	Females	(12)	-.14	(12)	.32	(12)	.66
Totals	Males	(53)	.17	(53)	-.64**	(51)	.34*
	Females	(53)	.43*	(53)	-.55**	(52)	.25

* $p < 0.05$

** $p < 0.01$

Table 8. Minimum two-week survival rates in M. townsendi on grid G. Number of voles released in parentheses. Voles were breeding during Summer 1973, but a decline in numbers was pronounced enough to warrant my separating the period into 'decline' and 'increase' phases given in (a) and (b).

Grid G

		Males		Females	
		FF	FS	FF	FS
Summer 1971		.82	.55**	.79	.84
		(44)	(40)	(58)	(90)
Winter 71-72		.84	.79	.89	.87
		(106)	(117)	(118)	(176)
Summer 1972		.76	.76	.84	.84
		(276)	(330)	(409)	(440)
Winter 72-73		.92	.88	.88	.88
		(366)	(400)	(370)	(482)
Summer 1973	(a)	.74	.70	.89	.86
		(102)	(101)	(95)	(144)
	(b)	.76	.74	.89	.86
		(112)	(147)	(82)	(112)

** $p < .01$

Table 9. Minimum two-week survival rates for M. townsendi on grid H. Number of voles released in parentheses. Voles were breeding during summer 1973, but a decline in numbers on all grids was pronounced enough to warrant my separating the period into 'decline' and 'increase phases given in (a) and (b).

Grid H

		Males		Females	
		SS	FS	SS	FS
Summer 1971		.71	.59**	.70	.70
		(14)	(29)	(23)	(30)
Winter 71-72		.84	.85	.82	.90
		(50)	(52)	(61)	(71)
Summer 1972		.65	.71	.85	.86
		(199)	(174)	(331)	(201)
Winter 72-73		.87	.85	.90	.86
		(233)	(169)	(250)	(161)
Summer 1973	(a)	.47	.79**	.84	.84
		(32)	(48)	(79)	(67)
	(b)	.75	.62	.82	.78
		(28)	(56)	(82)	(60)

** $p < .01$

Table 10. Minimum two-week survival rates for M. townsendi on control grid I. Number of voles released in parentheses. Voles were breeding during summer 1973, but a decline in numbers on all grids was pronounced enough to warrant my separating the period into 'decline' and 'increase phases given in (a) and (b).

Grid I

		Males			Females		
		FF	FS	SS	FF	FS	SS
Summer 1971		.85	.89	.85	.78	.94	.89
		(13)	(53)	(39)	(9)	(65)	(76)
Winter 71-72		.86	.88	.88	.94	.92	.88
		(35)	(213)	(116)	(49)	(242)	(162)
Summer 1972		.72	.72	.76	.80	.86	.84
		(47)	(339)	(287)	(107)	(564)	(475)
Winter 72-73		.80	.83	.86	.87	.86	.88
		(88)	(259)	(241)	(111)	(485)	(343)
Summer 1973	(a)	.87	.67	.84	.66	.78	.88*
		(14)	(44)	(62)	(22)	(138)	(98)
	(b)	.91	.53	.76**	.90	.80	.82
		(24)	(38)	(63)	(10)	(94)	(95)

** $p < .01$

Table 11. Percentage of adult *M. townsendi* males with scrotal testes on grid G. Total number of adult males in parentheses.

Grid G

		FF	FS	Totals
Summer 1971		97	97	97
	N	(31)	(30)	(61)
Winter 71-72		53	48	49
	N	(79)	(87)	(166)
Summer 1972		72	77	75
	N	(260)	(299)	(559)
Winter 72-73		13	16	15
	N	(263)	(254)	(517)
Summer 1973		84	74*	80
	N	(212)	(142)	(354)

* $p < .05$

Table 12. Percentage of adult M. townsendi males with scrotal testes on grid H. Total number of adult males in parentheses.

Grid H

		SS	FS	Totals
Summer 1971		95	89	92
	N	(21)	(18)	(39)
Winter 71-72		55	65	59
	N	(62)	(46)	(112)
Summer 1972		82	80	80
	N	(212)	(154)	(366)
Winter 72-73		16	29*	21
	N	(169)	(97)	(266)
Summer 1973		75	84	80
	N	(76)	(98)	(174)

* $p < .05$

Table 13. Percentage of adult M. townsendi males with scrotal testes on control grid I. Total number of adult males in parentheses.

Grid I

		FF	FS	SS	Totals
Summer 1971		100	94	69**	84
	N	(10)	(32)	(32)	(74)
Winter 71-72		26	46	51	45
	N	(30)	(160)	(84)	(278)
Summer 1972		87	83	77	81
	N	(46)	(313)	(255)	(614)
Winter 72-73		17	10	9	11
	N	(53)	(146)	(150)	(349)
Summer 1973		88	74	78	79
	N	(44)	(77)	(122)	(243)

** $p < .01$

Table 14. Percentage of adult M. townsendi females lactating on grid G. Total number of adult females in parentheses.

Grid G

		FF	FS	Totals
Summer 1971		42	47	45
	N	(43)	(76)	(119)
Winter 71-72		27	41	33
	N	(88)	(69)	(157)
Summer 1972		25	39**	32
	N	(346)	(338)	(684)
Winter 72-73		6	9	8
	N	(176)	(221)	(397)
Summer 1973		38	43	40
	N	(187)	(184)	(371)

** $p < .01$

Table 15. Percentage of adult M. townsendi females lactating on grid H. Total number of adult females in parentheses.

Grid H

		SS	FS	Totals
Summer 1971		15	36	22
	N	(27)	(14)	(41)
Winter 71-72		17	28	21
	N	(54)	(39)	(93)
Summer 1972		40	38	39
	N	(365)	(181)	(546)
Winter 72-73		7	6	7
	N	(161)	(80)	(241)
Summer 1973		36	32	34
	N	(140)	(93)	(233)

Table 16. Percentage of adult M. townsendi females lactating on control grid I. Total number of adult females in parentheses.

Grid I

		FF	FS	SS	Totals
Summer 1971		75	48	27**	38
	N	(4)	(48)	(59)	(111)
Winter 71-72		4	21	20	19
	N	(24)	(112)	(101)	(237)
Summer 1972		35	34	32	33
	N	(85)	(470)	(387)	(942)
Winter 72-73		6	5	5	5
	N	(32)	(182)	(151)	(365)
Summer 1973		33	33	39	36
	N	(21)	(132)	(139)	(292)

** $p < .01$

Table 17. Mean body weight of male *M. townsendi* on grid G for each season. Total number of males in parentheses.

Grid G	FF	FS
Summer 1971	49.14 ± 1.72 (42)	53.64 ± 1.82 (36)
Winter 1971-72	49.34 ± 1.17 (122)	51.76 ± 1.26 (117)
Summer 1972	54.62 ± 0.68 (315)	55.85 ± 0.56 (333)
Winter 1972-73	48.01 ± 0.48 (375)	47.15 ± 0.55 (400)
Summer 1973	55.02 ± 0.71 (245)	53.45 ± 0.77 (168)

Table 18. Mean body weight of male *M. townsendi* on grid H for each season. Total number of males in parentheses.

Grid H	FS	SS
Summer 1971	50.31 ± 2.05 (26)	50.96 ± 2.43 (26)
Winter 1971-72	54.55 ± 1.74 (55)	48.29 ± 1.31 (103)
Summer 1972	56.07 ± 0.74 (175)	52.44 ± 0.82 (281)
Winter 1972-73	45.71 ± 0.99 (170)	44.50 ± 0.61 (296)
Summer 1973	52.29 ± 1.04 (117)	50.06 ± 1.14 (99)

Table 19. Mean body weight of male M. townsendi on grid I for each season. Number of males in parentheses.

