POPULATION DYNAMICS OF <u>PEROMYSCUS MANICULATUS AUSTERUS</u>

AND <u>MICROTUS TOWNSENDII</u> WITH SUPPLEMENTARY FOOD

by

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Abstract

A number of field studies suggest that some vertebrate populations are limited by spacing behaviour. Small mammals of the genus Peromyscus and Microtus exhibit spacing behaviour by possessing home ranges, but they have contrasting patterns of population fluctuation. Deermice (Peromyscus sp.) fluctuate annually but maintain fairly constant numbers from year to year, whereas voles (Microtus sp.) 'cycle', reaching peak densities every 2 to 5 years. One use of the home range is for food-gathering. Therefore, these experiments were designed to investigate the influence of food availability on the home range and population dynamics of local deermice and voles (P. maniculatus austerus and M. townsendii).

The addition of food in late winter resulted in a doubling of the number of deermice. Immigration was 2.5 times that of an unfed control. This could be explained since resident deermice reduced the size of their home ranges.

Deermice populations with extra food increased their reproductive output compared with controls: larger numbers of mice bred, and for longer periods, more young were recruited, they grew faster and reached sexual maturity earlier. It is suggested that the onset and cessation of breeding in deermice are proximate responses to food availability. Deermouse dynamics may be closely tied to the temporal and spatial availability of food through the spatial organisation of individuals. It is also suggested that females, because of their energy demands for lactation, and their influence on the survival of young, may be more sensitive to these food conditions and hence exert a strong

influence on deermouse population dynamics.

Vole populations with low- and intermediate-levels of food peaked at twice the control density, and a population with a high-level of food reached seven times control density. Voles immigrated to established populations, and colonized vacant areas in proportion to the food available. Like deermice, residents reduced the size of their ranges. Breeding was enhanced in all fed vole populations.

Omnivorous deermice had larger ranges than did the herbivorous voles, but both species responded to extra food by reducing their range size, so the smallest deermouse ranges were the size of large vole ranges. The results indicate that home range size in both species is responsive to food availability, and that the concentration of food in the 'typical' habitats of these small mammals is different. If, as suggested, the heterogeneity of deermouse-food in the forest results in an annual cycle in numbers, then the reduced heterogeneity of vole-food in grasslands may influence vole dynamics.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ACKNOWLEDGEMENTS

GENERAL INTRODUCTION

A major field of interest in population ecology is the apparent tendency of natural populations to maintain their density at a certain level when they have the capacity to increase exponentially. A number of hypotheses have been advanced to explain this phenomenon. These hypotheses span a broad spectrum from those proposing that control is extrinsic to those suggesting that populations are intrinsically self-regulated.

One hypothesis that is consistent with recent research into population limitation in vertebrates was first suggested by Wynne-Edwards (1962,1965). He stated that animals which are capable of social behaviour can disperse themselves in space and time and so avoid overexploitation of their environmental resources. The extensive review of vertebrate population studies by Watson and Moss (1970) indicates that interference phenomena in the form of territorial and other types of dominance and spacing behaviour limit some vertebrate populations.

A problem arises when one attempts to look for the cause of these interference phenomena. For example, can one design a perturbation that will affect the spacing behaviour of individuals and produce a predictable change in their population dynamics? Two recent reviews on the role of behaviour in the regulation of animal populations offer little encouragement, but at the same time they illustrate the problem. Brown (1976) warns that, "The 'limitation', 'control' or 'regulation' of population numbers by behaviour is often discussed as if behaviour were the

only important factor." King (1973) suggests that, "Perhaps behavioural explanations of phenomena, like population regulation, are made when the explanations amenable to measurement and manipulation are unsatisfactory. Almost any type of behaviour can provide an impenetrable refuge for an infirm theory." A reason for the current skepticism as well as the difficulty of designing an experimental approach to the problem, is that the proximate causes of behaviour are multivariate in nature (Crook,1965). Extrinsically, the temporal and spatial pattern of physical resources and interspecific interactions (for example, food, nest sites, predators, and competitors) in the environment determines how animals move around and use the resources they require. Also, the individuals themselves: their number, size, sex, age, phenotypic experience and genetic make-up may determine when and how they interact. Therefore, the spatial arrangement of a given population is a result of extrinsic and intrinsic factors acting at specific and probably different times (Brown and Orians,1970).

Where the removal of dominant individuals results in the settlement and successful breeding of animals that previously were restricted, I consider that the operative behaviour is the spatial organisation of established members of the population. This spatial pattern of individuals could result from an integration of both extrinsic and intrinsic features (Figure 1). The dynamics of such a population may be a consequence of the spatial organisation of individual members. But it may also be directly influenced by certain features of both the extrinsic and intrinsic environment. In addition we have to allow for

Figure 1. A general model of spacing behaviour.

large arrows indicate major interactions

small arrows indicate other possible interactions

? Indicates possible feedbacks

EXTRINSIC	INTRINSIC
PHYSICAL RESOURCES : e.g., NEST SITES, FOOD INTERSPECIFICALLY: e.g., PREDATION COMPETITION	SEX, AGE, SIZE, BREEDING CONDITION, PHENOTYPIC EXPERIENCE GENETIC MAKEUP

SPATIAL   ORGANIZATION

DYNAMICS

NUMBER BREEDING
REPRODUCTIVE OUTPUT
IMMIGRATION
SURVIVAL
GROWTH RATE
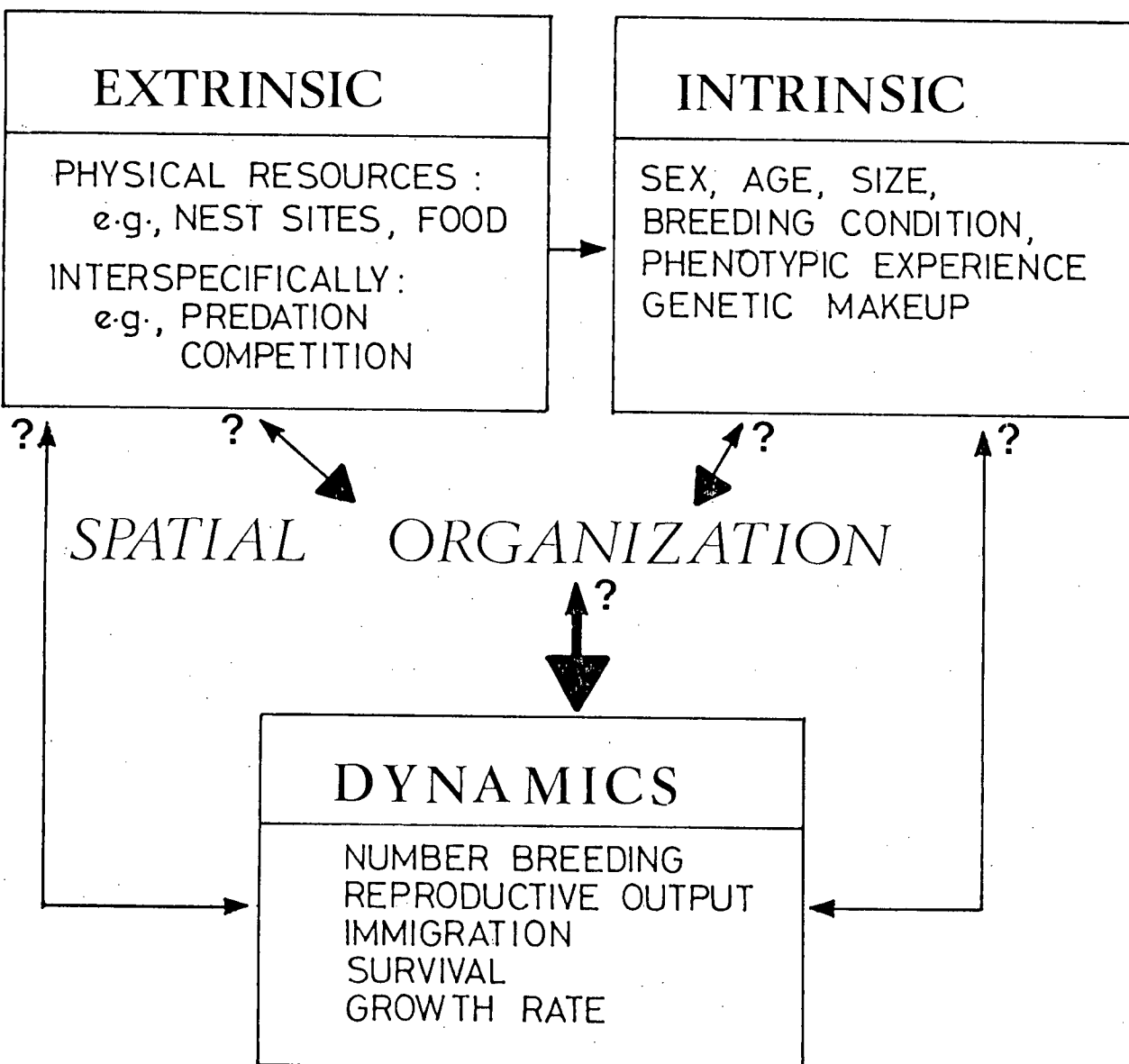
feedbacks, as indicated in Figure 1. For example, an increase in density, may feed back to spatial organisation. The ranges of individuals may become reduced in size or overlap more, causing animals to interact more frequently. Such an increase in interaction may lead to an intrinsic response, for example, some animals may leave or be excluded, while others may stay but cease reproduction temporarily. Further, the reduction or increasing overlap of ranges could result in a resource becoming over-utilized. But we can perturb such a system by increasing a resource such as food supply, then trace the effect of such a perturbation on the components. Later, removal of the perturbation may give insight into feedbacks that are operating.

One of the categories of dominance behaviour listed by Watson and Moss is 'a system of home ranges'. A home range was defined by Burt (1943) as "that area traversed by the individual in its normal activities of food gathering, mating, and caring for young". The small mammals Peromyscus and Microtus both exhibit this form of spatial organisation. Experiments by Sadleir (1965) and Healey (1967) on P. maniculatus and by Krebs et al. (1976) on M. townsendii, show that the removal of residents results in colonization by previously-excluded individuals. The general trends in population numbers have been fairly well established for these two groups of small mammals. The cyclic fluctuations of microtine rodents have been observed repeatedly: their numbers increase, peak and decline over a two- to five-year period (review by Krebs and Myers, 1974). Peromyscus, on the other hand, over most of its range appears not to fluctuate in such a cyclic manner. Instead, the

repeatable pattern is an annual cycle in numbers (McCabe and Blanchard, 1950 and Sadleir, 1965). These two species, therefore, have contrasting population dynamic patterns, but individuals of each exhibit the same interference phenomenon.

In this study, I have concentrated on one feature of the home range, namely its importance in food-gathering. These two small mammals differ in the nature of their food type. Peromyscus is an omnivorous seed-eater, exploiting a spatially and temporally variable food supply. Microtines, on the other hand, are grazers. Their food supply in open grasslands appears to be far less spatially and temporally restricted. McNab (1963) demonstrated that "croppers", for example grazers, had smaller home ranges than "hunters" such as granivorous small mammals. He ascribed this to the "concentration of food materials" within the habitats utilized by these groups.

By supplemental feeding I have attempted to manipulate the temporal and spatial availability of food to natural populations of Peromyscus maniculatus austerus (Baird) and Microtus townsendii (Bachman). I have measured the effect of this extrinsic manipulation on the home ranges and population dynamics of both species.

PEROMYSCUS MANICULATUS

1. INTRODUCTION

Peromyscus shows an annual cycle in numbers. The number of mice reaches a peak at the end of the breeding season in the fall or early winter. When breeding begins in spring there will be a sharp decline in numbers if population density is still high. This will not occur if population density is low at the end of winter (Petticrew and Sadleir, 1974). The density of mice then remains low throughout the ensuing summer breeding period.

McCabe and Blanchard (1950) were the first to suggest that Peromyscus populations might be controlled by some form of intrinsic behavioural mechanism. Sadleir (1965), working on P. maniculatus, hypothesized that juveniles survive poorly during the summer breeding season because they are competing with aggressive breeding adults. He predicted that the autumn rise in population is a result of better survival of juveniles, which may be correlated with a decline in aggressiveness of adults. Healey (1967) confirmed this correlation and demonstrated, both in the laboratory and the field that adult male aggression reduces survival and growth of juveniles. The central unanswered question is: what determines the number of animals that establish the size of the breeding population in the spring?

Fordham (1971) was the first to suggest that the number of male and female P. maniculatus in the breeding population may be

regulated differently. He supplied supplemental food to
P. maniculatus populations from mid-February to September, 1968.
The number of females increased, but the number of males
remained the same. Petticrew and Sadleir (1974) incorporated
this result into their general model of population regulation in
P. maniculatus. They propose that during the breeding season the
number of males is regulated in an 'undetermined manner' by
agonistic behaviour. But they suggest that the number of females
increases throughout the breeding season. In a recent paper,
Fairbairn (1977) suggested that females that bred early died and
so reduced the spring density of females. Finally, Petticrew and
Sadleir (1974) suggest that after the initial autumn increase in
density the numbers of both sexes of mice decline slowly for the
length of the non-breeding period.

A more general question is: what determines the onset and
cessation of breeding in the first place? This could be a
complicating feature because, as Petticrew and Sadleir (1974)
suggest, the length of the non-breeding season itself may have
some influence on the size of the population that will breed.
The use of food items by Peromyscus varies their seasonal
availability (Jameson, 1952). A variety of seeds are taken in
the fall, winter and spring, then the diet is expanded in summer
to include fruits and animal material, particularly insects. The
overall resource pattern in the forest is probably relatively
stable to Peromyscus populations. But certain food items,
especially those that provide the energy for female lactation,
are probably spatially and temporally variable to individual
mice. For example, the mast produced by trees and the products

of fruiting shrubs and plants are seasonally restricted and locally abundant. Sadleir et al. (1973) suggest that reproduction ceases in the fall because at normal winter temperatures so much energy is required for maintenance that lactation energy costs cannot be met. But a number of studies (on Peromyscus - Jameson, 1955; and on Apodemus sylvaticus - Smyth, 1966 and Hansson, 1971) have shown that the breeding season has been extended into the winter following especially abundant supplies of natural food. The breeding season might, therefore, be confined to a particular period of the year because of ambient temperature and food availability.

Experimental attempts to elucidate the relationship between food supply and the onset and cessation of breeding have so far produced no really consistent pattern. Bendell (1959) supplied supplemental food to a Peromyscus leucopus population; but found no effect on the length of the breeding season. Fordham (1970) found that male P. maniculatus came into breeding condition a month earlier on an area supplied with excess food than did control males. He also had pregnant females on his food grid two months before they appeared on his control area. In a long-term study on Apodemus sylvaticus in England, the start of the breeding season was advanced in populations with supplemental food by two to three weeks in three out of four years (Watts, 1970 and Flowerdew, 1972, 1973). However, the end of the breeding season in these studies was "hardly affected" by the addition of food.

I designed my experiments to provide a variety of times at which supplemental food was available to P. maniculatus.

Specifically, I was attempting to test the following hypotheses:-

H1: The breeding density of both male and female P. maniculatus will increase if food is added early in the year.

H2: The temporal and spatial abundance of food has a major effect on the onset, intensity, and cessation of breeding in P. maniculatus.

2. METHODS AND EXPERIMENTS

Study Area And Trapping Techniques

All five of my P. maniculatus populations were located in the University Endowment Lands (Figure 2). This area of forest is in the 'coastal douglas fir' zone (Krajina, 1969). Apart from the dominant Douglas fir (Pseudotsuga menziesii), there are some western red cedar (Thuja plicata) and western hemlock (Tsuga heterophylla) trees. The undergrowth consists chiefly of salal (Gaultheria shallon), with sword fern (Polystichum munitum), salmonberry (Rubus spectabilis), and trailing blackberry (Rubus ursinus) in certain areas.

Each P. maniculatus population was monitored in a grid of 7X7 trapping stations. The distance between traps on each grid was 50 ft (grids 2,3 and 4) and 15 m (grids 1 and 5), so the area of each grid was approximately 0.84 hectares. Grids were trapped at two-weekly intervals with Longworth live-traps (grids 2, 3 and 4) and Sherman traps (grids 1 and 5 up to November 1974) (see Appendix 1). Traps containing cotton batting and a large handful of whole oats were set late in the evening of the first day of each two-day trapping period. Mice were removed from the traps early next morning and the traps reset for a second night. During the interim non-trapping period the trap doors were locked open.

Each mouse captured for the first time was tagged with a numbered fingerling fish tag. On this and all subsequent captures of the individual, its number, grid location, and

Figure 2. Location of P. maniculatus grids on the university
endowment lands, Vancouver, B. C. Numbers correspond to
those assigned to each grid.

10th AVENUE

16th AVENUE

N

2

3

5

1

4

MARINE DRIVE
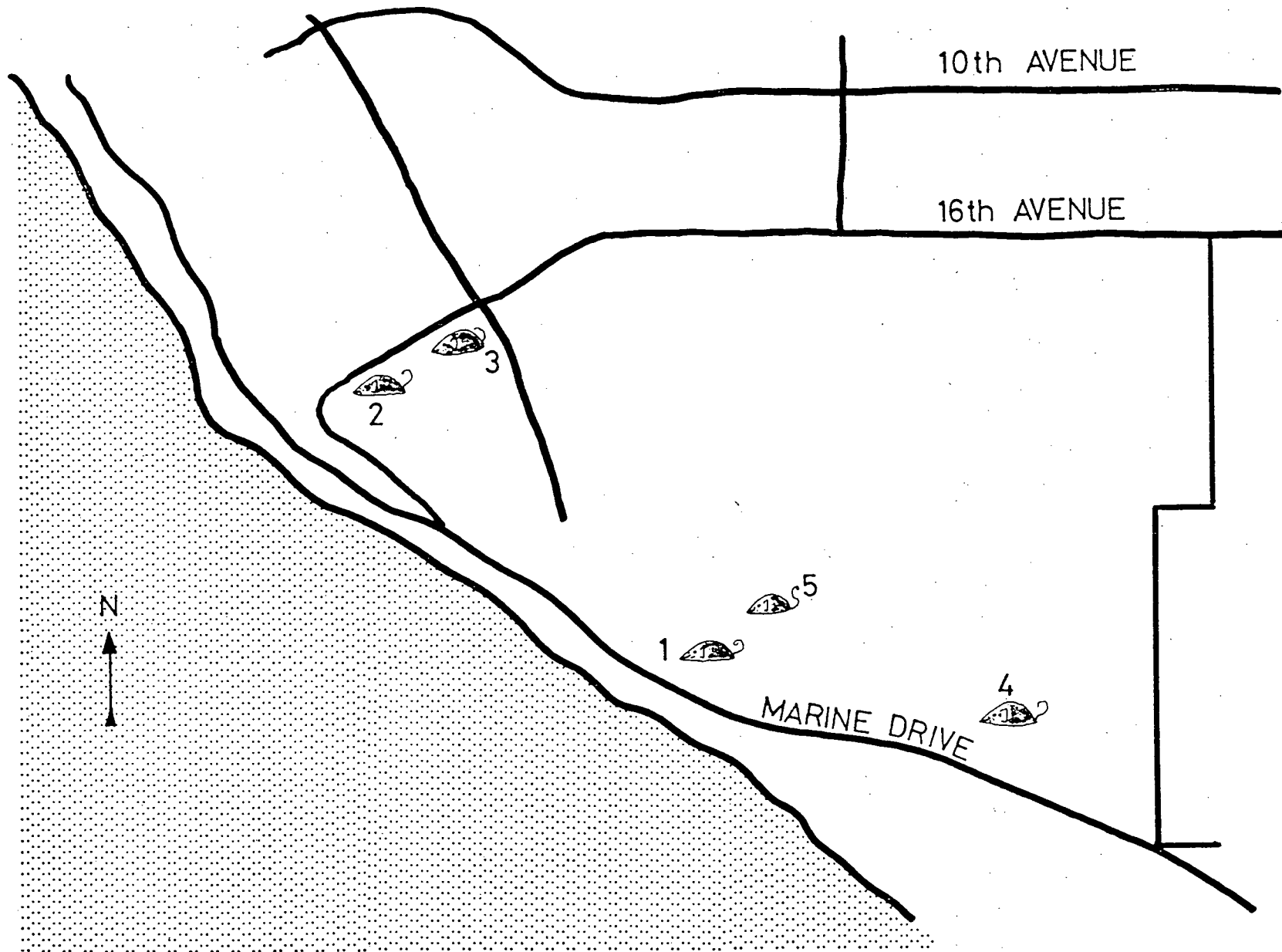
weight to the nearest gram were recorded. The breeding condition was assessed as follows: males - testes position (abdominal or scrotal), females - vaginal perforation and nipple size (small, medium or large). All litters in traps and obvious pregnancies were recorded.

Experimental Design

The experimental treatment is described here for each grid and summarized for all grids in Figure 4.

Grid 1

This grid was run as a control throughout the period of my research. Fairbairn (1976) trapped the grid as her control during the first year from November, 1973 to October, 1974. She used a slightly different trapping technique than I did (see Appendix 1). I took the grid over in November, 1974 and trapped it until the close of my study in August, 1975.

Grid 2

I started trapping mice on this grid in November, 1973. At the end of the second trapping period in December, I put out twenty-five feeding stations, which were 80-fl oz opaque plastic containers containing a known weight of whole oats (see Figure 3). At the end of each trapping period, that is, once every two weeks, I measured how much food had been consumed from each station and added a weighed amount of fresh oats. This supplemental feeding was continued for one-and-a-half years. All

Figure 3. The arrangement of traps and food stations.

X = trap site

O = trap site + food station

	A	B	C	D	E	F	G
1	X	X	X	X	X	X	X
2	X	O	O	O	O	O	X
3	X	O	O	O	O	O	X
4	X	O	O	O	O	O	X
5	X	O	O	O	O	O	X
6	X	O	O	O	O	O	X
7	X	X	X	X	X	X	X

food stations were removed at the end of June, 1975. The grid was trapped for a further month and closed in July 1975.

Grid 3

This grid was also set up in November, 1973. I began supplemental feeding one month later than on Grid 2. Again twenty-five feeding stations were provided and whole oats was added to this population. The same method of supplemental feeding was carried out on this grid. Food stations were withdrawn after the trapping period at the end of August, 1974. The population was monitored for a further fourteen weeks, then closed in November 1974.

Grid 4

This grid was established on June 26th, 1974. Supplemental food was added in twenty-five stations on August 9th, 1974. On October 18th, after ten weeks of supplemental feeding at this level, the stations were reduced to nine for the next ten weeks (stations were on rows: B, D, and F, at locations: 2, 4, and 6-see Figure 3). Stations were further reduced to four on December 28th (stations on rows: C and E, at locations: 3 and 5), and retained at this level for fourteen weeks. On April 18th, 1975 all four stations were removed, and the population was monitored for a further six weeks.

Grid 5

Throughout the whole of the first year this grid was run as

18

Figure 4. Summary of P. maniculatus experimental design.   Winter
        months are shaded.

▲ = food added

▽ = food reduced

▼ = food removed
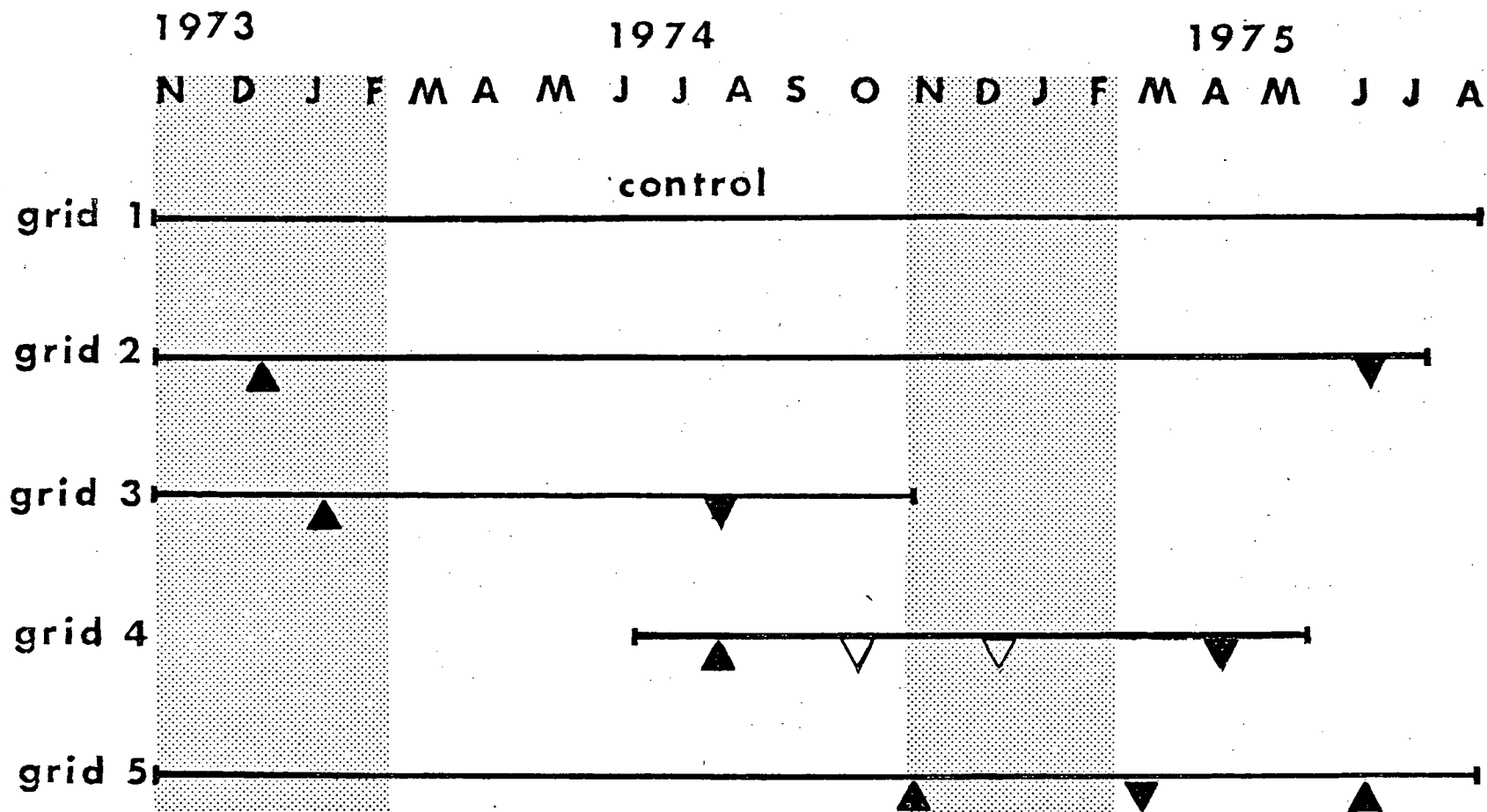
a control by Fairbairn (1976). I added twenty-five feeding stations on November 15th, 1974. The grid received supplemental food for the next four months. I removed all stations on March 7th and monitored the population for the next four months without a food supplement. On the 28th of June, 1975 I resumed feeding the population from twenty-five stations and continued this treatment until the close of my study on August 22nd, 1975.