Grid I	FF	FS	SS
Summer 1971	47.29 ± 2.58 (14)	47.96 ± 1.59 (54)	52.23 ± 2.05 (39)
Winter 1971-72	52.48 ± 2.06 (35)	50.71 ± 0.74 (213)	52.03 ± 1.17 (116)
Summer 1972	64.13 ± 1.11 (47)	60.79 ± 0.58 (339)	55.75 ± 0.66 (289)
Winter 1972-73	46.06 ± 1.24 (88)	44.28 ± 0.60 (254)	45.28 ± 0.63 (244)
Summer 1973	60.85 ± 1.46 (46)	55.41 ± 1.22 (93)	55.44 ± 0.98 (142)

Table 20. Average growth rates (% per day) adjusted by regression to a standard 35 g vole, of *M. townsendi* males on grid G. Sample size in parentheses.

Grid G		
	FF	FS
Summer 1971	1.87 ± .21 (31)	1.20 ± 34 (19)
Winter 71-72	0.64 ± .11 (94)	0.84 ± .13 (91)
Summer 1972	1.08 ± .12 (213)	1.09 ± .15 (240)
Winter 72-73	0.25 ± .08 (334)	0.22 ± .06 (349)
Summer 1973	0.51 ± .13 (160)	0.85 ± .16 (106)

Table 21. Average growth rates (% per day) adjusted by regression to a standard 35 g vole, of *M. townsendi* males on grid H. Sample size in parentheses.

Grid H	FS	SS
Summer 1971	0.75 ± .35 (17)	1.19 ± .36 (13)
Winter 71-72	0.76 ± .18 (82)	0.79 ± .12 (43)
Summer 1972	0.56 ± .16 (181)	1.70 ± .11 (123)
Winter 72-73	0.41 ± .09 (249)	0.31 ± .08 (141)
Summer 1973	1.30 ± .22 (55)	1.65 ± .23 (71)

Table 22. Average growth rates (% per day) adjusted by regression to a standard 35 g vole, of *M. townsendi* males on control grid I. Sample size in parentheses.

Grid I	FF	FS	SS
Summer 1971	0.84 ± .34 (11)	1.25 ± .19 (42)	1.64 ± .21 (32)
Winter 71-72	0.75 ± .21 (30)	0.66 ± .09 (178)	0.71 ± .10 (99)
Summer 1972	0.41 ± .40 (34)	0.54 ± .10 (241)	1.29 ± .12 (213)
Winter 72-73	0.19 ± .13 (68)	0.18 ± .08 (210)	0.29 ± .07 (202)
Summer 1973	0.79 ± .40 (34)	1.59 ± .30 (49)	1.32 ± .19 (99)

Figure 1. Westham Island receiving station: location of study grids. The central grid, I, was the control. Homozygous FF voles were removed from grid H and transferred to grid G, and homozygous SS voles were moved in the opposite direction.

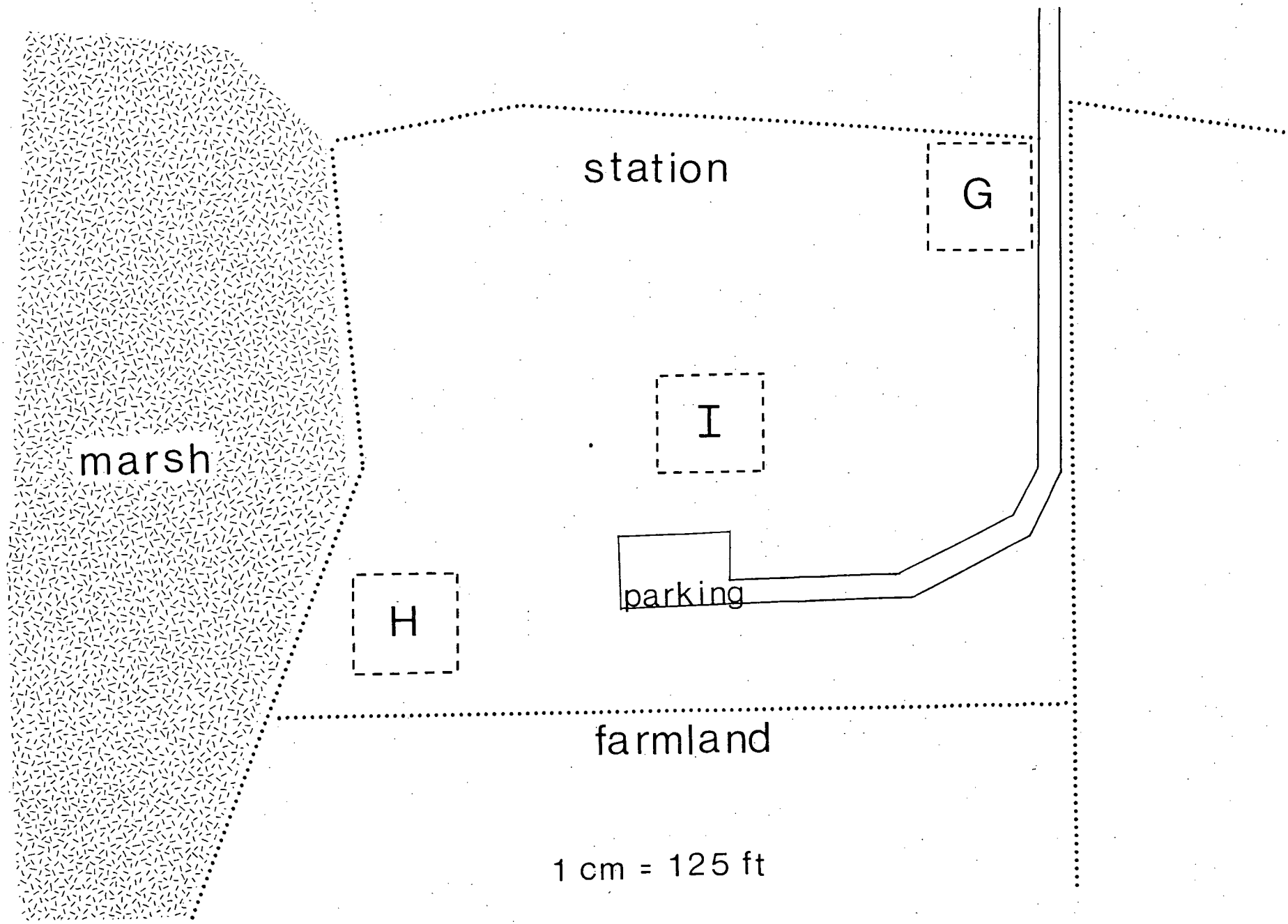

station
G
I
marsh
parking
H
farmland
1 cm = 125 ft

Figure 2. Starch gel showing LAP staining pattern in *Microtus townsendi* serum.