In Appendix 1, I have described events that may have reduced my trapping efficiency on each grid.

3. RESULTS

Section A: Trappability And Reliability Of The Data

Krebs (1966) abandoned using capture-recapture techniques for estimating the population size of voles because of the problems of non-random sampling. Hilborn et al. (1976) have shown that intensive trapping can provide accurate population estimates provided the trappability of the population is fairly high. Therefore, the reliability of my population estimates as well as the validity of the demographic analysis depends upon the trappability of mice on each grid.

In estimating the trappability of a population, I first discarded any mouse with only one or two captures. The estimate for the remaining mice is the number of times each individual was captured divided by the number of times it was potentially exposed to capture during its life on the grid, expressed as a percentage. The first and last captures are always subtracted. For example, a mouse living on the grid for eight trapping periods was captured six times, its trappability is:-

$$\frac{(6-2)}{(8-2)} \times 100 = 67\%$$

I have calculated this trappability of mice for each population per month (see Appendix 2).

On both control grids there was a considerable drop in trappability (males and females on grid 1, females only on grid 5) in January 1974. This did not occur in either sex on the

supplemental food grid 2: but females declined on grid 3, which was not supplied with supplemental food until the end of the month. Practically all other cases of low trappability coincided either with very cold weather or raccoon disturbance (see Appendix 1). Cold weather, especially snowfall, may reduce the mobility of mice. Also the Longworth trap mechanism may become frozen during very cold nights, and hence reduce the trappability of P. maniculatus.

Trappability in high density populations tends to be lower than in low density populations (e.g. see grand totals for grids 1 and 2 in Table I). In 1974 males had a higher trappability than females on four out of five grids. But females were more trappable than males in 1975 in three out of four grids.

Table I. The trappability of _P. maniculatus_ in each population. Minimum number alive is given in parentheses. ML=males, FM=females.

Season	Grid 1		Grid 2		Grid 3		Grid 4		Grid 5	
	ML	FM	ML	FM	ML	FM	ML	FM	ML	FM
Winter 1973-4	77(26)	69(20)	85(29)	74(35)	82(17)	87(15)	--	--	86(6)	67(3)
Summer 1974	82(33)	75(31)	64(53)	57(63)	85(30)	91(30)	69(33)	63(25)	81(24)	57(20)
Total 1974	80(45)	72(36)	72(64)	63(74)	83(38)	89(35)	69(33)	63(25)	84(27)	60(25)
Winter 1974-5	74(12)	68(13)	65(29)	77(20)	--	--	64(32)	69(19)	61(22)	76(21)
Summer 1975	73(23)	79(23)	49(28)	65(31)	--	--	57(20)	69(23)	83(29)	68(25)
Total 1975	73(25)	75(28)	55(42)	70(39)	--	--	62(36)	69(13)	75(41)	69(32)
Grand Total	77(65)	74(53)	66(97)	65(104)	83(38)	89(35)	63(52)	67(37)	73(58)	67(49)

Section B: Population Density

Hilborn et al (1976) have shown that the reliability of minimium number alive (MNA) as a population measure drops off dramatically when trappability falls below 65%. At a trappability of 65% and survival of 0.8, MNA gives a 10% underestimate of population size. I have noted by an '*' the periods when the trappability was equal to or lower than 65% on each P. maniculatus grid (see Appendix 3). This means that the error in MNA is -10% or worse in each population for those trapping periods.

Male Dynamics

Male numbers on the two control grids are given in Appendix 3, and plotted for grid 1 in figure 5. After the autumn increase in 1973, male density declined: on grid 1 from 25 to 9 and on grid 5 from 16 to 7. When breeding began in June 1974, there were 12 males on grid 1 and 7 on grid 5. Both control grids showed a slight autumn increase, but numbers on grid 1 then continued to decline.

The addition of food at the end of December 1973, clearly resulted in the male population on grid 2 increasing rapidly from 19 to 33 by the end of April (Figure 5). Food had a similar effect on grid 3, where it was added a month later; the male population here doubled in a month (Appendix 3). Through May and into June 1974, males declined on both grids in spite of there being superabundant oats. The population on grid 2 then remained fairly stable through the fall and winter but at a higher

Figure 5. Number of male and female mice on grid 1 and grid 2.
Winter months are shaded.

upper graphs = grid 1 (control)

lower graphs = grid 2 (long-term food)

▲ = food added to grid 2

dotted line = males

solid line = females

MINIMUM   NUMBER

grid 1

grid 2

1973 ▲   1974
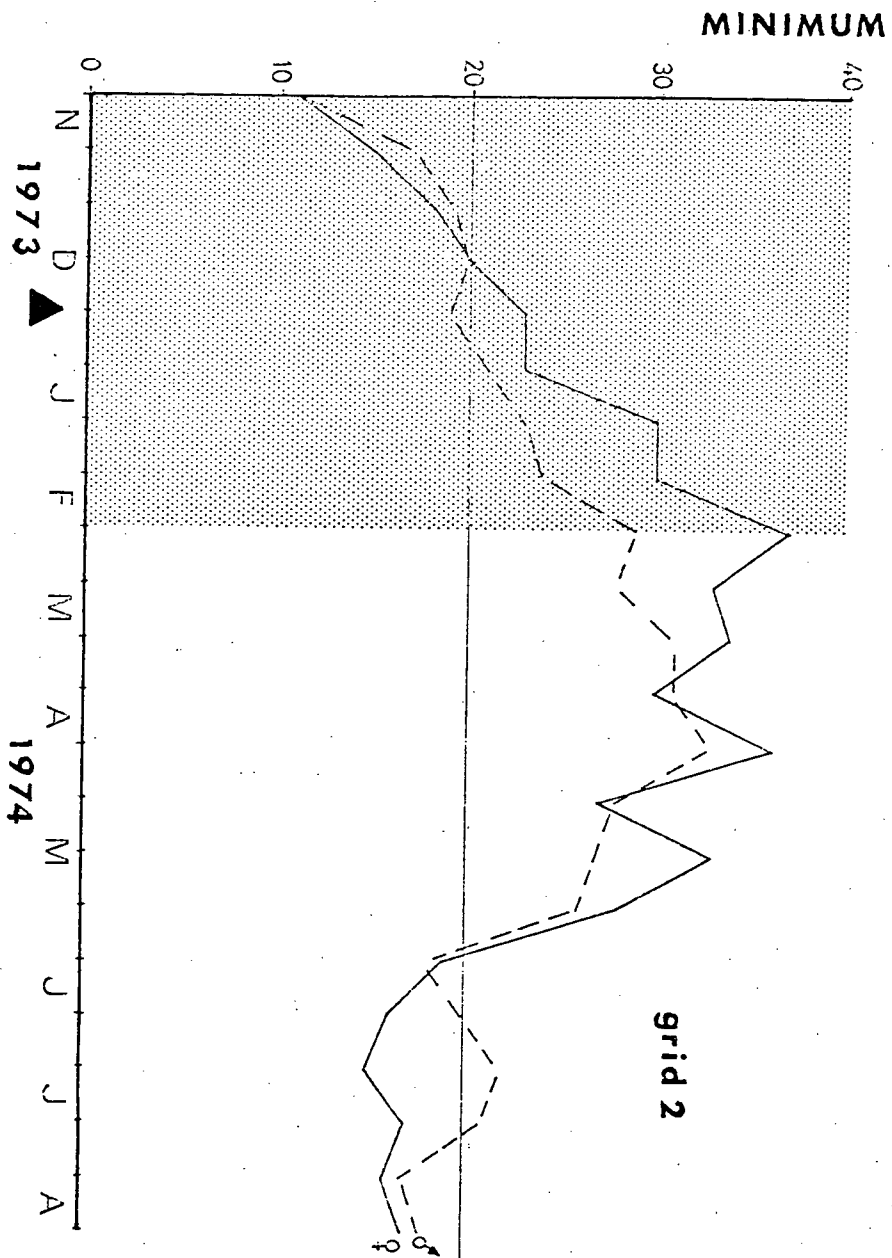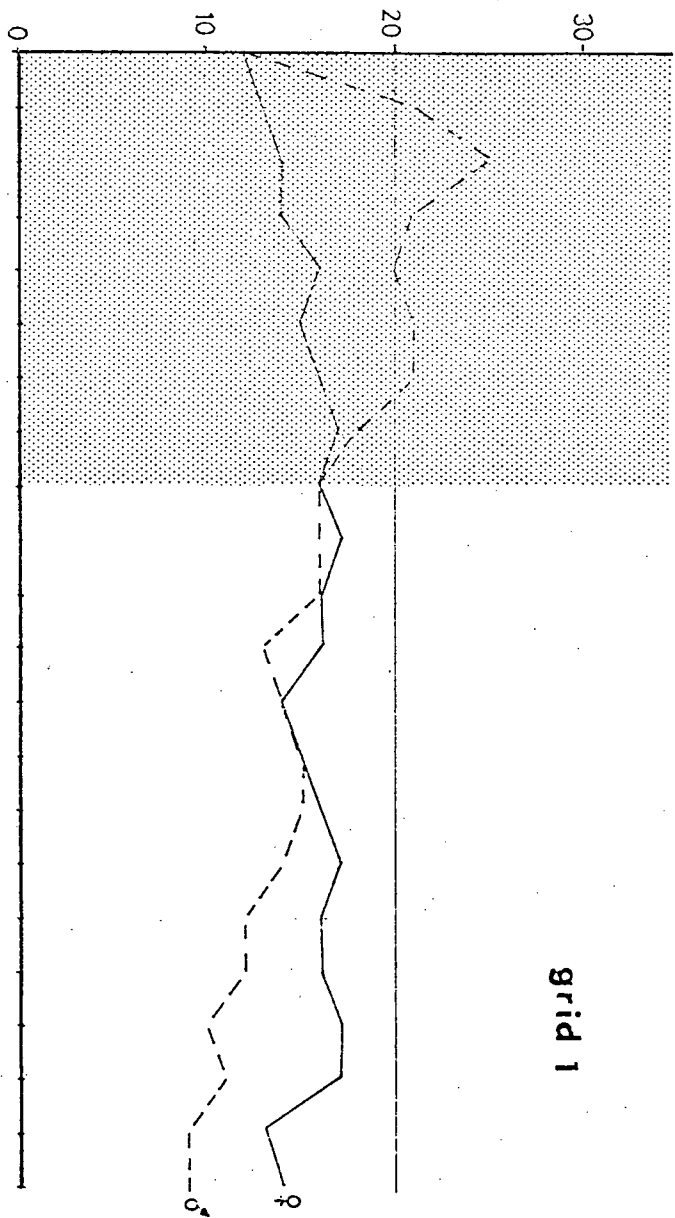
density than that of the controls (see Table II). In the last trapping in October, male density dropped from 20 to 14: this was probably the result of a raccoon invasion (see Appendix 1). At the end of February the following year, the number of males on grid 2, which was still receiving supplemental food, was 22 compared with 12 at this time on the control. Also on grid 5 with food this year, there were 16 compared with 9 males in the previous spring without food (Appendix 3). Through March to June 1975, traps in the grid 2 population were disturbed by raccoons and cats. These predators and the influx of M. oregoni may have resulted in the reduced density of P. maniculatus on grid 2 this summer.

Grid 4 has an interesting pattern of male dynamics over the 1974 winter period compared with that on the control (see Figure 6). When food was added in twenty-five stations at the beginning of August, male numbers rose from 15 to 23 by mid-October, while males on the control increased only from 9 to 12. With the reduction in food stations at this time to nine, males went out of breeding condition on grid 4, and numbers rose to a winter peak of 27 compared with 14 on the control. After food was restricted to four stations at the end of December, males declined from 27 to 19 by the end of April, while the control increased from 14 to 18. Then the food was completely removed, and males declined by nearly 50% (from 19 to 11) over the following six weeks that grid 4 was trapped. A spring influx of M. oregoni to all grids may have reduced the number of P. maniculatus a little (see Section H). But the early start and long duration of the decline on grid 4 alone suggests that once

Table II. The mean density of P. maniculatus on each grid over three month intervals in 1974-75. ML=males, FM=females.

Months	Grid 1		Grid 2		Grid 3		Grid 4		Grid 5	
	ML	FM	ML	FM	ML	FM	ML	FM	ML	FM
Nov-Dec 1973	19.8	13.8	17.2	17.4	11.0	6.8	--	--	14.2	20.0
Jan-Mar 1974	18.0	16.2	26.0**	31.2**	12.8*	12.5*	--	--	9.0	12.8
Apr-Jun "	13.6	15.7	26.0**	27.0**	10.4**	13.6**	--	--	7.4	11.43
Jul-Sep "	10.5	15.2	19.1**	16.6**	8.4*	7.8*	16.0*	14.2*	7.8	9.0
Oct-Dec "	10.1	11.9	17.3**	16.7**	12.3	8.3	22.5*	18.3*	12.4*	12.3*
Jan-Mar 1975	12.8	13.2	18.5**	15.7**	--	--	22.5*	15.8*	15.8*	18.0*
Apr-Jun "	17.4	16.1	17.1**	18.0**	--	--	16.2	10.6	16.6	18.0
Jul-Aug "	10.3	13.3	14.0	7.5	--	--			13.0**	14.3**

** = full complement of food for the whole period

* = partial complement or fed for only part of the period

Figure 6. Number of mice on grid 1 and grid 4. Winter months are
      shaded.

              upper graph = grid 1 (control)

              lower graph = grid 4 (reduced-food)

                    ▲ 1 = food in 25 stations

                    ▲ 2 = food reduced to 9 stations

                    ▲ 3 = food reduced to 4 stations

                    ▼ 4 = food removed

          dotted line = males

           solid line = females
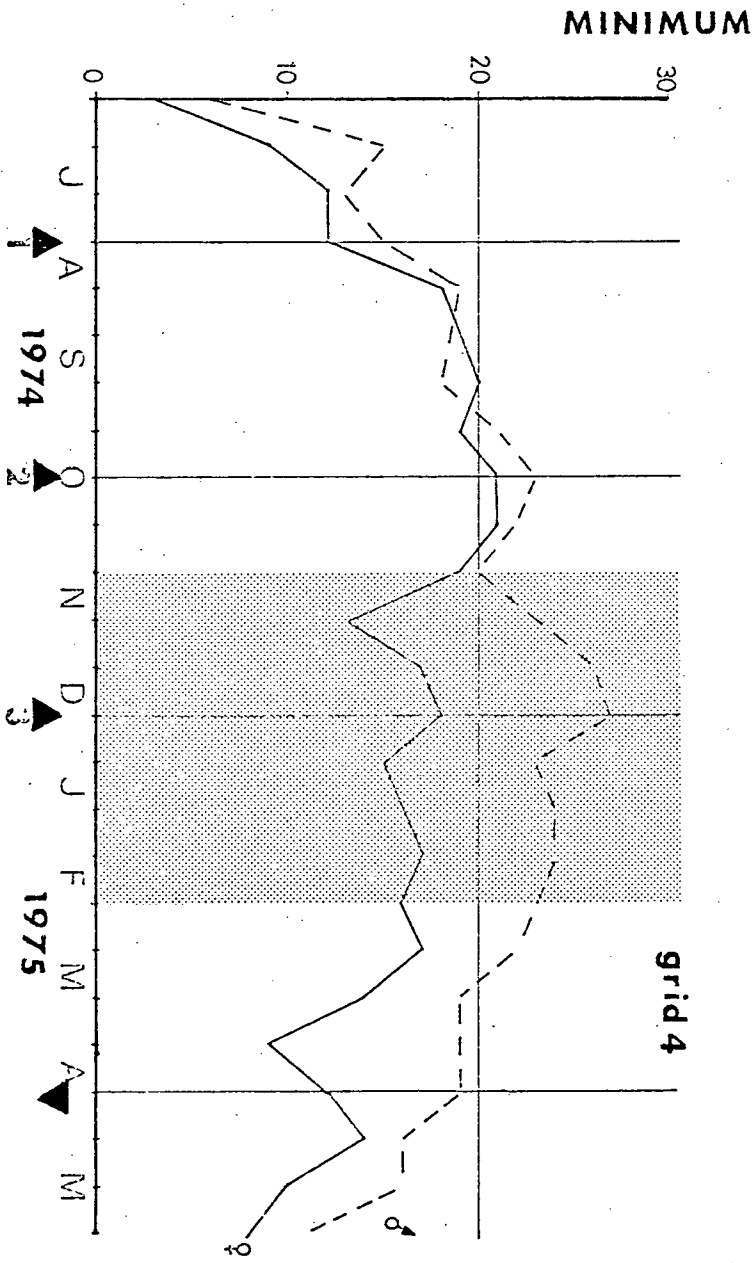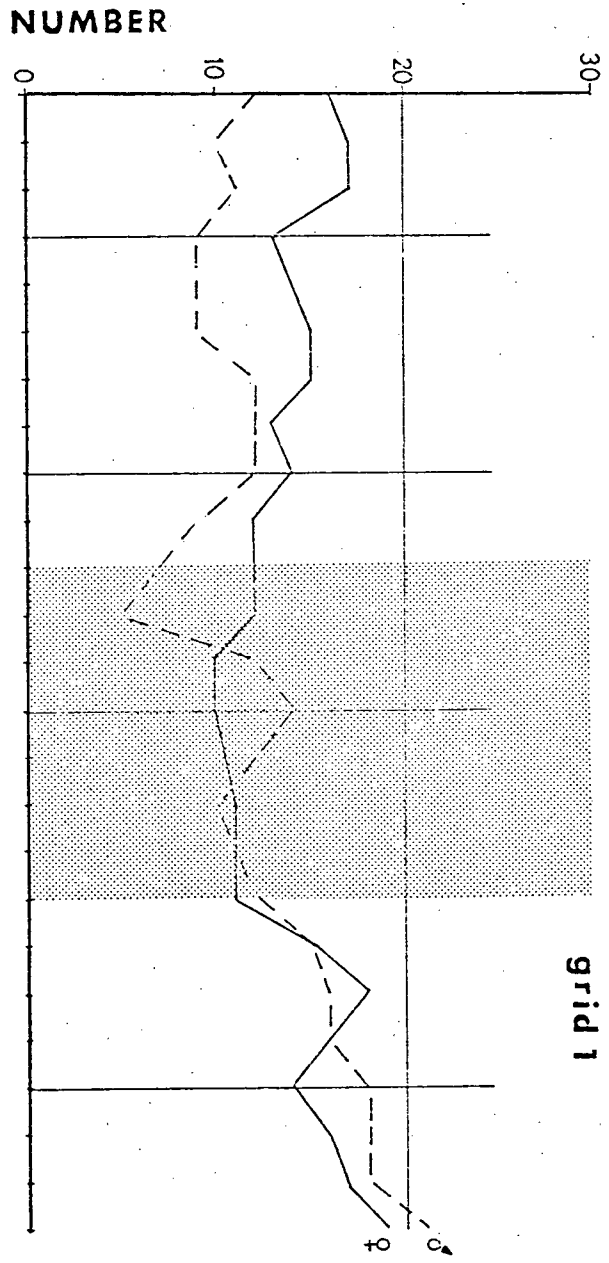
the food was reduced to 4 stations, this was insufficient to maintain the high density population through the spring.

Female Dynamics

Female mice on the control grids reached winter population peaks in December 1974 (Appendix 3). On grid 1, females maintained fairly stable numbers through the spring 1974 (Figure 5), while females on grid 5 declined. On both grids the lowest numbers were reached when the breeding season was fully underway in late summer 1974.

After food was added to grid 2, females increased and reached peak numbers more rapidly than did males (Figure 5). On grid 3 females doubled their numbers five weeks after the food was added at the end of January 1974 (see Appendix 3). As in males, female numbers declined over the summer on both food grids.

The mean winter population of females on the control was 11.9 compared with 16.7 on grid 2 with food (Table II). This was in spite of a reduction in females from 22 to 15 following the raccoon invasion (Appendix 1). On this long-term food grid spring numbers peaked at 22 at the end of March compared with 16 on the control. As with males, female spring densities in 1975 on grid 2, although higher than those on the control, are lower than those in 1974. As suggested, this may have resulted from raccoon or cat disturbance and the immigration of M. oregoni. Also, 1975 was a more nearly normal breeding year on the control (see Section C), which suggests that natural food conditions may have been better in 1975. Also, immigration to the control was

higher and closer to the rate for grid 2 this year (see Section E). On grid 5, which was supplied with food in twenty-five stations in November 1974, females increased to 21 by the end of March 1975 compared with 11 in March 1974. By contrast, females on grid 4 started to decline when the food stations were reduced to nine on October 1974 and continued to decline throughout the spring (see Figure 6).

Summary

The addition of food early in the spring resulted in the numbers of both sexes doubling or nearly doubling on the experimental grids 2 and 3. The mid-winter addition of food to grid 5 reversed the normal slow winter decline in numbers. The response of both sexes to the removal of food varied according to the time of year. Spring removal of food (grids 4 and 5) tended to cause a reduction in both sexes. The summer removal from grid 2 had a strong effect on females, which declined from 20 to 6 in four weeks. Late fall removal (grid 3) caused animals to go out of breeding condition (see Section C) and proceed into a normal fall increase. There was a tendency for both sexes on all grids to decline in the summer of 1975 as *M. oregoni* immigrated (see Section H).

Section C: Breeding Season

Densities change by births, deaths, and movements. In this section I assess the effects of supplemental feeding on the potential reproductve effort of the populations. I have defined the breeding season based on the external examination of mice captured in the field at each two-week trapping period. I considered all males and females weighing 17g or more as adults (see Appendix 4). A breeding adult male has scrotal testes and a breeding female has medium or large nipples. I defined the breeding season as the period when 50% or more of the adult males or females are in breeding condition. In Appendix 5, I present a table of the percentage of adult males and females breeding in each trapping period in all five P. maniculatus populations.

Food And The Onset And Cessation Of Breeding

I was interested in measuring the effect of supplemental food on the onset, intensity, and extent of the breeding season on food grids 2 and 3 compared with events on the control grid 1. No males were breeding on any grids in November or December 1973. Food was added to grid 2 after the second trapping period in December 1973. One month later 5 males had scrotal testes, and six weeks later over 50% of the males were breeding in this population. Food was supplied one month later to grid 3. In the following two-week trapping period over 50% of the males had scrotal testes. This level of breeding intensity was not reached on the control until the beginning of June, four months later

than on the food grids.

Males in the control population ceased breeding completely at the end of August 1974. Two males on grid 2, and all four males on grid 3 were still breeding. The food was removed from grid 3 during this trapping period, and no more males were recorded breeding here. I was unable to trap the experimental grids in the first week of September or feed the grid 2 population. Practically all the food stations were empty when I came to refill them at the end of the month. Male reproduction had ceased completely at this time on grid 2, but started again the following period and continued for the rest of the study. Apart from one male that was scrotal on the control in October, no animals resumed breeding on this grid until December. The onset of the breeding season on the control was much earlier in 1975, over 50% of the males were scrotal by the end of February. In fact, apart from a drop at the beginning of May, the pattern of reproduction on the control grid in 1975 was very similar to that on the long-term food grid.

The pattern of breeding in females was very similar to that in males. One month after the addition of food to grid 2, females were lactating in January (see Appendix 5). On grid 3 females were lactating six weeks after food addition. In both cases females had perforate vaginas in the trapping period immediately following food addition. One female was found lactating in March on the control, but no others were found until July. Females on the control bred for only one month compared with five months on grid 2. Breeding stopped in females on all three grids for the whole of October. No breeding was

recorded on grid 3 once the food was removed, but females on food grid 2 started breeding in November, and more than 50% were lactating by the end of January. Like the males on grid 1, females bred much earlier on the control in 1975 than in 1974. The intensity of breeding dropped below 50% in May on the control while females on grid 2 continued at 50% or more. There was no response in either males or females to the removal of food from grid 2 in June 1975.

Food And Winter Breeding

On grid 5, I was interested to see if a population would start to breed if food were provided in the middle of winter. Secondly, I wanted to see if the breeding condition in late spring would be affected by removal and later re-addition of the supplemental food. Grid 5 was run as a control from November 1973 to September 1974. The pattern of reproduction was very similar to that on grid 1 (see Appendix 5). I added food to this population at the beginning of November 1974. Males became scrotal and females perforate by the next trapping period. Some females were lactating at the end of December. I removed food from this population in early March. Male reproduction declined slightly, but the number of females lactating dropped from 8 to 1 two months after food stations were removed. Over this period female lactations on the control declined from 7 to 3 and did not change on the long-term food grid. I re-introduced food to the grid at the end of June but neither sex responded noticeably.

On grid 4, I was interested in seeing how many feeding

stations were needed to prevent a cessation of breeding in winter. Male breeding had almost ceased when I added food in twenty-five stations at the beginning of August, then ceased when the food ran out in September (see Appendix 5). Three males became scrotal in October, but ceased breeding after the number of food stations was reduced to nine at the end of the month. Female lactation increased from 43% to 82% lactating after the food was added in twenty-five stations. But at the end of October and through November only one female was pregnant and lactating; she was trapped twice out of a possible three times at one of the nine food locations on the grid. By the time the food stations were reduced to four at the end of December, no mice were breeding on grid 4.

Weather And Breeding

The breeding performance of males and females on the control grid differed in the onset and intensity of breeding in 1974 and 1975 (see Figure 7). February 1974 had close to the average mean temperature, precipitation, and hours of sunshine (see Appendix 5). But March had double the normal precipitation for the month; this continued through a cool, rather cloudy April. Some males did become reproductive on the controls, but only one female was recorded breeding at the end of March. May 1974 had the lowest average temperature ever recorded for this month in Vancouver. May also had two-and-a-half times the normal rainfall and 41 hours below the normal sunshine for the month. Reproductive activity halted in males, and no lactating females were caught on the controls by the end of May. The weather

Figure 7. Summary of breeding season data for grids 1, 2, 3, and 5. Winter months are shaded.

▲ = food added

▼ = food removed

wide line = 50% or more adults breeding

middle line = less than 50% of adults breeding

narrow line = no breeding
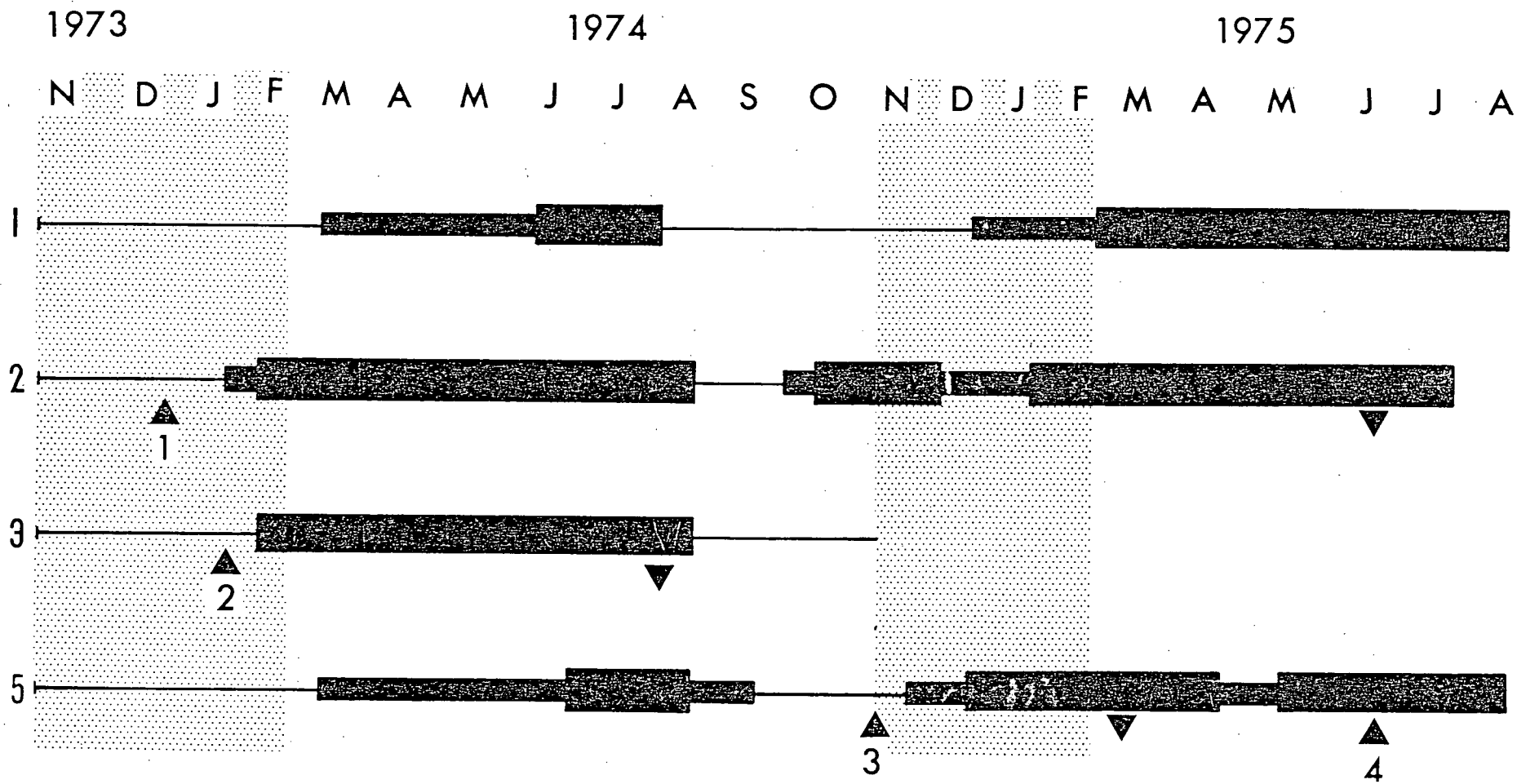
improved through June when breeding began. In contrast, October set a new record for the hours of sunshine. Similarly, December was much milder than normal. One male on grid 1 had scrotal testes in October. In December four males had scrotal testes and three females had perforate vaginas in the control population. The spring of 1975 was not much warmer than that of 1974, but the hours of sunshine and the total precipitation were much closer to normal.

Summary

The addition of supplemental food to grids 2 and 3, at the end of December 1973 and the end of January 1974 respectively, enabled mice on these grids to breed earlier and for much longer in spite of the poor weather in 1974 (see Figure 7). Breeding stopped on the control grid at the beginning of August 1974. It ceased completely on grid 3 when food stations were removed at the end of the month and temporarily on grid 2 when the food stations were emptied. Otherwise mice on grid 2 with food in twenty-five stations continued to breed throughout the winter. Both sexes on grid 5 were stimulated to breed immediately after food was added to this grid in mid-winter 1974. The results for grid 4 with regard to a threshold level of food abundance for winter breeding in P. maniculatus are not clear. But when the food stations were reduced from twenty-five to nine, breeding ceased in this population during the winter of 1974.

Section D: Breeding Success

Breeding on the food grids began four months earlier than on the controls in 1974. The duration and intensity of breeding on these grids was also much greater than on the controls (see Section C). Did this greater reproductive effort result in a higher production of young mice? Estimating the recruitment of young mice to a population, particularly in the breeding season, is difficult. First, according to Sadleir's hypothesis (1965), male P. maniculatus are aggressive to all juveniles. Secondly, young may be present in the population but 'passively' prevented from entering the traps because larger mice are caught first.

I held all mice caught on grids 1 and 5 during the first night in the August 20-22 trapping session. This meant that all 49 traps were available to any mice remaining on these grids. In Table III, I compare the number of new subadult and juvenile mice caught in this trapping period with those caught in the preceeding period in August 6 - 8th. On each grid the total number of new young mice was much higher in the 'removal' period (August 20 - 22nd) compared with the previous 'normal' trapping period (August 6 - 8th). There were the same number of breeding males on grid 1 in both trapping periods. Further, on grid 5 the number of breeding males increased to 6 out of 6 compared with 4 out of 5 in the August 6 - 8th period. Therefore, there was presumably no decrease in reproduction-related aggressive behavior of adult males between the two trapping periods. In addition, 9 out of 16 (grid 5), and 7 out of 14 (grid 1) new young mice in the August 20 - 22nd period were caught in the first check. This suggests that the second factor, namely the

Table III. New young mice caught on grid 1 and grid 5 in the last two trapping periods.

	August 6-8			August 20-22		
	Sub-ad.	Juv.	Total	Sub-ad.	Juv.	Total
Grid 1	1	1	2	8	6	14
Grid 5	2	4	6	10	6	16

'passive' exclusion from traps, was not the reason for the low catch of juveniles in August 6 - 8th.

Two recent laboratory studies on Peromyscus suggest that maternal aggression may be important in the dispersal of young mice. Rowley and Christian (1976) found that lactating female P. leucopus had high levels of aggression, and that they, not males, were aggressive towards their own young. Savidge (1974) working with P. maniculatus bairdi, found that a female's aggression towards her young was manifest only if the female was pregnant with a subsequent litter. If these results apply to field populations, then reproductive females may have influenced the observed changes in the recruitment of young mice between the two trapping periods in August 1975. On grid 1, four females were lactating and two of these plus two other females were pregnant in the August 6 - 8th period, but in the following period no females appeared to be pregnant although five were lactating. On grid 5 no females in either period were pregnant, but five were lactating in August 6 - 8th compared with only two on August 20 - 22nd.

An index of reproductive output is the number of juveniles (all mice weighing 13 g or less) recruited to each grid. In 1974 61 juveniles were captured on grid 2 with supplemental food compared with only 17 on the control (Table IV). Food was removed from grid 3 in August 1974, yet this grid produced 43 juvenile recruits. Reproductive output on the control in the first half of 1975 was double that of 1974. But grid 5, which was receiving food for the first two months of 1975, had 4 times the number of juveniles it had in the previous control year.

Table IV. Juveniles recruited into each population in each six-month period.

| | 1974 | | 1975 |
	Jan-Jun	Jul-Dec	Jan-Jun
Grid 1	8	9	18
Grid 2	36**	25**	27**
Grid 3	22*	21*	--
Grid 4	--	20*	16*
Grid 5	7	19*	29*

** = grid receiving food throughout period

* = grid receiving food for part of period

The overall breeding success was higher on grids with supplemental food, but a larger number of adults were breeding on these grids (Appendix 5). Was juvenile survival increased? I estimated early juvenile survival by counting the number of juveniles recruited at time t, then dividing this by the number of females lactating at time t-4 weeks (Krebs,1966). This index assumes that all young from a litter are recruited at a juvenile weight, so it ignores those that may be recruited later as subadults or adults. In the first half of 1974 early juvenile survival was highest on grid 2, which was receiving supplemental food over the whole period (Table V). The early survival of juveniles in the fall - winter 1974 was higher on grids 2, 3, 4, and 5 than on the control. All these grids were receiving some level of supplemental food over this period.

Summary

The overall breeding success, in terms of the number of juveniles recruited, was increased by the addition of food. During the breeding season, this was chiefly a result of the much higher reproductive activity on the supplemental food grids. Early juvenile survival in the fall and winter was higher in populations that received some level of supplemental food. But early juvenile survival during the summer was low in the high density populations of breeding adults.

Table V. Index of early juvenile survival. The number of lactating females is given in paretheses.

| | 1974 | | 1975 |
	Jan-Jun	Jul-Dec	Jan-Jun
Grid 1	0.00(1)	0.22(27)	0.38(34)
Grid 2	0.26(87)**	0.40(43)**	0.20(86)*
Grid 3	0.01(41)*	0.54(13)*	--
Grid 4	--	0.38(21)*	0.35(26)*
Grid 5	0.00(4)	0.45(20)*	0.36(53)*

** = grid receiving food throughout period

* = grid receiving food for part of period

Section E: Immigration And Survival

The first juveniles were recruited to the supplemental food grid 2 at the end of March 1974. The population of males on this grid had already increased from 19 to 31, and females from 23 to 37 in response to the addition of food. Therefore, the rapid increase in numbers must have resulted from the immigration of mice onto grid 2.

Immigration

I measured immigration as the total number of new mice captured during each two-week trapping period. In the first half of 1974 number of immigrants onto grid 2 was much higher than onto the control (Figure 8). Females in particular showed a high level of immigration: by the end of June 1974, a total of 68 had entered the grid 2 population compared with 15 on the control. Immigration to the control increased during July - September 1974 and was only slightly below that to grid 2. But through the winter immigration to grid 2 rose to 54 mice compared with only 20 on the control. Total immigration to grid 5 was only 22 in the winter of 1974/5. But when food was present overwinter in 1975/6, immigration rose to 69 mice.

The pattern of immigration of the two sexes was different (Table VI). On both grids 1 and 2 the sex ratio of immigrants was practically even in the spring and late summer. But female immigrants predominated in early summer and males during the winter. This resulted in an even immigrant sex ratio (grid 1 65:59, grid 2 154:162). The age distribution of immigrants of

Figure 8. Immigration of mice to grid 1 and grid 2. The data are
    summed for each three-month period of the study.

            dotted line = grid 1 (control)

            solid line = grid 2 (long-term food)
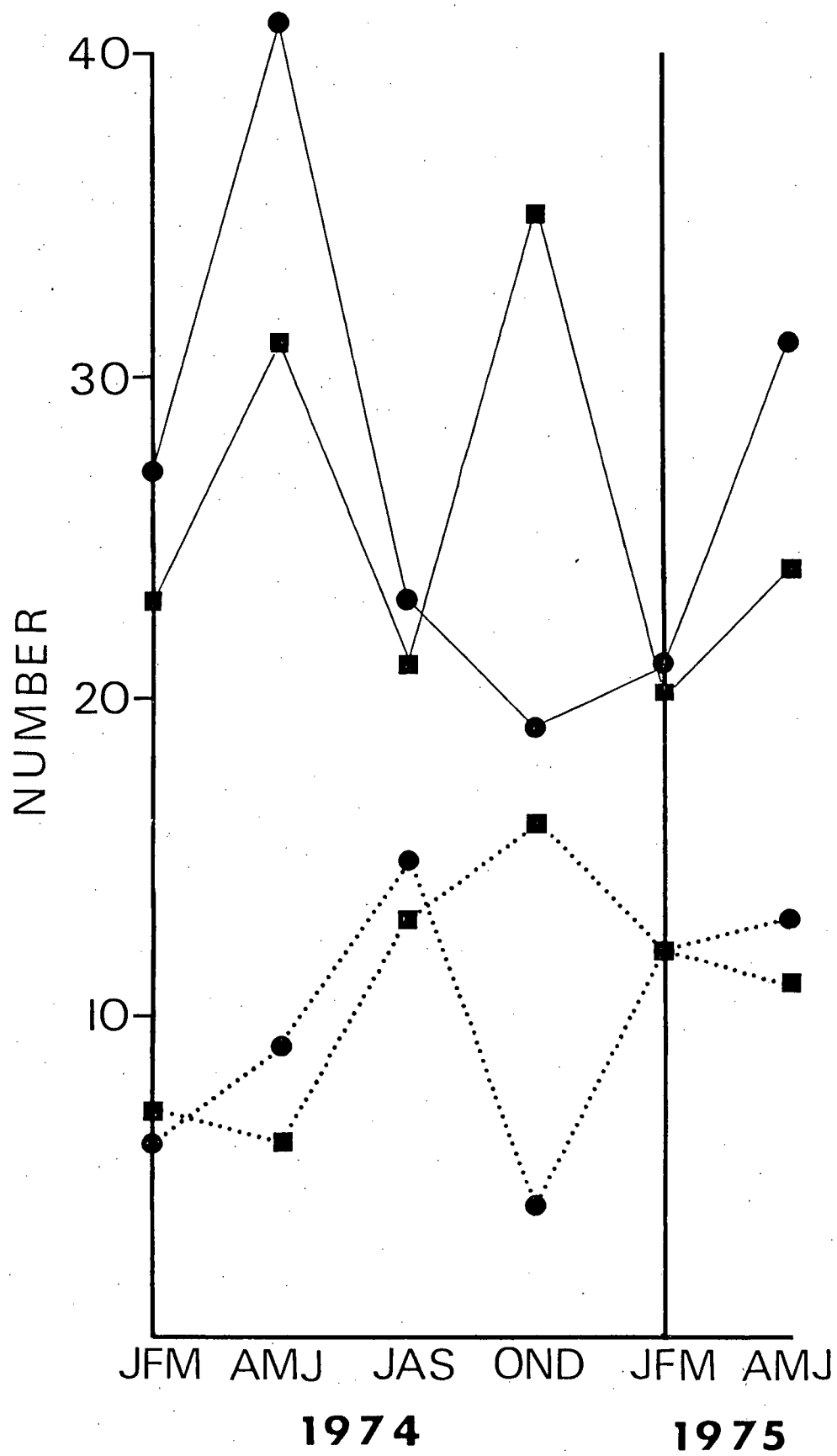
                    ● = females

                    ▉ = males

Table VI. The sex and age of immigrants to grids 1 and 2 in each three-month period. The ratios are the number of males:females.

	Grid 1			Grid 2		
	Ad.	Sub-ad.	Juv.	Ad.	Sub-ad.	Juv.
Jan-Mar 1974	1:1	4:2	2:3	16:8	4:9	3:10
Apr-Jun "	3:1	2:6	1:2	10:18	10:11	11:12
Jul-Sep "	7:6	3:5	3:4	9:5	5:9	7:9
Oct-Dec "	6:0	10:2	0:2	17:3	14:11	4:5
Jan-Mar 1975	5:3	3:3	4:6	3:6	11:6	6:9
Apr-Jun "	5:4	3:4	3:5	12:14	6:11	6:6
Total	27:15	25:22	13:22	67:54	50:57	37:51

each sex is also given in Table VI. There are significantly more females among juvenile recruits (chi square, 4.30, p<0.05). The sex ratio is even in mice immigrating to the sub-adult age class. But males tend to predominate in the adult class (chi square, 3.83, 0.05<p<0.1). Therefore, females tend to immigrate as younger mice and males to immigrate later as adults. In the winter period, when the immigrant sex ratio is skewed towards males, we see that the age structure also reflects this trend. All male immigrants on the control and 31 out of 35 on grid 2 are in the adult or sub-adult age class in October-December.

Survival

Immigration to the long-term food grid was higher than that to the control, but the density of mice on this grid declined. If mortality or emigration was higher on the food grids, the changes in density might be explained. At present, we cannot separate emigration from death in mice that cease being trapped. All we can calculate is the return of marked mice each trapping period. The value of this survival estimate is closely dependent on the trappability of mice, since only mice caught in consecutive trapping periods can be used in the calculation. I calculated the mean minimum survival per 14 days for each three-month period of the study, and plotted the results for adult males and females in Figure 9. In the juvenile and sub-adult age categories, the survival of males and females was very similar, so I have combined the sexes for these two age groups (Table VII).

The survival of adult males and females on both the control

Figure 9. Minimum 14 day-survival of adults on grid 1 and grid
     2. The horizontal line is drawn at survival=0.75.

          dotted line = grid 1 (control)

          solid line = grid 2 (long-term food)
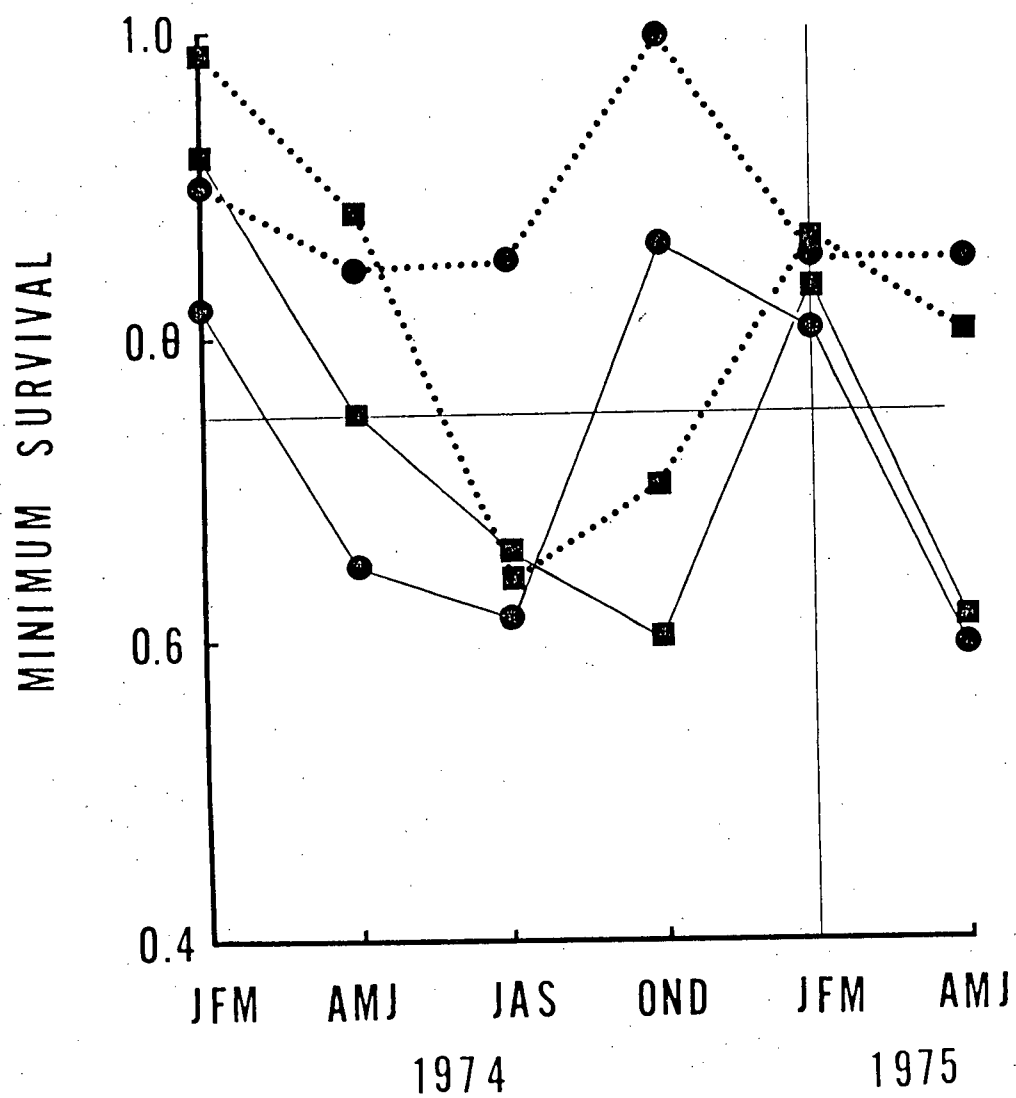
               ● = females

               ■ = males

and the long-term food grid is high in January-March in both years. Adult female survival declined in summer then rose to 100% in October to November on the control. Adult female survival on the food grid was much lower than that on the control in summer, but trappability was lower and more females were breeding on grid 2. The high winter survival of females on both grids coincides with the lowest rate of female immigration (see Figure 8). The lower survival of the grid 2 females may be associated with their greater reproductive effort; they may be dying, or emigrating, or both. Myers and Krebs (1971) found that a high proportion of adult female *Microtus pennsylvanicus* that moved into a removal area in summer was in breeding condition.

Adult male survival also declined in summer, but, in contrast to females, it remained low on both grids through October to November. This low male survival in early winter coincides with the period of maximum immigration of males onto the grids.

Excluding the winter months, the survival of juvenile and sub-adult mice is low in summer when most adults are in reproductive condition (see Table VII). If the October-December samples are not included, there is a weak negative correlation ($r=-0.76$) between the combined survival of juveniles and sub-adults and the number of lactating females on grid 1. A stronger relationship ($r=-0.93$) exists on the supplemental food grid, if the October-December period is excluded. In contrast, there is no relationship ($r=0.18$) between the survival of young and the number of males with scrotal testes on the control but a weak one ($r=-0.71$) on grid 2. In spite of the negative effect of

Table VII. Mean minimum 14-day survival of sub-adult and juvenile mice on grids 1 and 2. Sample size is in parenthses. Lfm is the mean number of lactating females, Sm is the number of scrotal males.

	Grid 1(control)			Grid 2(food)		
	Sub-ad.	Juv.	Lfm/Sm	Sub-ad.	Juv.	Lfm/Sm
Jan-Mar 1974	0.87 (63)	0.92 (12)	0.0/0.5	0.88 (56)	0.74 (19)	4.0/10.7
Apr-Jun "	0.93 (69)	0.50 (6)	0.0/3.9	0.65 (34)	0.48 (25)	10.9/15.9
Jul-Sep "	0.62 (21)	0.50 (8)	5.2/2.5	0.80 (45)	0.90 (20)	4.6/4.6
Oct-Dec "	0.74 (42)	0.75 (4)	0.0/0.1	0.58 (74)	0.70 (10)	1.6/4.3
Jan-Mar 1975	0.92 (13)	0.73 (11)	3.4/4.2	0.82 (33)	0.88 (16)	6.0/4.7
Apr-Jun "	0.92 (37)	0.67 (15)	3.0/9.3	0.73 (30)	0.42 (12)	7.7/8.3

reproductive adults, for a given number of lactating females, the survival of young deermice is higher in the presence of extra food.

Summary

The provision of food increased the number of immigrants to a population at all times of the year. Total immigration to a population which was fed for one-and-a-half years was 2.5 times greater than that to a control population. But survival of adult mice in this long-term food population was lower than on the control. The lower survival of adults with food may be associated with the increased reproductive activity of mice in the presence of supplemental food. This may have resulted from these reproductively active mice emigrating or dying. The results of these experiments indicate that breeding females have more influence on the survival of young than males.

Section F: Weights, Sexual Maturity And Growth

A number of studies have shown that the mean weight of individuals in populations of north temperate small mammals decreases in the fall and winter (see Iverson and Turner, 1974 for a review). These authors analyse in detail the winter weight dynamics of Microtus pennsylvanicus in Manitoba over two years. They conclude that the fall and winter decrease in mean weight is due partly to the recruitment of small mice that fail to gain weight, and weight loss by larger individuals. They suggest that the lower winter weights are adaptive because by decreasing its energy requirements an individual minimizes the amount of time it spends foraging and hence reduces its exposure to predators and bad weather. However, they feel that the lack of food is not the proximate cause of this reduction in weight.

P. maniculatus populations show this decrease in mean weight during the winter (Sadleir, 1965 and Stebbins, 1978). I was interested to test the hypothesis that food was not a proximate factor in determining the failure of small newly-recruited P. maniculatus to gain weight and larger individuals to maintain weight during the winter.

A second interesting feature of winter weights in mice is discussed by Flowerdew (1973). He shows that there is a trend in Apodemus sylvaticus towards an earlier start to the breeding season for a given increase in weight late in the winter. If this applies to P. maniculatus, the addition of supplemental food should cause the mice to breed earlier because they can increase their overwintering weight.

Winter Weights Of Larger Mice

In Figure 10 I have plotted the weight records for three long-lived mice from the controls and three from food grid 2. All three adult mice on the controls show the characteristic decline in weight in winter 1973. The two long-lived females, 1040 and 594, also declined in weight in the following winter. The two males on grid 2 responded immediately to the addition of food at the end of December 1973. Both increased in weight and became scrotal by the end of January and the beginning of February, while male 1005 on the control never became scrotal. Female 2759 was pregnant in April, while the two control females were not pregnant until June and July 1974. Control females 594 (grid 5) and 1040 (grid 1) showed an almost identical decline in weight into the fall 1974. But as soon as the food was added to grid 5 the weight of female 594 increased and she became pregnant in December. These immediate responses to the addition of food suggest that indeed the winter decline in weight of larger mice can be reversed in what appears to be a proximate response to food.