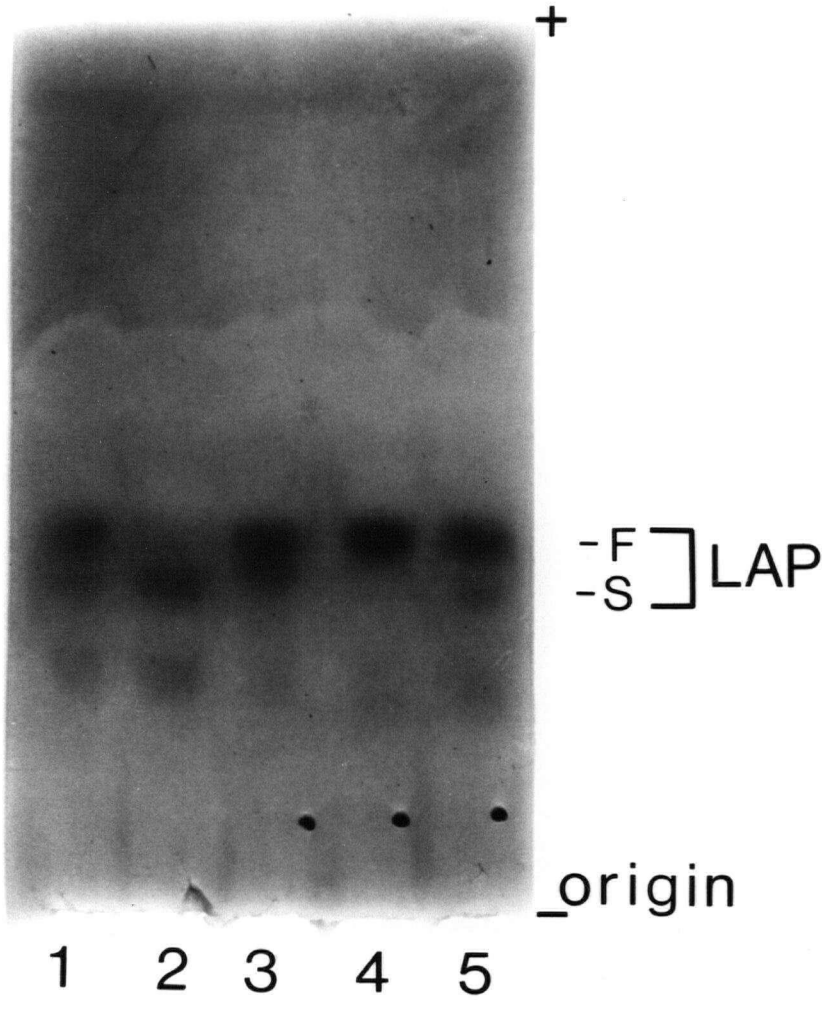

+
-F
-S
LAP
origin
1
2
3
4
5

Figure 3. Population density of Microtus townsendi on grid G.

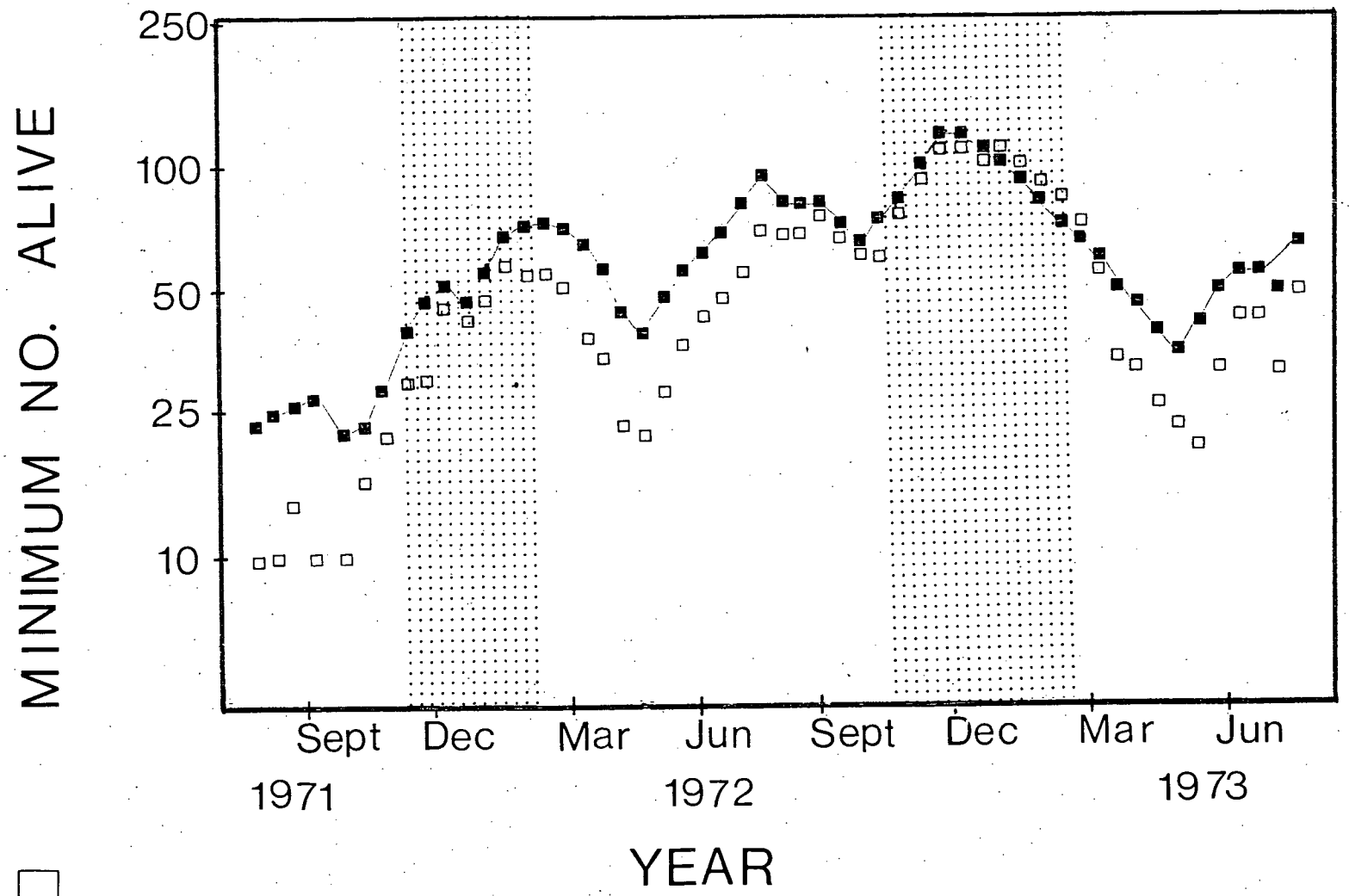

MINIMUM NO. ALIVE
250
100
50
25
10
Sept
Dec
Mar
Jun
Sept
Dec
Mar
Jun
1971
1972
1973
YEAR
males
females

Figure 4. Population density of *Microtus townsendi* on grid H.