Winter Weights Of Smaller Mice

The maintenance of a low winter weight in young recruits is clearly shown in all four mice in Figure 11. The two mice on grid 1, male 891 and female 888, continued at low sub-adult weights into the spring of 1974. But male 2796 and female 2788, which showed the same pattern initially as the control mice, increased in weight rapidly after the addition of food. In fact,

Figure   10.   Winter   weights of   individual   large   mice on   the
     controls and food grids.

              dotted line = control grids

              solid line = food grids

                   ▲ 1 = food added to grid 2

                   ▲ 2 = food added to grid 5
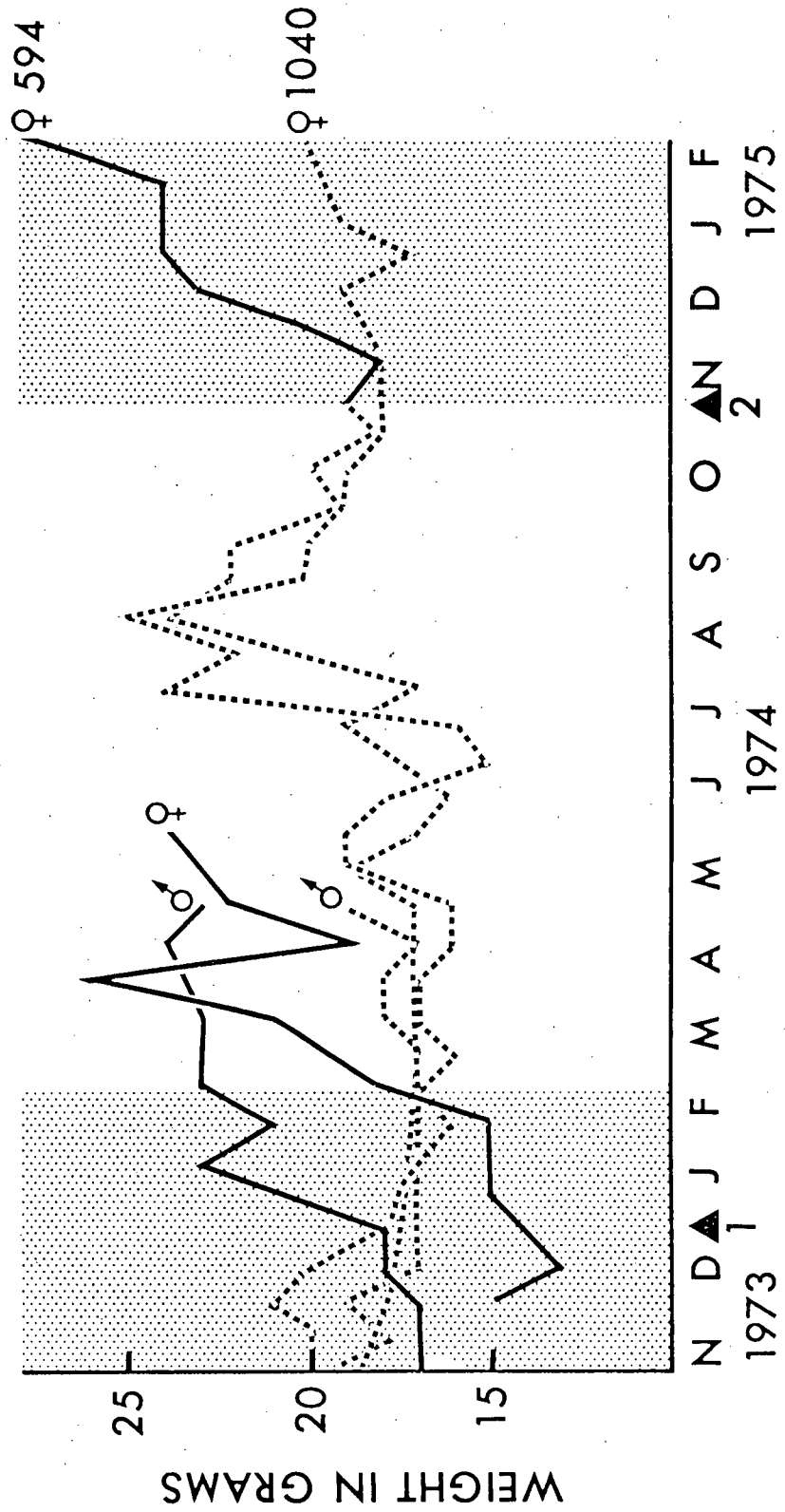
Figure 11. Winter weights of individual small mice on the controls and food grids.

dotted line = control grids

solid line = food grids

▲ = food added to grid 2

WEIGHT IN GRAMS
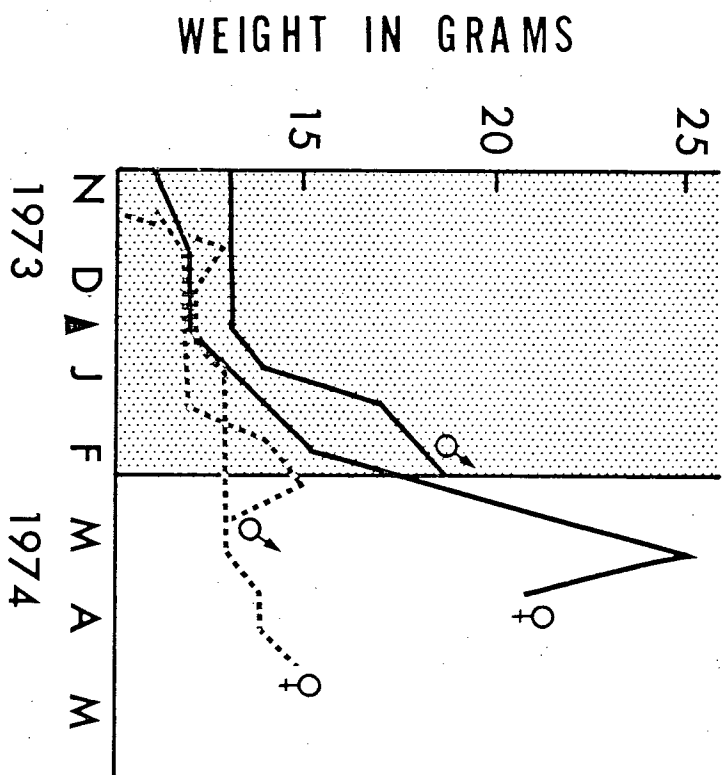
both mice reached adult weights and were breeding by the end of
February. These weight responses of small mice again seem to
have resulted from a proximate response to the increased
availability of food.

Overwintering Weight And Breeding Condition

To avoid the problem of the increase in weight of females
associated with pregnancy and lactation, I have considered the
weight distribution of males only in this sub-section. The mean
weights of males on the control grid 1 and food grid 2 were
similar in November-December 1973 before food was added
(Appendix 7). Following the addition of food to grid 2 at the
end of December, the weights of all age classes of males started
to increase (see Figure 12). A month later the mean weights of
males on the food grid were significantly higher than those on
the control. The mean weight remained significantly higher for
the next six weeks. All males were in the adult weight class,
that is over 17 g, by the end of February. In the following
trapping period the mean reached 21.2 g on grid 2, which was the
highest recorded during the study. The mean weight was not
significantly higher at the end of March when the first
juveniles were recruited, but rose again and was significantly
higher for the whole of April. A similar pattern of weight
increase occurred on grid 3. One month after food was added at
the end of January 1974, the mean weight of males was
significantly higher than that on the control ($p < 0.05$). The
mid-winter addition of food to grid 5 also gave the same result
as these early spring additions. Food was added to grid 5 at the

Figure 12. Weight distribution of males on grid 1 and grid 2.

open rectangles = grid 1 (control)

closed rectangles = grid 2 (long-term food)

▲ = food added to grid 2

x = mean weights significantly different (p=0.05)

WEIGHT IN GRAMS
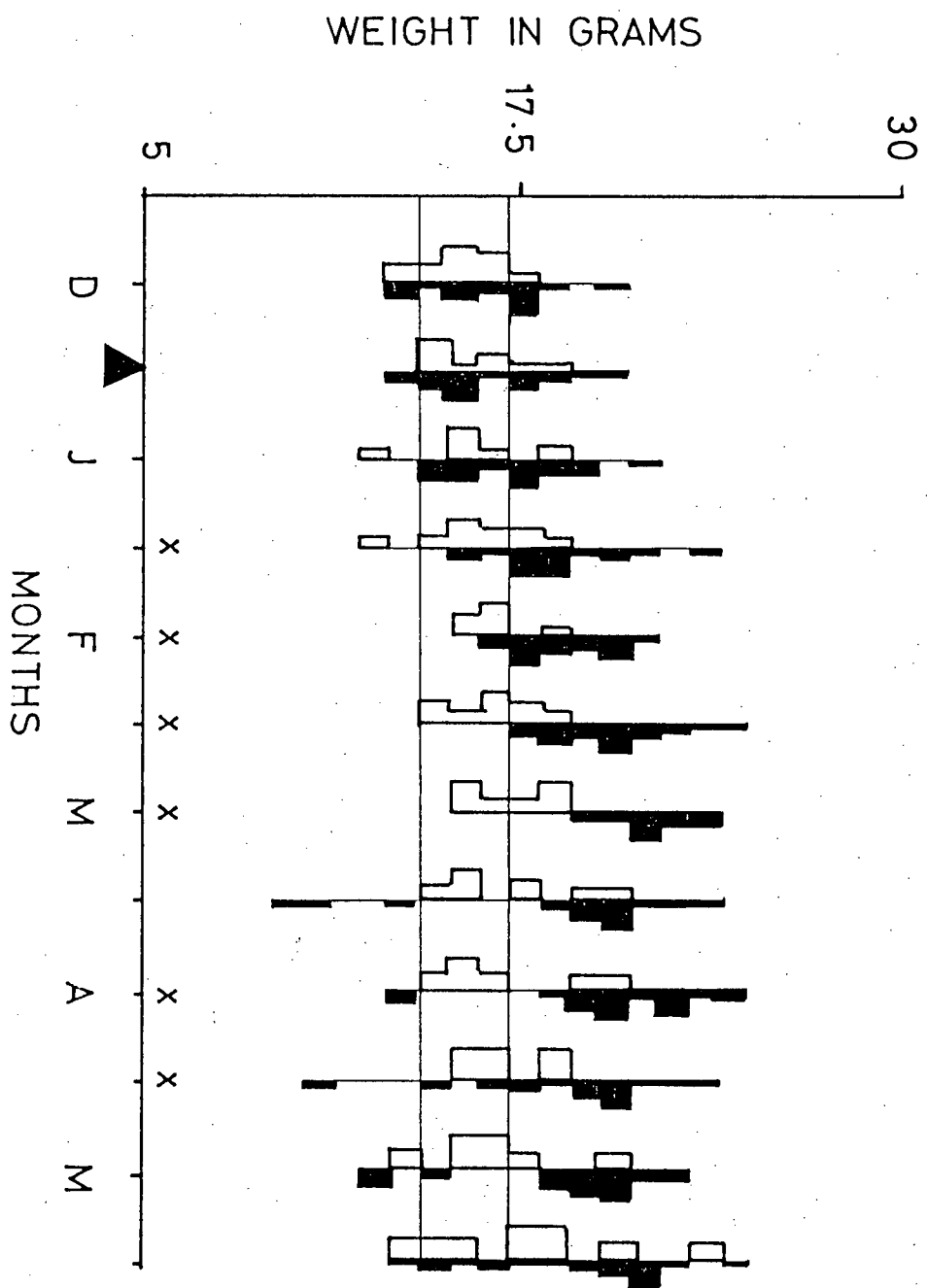
beginning of November 1974. The mean weight of males was significantly higher one month after food addition compared with that in the same period the previous control year. The mean was significantly higher than that on the control at the beginning of December 1974, six weeks after food addition.

The increase in weight in response to the addition of food had a direct influence on the breeding condition of males. The breeding season was underway on grid 2 by the first period in February 1974, which was two weeks after the mean weight of males reached over 18 g. On grid 1, 50% of the males were breeding by the first week of June, which is one month after the mean weight reached and remained at or above 18 g. On the lower-density food grids 3 and 5, 50% of the males were scrotal one month after the mean weights had reached 17 g in spring 1974 and winter 1975 respectively. The patterns for the remaining onsets and cessations of breeding are not so clear. One problem is that the mean weight is dependent on the age distribution of mice in the sample. Secondly, the age at which individuals reach sexual maturity in a population may change throughout the breeding season.

Sexual Maturity

I was interested to see if there was a change in the age of sexual maturity through the breeding season and in response to food. Unfortunately there is no convenient method of aging mice in the field apart from weight. Leslie et al. (1945) used a quantitative technique to estimate median body weight at sexual

maturity. In Figure 13 I have plotted this median body weight of males at sexual maturity for both years combined on the food and control grids. Since 50% or more males on grid 1 in 1974 bred only from June to August, I have grouped the data so that these three months form a period.

There is a trend on the control for a decrease in the median body weight at sexual maturity with the progress of the breeding season. Only the heaviest males were sexually mature during the early breeding season. The addition of supplemental food significantly reduced the weight at maturity of these early breeding males (p<0.05). Over the whole period of food addition, sexually mature males were significantly lighter on both grids 2 and 3 compared with those on the control. The late summer median was lower on grid 2 compared with that on the control, but on the lowest density food grid 3 (av. den. 8 males) it was still lower than that on either grid 1 (av. den. 11) or 2 (av. den. 17). This suggests that density as well as food may have been important in determining the age of sexual maturity.

Growth

Supplemental food increased the reproductive potential of mice because individuals were able to gain weight and become reproductively active earlier. Second, the age of sexual maturity was lowered in males. A third possibility is that surplus food may also have increased the growth rate of mice.

Growth rates of mice in these populations can be calculated from weight changes of individuals between trapping periods. Pregnant females are excluded from this analysis. Within each

Figure 13. Median body weight at sexual maturity on grids 1, 2,
    and 3. The 95% confidence limits are given.

◇ = grid 1 (control)

◆ = grid 2 (long-term food)

■ = grid 3 (short-term food)
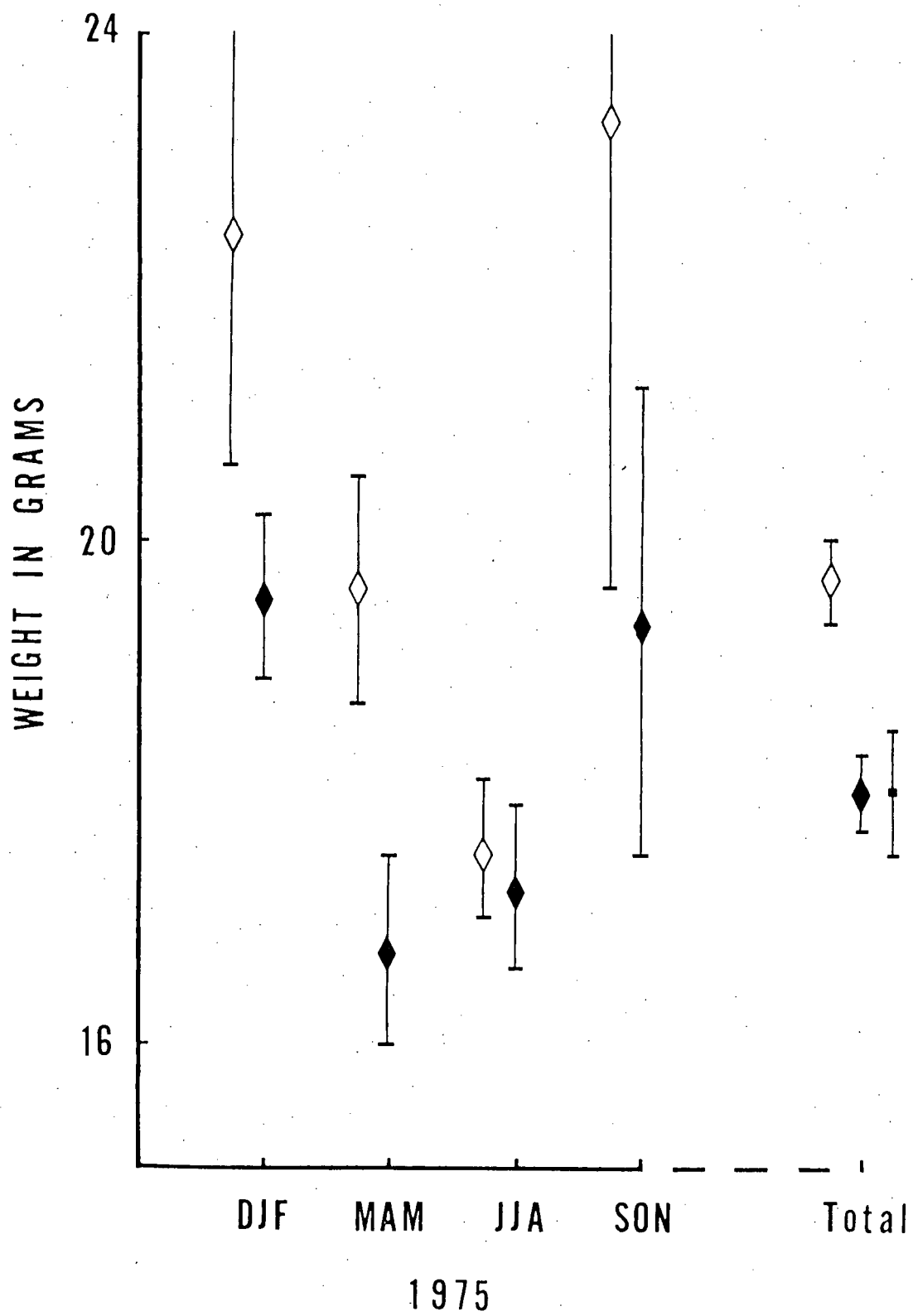
four-week period, a linear regression was calculated for each sex on the change in weight against the mean weight. This was then adjusted for an average juvenile (12 g), an average sub-adult (15 g), and an average adult (18 g) mouse to give an instantaneous relative growth rate. The growth rate data for each sex-age group are given in Appendix 8.

After food was added to grid 2 at the end of December 1973, the growth rate of all sex-age groups of mice increased. First, both sexes in all age classes had growth rates less than zero on only seven occasions after food was added to grid 2 compared with forty occasions for all sex-age groups on the control. Second, adult males and females on the food grid had higher growth rates (sign test, males p=0.01, females p=0.02) than voles on the control. This was also the case for each sex in the sub-adult (sign test, males and females p=0.02), and juvenile (sign test, males p=0.06, females p=.02) age classes. Third, adult males and females, and sub-adult females on grid 2, all had lower growth rates than mice on the control in September 1974; this is the period when the food stations were emptied. Fourth, mice on the control had fewer growth rates below zero in the spring of 1975 compared with the previous year, when the onset of breeding was so late. Finally, the highest growth rates in adult males on the control were recorded six weeks before the 50% breeding level was reached. Adult females had high growth rates a month later. But on the food grid both sexes and all age groups had high growth rates at the same time.

Food Consumed

It is difficult to obtain a meaningful measure of food consumption. The weight of food removed from feeding stations was recorded every two weeks. But mice may store the oats, so that the total measured need not represent the consumption of food over the two-week period. Consumption per individual may be an even less satisfactory measure. First, because MNA was not always a good measure of population size. Secondly, because it is not known whether all mice in the population had access to the food stations. For example, Dunford (1970) found that several chipmunks initially fed from seed piles that he provided. But after a short time one or two animals would become dominant and chase away subordinates so that the latter ceased to use the seed piles. Finally, not all mice require the same amount of food, so individuals probably took different quantities of oats.

The mean weight of oats removed every two weeks from the grid 2 food stations, and the mean consumption per individual in the three-month periods of the study are given in Table VIII. Least oat food was removed from stations in late summer. This may reflect the use of alternative food items which become avalable in the forest at this time of year. Dietary analyses indicate that P. maniculatus switches from seeds to other food items, particulary arthropods, in the summer (Jameson 1952 and Batzli 1977). In both years the largest quantity of oats was removed from the feeding stations in the first half of the year. This is the period of maximum weight gain. January to March is the period when males gain weight before becoming reproductive,

Table VIII. The mean weight of oats removed from feeding stations and mean consumption per mouse on grid 2.

Three-month Period		Kg of Oats Removed per two-weeks	G per mouse per two-weeks
Jan-Mar	1974	1.8	31
Apr-Jun	''	1.8	35
Jul-Sep	''	1.3	35
Oct-Dec	''	1.2	37
Jan-Mar	1975	1.8	52
Apr-Jun	''	2.1	60

and April to June coincides with the maximum number of lactating females. Millar (1975) demonstrated that lactating female P. leucopus required 2.6 times the amount of food taken by non-breeding females. The mean consumption per individual indicates that mice ate the same quantity of oats throughout 1974. However, it is not possible to say whether this is a true measure of consumption. The higher consumption in 1975 may indicate that the emigrating M. oregoni were removing some of the oats this year.

Summary

The winter decline in weight of larger mice and the maintenance of a low winter weight by smaller mice can be reversed by providing supplemental food. The response is immediate, which suggests that these winter weight changes in P. maniculatus may be proximate responses to the availability of food. The resulting increase in overwintering weight enabled mice to come into breeding condition much earlier than on the control. The consumption of supplemental food also lowered the age of male sexual maturity so that smaller males came into breeding condition earlier than on the control. Finally, mice of all age-sex classes had higher growth rates in the presence of extra food.

Section G: Home Ranges

Stickel (1968) indicated that the home ranges of P. leucopus vary in size between habitats. She suggested that home range size may be larger in areas with lower food supplies. A recent short-term study by Metzgar (1973) suggests that feeding and exploratory home ranges of P. maniculatus are not spatially distinct activities. If food-gathering is an important component of P. maniculatus movement, the addition of food should reduce home range size. If individuals in the present study concentrated their movements around feeding stations, this might leave room for immigrants to the food grids.

I estimated home range size by Koeppl et al.'s technique (1975). This model calculates an elliptical home range from the distribution of grid capture points of an individual animal. The model does not calculate ranges for individuals that are captured at only one location, or at two or more locations in a straight line. I calculated a home range estimate for such individuals (Appendix 9). Unfortunately, the 0.8-hectare grids used in this study are too small to give good home range data. Over half the mice in all populations had 50% or more of their capture points in the outer lines of traps on these grids. Since the percentage with such captures was almost equal for all populations I have included these mice in the data analysis. But mice with 100% of their captures in the outer line of traps were excluded.

Home range size is highly variable within each population (see Table IX). Males have larger home ranges than females. For example, during the one-and-a-half years of food addition to

Table IX. The mean home range size (sq m) of male and female mice on control and food grids.

| | Grid 1(control) | | Grid 2(food) | |
	Males	Females	Males	Females
Nov-Dec 1973	1442(10)	1073(10)	1035(13)	903(11)
Jan-Mar 1974	2273(14)	1352(10)	1489(18)	796(15)
Apr-Jun "	1511(13)	1548(10)	1203(14)	639(14)
Jul-Sep "	2784(9)	2881(10)	1338(9)	815(8)
Oct-Dec "	1516(6)	1571(10)	1513(7)	867(8)
Jan-Mar 1975	2241(6)	2008(8)	2089(11)	919(11)
Apr-Jun "	2105(15)	1795(14)	3365(7)	868(11)
Means(1974-75)	2009(45)	1615(37)	1473(45)	974(66)

	Grid 5 (without food)		Grid 5 (with food)	
	1757(17)	1753(14)	1584(13)	1151(18)

The means are for home ranges calculated for the whole data set from January 1974 to June 1975.

grid 2, males on the control had home ranges 1.24 times larger than those of the females, and on grid 2 they were 1.51 times larger. On a seasonal basis, home ranges of males on the control are large in late winter and spring (Jan.-Mar.). They decrease in early summer, peak in late summer (Jul.-Sep.), and finally decrease again in the fall and early winter. Females on the control had a seasonal pattern in home range size similar to that of the males, except in the spring of 1974, when they showed little home range expansion. But in 1975, when breeding was underway much earlier, female home ranges were also high in the late winter-spring period. Stickel (1968) also reported that home ranges were large at the onset of breeding.

The distribution of home range sizes calculated for males and females during the whole period of food addition are given in Figures 14 and 15. The mean home ranges over the whole period are significantly smaller on grid 2 (males: t=2.41, p<0.02, and females: t=4.52, p<0.001). In each three-month period (see Table IX), except for males in Apr.-Jun. 1975, home ranges of both sexes are smaller in the long-term food population (grid 2). But on the low density grid 3 population which received food one month after grid 2, males had larger home ranges (3027sq m) even than those on the low density control grid 5 over this period (2638sq m). Females in this population had smaller home ranges (1488sq m) but not significantly smaller than those on grid 5 (2076sq m). Certain topographic features of this grid may have had some influence (see Appendix 1). Over the whole period that grid 5 received food (Nov.-Feb. + Jul.-Aug.), compared with the same period the previous control year, the mean home ranges of

Figure 14. Frequency distribution   of   male   home   range
    sizes on the control(grid 1) and food grid(2).
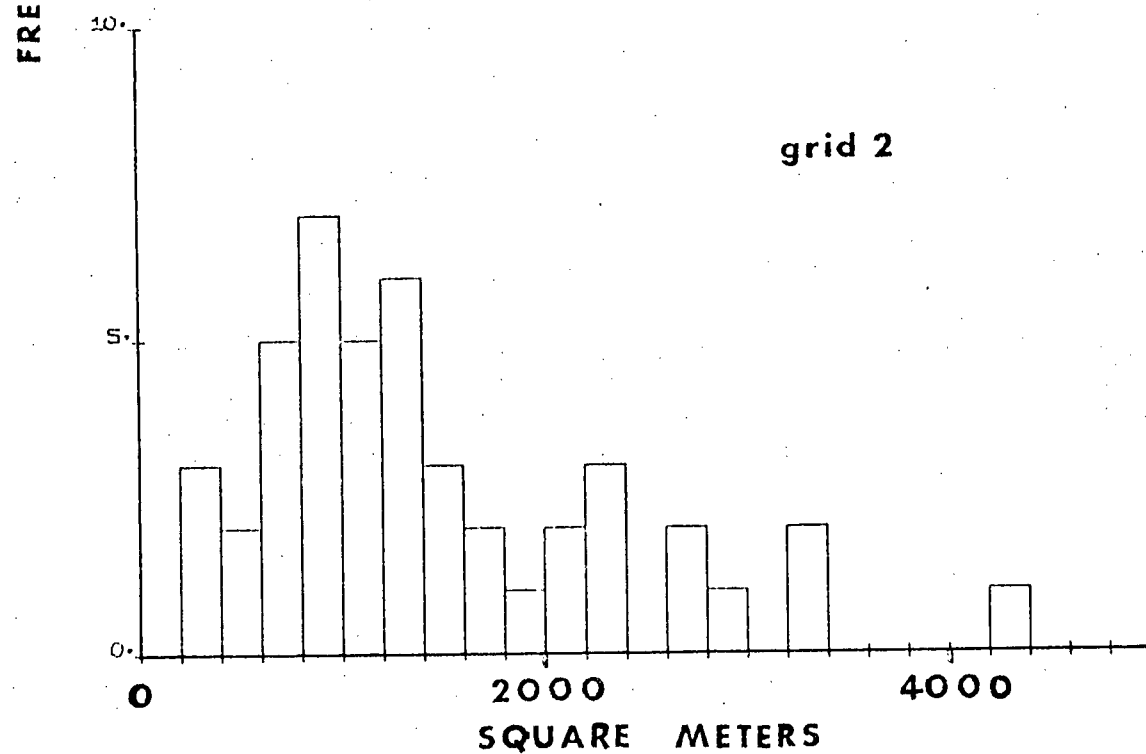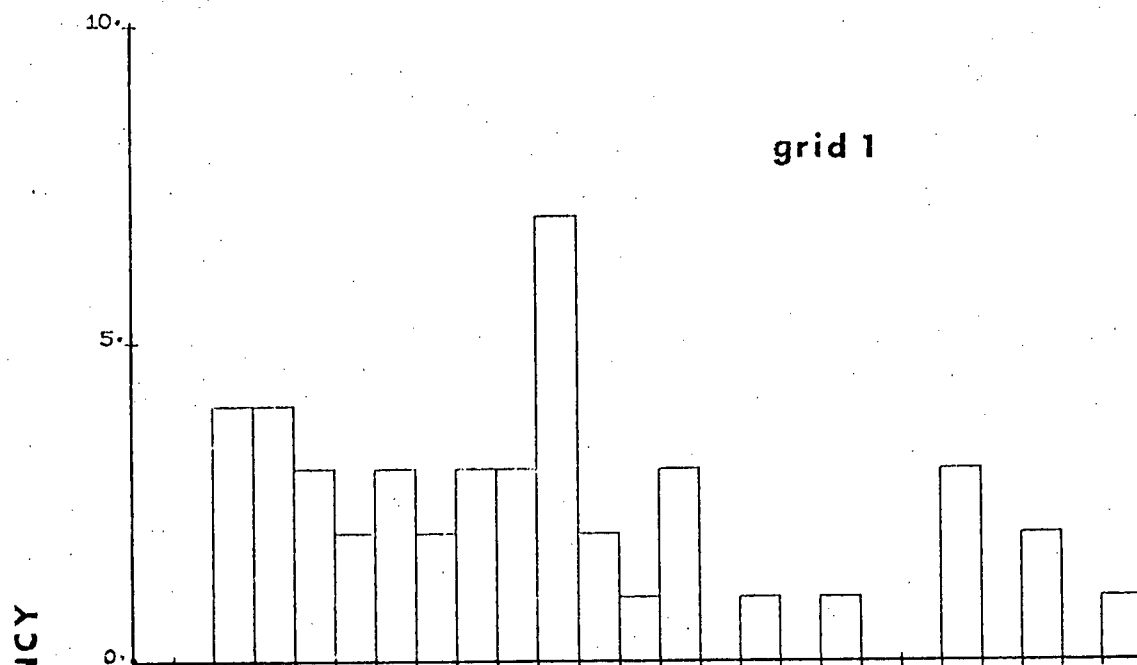
Figure 15. Frequency distribution of female home range sizes on the control(grid 1) and food grid(2).
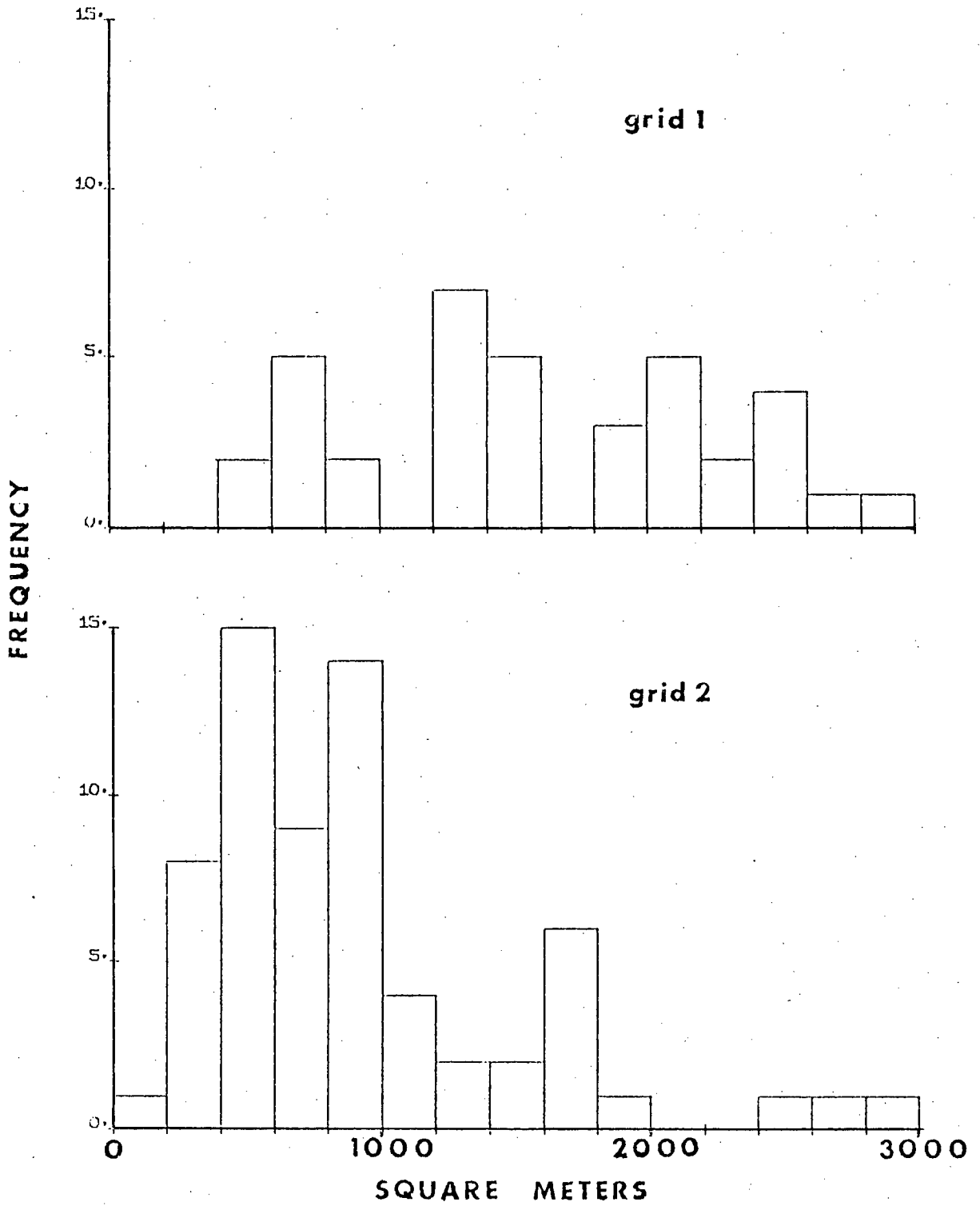
males and females were smaller. Females again had statistically smaller home ranges when the population was supplied with excess food (t=2.13, p<0.05).

Summary

Home ranges of P. maniculatus are flexible. Home ranges on the control changed seasonally, with a tendency for there to be larger home ranges in both sexes during the breeding season. Mice reduced the size of their home ranges in response to the addition of food. This response to food indicates that food-gathering is an important determinant of the movement pattern exhibited by P. maniculatus. The reduced movement of males and females in response to supplementary food could have made 'space' available for immigrants. In fact, the period with the highest rate of female immigration coincides with the smallest home range size recorded in the study. Also, home ranges of females in particular tended to be smaller during periods of highest food consumption (Table VIII). This suggests a cause-effect relationship between food availability and movement patterns. Males also reduced the size of their home ranges, yet in spite of being lighter than lactating females and having lower energy requirements, they maintained larger home ranges than did such females. This suggests that males maintain larger home ranges than are energetically neccessary. But, since the overall sex ratio for the fed population remained at 1:1, males with extra food may tolerate more range overlap than females.

Section H: Microtus oregoni: A Possible Competitor?

In previous sections I have alluded to possibile competition from M. oregoni that immigrated into all P. maniculatus populations in 1975. When I started trapping the P. maniculatus populations on grids 2 and 3, I tagged any M. oregoni that entered the traps. Over the first summer on these grids, M. oregoni made only sporadic appearances or disappeared, so I ceased tagging them. Unfortunately, when they reappeared I did not have the time to tag them individually. The number of M. oregoni given in Table X is therefore a minimum population count. It represents the largest number I recorded in either check each trapping period. However, in the penultimate trapping period on grid 2, I caught 23 M. oregoni in one check. Then, in the last trapping period I removed all individuals of both species that were caught in the first check, so all 49 traps were available to any remaining mice of either species. The total number of M. oregoni recorded in this trapping period was 25, only 2 more mice than my count for the previous normal trapping period. Therefore, the figures given for the M. oregoni population may not be too unrealistic.

Table X shows the mean number of M. oregoni for each three-month period on each grid. There are unfortunately no data for the two controls in the first half of the study (Appendix 1). There was an increasing immigration of M. oregoni to all grids in 1975. The number of M. oregoni compared with the number of P. maniculatus (Table II) indicates that there is a reciprocal change in numbers of the two species. Petticrew and Sadleir (1974) found a similar reciprocal change in numbers of

Table X. The mean number of _M. oregoni_ in each _P. maniculatus_ population.

	Grid 1	Grid 2	Grid 3	Grid 4	Grid 5
1973 Nov-Dec	--	1.40	1.60	--	--
1974 Jan-Mar	--	1.00	1.50	--	--
Apr-Jun	--	0.29	0.57	--	--
Jul-Sep	--	2.50	8.40	7.60	--
Oct-Dec	0.57	2.25	10.25	2.86	0.0
1975 Jan-Mar	8.0	5.17	--	7.8	3.8
Apr-Jun	9.86	6.4	--	4.8	8.71

these two species in one of their populations in the UBC
Research Forest at Haney. They concluded that some type of
competitive interaction may have occurred. Redfield et al.
(1977) showed that M. townsendii actively excluded
P. maniculatus from grassland areas in the Fraser River Delta.
In the present study I was interested to see whether food
manipulations had any affect on the proportions of the two
species occurring in the forest. Also, I wanted to see if the
M. oregoni immigration was having any effect on the
P. maniculatus populations.

Food Manipulation And Species Numbers

In the last half of 1974 there were few if any M. oregoni
on grids 1, 2 and 5. But on grids 3 and 4 numbers were higher.
An interesting change in numbers of both species occurred in
August 1974, when food was removed from grid 3 and added to grid
4. On grid 3, in the first trapping period in August 1974, there
were 9 M. oregoni and 16 P. maniculatus. The food stations were
removed during this trapping period. Two weeks later there were
16 M. oregoni and 15 P. maniculatus. The numbers of
P. maniculatus and M. oregoni on grid 4 at the beginning of
August were 27 and 13 respectively. After two weeks of food the
number of P. maniculatus rose to 36 and the number of M. oregoni
declined to 4. Similar changes in numbers of the two species
occurred with the removal of food stations from grid 2 in June
1975. M. oregoni increased from 13 to 23, and P. maniculatus
declined from 35 to 19. Finally, on grid 5, when food was
removed in March 1975, M. oregoni increased from 3 to 13 in two

weeks, but P. maniculatus in this case increased initially, then declined. There is some indication of a decrease in P. maniculatus and an increase in M. oregoni when food stations are removed from a population. There is also an indication of a reverse pattern of change of numbers when food is added to a population.

Removal Of M. oregoni

In the last trapping period of the study, I removed some of the M. oregoni from control grid 1 and food grid 5. In both populations I removed all M. oregoni that were caught in traps on the first four rows of each grid (rows D to G, see Figure 3). I did this partial removal of M. oregoni for two trapping periods (at the end of July and the beginning of August). Table XI presents the total number of traps occupied by each species for these last three trapping periods.

M. oregoni on rows A to C almost certainly moved into rows D to G to replace voles removed. For example, on grid 1 there were 10 voles in the A to C rows and 12 in the D to G rows initially. By August 20-22, the number of voles was reduced by half. From the total number of traps occupied by each species, we see that after 2 weeks of M. oregoni removal this species was reduced on grids 1 and 5. P. maniculatus, on the other hand, increased on both grids. The changes in MNA of P. maniculatus also reflect this trend: on grid 1 numbers rose from 20 to 32 and on grid 5 from 25 to 35. The presence of M. oregoni appears to have depressed the numbers of P. maniculatus in both populations in 1975. But the reduction of P. maniculatus in the

Table XI. The number of P. maniculatus and M. oregoni during partial removal of the vole from grids 1 and 5. M.O. = M. oregoni and P.M. = P. maniculatus. The numbers are the number of traps occupied by each species.

| | Grid 1(control) | | | | Grid 5(food) | | | |
| | Rows A-C | | Rows D-G | | Rows A-C | | Rows D-G | |
	M.O.	P.M.	M.O.	P.M.	M.O.	P.M.	M.O.	P.M.
Jul 23-25	10	5	12*	12	17	12	16*	14
Aug 6-8	12	12	14*	10	9	14	5*	13
Aug 20-22	5	13	6	22	6	16	5	21

* = voles removed

presence of extra food on grid 5 was not as great as on the control.

To see which age group was being affected by this interspecific interaction, I have counted the number of recruits in the month before M. oregoni removal and in the month during patial removal. It was not possible to compare recruitment on the two halves of the grids during the removal periods because M. oregoni distributed themselves evenly across the grid in the intervening two weeks. On both grids combined adult recruitment did not change, but sub-adults and juvenile recruitment increased from 5 to 37. This indicates that sub-adults and juveniles were prevented from entering the P. maniculatus populations with large numbers of M. oregoni.

Summary

It is not possible to say what mechanism produced the change in numbers observed in the two species in response to the addition and removal of food. But it is interesting to note that P. maniculatus home ranges on both control and food grids were larger in 1975 in the presence of M. oregoni than in 1974 in their absence. This may indicate that the two species were using some resource in common, even if only 'space'. Individual P. maniculatus may then have been forced to compensate for this by enlarging their home ranges in the presence of the vole. But the responses of both species to the removal of food suggests that P. maniculatus can outcompete M. oregoni if food is provided. Such a response may result if P. maniculatus is more

successful at defending a localized food supply than the vole. The removal experiments suggest that subadult and juvenile *P*. *maniculatus* recruitment was reduced by *M*. *oregoni*.

4. DISCUSSION

The results of increasing the temporal and spatial availabilty of food to P. maniculatus populations are summarized in Figure 16. Supplemental feeding changed the size of the breeding population, the extent and intensity of breeding, and the spatial organisation of individual mice.

Male And Female Numbers

The late winter (December 1973 and January 1974) addition of food resulted in a doubling or near-doubling of the number of both sexes of P. maniculatus, thus confirming the first prediction (see H1. Introduction). Similar, though less dramatic, numerical responses followed the late summer (August 1974) and mid-winter (November 1974) additions of supplemental food. The large late winter increase in both sexes occurred before juveniles were born and resulted from an increase in immigration to the food grids. The results contrast with those of Fordham (1971), who added food to P. maniculatus populations in mid-February and observed an increase in female density, but no change in males. Since in a 'normal' year, males can have scrotal testes by February (present study and Sadleir 1974), it is possible that Fordham added food after the potential breeding males had expanded their home ranges and possibly excluded any surplus males. The early provision of supplemental food in the present study preceeded any weight gain and home range expansion in males.

Figure 16. Summary of the effect of supplemental food on
    P. maniculatus populations.

EXTRINSIC
PERTURBATION

INTRINSIC
RESPONSE

Increase food ⟶ Increased growth

Incr. winter weight ⟶

Decr. age of maturity ⟶

SPATIAL ORGANIZATION

Decr. home range size

DYNAMICS

Incr. immigration

Incr. breeding popn. ♂ & ♀ ⟵

Incr. reproductive output
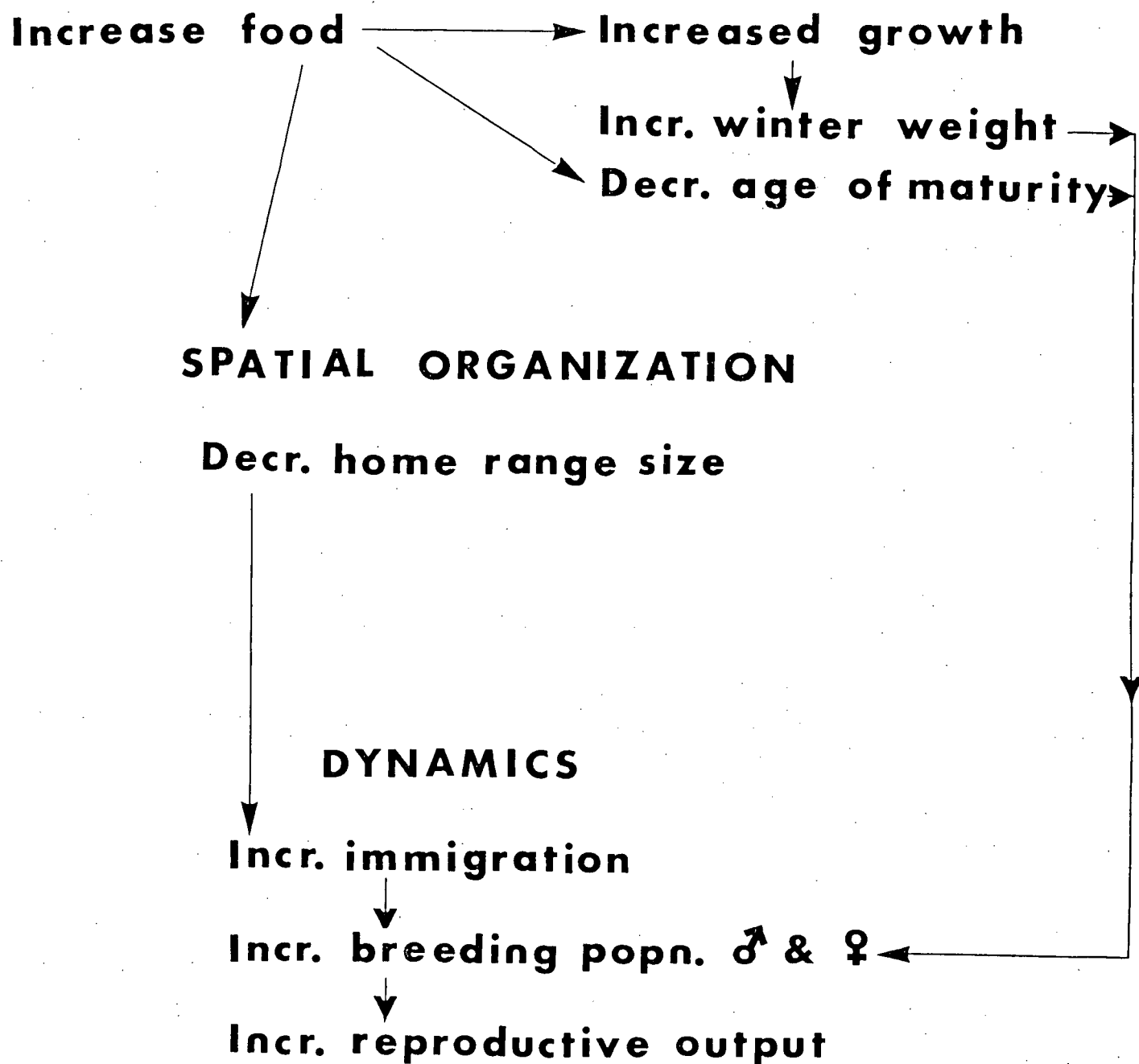
These numerical responses of P. maniculatus to the addition of food in late winter suggest that food availability influences the size of the breeding population. This response may vary with the stage of the breeding cycle, the amount of natural food present, and the number of feeding stations. The importance of the stage in the breeding cycle is indicated in the smaller numerical responses of populations to late summer and mid-winter food addition and removal. The complete and temporary removals of food in late summer and fall caused males first to go out of reproductive condition and then to increase in density. This numerical response is probably a consequence of the decline in male agonistic behaviour associated with the cessation of reproduction (Peromyscus: Sadleir 1965 and Healey 1968, Microtus: Turner and Iversen 1973). Food removal earlier in the breeding season had little effect on males but did affect females. For example, the late summer removal of food was followed by a drastic decline from 20 to 6 females over six weeks, but 70% or more adult females continued to lactate. By contrast, spring food removal produced no change in density but reduced the percent of females lactating from 73% to 20%.

The other two factors that modified the numerical response of P. maniculatus to supplemental food involve the food itself. The consumption of supplemental oats declined during late summer, which coincides with the period when granivorous rodents are known to expand their diet to include arthropods, leaves, fruits and seeds of growing plants (Peromyscus: Jameson 1952 and Batzli 1977: Apodemus: Hansson 1971). If the P. maniculatus populations supplied with oats expanded their diet to include

such natural food items, and re-adjusted their home ranges to include these items, then this could explain the summer decline in density on the food grids. This might also explain why other populations of granivorous mice supplied only with supplemental seed food tend to decline in density over summer in spite of the extra food (Peromyscus: Fordham 1971 and Smith 1971: Apodemus: Watts 1969 and Flowerdew 1972). Finally, the reduction in the number of feeding stations over winter was followed by a steepening of the normally slow overwinter decline in density. Meanwhile, two populations fed at high levels were stable or increased. This suggests that the number of food stations also affected the populations' response to food.

Breeding Season

Peromyscus normally does not breed in winter. But a number of studies have shown that the onset, duration, and cessation of breeding can be highly variable in one location from year to year (see Sadleir 1974 for a review). In the present study P. maniculatus in a control population started to breed three months later in 1974 than 1975. The duration of the breeding season itself (at least 50% of males scrotal or females lactating), was only two and a half months compared with over six months in 1975. The average monthly temperatures were below normal in both years, but May 1974 had the lowest mean temperature on record. Male reproduction halted and females ceased breeding on both controls by the end of May 1974, whereas no breaks in reproduction occurred in either sex in 1975. Total precipitation and hours of sunshine were closer to normal in

1975. In fact, the unusually early onset of breeding this year was probably a direct response to particularly mild weather in December 1974.

In spite of the rather 'wintry' weather in 1974, mice in two populations with supplemental food started to breed. This advanced the onset of breeding in 1974 by four months compared with that on the control. In fact, breeding in the long-term food population continued for seventeen months apart from a two-week cessation in the fall 1974. This cessation was probably in response to a temporary exhaustion of food supplies at this time. The mid-winter addition of food to another population resulted in males becoming scrotal and females perforate after two weeks. These results confirm the predictions of Watts (1970) and Sadleir et al. (1973), that abundant food supplies can override the normal cessation of reproduction exhibited by granivorous small mammals in temperate winter climates.

This relationship between food supply and reproductive condition is also indicated in the winter weight responses of mice to supplemental food. Mice on all grids showed the winter weight decline characteristic of north temperate small mammals (Iverson and Turner, 1973). But in all three populations that received food in winter, mice increased in weight immediately after food was made available. This resulted in some individuals becoming reproductive in two weeks after the early November addition and four weeks after the late December addition. The delay in the latter case is a result of mice in this population having reached the minimum overwintering weight by the time food was added. The presence of extra food reduced the cost of energy

aquisition and enabled deermice to maintain positive growth rates and reproduce in spite of winter weather conditions. Flowerdew (1972) also found that the mean weights of Apodemus sylvaticus supplied with supplemental food were 20% higher than those of controls. These results suggest that weight changes and, in turn, the onset and cessation of breeding are proximate responses to food availability in granivorous rodents.

The consumption of supplementary food also enhanced reproductive output. Larger numbers of male and female mice bred on food grids than on controls. The median body weight (which is equated with age) of sexually mature males was high at the beginning of the breeding season on the control and then declined. But the addition of food reduced the weight at sexual maturity, particularly in the early breeding season. Also mice of both sexes on food grids had higher growth rates than controls at all times of the year. Therefore, younger mice were able not only to breed but also to reach breeding weights earlier. Finally, the highest growth rates coincided with periods when most oats were removed from food stations. These results indicate that the abundance of food, through its influence on the weight of individuals, affects the onset, cessation, and intensity of breeding in P. maniculatus.

Spatial Organisation

In a population supplied with supplemental food for one-and-a-half years, male deermice had average home ranges 0.73 times the size of male home ranges in a control population. Females reduced the size of their home ranges even further to

0.60 times that of controls. If home ranges space individuals in a population (Watson and Moss 1970), then this reduction in response to food represents a reduction in the use of 'space' by the residents. This could explain the high rate of immigration to food populations. In fact, female immigration was highest during the three-month period when the lowest mean home range was recorded. Further, females in particular tended to have smaller home ranges during periods of highest oat removal from feeding stations. These results suggest that food-gathering is an important determinant of home range size in both male and female _P. maniculatus_.

The response of _P. maniculatus_ to the immigration of _M. oregoni_ in the present study could also be interpreted in terms of spatial organisation. Deermice in all populations had larger home ranges in the presence of _M. oregoni_. This interspecific competitor may have decreased the availability to deermice of food or some other extrinsic factor. Individual deermice may have been forced to occupy larger home ranges, and perhaps also exclude subordinate conspecifics. This would explain the decline in deermouse density and the exclusion of juvenile and sub-adult mice in the presence of _M. oregoni_. 'Density compensation' in the presence of a coexisting competitor has been observed in bird species (Cody, 1974). The reduction in _M. oregoni_ numbers and the increase in _P. maniculatus_ when supplemental food was provided requires further explanation, however. Perhaps deermice are better at exploiting seed foods (Caldwell, 1964), especially the clumped distribution in food stations used in the present study.

Implications For Population Regulation In Peromyscus

What bearing, if any, do the results of the present study have on the general population model for P. maniculatus proposed by Petticrew and Sadleir (1974)? Deermice share with other small mammals the frequently observed spring decline in population size at the onset of breeding. The extent of this decline is variable and depends on the length of the previous non-breeding season in granivorous mice (Fuller 1969, Watts 1969 and Petticrew and Sadleir 1974). The end result, whether a large decline from high densities, or a small one or none at all following lower overwinter densities, is a low density breeding population from year to year. The manner in which this is achieved is as yet undetermined (Petticrew and Sadleir 1974).

The present study suggests that the availability of food may determine both the onset and cessation of breeding and hence the length of the non-breeding season. Mice in populations supplied with extra food in mid- and late-winter not only put on weight and came into breeding condition but also increased in density. This increase resulted from immigration in response to the reduction in home range size by residents receiving extra food. Like the European wood mouse (Flowerdew 1973), deermice in this study had to gain weight from low overwintering weights before starting to breed. This pre-reproductive weight gain in control populations was associated with home range expansion. Since the food experiments indicate that the size of home ranges is affected by food availability at this time, I suggest that males expand their home ranges in the spring in order to obtain the extra food required to gain weight and reproduce. This

increase in male home ranges could exclude subordinates (observed in arena studies by Eisenberg 1968) and hence help to explain the normal spring decline in male density. Further, if larger males are dominant (Turner and Iverson 1973), this could explain why dispersers are light-weight males (Fairbairn 1977) and also why only the heaviest males become reproductive in the early breeding season (present study).

Petticrew and Sadleir (1974) suggest that male density is regulated throughout the breeding season, whereas females can increase through the season. They also suggest that juvenile numbers are limited by the agonistic behaviour of reproductive males. In the present study, no correlation was found between the number of breeding males and juvenile survival. Instead, there was a negative correlation between juvenile survival and the number of lactating females. Redfield et al. (1978) also found that juvenile recruitment in M. townsendii was related to female but not male density. Female P. maniculatus in the present study appeared to maintain nearly constant population size through the breeding season than did males on the control in 1974 (Figure 5). Over the long breeding season in 1975, both sexes increased and then declined, possibly in response to M. oregoni immigration (Appendix 3). Over the same two-week period (May 29 - June 12) in the 1974 breeding season both sexes declined on the food grid (Figure 5). This large decline may have coincided with the summer switch in diet from seed to non-seed food items. If so, not only were the sexes behaving similarly, but they also may have responded to the distribution of their perhaps preferred natural food supply. The number of

females on the food grid after this decline was almost identical to that on the control. The results of these experiments suggest that female reproduction is sensitive to environmental conditions, and that females thereby have a strong influence on population dynamics in P. maniculatus. After the spatial re-organization of males in the spring an increasing number of males become scrotal. With sufficient food and warmer weather some females may then become pregnant and lactate after two to six weeks. If insufficient food is available, or weather is poor, females may not come into breeding condition until later. The long delay in the onset of female lactation on the control in the cold spring of 1974 contrasts with there being no delay the same year on grids with extra food.