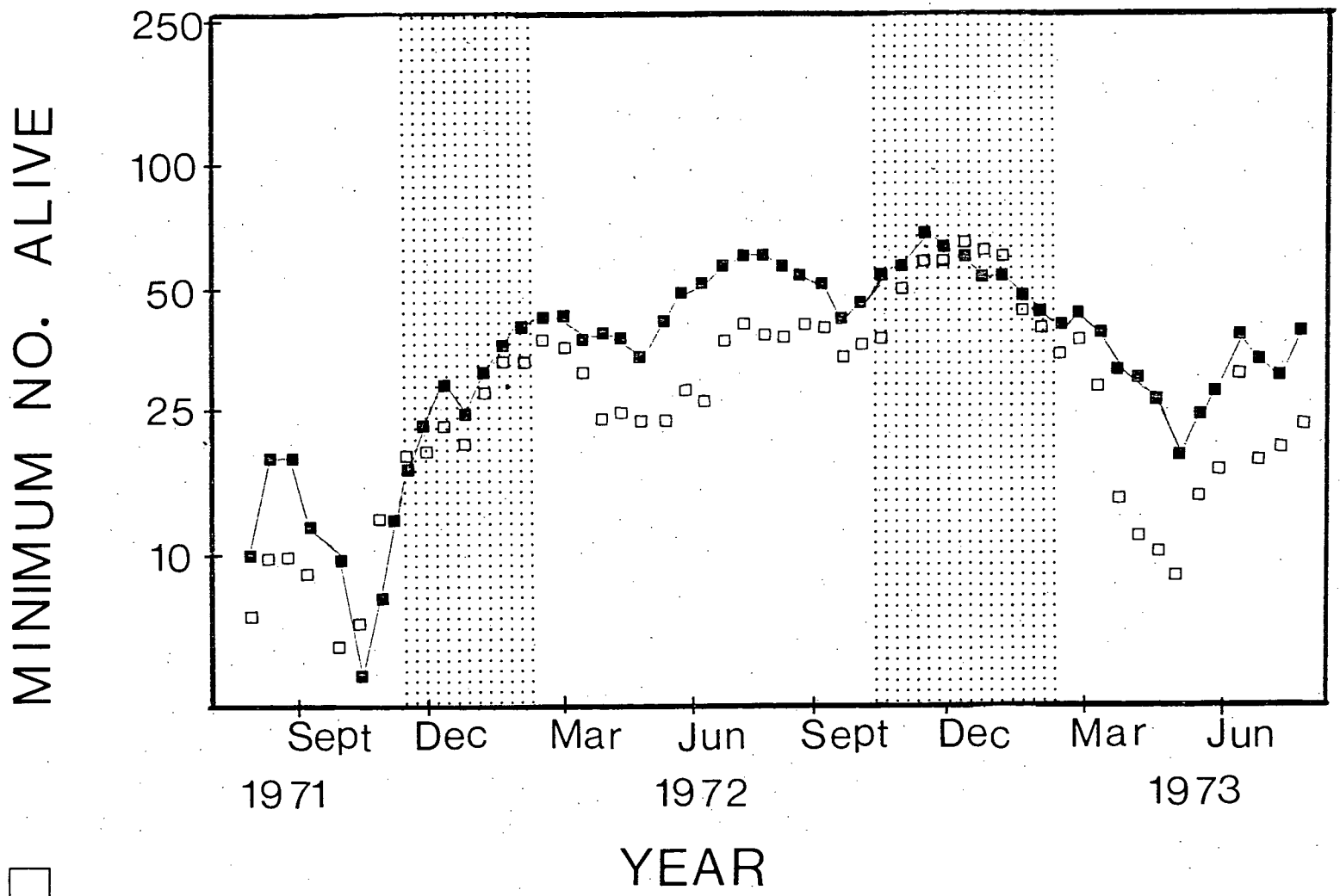

MINIMUM NO. ALIVE
250
100
50
25
10
Sept
Dec
Mar
Jun
Sept
Dec
Mar
Jun
1971
1972
1973
YEAR
males
females

Figure 5. Population density of Microtus townsendi on grid I.

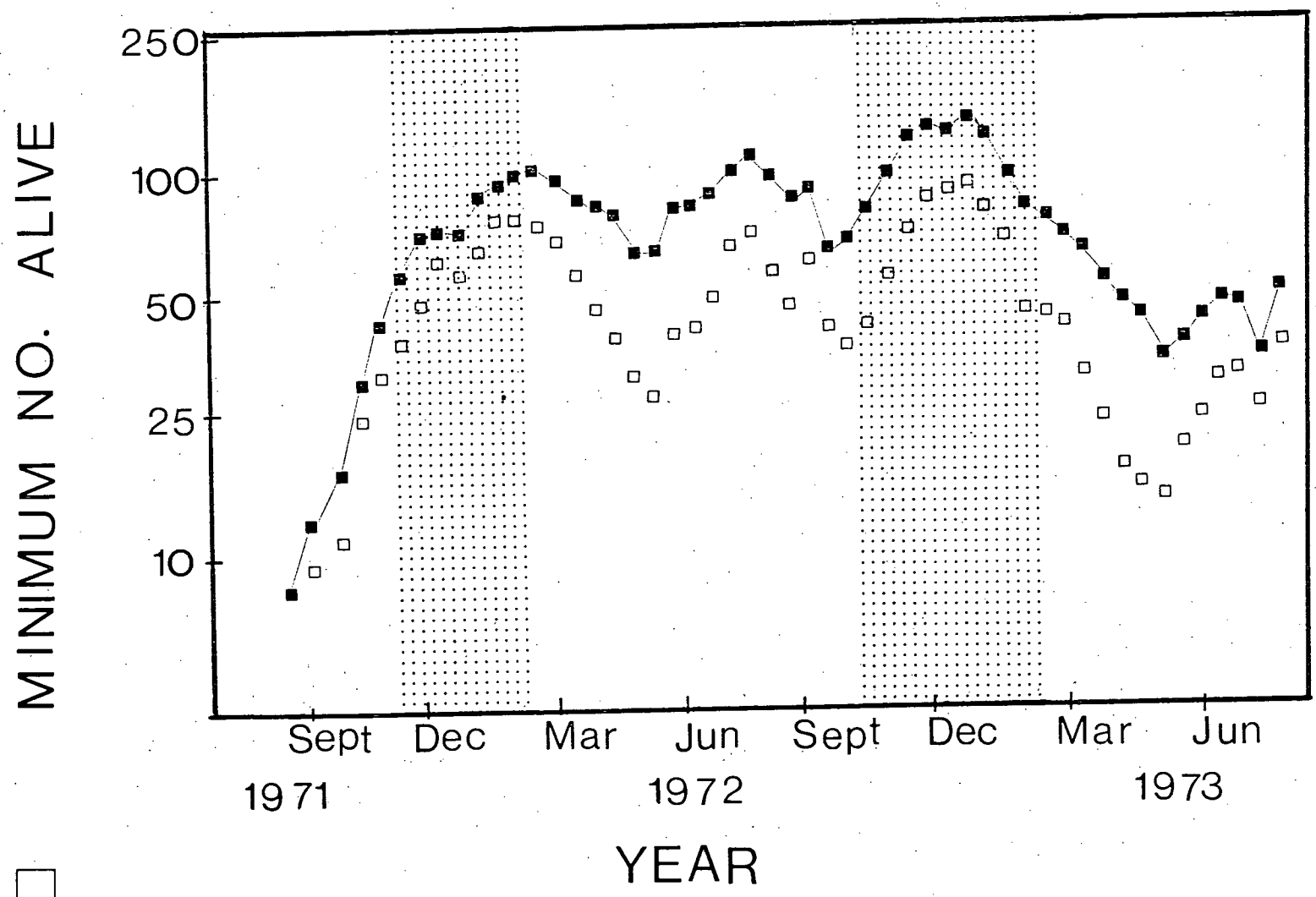

MINIMUM NO. ALIVE
250
100
50
25
10
Sept
Dec
Mar
Jun
Sept
Dec
Mar
Jun
1971
1972
1973
YEAR
males
females

Figure 6. Allele frequency of F on grid G, from which all SS voles were removed.