Petticrew and Sadleir (1974) suggest that over the non-breeding period both sexes of P. maniculatus are regulated by the length of such seasons. At lower temperatures energy demands increase, and on the control, mice lost weight, ceased reproduction, and declined in number. This response was reversed immediately in winter by the addition of food to experimental grids. Mice on such grids gained weight, reproduced, and maintained fairly stable winter densities. By contrast, P. maniculatus supplied with decreasing levels of food overwinter tended to respond to each food reduction by a steepening of their overwinter decline (Figure 6). This suggests that not only is the length of the non-breeding season determined by a combination of food availability and weather conditions, but also that the pattern of decline within such periods can be influenced by food availability.

I suggest that natural populations of P. maniculatus, through their spatial organisation in home ranges, are highly responsive to the extrinsic environment. By means of this spatial arrangement, individuals attempt to gain access to required resources, maintain high weights, and reproduce. The system is probably tightly regulated in P. maniculatus by the seasonal restrictions of their food supply, which results in their losing weight over winter and ceasing to breed. Because of their high energy demands for lactation, females are probably more sensitive to these conditions than males and may exert more influence on population dynamics during the breeding season.

Such a dynamic system could be maintained through the interaction of individuals as a result of their spatial organisation. Interaction could be through direct contact, or through olfactory stimulation as a result of scent-marking by individuals (Eisenberg 1968). For example, through increased interaction, individuals could monitor a reduction in resource quantity or quality, and then respond by emigrating to an area of lower interaction if such exists, or reducing the size of their home ranges and ceasing to breed. There are records of low rates of lactation in dense populations and complete reproductive cessation in extremely dense populations of granivorous mice (see Terman 1968 for review, and Canham 1969). It is interesting to speculate that these females may have experienced such high rates of interaction when attempting to gain access to resources that reproduction was no longer possible. In the very dense population, the high rates of interaction per se may have had a detrimental effect, such as

pregnancy block (Bruce 1959, Eleftheriou et al. 1962, and Clulow and Langford 1971). The end of the normal breeding season might result from a combination of higher energy demands and increased interaction over decreasing food availability in the autumn. Reduced access to food could result in loss of weight and cessation of reproduction. The associated decline in reproductive behaviour results in the observed increase to winter densities. Some of these suggestions are highly speculative. But the presence of such a dynamic system of spatial organisation could explain the observed impact of supplementary feeding in the present study. Also such a system, combined with the omnivorous nature of their diet, could account for the rapid and successful exploitation of new food resources in general by Peromyscus, especially human garbage (Courtney and Fenton 1976).

MICROTUS TOWNSENDII

1. INTRODUCTION

In spite of half a century of research, the population dynamics of voles remains somewhat of an enigma. The general population trend of a two- to five-year 'cycle' in numbers has been observed repeatedly (see review by Krebs and Myers 1974). But there is no consensus on the underlying mechanism. The hypotheses range from single factor extrinsic (weather, food, predation) or intrinsic (behaviour, genetics) explanations, to recent suggestions that involve a combination of several factors (Bunnell 1973, Batzli 1975, Collier et al. 1976, Gaines and Rose 1976).

Krebs et al. (1969) put a fence around an otherwise natural population of Microtus pennsylvanicus and M. ochrogaster, thus preventing immigration and emigration. The fenced population increased to unusually high densities, which resulted in voles overgrazing their food supply and consequently some individuals starving. This experiment has been repeated with similar results on Microtus townsendii (Boonstra and Krebs 1977). These experiments suggest that natural vole populations are normally able to prevent serious overgrazing of their food supply. Further, removal experiments on these species (Myers and Krebs 1971, Krebs et al. 1976) indicate that voles could do this by inducing dispersal of some individuals and hence limit population size in a given area. Finally, Krebs et al. 1976,

found that the recruits to areas from which resident voles had been removed, were breeding at lower weights than voles on the control. This shows that excluded voles were capable of breeding, and that smaller voles on the control were being prevented from breeding in the presence of larger animals. These microtines thus fulfill the first three conditions that Watson and Moss (1970) suggest indicate that spacing behaviour can limit population size at least in the short term (Table XII). It is not known whether this is the case over long periods of time (condition D).

There is very little evidence for or against condition E (Table XII) in microtines. Krebs and Delong (1965) provided surplus oats to a low density vole population for ten months. The population increased at 3% per week over five months (reaching 8 times its original density), then declined over the summer to the low starting density in contrast to the control, which continued to increase. But this experiment has been criticised because of the type of food used (Watson and Moss 1970, Batzli and Pitelka 1971). Also, there were many differences in the vegetation between the control and the experimental area, which was 10 km away. The status of the experimental area was uncertain, but the control was clearly an 'increasing' population.

I was interested in testing condition E on _Microtus townsendii_, and seeing if the number of individuals that could be supported in a given area over a long period of time was related to food distribution (Section I). Second, I wanted to see if immigration to a new area, and the size of the colonizing

Table XII. Factors suggested as necessary to show that spacing behaviour limits population size.

A. A substantial part of the population does not breed.

B. Such non-breeders are capable of breeding if dominant or territorial animals are removed.

C. Breeding animals are not completely using up some resource.

D. Long-term limitation by spacing behaviour.

E. If conditions A to D are met, and numbers change following changes in food, then food and behaviour are both limiting population size.

Taken from Watson and Moss(1970) p. 170.

population was affected by food distribution (Section II).
Finally, voles, like P. maniculatus, often exhibit a spring
decline in density, and I wanted to see if this was influenced
by the availability of food, or by dominant resident voles
(Section III).

2. METHODS AND EXPERIMENTS

Study populations of M. townsendii were situated in two grassland areas south of Vancouver in the Fraser River Delta of B.C. The Ladner study area is 4.8 km east of Ladner in the abandoned airbase bordering Boundary Bay. The Reifel grassland is situated on Westham Island, which is 6.4 km west of Ladner. Both grasslands have been undisturbed for at least ten years. The Reifel grassland is a relatively confined area bounded by farmland, water-filled ditches and a dyke beside the sea. In contrast, the Ladner grassland is bounded on only one side by the Boundary Bay dyke.

Two sizes of grid were marked out in these grasslands. Large grids had 100 trap stations at 7.62 m intervals, usually in either a 10X10 (0.47 hectares) or a 5X20 (0.44 hectares) pattern. Small grids had either 50 traps in a 5X10 pattern (0.21 hectares) or 49 traps in a 7X7 pattern (0.21 hectares). Variations in the shape of larger grids were made to fit habitat restrictions: these are described in more detail in the relevant sections. The trapping regime was the same as that used in P. maniculatus, except that M. townsendii were checked during the intervening day as well as the two overnight periods in each winter trapping session. In summer, the daytime trapping period was abandoned altogether in order to avoid mortality from overheating. The type of data recorded on each vole was identical to that recorded for P. maniculatus.

Grids E, R, T And M : Long-term Food Supplementation

These four grids were located in the Ladner study area (see Figure 17). Grid E was the control population trapped by Krebs et al.(1976) from May 1971 to September 1975. Grids R and T were set up in July 1972. Initially, the 100 traps on grid R were placed in a 4X25 pattern, and grid T had 7 rows of 13 traps and one row of 9 traps. But the area between grids R and T and the control (grid E) became a shallow lake in late fall, so I realigned both experimental grids on October 29th to avoid flooding the traps. Both grids were made into 5X20 grids running close and parallel to the runway. At the end of March 1973, a high density of food stations (1 per 22 sq m) was introduced to grid T and a low density to grid R (1 per 73 sq m). I had intended to run these two grids as long-term food grids with high and low densities of food available for the duration of the study. Unfortunately both were destroyed by ploughing in April 1974 after only one year of supplemental feeding. In May 1974 I set up grid M and provided it with food stations at an intermediate density (1 per 45 sq m) at the end of August 1974. This grid was monitored every two weeks until the end of the study in September 1975. Food stations were removed from grid M ten weeks before the end of the study.

Grids 1, 2, and 3 : Colonization and Food Density

These three small grids were set up on the area that was ploughed in April 1974 (see Figure 17). By the end of November

Figure 17. Location of M. townsendii grids at Ladner, B. C.
Numbers and letters correspond to those assigned to each
grid.

scale: 100 feet

road:

ditch:

N

3

1

T

M

2

R

runway

marsh

Grid E
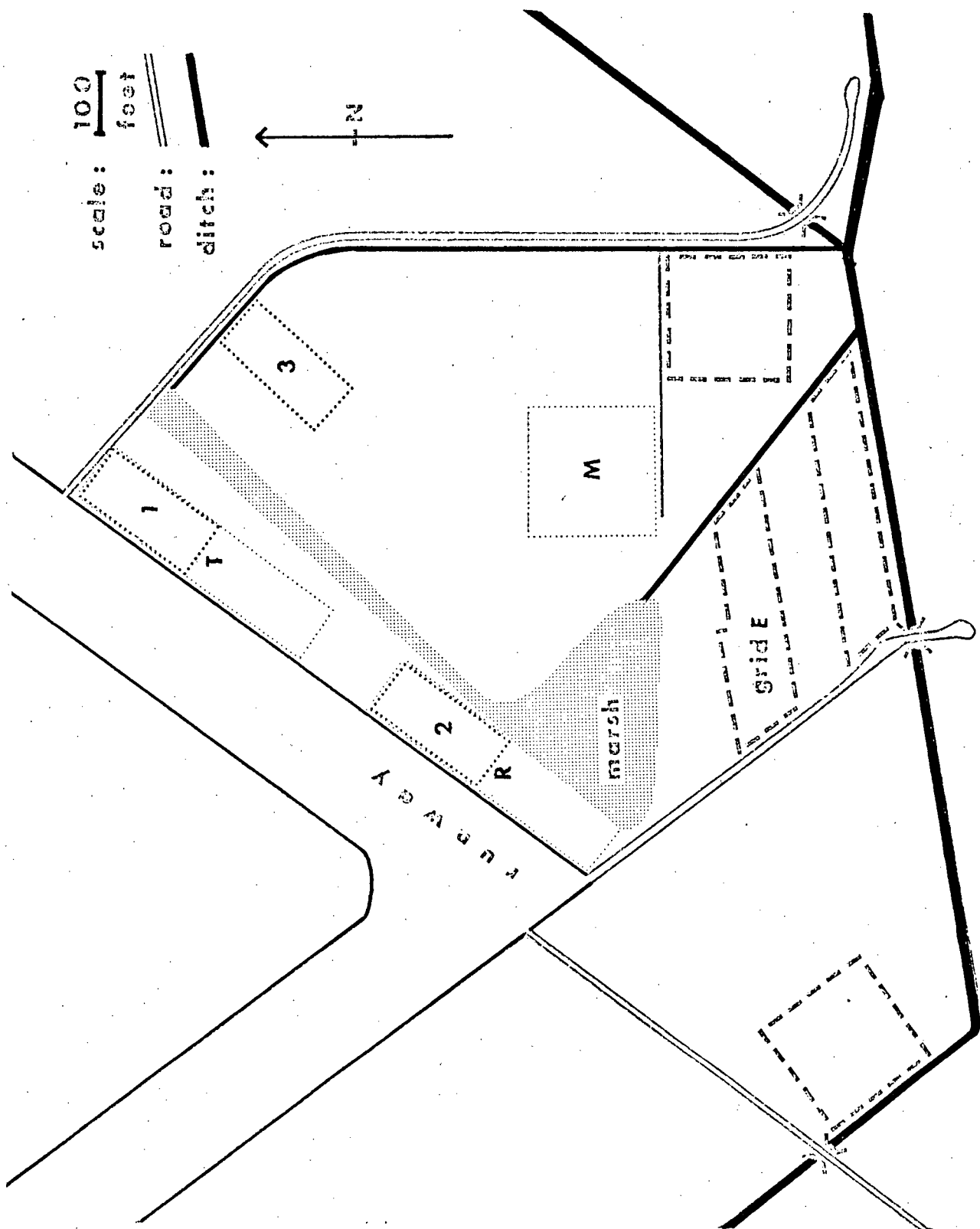
1974, grass was re-growing and some mice were immigrating into the area. I was interested in monitoring immigration to high, low, and zero supplemental food levels in the breeding and non-breeding season.

Grids I and G : Spring Decline and Food

Grid I was the control used by LeDuc and Krebs(1975). It was trapped continuously from July 1971 to September 1975. Grid G was also used by these authors. The dynamics of voles on the two grids was practically identical. In particular they exhibited a non-breeding season which terminated in a substantial spring decline. I decided to use the two grids to test the effect of food availability on the magnitude of the spring decline. On December 1st 1974, food stations were put out at each trap location (1 per 47 sq m) on grid G. All food stations were removed on June 27th 1975, eight weeks before the grid was last trapped.

I looked at the data available from previous years on the voles that remained on grid I after each spring decline. There was some indication that such voles were large and came into breeding condition early. At the low point of the decline, all males tended to be scrotal adults and half the females were perforate and some were lactating. I therefore decided to test the hypothesis that if such voles were removed from the population the voles that normally disappeared during the decline would stay and reproduce. Two small grids were set up at the beginning of January 1975. All males weighing > 70 g and

females weighing > 54 g were removed from one grid (Alpha). The second grid (Beta) was the control, where the same number of voles was removed but as a random sample across all size classes. Finally to determine what voles dispersed from established populations at Reifel through the 1975 spring decline, I removed voles continuously from a 10X10 grid and a narrow strip grid of 2X13 traps.

Food Supply

Microtines are herbivores, and the most effective method of manipulating their food supply would be to provide them with extra green vegetation or change their grass food supply in situ by fertilization or destruction. But the logistics and expense of the former on a large scale over a long period of time, and the consequence of the latter on habitat structure made them unacceptable. Further, I wanted to control the distribution of food fairly closely. Following the advice of Dr. G. O. Batzli (personal communication), I provided voles on grids R and T with a laboratory chow (Purina #5321) for the duration of this experiment. The chow was readily taken by M. townsendii both in the laboratory and from food stations in the field. But the pellets were very sensitive to moisture; after a period of rain they became mushy, and developed mildew a few days later. M. townsendii readily took whole oats from live-traps, so in all other food experiments I used oats with a large handful of chow. The experimental design is summarized in Figure 18.

Figure 18. Summary of M̲. t̲o̲w̲n̲s̲e̲n̲d̲i̲i̲ experimental design. The winter months are shaded.

▲ 1 = food added to grids R and T

▲ 2 = " " " grid M

▲ 3 = " " " grids 1 and 2

▲ 4 = " " " " 2 and 3

▲ 5 = " " " grid G

▼ = food removed
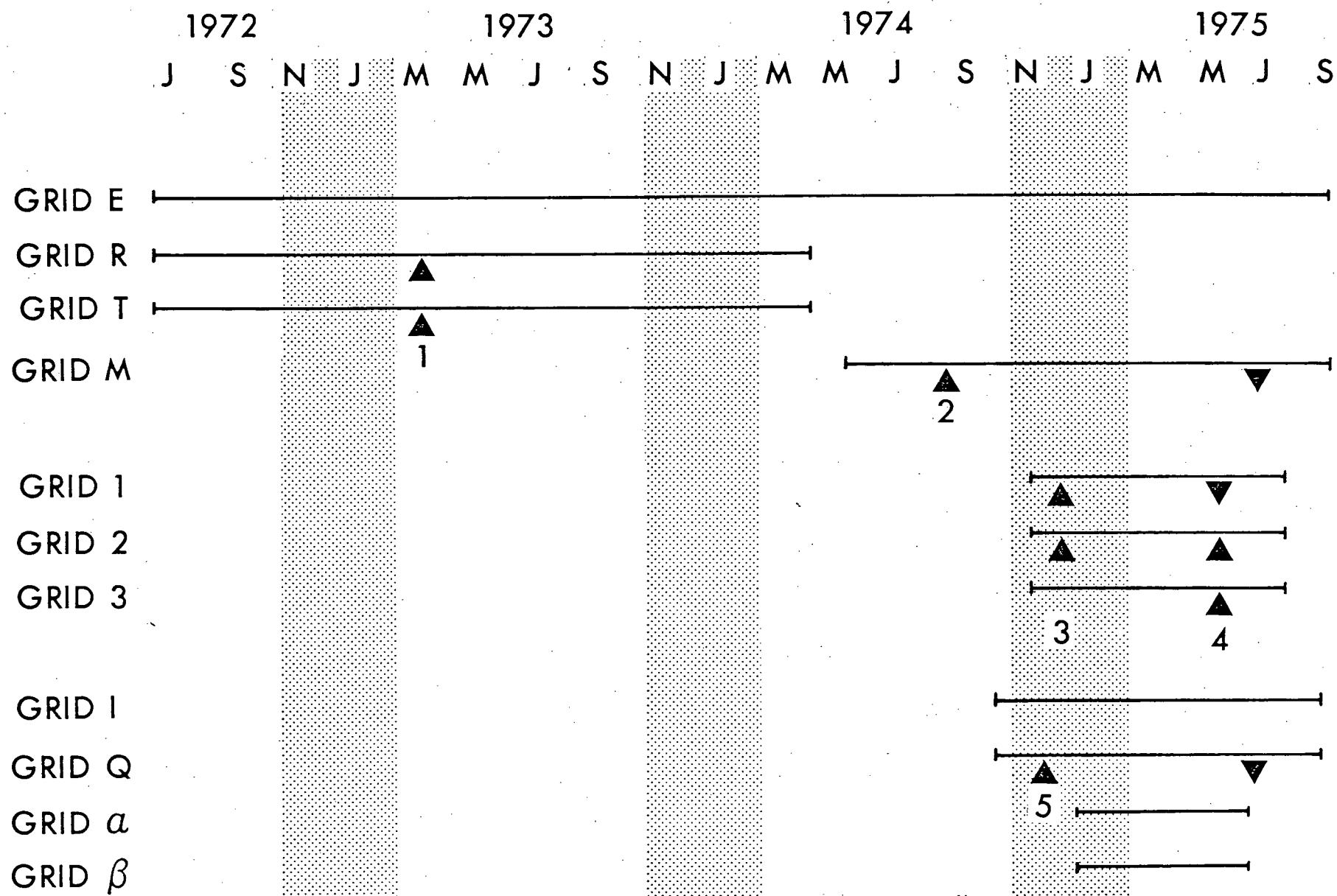
3. RESULTS

Section I : Long-term Food Supplementation

Trappability

The trappability of voles on the control grid (E) and the experimental grids (R, T, M) was calculated in the same manner as described for $P.$ maniculatus. The voles are more trappable than the deermice at similar densities (see Table I and Table XIII). But the trappability of voles declines progressively as the number of individuals increases. Male and female voles are equally trappable.

Population Density

The density of voles on the control grid (E) was very low when it was first established in June 1971 (see Krebs et al. 1976). From a winter (November) high of 27 voles the population declined to 12 in March 1972. When grids R and T were established in July 1972, the control was increasing towards its second winter peak of 58 voles (Figure 19). Before the realignment of traps on October 29 1972, the number of voles on both grids R and T were similar at 63 and 68 voles respectively compared with 48 on the control. But after realignment, the density on these two grids increased rapidly. I think part of

Table XIII. The trappability of voles on grids E, R, and T. Minimum number alive is given in parentheses. ML=males, FM=females.

Season	Grid E		Grid R		Grid T		Grid M	
	ML	FM	ML	FM	ML	FM	ML	FM
Winter 1972-3	91(33)	09(36)	85(46)	87(59)	81(72)	81(86)	--	--
Summer 1973	78(68)	83(57)	74(112)	76(104)	54(167)	65(183)	--	--
Winter 1973-4	85(36)	82(28)	90(57)	79(61)	68(135)	60(130)	--	--
Summer 1974	89(80)	81(79)	--	--	--	--	-	
Winter 1974-5	78(93)	77(89)	--	--	--	--	59(120)	49(153)
Grand Total(1)	85(124)	85(104)	78(166)	79(156)	68(264)	68(259)	--	--
Grand Total(2)	71(209)	71(188)					47(226)	41(290)

E = Control, R = Low-food, T = High-food, M = Intermediate-food

(1) = Trappability Over The Period July 1972 To March 1974

(2) = Trappability Over The Period May 1974 To September 1975

Figure 19. Number of voles on grids E, R, and T.

▲ = grid E (control)

x = grid R (low-food)

✦ = grid T (high-food)

▲ = food added to grids R and T
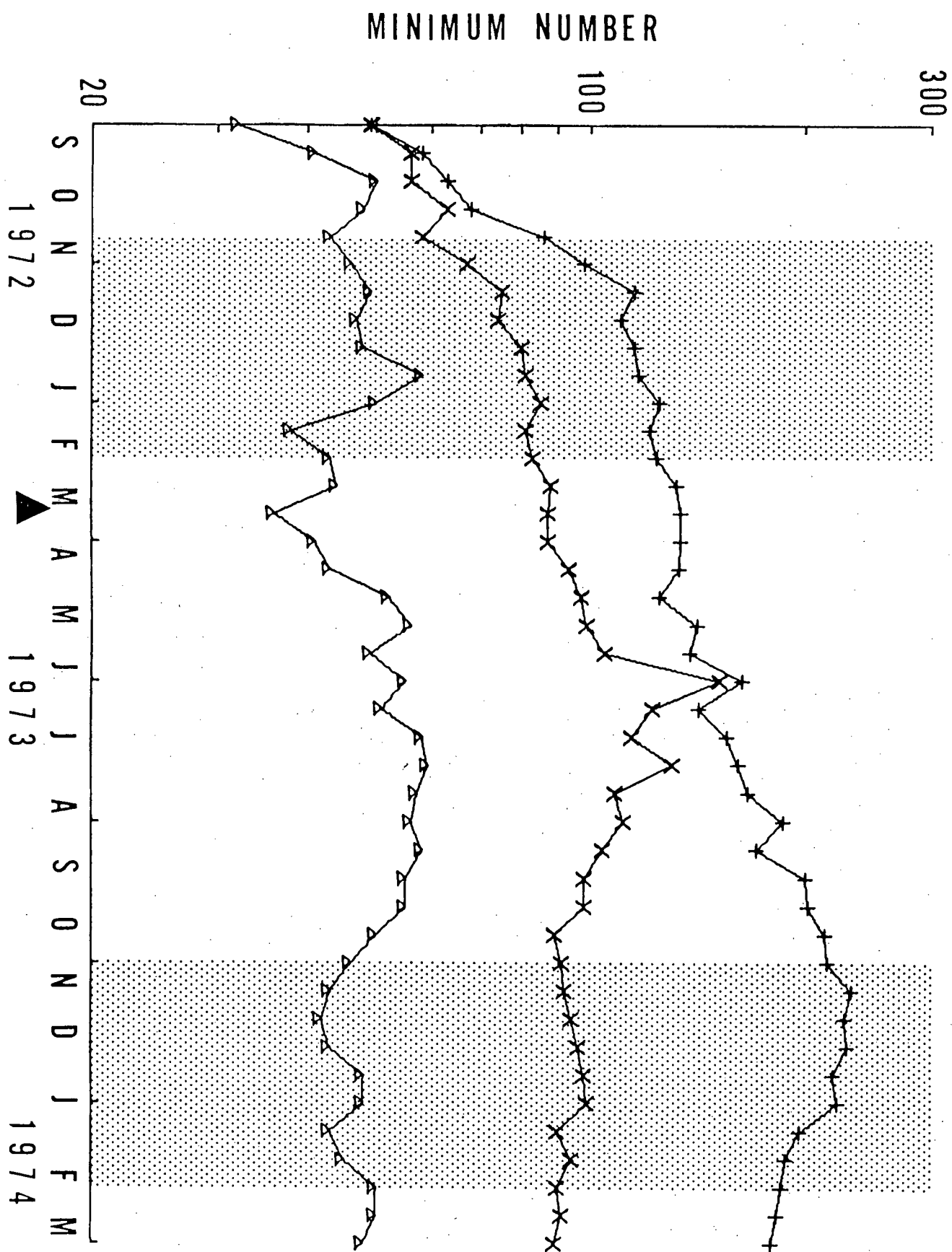
the reason for this increase is that mice from the 'marsh' area that became a winter 'lake' emigrated to the slightly higher ground along the edge of the runway where the two experimental grids were positioned (Figure 18). The lake remains until April or May depending on the precipitation, then it becomes a temporary breeding habitat for M. townsendii in summer. I delayed adding food stations to grids R and T in the hope that the density of voles would decline to the level of the control. But over the three months (January to March), the control declined at an average of 1% per week, while grid R continued to increase at 2% per week and grid T at 4% per week. The sex ratio on both experimental grids was biased in favour of females (R 37:50, T 59:75), while on the control it was even (19:17).

The number of voles on grids R and T continued to increase after food was added on March 18 1973 (Figure 19). The number of voles on the low-food grid (R) increased at 6% per week over the next three months to peak at nearly 3 times the control density. But the number of voles then declined steadily (2% per week) on the low food grid (R) through the late summer and autumn (July to October). The control (E) population declined at 3% per week during October and November, while the low-food population increased at 1% per week. The population (T) of voles supplied with a high-level of food, in contrast to both the control and low-food population, continued to increase at 2% per week throughout the whole period (March to December 1973). Initially, females increased more quickly than males on the high-food grid and became significantly (chi square, 6.303, p<0.025) more abundant over the period April to June 1973 (Appendix 10). But

by the end of the year the sex ratio was even.

The overall density of voles on the control and low-food grid did not change appreciably over the first three months of 1974. The sex ratio on the control became slightly biased towards males, while on the low-food grid males declined in numbers and females increased. Over the same period, the density of voles in the high-food population declined because the number of males declined by 30%. Therefore, both food grids had populations biased towards females.

Grid M was set up as a 10X10 grid of traps at the end of May 1974. The density of voles on the grid M was close to that of the control (Figure 20) at the end of August, when an intermediate density of food stations was added to grid M. The number of voles on both grids increased rapidly (control 7.3%, intermediate-food 9.6% per week) over the next four months. Again, the population increase on the food grid was uneven between the sexes, females increased faster than males. The control population remained fairly stable over the early summer then increased again towards the end of the study in the fall of 1975. The intermediate-food population diverged from the control in December and increased to double its number by March. This increase was contributed to equally over this time by both sexes. Over the next three months male density declined while females increased still further with intermediate food.

Figure 20. Number of males and females on grids E and M.

unjoined points = grid E (control)

joined points = grid M (intermediate food)

x = males

+ = females

▲ = food added to grid M
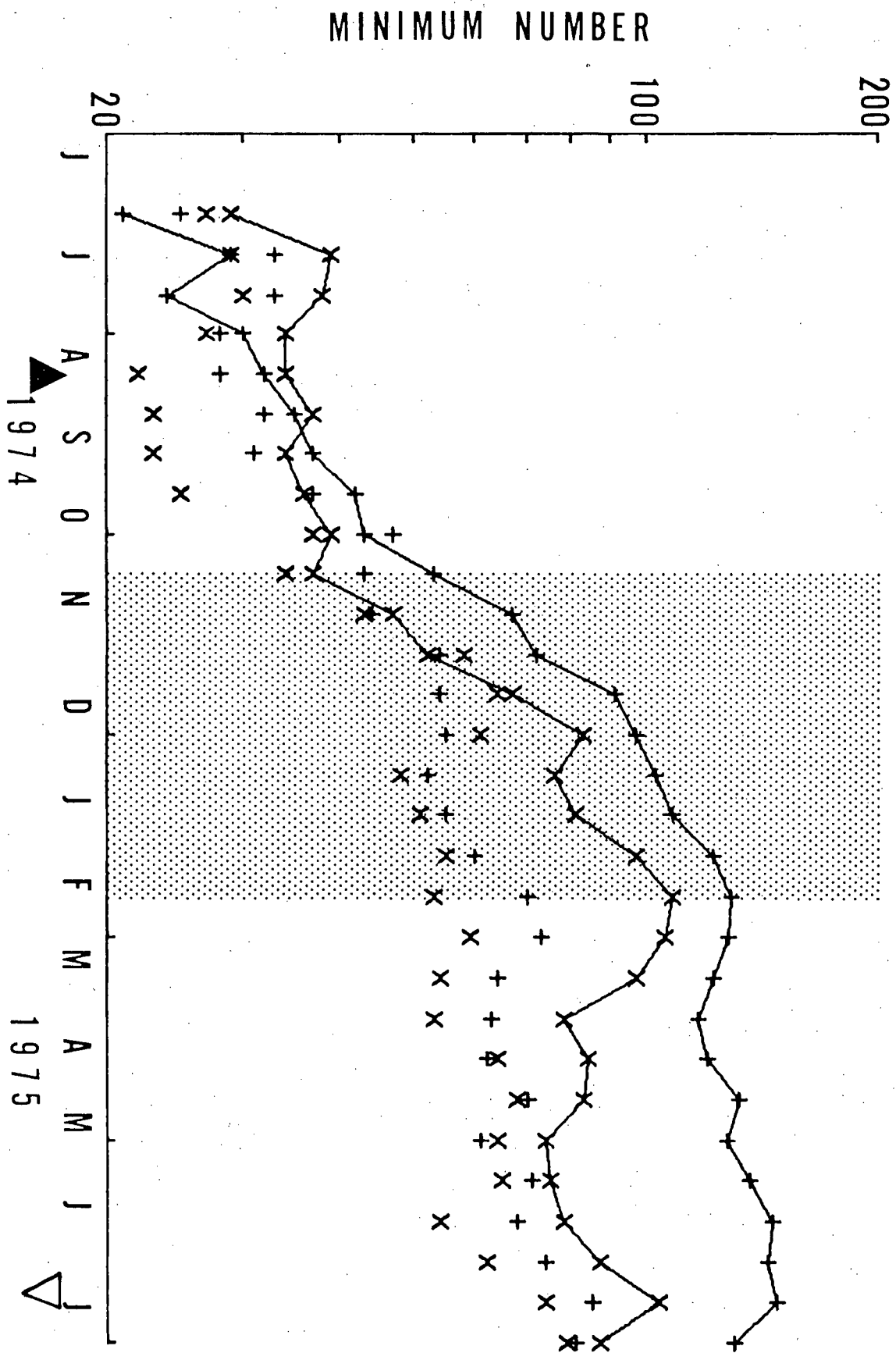
Immigration

The total number of new voles captured on all grids in each three-month period of the study is shown in Figure 21. There is a fairly consistent pattern of capture of new voles on the control over the first two years of the study. Over the summer months the number of new voles is higher than over the winter periods. But after September 1974 nearly twice as many new voles were captured over the 1974/5 winter as over the previous two winters combined. Twice as many new voles were recorded over the following summer compared with the previous year.

Grids R and T had more new voles than the control in the nine months before food was provided. During the summer 1974, following food addition, the number of new voles on the low food grid (R) rose to 1.9 times the control number and on the high-food grid (T) to 2.5 times the control number. The low-food population had almost the same number of new voles as the control over the 1973/4 winter, but the high food grid maintained 2.9 times the control number. The number of new voles captured on the intermediate-food grid (M) was 1.7 times that on the control overwinter (1974/5) and twice the control numbers over the summer 1975.

The age and sex composition of new voles entering each population is given in Appendix 11. In terms of the sex composition of each age class, immigrants to all populations of M. townsendii exhibit the same general pattern as P. maniculatus . The sex ratio in the sub-adult category is close to even. Females predominate in the juvenile age class, while new adults

Figure 21. New voles captured on grids E, R, T, and M.

◇ = grid E (control)

▪ = grid R (low food)

● = grid T (high food)

◆ = grid M (intermediate food)

▲ 1 = food added to grids R and T

▲ 2 = food added to grid M
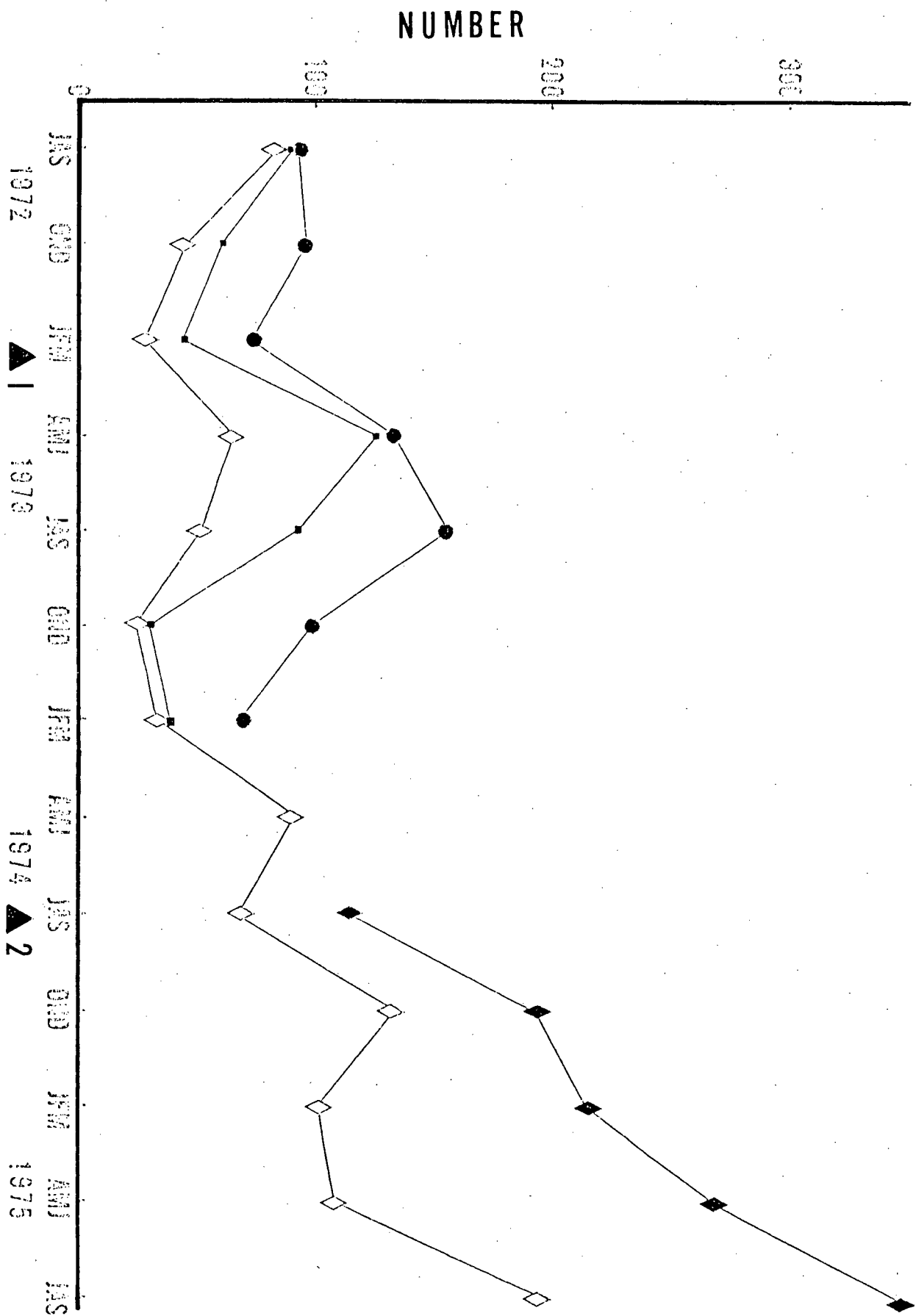
in all populations are predominately males.

After food was added to grids R and T both populations increased over April - June 1973 because of high immigration of voles of all age classes. Over the next three months, adult immigration dropped on both experimental grids to the same levels as on the control. Sub-adults and juveniles entered the low-food population (R) at the same high rate as in the previous three months but then declined over winter to control levels. Meanwhile, the high-level food grid (T) had twice as many immigrants in the sub-adult age group in late summer and continued with high rates into the winter in contrast to the control and low-food grids. The first new voles on the intermediate-food grid (M) were in the adult and sub-adult age class. But over the last six months(January to June), twice as many voles immigrated to grid M as to the control.

Over the year that food was added to grids R and T, the sex ratio of new voles to the control was biased towards males (106:70). Males also predominated (181:152) amongst immigrants to the control over the nine months of intermediate food addition to grid M. The number of males amongst new voles on each food grid, in order of food level from low to high, was: 1.5 times, 1.8 times, and 2.2 times the number on the control. Similarly, new females on each food grid in order were: 1.7 times, 2.3 times, and 3.1 times those on the control. Therefore, both sexes entered food grids in proportion to the food available.

Breeding Season

I have separated the breeding data for the sexes of M. townsendii. Although some female M. townsendii were perforate in every trapping period of the study except one, the breeding intensity, in terms of the percentage of females lactating, seldom rose above 50%. Males, on the other hand, sustained a high level of breeding in each season. The data are summarized in Figure 22, where the breeding activity of adults (voles weighing >42 g) on each grid is given for the duration of the study. In a few instances sub-adults (voles weighing 30 to 42 g) were considered if the percentage breeding was higher than in the adult age class.

Before food was added to grids R and T, male voles on all grids were breeding. The intensity of breeding in males in the highest-density population on grid T was slightly less than in the other two populations. The following winter, males on the control had stopped breeding by the end of December 1973. On grid R, which had a higher density of voles and a low level of food, males had gone out of breeding condition six weeks earlier. But with a high level of food, males on grid T continued to breed. In fact they stopped breeding for only six weeks on grid T compared with 12 weeks on grid R, and ten weeks on the control.

The breeding activity of females was more sporadic and less intense than that of males. There was no appreciable increase in breeding intensity of females with extra food, but the period of non-breeding was shorter in the presence of a high density of food. On grid R with a low density of food but twice the density

Figure 22. Breeding activity on grids E, R, T, and M.

wide line = 50% or more adults breeding

middle line = less than 50% of adults breeding

narrow line = no breeding

grid E (control)

grid R (low food)

grid T (high food)

grid M (intermediate food)

▲ 1 = food added to grids R and T

▲ 2 = food added to grid M

▼ = food removed
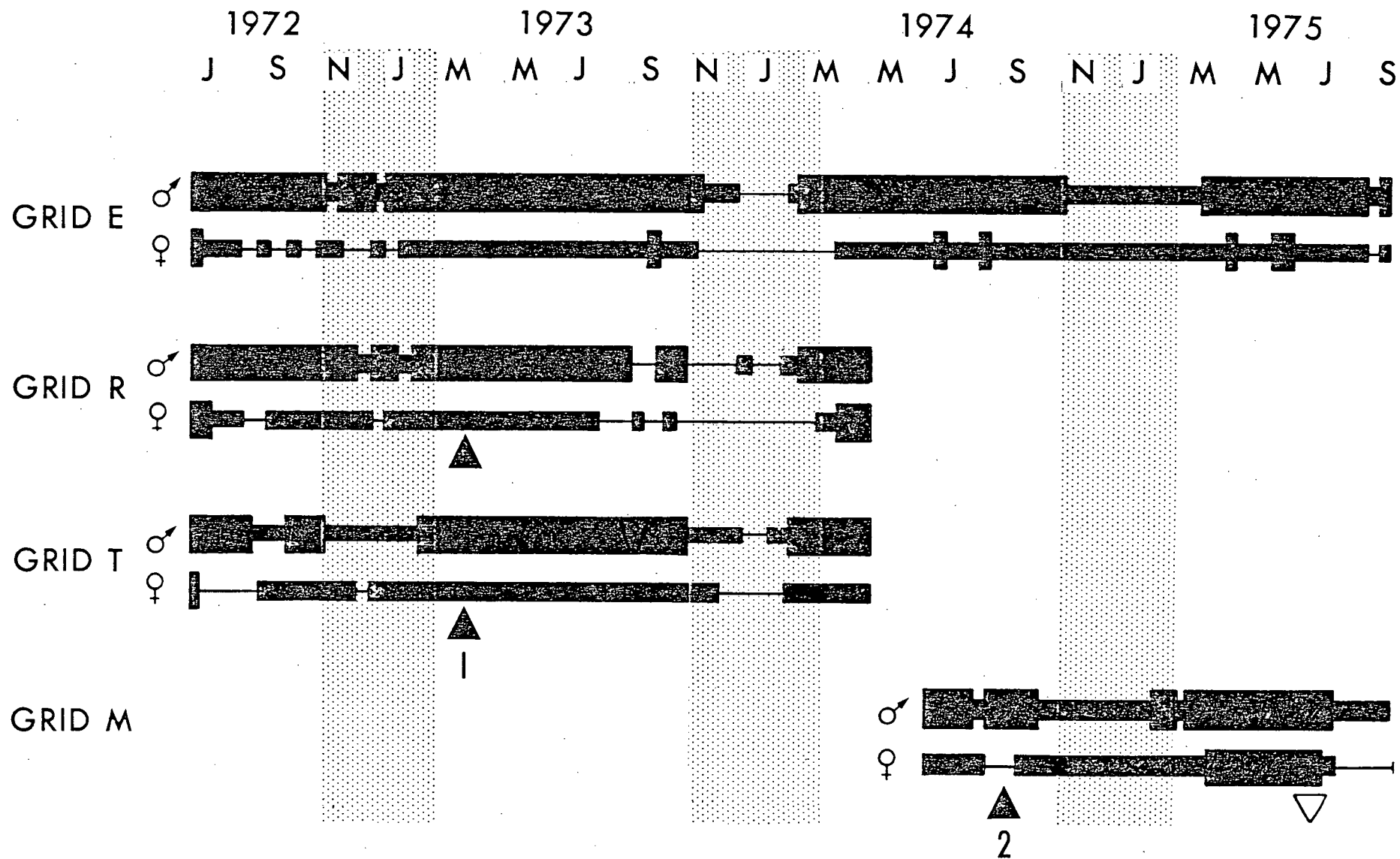
of voles compared with the control, females ceased breeding for twenty-six weeks compared with eighteen weeks on the control. Females in the high-density population with a high level of food(T) did not breed for twelve weeks.

Apart from one trapping period at the end of August 1975, males and females bred continuously on the control from spring 1974 until the end of the study. More than 50% of the males were scrotal on the intermediate-food grid in February 1975, this was six weeks earlier than the control males. Females lactated at a consistently higher intensity in the presence of intermediate food compared with control females in 1975. After the removal of food stations at the beginning of July, male reproduction dropped below 50% two weeks later and female breeding ceased completely, while both sexes on the control continued at their summer intensity.

In summary, breeding of voles in the control population at Ladner was nearly continuous throughout the study. This made it difficult to observe the influence of additional food on vole breeding. But, a population with double the control density of voles, and only a low-level of extra food, appeared to have a shorter breeding season than the control. But the addition of a high-level of food appeared to shorten the non-breeding season of both sexes in a high density vole population. Finally, in 1975, voles with an intermediate level of food bred more intensively than control animals. When food was removed from this population, reproduction in both sexes was reduced.

Breeding Success

Reproductive output, in terms of the number of young recruited, varied widely on the control over the duration of the study at Ladner. For example, in the three-month period October to December 34 young were recruited in 1972, 23 in 1973, and 88 in 1974. Before food was added to grids R and T, 76 young had been recruited to the control grid. The number recruited to grid R was 1.4 times higher (113) and to grid T was 1.9 times higher (148) than the number to the control. Over the six months following food addition 59 young were recruited to the control (E). The low-food population had 163 young (2.8 times grid E), and the high-food grid had 215 young (3.6 times grid E) over this period. So the number of young entering the food grids was twice the pre-food level. Before food addition to grid M, the number of young voles present was similar to the number on the control. But during the next nine months over twice as many young(337) were recruited to the intermediate-food population than to the control(159).

Early juvenile survival is shown in Table XIV. Before food was added grid T had higher juvenile survival but a lower rate of female lactation than grid R. Juvenile survival on grid R was lower than on the control. In the six months after food addition, the number of lactating females on both food grids was equal. Juvenile survival on the food grids was lower in the first half of 1973 than on the control. But in the second half of the summer it improved on the food grids, and was highest on the high-food grid (T). Before food was added to grid M,

Table XIV. Early juvenile survival on grids E, R, T, and M. The number of lactating females is given in parentheses.

Date	Grid E (control)	Grid R (low-food)	Grid T (high-food)	Grid M (int.-food)
Jul-Sep 1972	2.13(15)	0.44(10)	4.33(9)	
Oct-Dec "	3.78(9)	2.50(18)	4.79(14)	
Jan-Mar "	0.77(13)	0.56(43)	1.27(33)	
Apr-Jun "	0.96(28)	0.77(105)	0.78(105)	
Jul-Sep "	0.91(35)	1.26(65)	2.02(66)	
Oct-Dec "	1.64(14)	25.00(1)	2.77(26)	
Jan-Mar 1973	13.00(1)	3.75(4)	1.90(10)	
Jul-Sep "	0.87(46)			2.05(17)
Oct-Dec "	2.84(31)			1.49(71)
Jan-Mar 1974	0.90(49)			1.40(77)
Apr-Jun "	0.16(168)			0.56(220)

juvenile survival was higher than on the control, but the number of females was also lower. In the first six months of 1975 the number of lactating females was higher in the presence of food, and juvenile survival was also better than on the control.

Weights And Growth

The mean weights of males on grids E, R, and T are plotted in Figure 23. There is a strong annual cycle in mean weight on all grids. The lowest mean weights are recorded in early to mid-winter and the highest weights in early summer.

The addition of food to grids R and T in 1973 resulted in the mean weight of these populations becoming significantly higher than that on the control by the following trapping period. On grid T with the highest level of food the mean was significantly higher than the means on both grid R and the control. Four weeks later grid T reached its peak of 57g while the control was still only at 53g. The lowest winter weights on the control were lower than those on the low-food grid, which in turn were lower than those on the high-food grid. In fact, voles on grid T maintained higher mean weights than did the controls from the end of November 1973 to the ploughing of the grid in April 1974.

Instantaneous relative growth rates were calculated for voles as described for P. maniculatus. Before food was added to grids R and T, the growth rates on these high-density grids was lower than on the low density control (E) (see Appendix 12). In the period immediately following food addition, the growth rates

Figure 23. Mean weights of voles on grids E, R, and T.

top = grid E (control)

middle = grid R (low food)

bottom = grid T (high food)

▲ = food added to grids R and T

GRID E

GRID R

WEIGHT IN GRAMS

GRID T

J F M A M J J A S O N D J F M

1973   1974
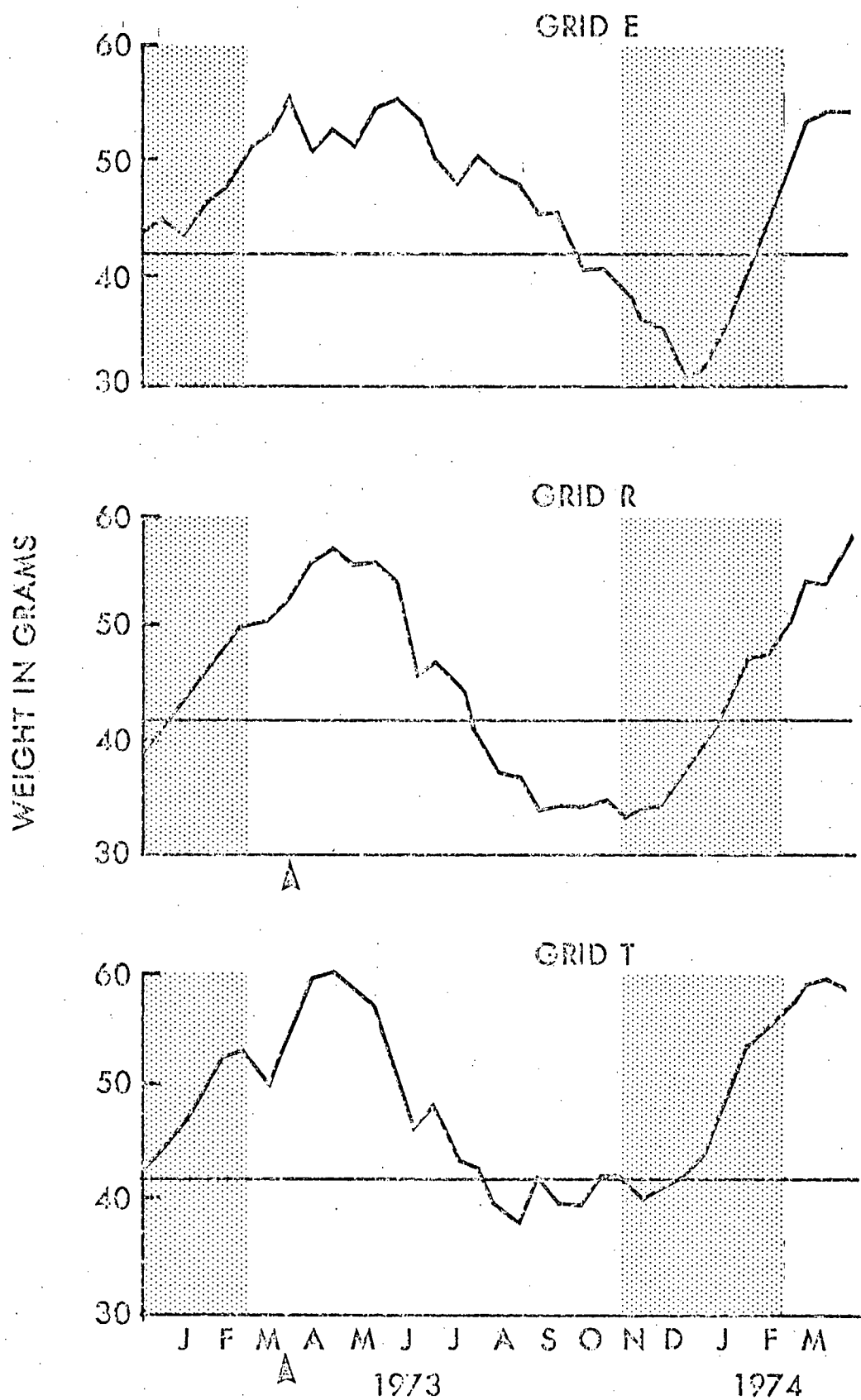
in all age-sex groups were higher on the low-food grid (R), and highest on the high food grid (T). A month later, all voles on the control had extremely high growth rates. All age-sex groups in the low food population (R), except juvenile females in August, had lower growth rates than controls through the summer (June to August). Voles in the high-food population (T) had higher growth rates than voles on grid R, but apart from all males in May, each age-sex group had lower growth rates than voles on the low-density control until the end of July. Therefore, voles with access to dry, supplemental mouse chow in mid-summer had lower growth rates than voles on a low density control grid. This situation was reversed in the winter months. Voles on grid R had higher growth rates than voles on the control 19 out of 24 possible times (sign test, p=0.003). On the high-food grid (T) voles had higher growth rates 24 out of 30 times in the period from August to December 1973. In late winter, the growth rate of voles on the control increased, and, as in _P. maniculatus_, males increased before females. At this time on the food grids, as in _P. maniculatus_ with food, males and females had higher growth rates at the same time.

Growth rates of voles on the control through the 1974/5 winter were much higher than in both previous winters. In fact, no negative growth rates were recorded on the control in this mild winter. However, voles on the intermediate food grid (M) had higher growth rates than control voles 35 out of 42 times. But again, the extra food, this time admittedly oats, did not increase growth rates in the summer 1975 on grid M.

Survival

The survival of voles on all grids fluctuated between 0.80 and 0.90 from July 1972 to March 1974 (Table XV). In the nine months before food was added, vole survival on grids R and T was higher than on the control. The addition of supplemental food to both experimental grids did not change the survival in their vole populations. But survival on grid M, with an intermediate level of food, was lower in both sexes compared with the control from October 1974 to June 1975. In particular, male survival was below .80 in 17 out of a possible 18 sample periods. In the two months following food removal, male survival declined to 0.43 and female survival to 0.52 compared with 0.77 and 0.78 respectively on the control.

Home Range Size

Home ranges of voles were calculated by the same method as described for P. maniculatus. Voles with one capture point, and more than one capture in a straight line (but not on the peripheral rows of the grids) have been included using the estimates given in Appendix 9. The home ranges were calculated for blocks of data, one for the nine months before food was added to grids R and T (July 1972 to March 1973), one for the same time period a year later, when grids R and T were receiving supplemental food, and one the following year, when grid M was being fed (see Table XVI). In the control year (1972/3) there were no significant differences in home range size of the sexes on the control from those on the experimental grids. But during

Table XV. Survival of voles on grids E, R, T, and M. The number of voles is given in parentheses, followed by the number of periods that survival was >0.90 / and <0.80.

	July 1972 to March 1973		July 1973 to March 1974	
Grid	Males	Females	Males	Females
E	0.83(332) 7/6	0.87(381) 11/3	0.86(433)5/6	0.89(378) 10/1
R	0.88(445) 12/3	0.89(615) 12/3	0.87(780) 9/3	0.90(726) 9/1
T	0.88(603) 7/3	0.93(757) 15/1	0.87(1104)8/2	0.90(249) 13/1

	October 1974 to June 1975	
E	0.83(725) 3/8	0.85(787) 5/4
M	0.69(792)1/17	0.78(919) 5/18

E = control, R = low-food, T = high-food, M = interm.-food

Table XVI. Mean home range size (sq m) of voles on grids E, R, T, and M. The periods are July to March in each year.