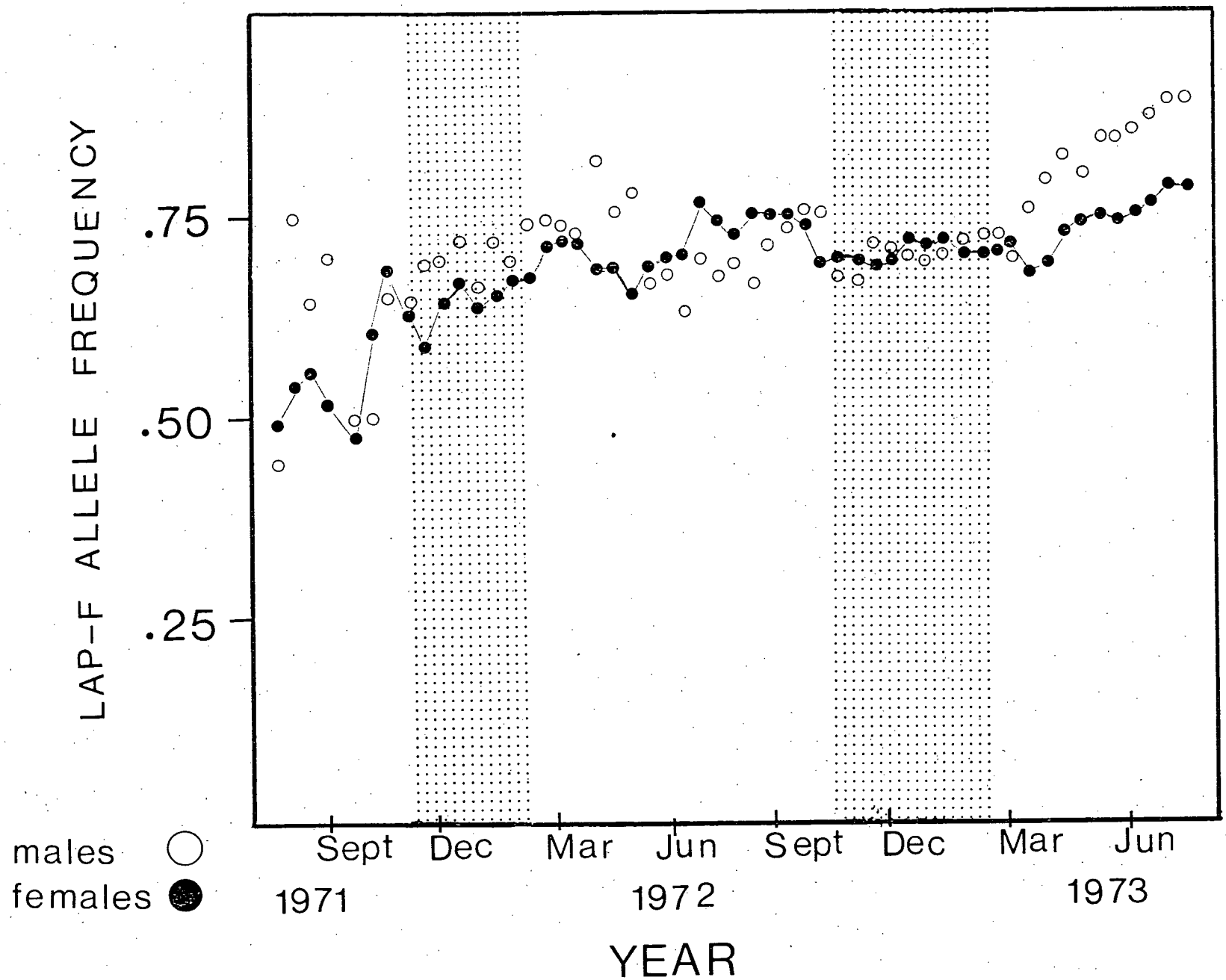

LAP-F ALLELE FREQUENCY
.75
.50
.25
males
females
Sept
Dec
Mar
Jun
Sept
Dec
Mar
Jun
1971
1972
1973
YEAR

Figure 7. Allele frequency of F on grid H, from which all FF voles were removed.

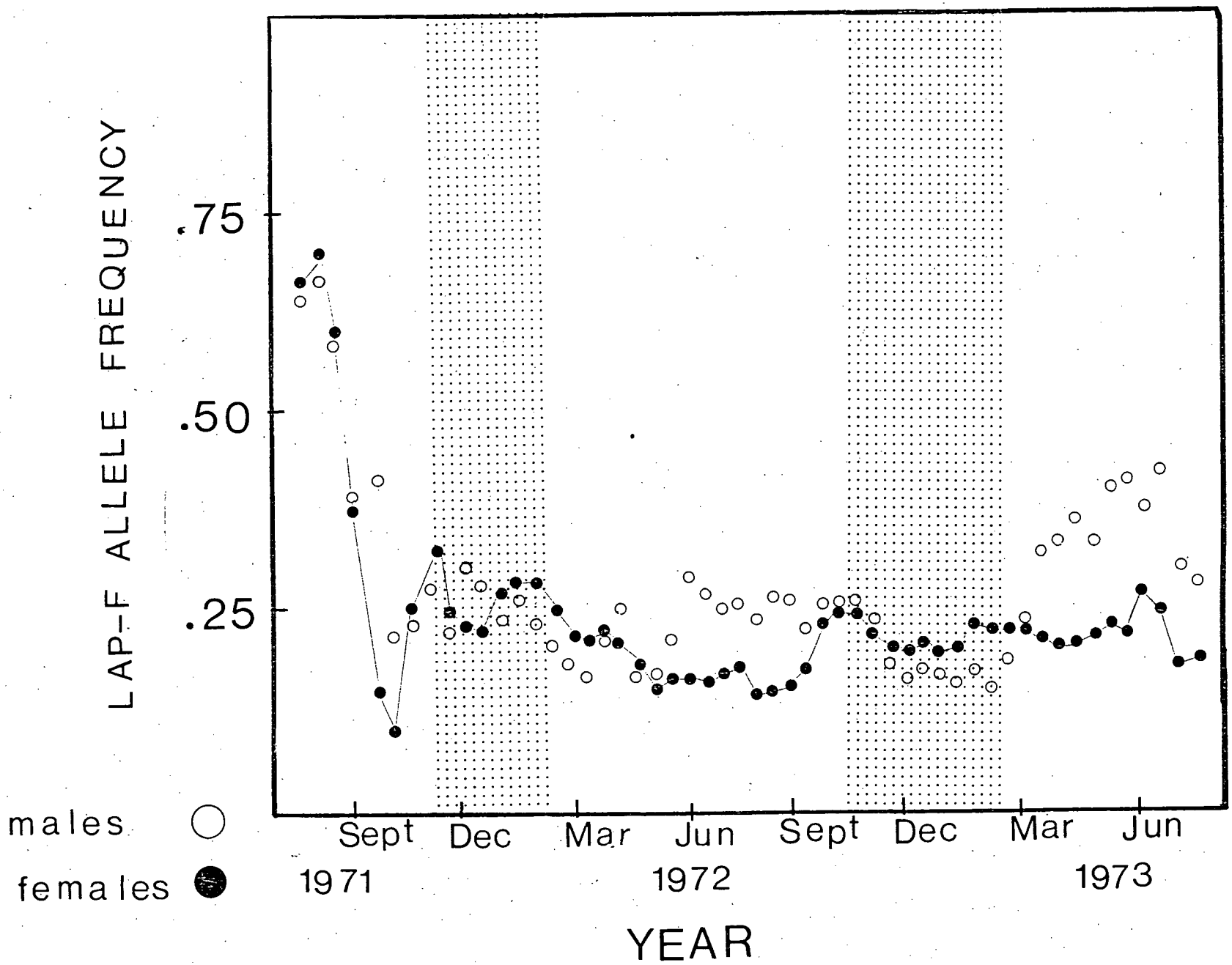

LAP-F ALLELE FREQUENCY
.75
.50
.25
males
females
Sept
Dec
Mar
Jun
Sept
Dec
Mar
Jun
1971
1972
1973
YEAR

Figure 8. Allele frequency of F on grid I, the control grid.

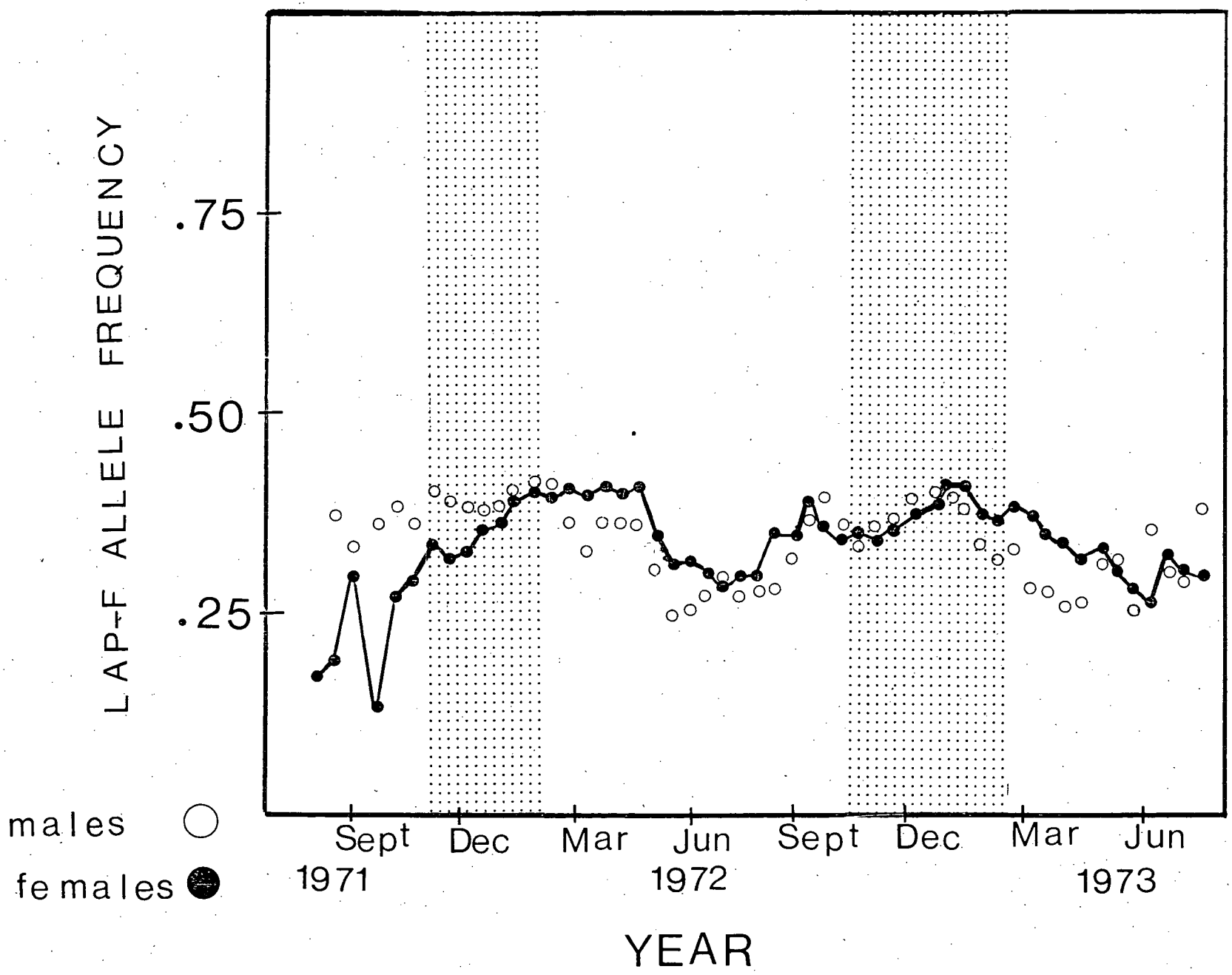

LAP-F ALLELE FREQUENCY
.75
.50
.25
males
females
Sept
Dec
Mar
Jun
Sept
Dec
Mar
Jun
1971
1972
1973
YEAR

Figure 9. Histogram of mean bi-weekly survival rates of male Microtus townsendi during the three summers.

** $p < .01$ * $p < .05$

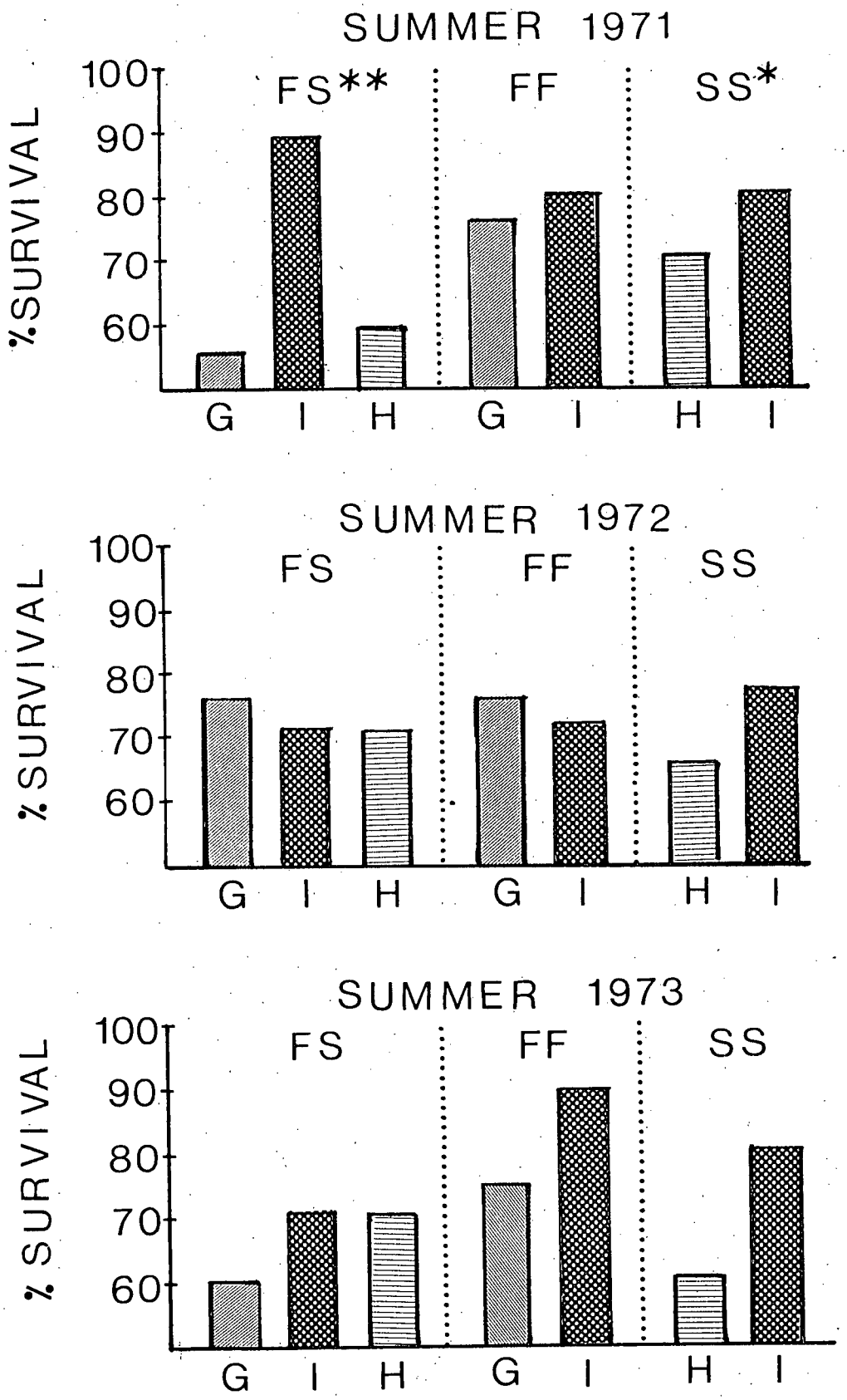

SUMMER 1971
% SURVIVAL
100
90
80
70
60
FS**
FF
SS*
G I H G I H I
SUMMER 1972
% SURVIVAL
100
90
80
70
60
FS
FF
SS
G I H G I H I
SUMMER 1973
% SURVIVAL
100
90
80
70
60
FS
FF
SS
G I H G I H I

Figure 10. Histogram of mean bi-weekly survival rates of female Microtus townsendi during the three summers.

** $p < .01$

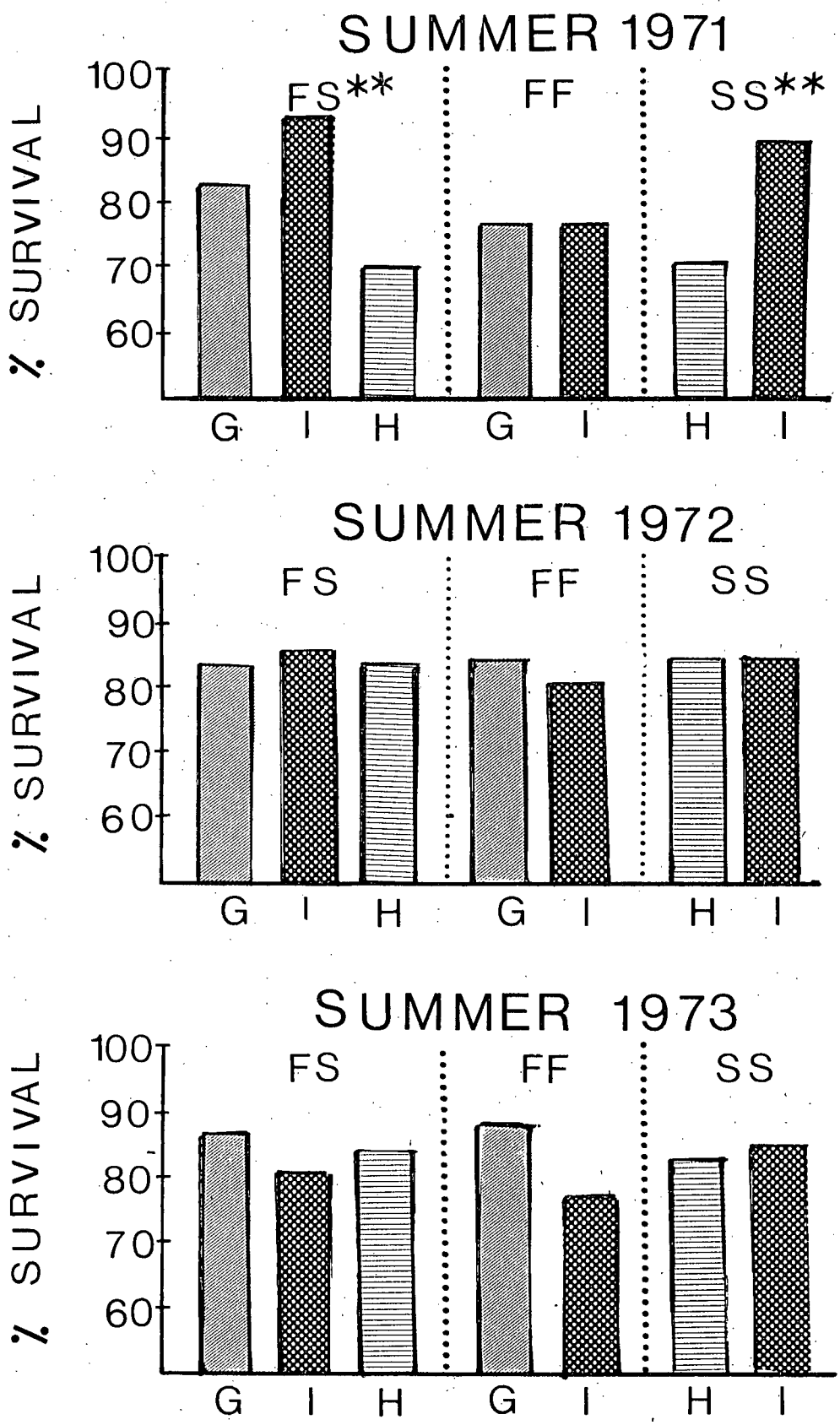

SUMMER 1971
% SURVIVAL
100
90
80
70
60
FS**
FF
SS**
G I H G I H I
SUMMER 1972
% SURVIVAL
100
90
80
70
60
FS
FF
SS
G I H G I H I
SUMMER 1973
% SURVIVAL
100
90
80
70
60
FS
FF
SS
G I H G I H I

Figure 11. Histogram of body weight distributions of male Microtus townsendi on grid G.

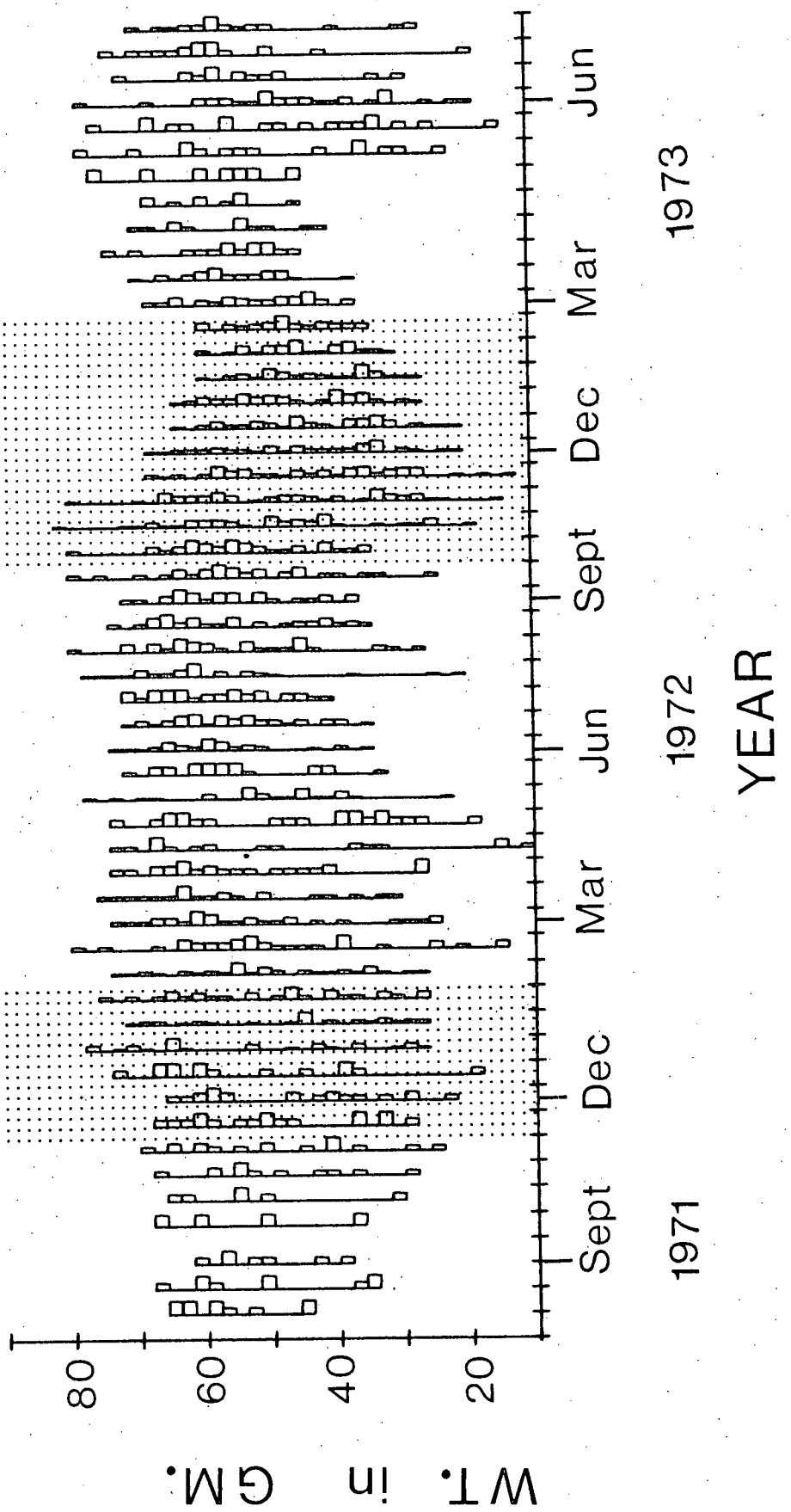

WT. in GM.
80
60
40
20
Sept
Dec
Mar
Jun
Sept
Dec
Mar
Jun
1971
1972
1973
YEAR

Figure 12. Histogram of body weight distributions of male Microtus townsendi on grid H.

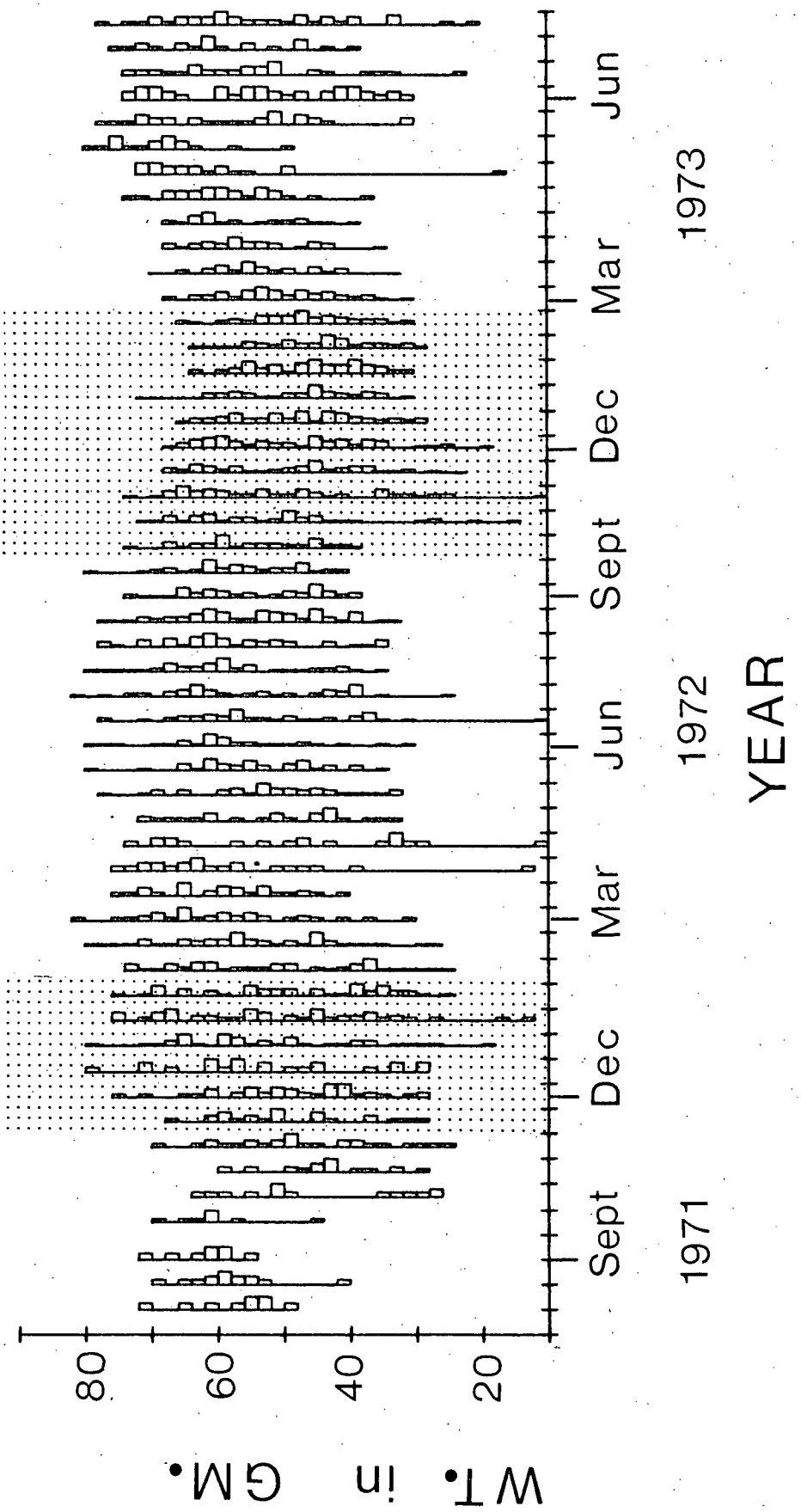
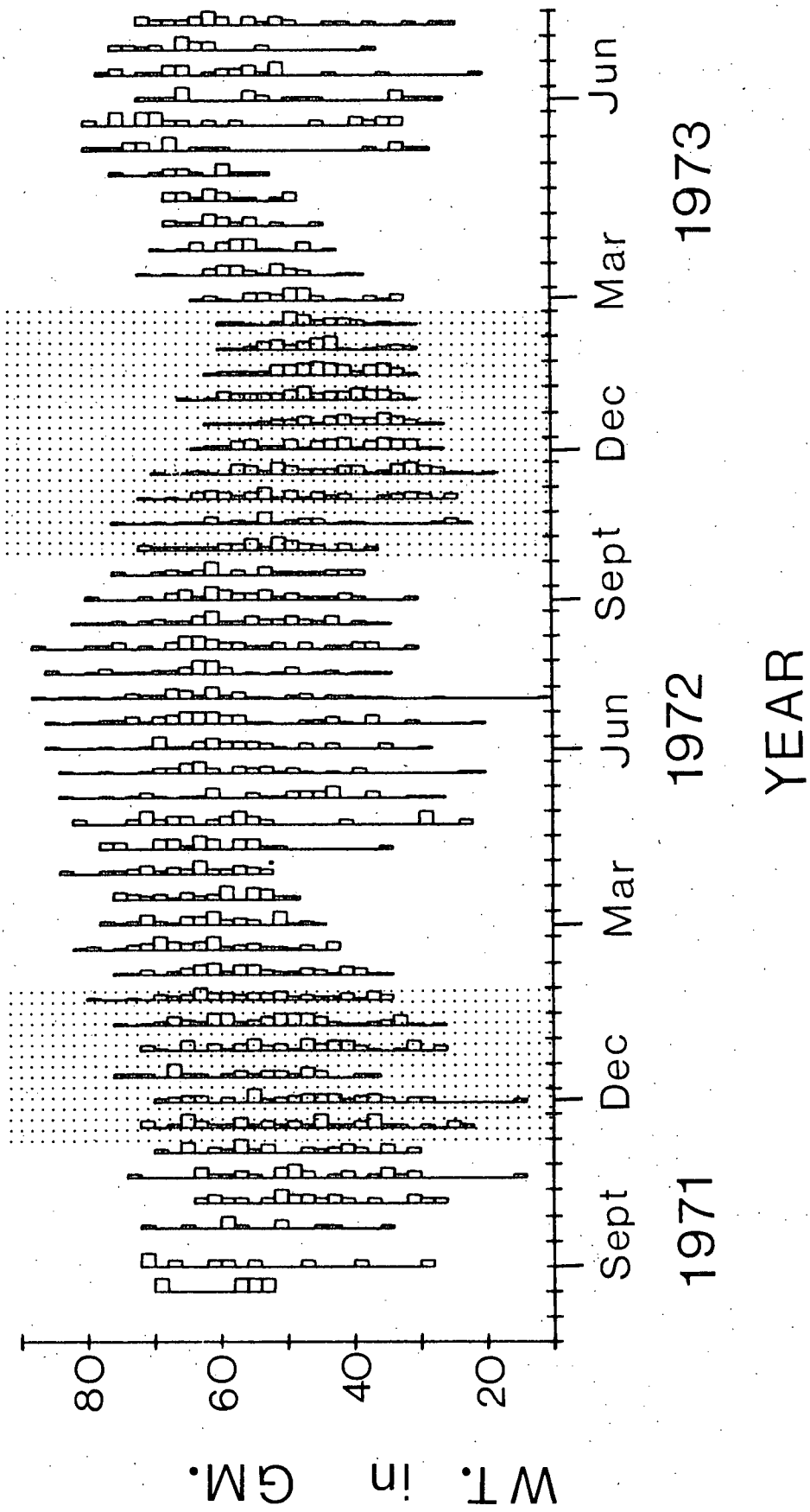

WT. in GM.
80
60
40
20
Sept
Dec
Mar
Jun
Sept
Dec
Mar
Jun
1971
1972
1973
YEAR

Figure 13. Histogram of body weight distributions of male Microtus townsendi on grid I.


WT. in GM.
80
60
40
20
Sept
Dec
Mar
Jun
Sept
Dec
Mar
Jun
1971
1972
1973
YEAR

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