		1972/3	1973/4	1974/5
Grid E	Males	804(42)	1134(51)	670(85)
	Females	546(45)	608(38)	391(79)
Grid R	Males	1050(50)	445(79)*	--
	Females	578(65)	331(78)*	--
Grid T	Males	795(74)	328(102)***	--
	Females	423(89)	261(114)***	--
Grid M	Males	--	--	447(87)**
	Females	--	--	231(92)**

*** = high food

** = intermediate food

* = low food

the period of food addition, males on grid R and grid T had significantly smaller home ranges than did males on the control (grid R: t=3.12, p<0.01; grid T: t=3.66, p<0.001). Similarly, females on the experimental grids had smaller home ranges than did controls over this period (grid R: t=3.14, p<0.01; grid T: t=3.88, p<0.001). Although males and females on the control had smaller home ranges in the 1974/5 period than in the previous two periods, those with an intermediate level of food (grid M) had significantly smaller home ranges than control voles (males: t=2.63, p<0.01; females: t=3.33, p<0.001). Females had smaller home ranges than males in all periods on all grids (except grid T with high-food).

Section II : Colonization and Food Density

The most significant response to food addition in both
P. maniculatus and M. townsendii was a large increase in
immigration. In the next series of short-term experiments (see
Figures 17 and 18), I attempted to see if immigrants to vacant
areas were settling in response to the spatial pattern of food.
The experiment was planned for the winter non-breeding season
(1974/75) and the summer breeding season (1975).

At the outset of the experiment on November 18-20th 1974, I
removed all voles from all grids. On November 25, a high density
of food stations (1 per 11 sq m) was placed on grid 1, a lower
density (1 per 33 sq m) on grid 2, and none on grid 3. After
three weeks of immigration to these three food levels, all voles
were removed in the mid-December trapping period. I reduced the
density of food stations on grid 2 to one per 68 sq m. Voles
were then allowed to immigrate freely for the next four months
to all three grids. I reduced the density of food stations on
both grids 1 and 2 by half in January 1975. Food cans were
removed at the end of April, and all voles were removed for the
next three trapping sessions. The experimental treatments were
then switched so that no stations were placed on grid 1, grid 2
had a high density of food (1 per 87 sq m), and grid 3 now had a
low density (1 station per 136 sq m).

Population Density

The number of voles removed (vertical lines) and the minimum number alive for the intervening colonization periods are shown in Figure 24. Practically the same number of voles were removed from all three grids before food was added, and also after the first week of food addition. But over the second and third week of food addition to grids 1 and 2, 37 new voles entered the high-food population (1), 28 entered the low-food population (2), and only 19 entered the control population (3).

Over the four-month colonization period, the population with a high level of food (1) increased at an average of 50% per week compared with 30% and 35% respectively on the low-food grid (2) and the control (3). After the three removal periods in April and May 1975, the total number of voles (males:females) that had colonized the high-food grid was 188 (97:91), compared with 116 (62:76) on the low-food grid (2), and only 53 (16:37) on the control. Therefore, three times as many voles colonized an area with high-food compared with one with no food, and twice as many colonized an area with low-food compared with one with no food.

The second colonization experiment was not run for a long enough period. However, voles again colonized the highest-food area (2) at a higher rate (22% per week) than they did the low-food area (10% per week) and the control (10% per week).

Figure 24. Number of voles on grids 1, 2, and 3. Vertical lines
     are the number of voles removed.

⬤ = grid 1 (high food then no food)

◯ = grid 2 (low food then high food)

▼ = grid 3 (no food then low food)

▲ 1 = high food to grid 1 and low to grid 2

▼ = food removed

▲ 2 = high food to grid 2 and low to grid 3
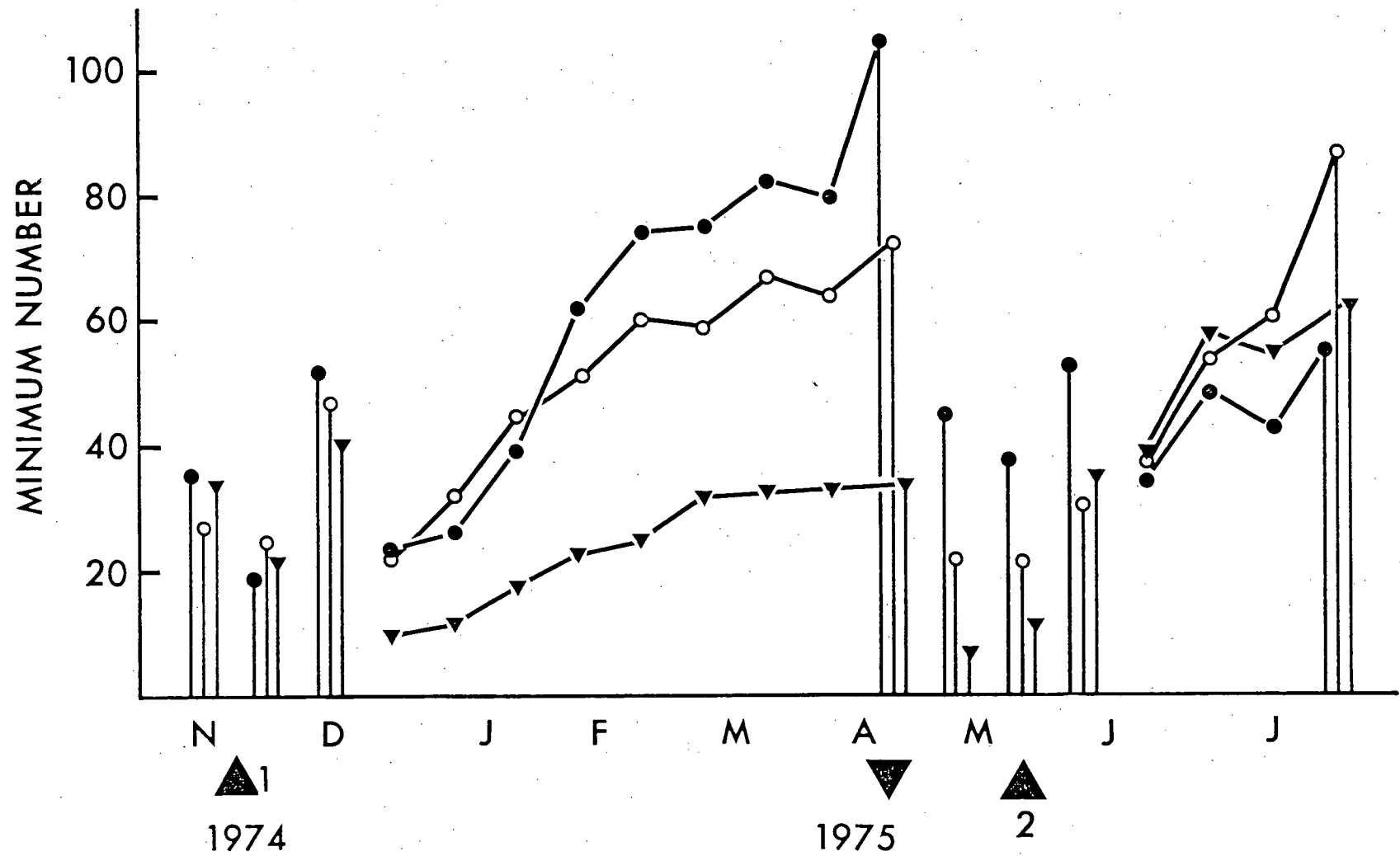
Immigration

A total of 241 new voles was captured on the high-food area (1) over the first colonization period (Table XVII). Only half this number(136) of new voles was captured on the low-food area (2) and slightly greater than a quarter the number(77) on the control (3). In the two-month colonization period in summer 1975, 153 new voles were captured on the high-food grid (2), 143 on the low-food area (3), and 106 on the control (1).

During the first colonization period, the number of new female voles on the low food area (2) and the control (3) were similar. But nearly three times the control number of females entered the high-food area (1). New males, on the other hand, entered the populations in proportion to the food available. Over the short summer period, the trend in the sexes was reversed, namely, females appeared to be more responsive to the different food levels.

During the first colonization period, the age-sex composition of immigrants reflects previous trends found for both species in this study. Namely, the sex ratio of sub-adults entering all grids combined was close to even. Adult immigrants were predominantly males (163:110), and juveniles were predominantly females (24:44). A second feature is that an increasing number of smaller voles immigrated to areas in proportion to the food available. During the first colonization period, only 27% of the immigrants to the control (3) were juveniles and sub-adults compared with 35% and 47% of those to the low- and high-food areas respectively.

Table XVII. New voles captured on grids 1, 2, and 3 in each colonization period. Ratio of number of males:females

		Jan. to May 1975	Jun. to Jul. 1975
Grid 1	Adults	78:51**	36:26
	Sub-adults	34:35**	16:24
	Juveniles	15:28**	2:2
Grid 2	Adults	56:32*	38:41**
	Sub-adults	19:12*	20:30**
	Juveniles	8:9*	7:17**
Grid 3	Adults	29:27	46:33*
	Sub-adults	7:6	18:27*
	Juveniles	1:7	9:7*

** = high food

* = low food

Breeding Condition And Reproductive Success

All voles bred through the winter 1974/5 at Ladner, so it was not possible to detect any influence of food on the breeding season on grids 1, 2, and 3. The number of males and females in reproductive condition is shown in Table XVIII. Over the winter-spring colonization period, males and females bred at a higher intensity on grids with extra food. The number of females breeding in the food populations (1 and 2) was in proportion to the amount of food available. Over the short summer colonization period, males bred equally intensively on grids with and without food, but females again bred more intensively in the presence of extra food.

The number of young (<40g) recruited reflected the intensity of female breeding in each population. Between January and May, 52 young voles were recruited to the high-food grid (1), 28 to the low-food (2) and only 10 to the control (3). Over the two month summer colonization, 26 young were recruited to the high-food population (2), 18 to the low-food (3) and only 9 to the control.

Early juvenile survival was also higher in both colonization periods in proportion to the food made available to the population. In the high-food populations, 1.41 juveniles were captured per lactating female in the first period, and 1.73 in the second. Early juvenile survival in the low-food populations was 1.00, and 1.39, and on the controls it was 0.50, and 0.82 in each colonization period respectively.

Table XVIII. Mean number of males scrotal and females lactating on grids 1, 2, and 3.

		Jan. to May 1975	Jun. to Jul. 1975
Grid 1	Males	11.3**	12.8
	Females	7.4**	3.0
Grid 2	Males	12.7*	12.0**
	Females	5.0*	5.3**
Grid 3	Males	4.1	15.3*
	Females	3.9	5.0*

** = high food

* = low food

Section III: Spring Decline And Food Supplementation

The fluctuations in the number of mice on grids I and G were very similar to one another from July 1971 to July 1973 (see LeDuc and Krebs 1975). The pattern of change in numbers is also remarkably consistent between years over this period and again in 1974. Table XIX lists the trapping periods when the population on grid I reached maximum and minimum numbers each year. The population was unusual in 1971: it was at a low-density when trapping began, and reproduction continued throughout the first winter (see LeDuc and Krebs 1975). In 1972 and 1973 the population peaked in December then declined over the spring to reach its lowest levels in late April and early May in all three years. In 1973 and 1974 the number of voles at the end of this spring decline was almost equal at 46 and 41 respectively, and 100% of the adult males were scrotal. This pattern is suggestive of the annual cycle in numbers exhibited by P. maniculatus. The population declined in the spring to a low-density breeding population. Then, when breeding ceased in the fall the population increased to a winter peak in density.

Food stations were placed on grid G on December 1st 1974. Both grid G and the control grid I populations were well into their winter increase by this time. But the density pattern over this winter turned out to be completely different from that in all other years. Males on grid I peaked early in January at a much higher density than in previous years, and females continued to increase in numbers until March. Further, neither sex exhibited a spring decline in density; by the end of April

Table   XIX.   Periods of   maximum and   minimum   numbers at Riefel from 1972 to 1975.

Maximum numbers	Total	Males	Females
10 to 12th January 1972	170	77	93 (+2)
12 to 14th December 1972	231	93	138
22 to 24th December 1973	233	118	115
6 to 8th January 1975	327	149	174 (+10)
Minimum numbers			
1-3rd May 1972	88	26	62 (-2)
30 April to 2 May 1973	46	14	32
15 to 17th April 1974	41	15	26 (+2)
28 to 30th April 1974	273	95 (+2)	178

(- or + #) indicates the weeks before or after the date given that numbers peaked for this sex

1975, the number of males and females was six times that of the previous two years (see Table XIX). This, combined with the very low trappability of voles in the extremely dense population on grid I throughout the summer of 1975, and the resulting overgrazing, made any attempt at data comparison between the two grids meaningless. Similarly, the number of dispersing voles was fairly low on the removal areas which made the results of the selective removal experiment almost meaningless.

It would be very interesting to conduct these experiments again under more tightly controlled conditions. In order to overcome the possibility of being swamped by voles immigating to the extra food, I would conduct the feeding experiment and selective removals on fenced grids with a dispersal 'sink' included (of the type now being used by Beacham, Ph. D. in progress).

4. DISCUSSION

It is hard to interpret the the effect of the three levels of long-term food supplementation on the dynamics of these M. townsendii populations. This is because of:-

1. The control grid (E) exhibited an unusual pattern of fluctuation over the four years of the study. The density of voles was fairly stable for the duration of the low- and high-level food experiments. But, during the period of intermediate food supplement to grid M, the number of voles on the control proceeded to increase fairly steadily.

2. It is difficult to decide what influence the seasonal availablity of breeding habitat had on experimental grids R and T. In the summer the 'lake area' dried out and was colonized by voles, but in the autumn and winter the area became a shallow lake.

3. The two long-term food grids were destroyed after only one year of supplementary feeding.

4. Apart from grids R and T, I was not able to feed these M. townsendii a suitable supplementary food. In fact, I doubt the effectiveness of the chow that was used on grids R and T in wet and very dry weather conditions.

Before food was added, the density of voles on experimental grids R and T increased; this was probably in response to flooding of the 'marsh'. In retrospect, I should have delayed adding food until the lake had dried out in the summer of 1973, because some voles might have left both areas (R and T) to colonize the new habitat, and hence the densities on these grids

might have been closer to that on the control (E). However, after one year of low-level food supplement, the grid R population still had twice the number of voles that were present on the control (E). The grid T population reached 4.2 times the control density after one year of high-food compared with its pre-food density of 2.8 times the control density. After nine months of intermediate food, grid M had double the control density of voles, having been at the same density prior to food addition. Therefore, over the periods that these experiments were conducted, areas with extra food were able to maintain higher vole populations than that on a control area with no food. Also, populations with intermediate and high densities of food stations doubled their pre-food numbers.

The number of new voles captured on an area was always higher in populations with extra food. Also voles immigrated into the populations in proportion to the extra food available. This may have been facilitated by males and females reducing the size of their home ranges on areas with extra food compared with those of voles on the control areas. The colonization of vacant areas provided with different levels of food confirmed the observations for the long-term food grids. The largest populations were established on areas with the highest levels of extra food. Also, such areas had higher numbers of immigrants in proportion to the food available.

It was difficult to detect any influence of food availability on the breeding season in M. townsendii, partly because breeding was almost continuous on the controls. The non-breeding season was shorter in a population with a high

level of food compared with one with no extra food. Also more
male and female voles bred on areas with extra food. Larger
numbers of young voles were recruited to food populations than
to the controls, and early juvenile survival was improved with
extra food. Finally, mean growth rates of voles were higher over
winter on areas with additional food.

Since the present study was initiated, two feeding
experiments conducted on the European bank vole
Clethrionomys glareolus have been reported. Flowerdew (1973) in
England found no significant change in the breeding season of
bank voles supplied with extra wheat food. But these voles did
have higher overwintering weights than did the controls.
Andrzejewski (1975) in Poland found that 90% of female bank
voles had an open vagina in early spring on a plot with
high-level oat food, compared with 53% on a low-food area and
only 23% on a control plot. Both studies reported little change
in survival of voles on their food plots. Andrzejewski (1975)
found a large increase in immigration to his food plots, but
Flowerdew (1972, 1973) found an increase one year but not the
next. In a later short-term experiment, Flowerdew (1976)
concluded that his equivocal response resulted from the fact
that the bank voles did not significantly change their
distribution in response to the extra food. In another
experiment in Poland, Andrzejewski and Mazurkiewicz (1976) found
that an island population of bank voles with supplemental food
had smaller home ranges than they had had in previous non-food
years.

The equivocal nature of some of the results of these food

experiments on voles may be a consequence of the type of supplementary food that was provided. If voles prefer green plant food, as suggested by Batzli (1974), or require it to reproduce, as suggested by Negus et al. (1977), then such results might be explained. But in spite of the type of supplementary food used in the present study, the results indicate that voles are sensitive to the availability of food resources in their environment.

GENERAL CONCLUSIONS

The small mammals P. maniculatus and M. townsendii exhibit spacing behaviour by the possession of home ranges. This behaviour may limit the number of breeding individuals in a given area. Two recent experiments by Fairbairn (1976) on P. maniculatus and Krebs et al. (manuscript) on M. townsendii provide more thorough evidence for this. By using a 'pulsed removal' design these authors showed that dispersers into an area from which residents had been removed were able to colonize and establish viable populations. Thus both P. maniculatus and M. townsendii fulfill conditions A and B (Table XII) of the experimental design suggested by Watson and Moss (1970) for showing that spacing behaviour limits population size. P. maniculatus in the present study was able to breed in winter when extra food was provided. This may indicate that food itself limits breeding in P. maniculatus at this time of the year. There is no evidence, at present, as to whether food or any other extrinsic resource is limiting for these small mammal populations (condition C). Further, it is also not possible to say whether spacing behaviour limits these populations over long periods of time (condition D).

The overall purpose of the present study was to see if spacing behaviour (measured as home ranges) of P. maniculatus and M. townsendii could be changed following an experimental change in food availability (testing condition E, see Table XII). P. maniculatus with extra food reached a maximum density

of 82 mice/hectare compared with 33 mice/hectare on the control. M. townsendii with a high level of extra food peaked at 734 voles/hectare compared with 209 voles/hectare in a low food population, and 98 voles/hectare on the control. The following year, an intermediate food population of M. townsendii peaked at 504 voles/hectare compared with the control, which this year had 280 voles/hectare. Females in both species responded more quickly than males to the addition of food. Immigration to all populations of both species with extra food was always higher than to the controls. The age-sex distribution of the immigrants to all populations showed the same pattern: there were significantly more females in the juvenile class, and significantly more males in the adult class. Residents in populations of both species reduced their home range size in the presence of extra food, and this probably facilitated the increased immigration. Therefore, the home ranges of these small mammals were responsive to changes in food availability, and this affected their population dynamics, thus providing evidence for condition E (Table XII). But having done this, I think it remains to be determined whether any other factors (as suggested in Figure 1) can act on spacing behaviour in this way.

Flexibility of spatial organisation in response to food availability has recently been documented for other vertebrates. Mares et al. (1976) showed that Eastern chipmunks reduced the size of their home ranges in response to three weeks of food supplementation. Iguanid lizards reduced the size of their territories in response to only 14 days of food addition (Simon 1975). Both species expanded their respective home ranges

following withdrawal of the extra food. These studies, like the present one, are short-term experimental perturbations. But a study by Zach and Falls (1975) indicates that such responses can and do occur naturally. They observed that ovenbirds responded to a spruce budworm outbreak by reducing their territory size and increasing in density. These studies indicate that the spatial organisation of established individuals can change in response to perturbations in food availability, and that this in turn can change the number of individuals that occur in a given area.

P. maniculatus and M. townsendii have different food habits. The results of the present study confirm McNab's (1963) observation, that the granivores have larger home ranges than the herbivores. But after the provision of extra food, female P. maniculatus reduced their home ranges to the size of those of male M. townsendii. This supports McNab's (1963) conclusion that the difference in home range size in the two groups is a result of the distribution of food in the habitat. Further, the present study indicates that both species can respond to different food densities. Therefore, it is interesting to speculate that the spatial and temporal pattern of food in the 'typical' habitats that the two groups of species have been studied in previously may have influenced the dynamics observed.

I have suggested that P. maniculatus survives the temporal restriction of its food supply in the forest overwinter by ceasing to breed, and hence exhibits an annual cycle in numbers. By contrast, the food supply in a typical homogeneous grassland habitat appears to be far less restricted for low density

Microtus populations. For example, a low density, increasing population of microtines usually breeds through its first winter, which may indicate no temporal restriction of food and result in high population densities. On the other hand, the results of the present study indicate that P. maniculatus will breed overwinter in the forest if extra food is made available. Further, a population of M. pennsylvanicus living in woodland habitat (Grant, 1975) appeared to cease reproduction in winter. Perhaps a Microtus population would exhibit an annual cycle if its food supply could be temporally restricted. Perhaps grassland populations of M. townsendii are a case in point. Temporal and spatial heterogeneity of whole pieces of habitat may be imposed by the winter flooding of these grasslands. In summer such areas are good breeding habitat, and the voles move out to use them. But in winter they have to leave them for patches of higher ground, which themselves may not be high enough to allow deep burrows. This increased density may, through increased interaction, as suggested for P. maniculatus, cause a decline in weight and halt reproduction, thus giving rise to an annual cycle in numbers. Finally, a major difference between the two groups is the fact that the food supply of voles is also their cover protection. Under conditions of peak density, voles have been observed to reduce their major food plants by as much as 85% (Batzli and Pitelka 1970). Locally, the spatial and temporal heterogeneity of vole habitat could serve to protect patches of grass from such overexploitation by M. townsendii. Then, for example, if an impact of high densities of voles is a reduction in cover, this will occur in patches.

But, as the water-table subsides in the spring, the remaining
voles will be able to invade the previously flooded patches,
which now may be favourable refugia, as well as burrow deeper in
the old patches. A similar patchwork of favourable and
temporally unfavourable habitat on a larger scale may be
important to microtine dynamics in general. These speculations
are too parsimonious, but they should be readily testable.

It would still be interesting to determine the effect of
food and removal of dominants on the spring decline in voles, as
outlined in Section III above. Since voles responded to extra
food by increased immigration, this experiment should be
conducted in an enclosure with a dispersal sink (see Beacham Ph.
D. in progress). A suitable 'herbivore-food-supplement' should
also be used. Second, if future feeding experiments are carried
out in open populations of either species, it would be
interesting to provide food to the central part of a large
trapped area. It should then be possible to determine whether
the immigrants are local animals or not. Third, it would be
interesting to test some of the ideas raised on the influence of
habitat heterogeneity. Specifically, can P. maniculatus be
induced to 'cycle' if a continual supply of suitable food is
provided? Can the winter weight syndrome be reversed and
reproductive condition manipulated in both species by the
provision of extra food in the fall? Can this also be done by
reducing population density in the fall, hence allowing the
remaining animals unmolested access to resources? If
reproduction can be maintained into the winter, what effect does
this have on future population dynamics, and in voles, on the

structure and quality of the grasses. Finally, if a patchwork of good and poor habitat of different sizes can be created, what effect does this have on the movement patterns of individual voles, their reproductive condition, survival, and population dynamics?

LITERATURE CITED

Andrzejewski, R. 1975. Supplementary food and the winter dynamics of bank vole populations. Acta theriol. 20:23-40.

Andrzejewski, R., and M. Mazurkiewicz. 1976. Abundance of food supply and size of the bank voles home range. Acta theriol. 21:237-253.

Batzli, G. O. 1977 population dynamics of the white-footed mouse in floodplain and upland forests. Amer. Midl. Nat. 97:18-32.

Batzli, G. O. 1975. Populations and energetics of small mammals in the tundra ecosystem. In J. J. Moore (ed.) Tundra: Comparative analysis of ecosystems. Cambridge Univ. Press.

Batzli, G. O. 1974. Influence of habitat structure on a population of voles. Bull. S. Calif. Acad. Sci. 73:83-85.

Batzli, G. O., and F. A. Pitelka. 1971. Condition and diet of cycling populations of the California vole, Microtus californicus. J. Mammal. 52:141-163.

Batzli, G. O., and F. A. Pitelka. 1970 influence of meadow mouse populations on California grassland. Ecology, 51:1027-1029.

Bendell, J. F. 1959. Food as a control of a population of white-footed mice Peromyscus leucopus noveboracensis. Can. J. Zool. 37:173-209.

Boonstra, R., and C. J. Krebs. 1977. A fencing experiment on a high-density population of Microtus townsendii. Can. J. Zool. 55:1166-1175.

Brown, J. L. 1976. The Evolution of Behaviour. Norton, New York.

Brown, J. L., and G. H. Orians. 1970. Spacing patterns in mobile animals. Ann. Rev. Ecol. Syst. 1:239-262.

Bruce, H. M. 1959. An exteroceptive block to pregnancy in the mouse. Nature, Lond. 184:105.

Bunnell, F. L. 1972. Lemmings - models and the real world. Proc. 1972 Summer Computer Simulation Conference, Simulation Councils, Inc. Pp 1183-1193.

Burt, W. H. 1943. Territoriality and home range concepts as applied to mammals. J. Mammal. 24:346-352.

Caldwell, L. D. 1964. An investigation of competition in natural populations of mice. J. Mammal. 45:12-30.

Canham, R. P. 1969. Early cessation of reproduction in an unusually abundant population of Peromyscus maniculatus borealis. Can. Field. Nat. 83:279

Clulow, F. V., and P. E. Langford. 1971. Pregnancy-block in the meadow vole, Microtus pennsylvanicus. J. Reprod. Fert. 24:275-277.

Cody, M. L. 1974. Competition and Structure of Bird Communities. Princeton University Press, Princeton, New Jersey. 318pp.

Collier, B. D., N. C. Stenseth, S. Barkley and R. Osborn. 1975. A simulation model of energy aquisition and utilization by the brown lemming Lemmus trimucronatus at Barrow, Alaska. Oikos 26:276-294.

Courtney, P. A., and M. B. Fenton. 1976. The effects of a small rural garbage dump on populations of Peromyscus leucopus rafinesque and other small mammals. J. Appl. Ecol. 13:413-422.

Crook, J. H. 1965. The adaptive significance of avian social organisations. Symp. Zool. Soc. Lond. 14:182-218.

Dunford, C. 1970. Behavioural aspects of spatial organization in the chipmunk. Behaviour 36:215-231.

Eisenberg, J. F. 1968. Behavior patterns, p. 451-495 In J. A. King (ed.) Biology of Peromyscus (Rodentia). Spec. Publ. No. 2 Amer. Soc. Mammal.

Eleftheriou, B. E., F. H. Bronson, and M. X. Zarrow. 1962. Interaction of olfactory and other environmental stimuli on implantation in the deer mouse. Science 137:764

Fairbairn, D. J. 1977. The spring decline in deermice: death or dispersal? Can. J. Zool. 55:84-92.

Fairbairn, D. J. 1976. Population processes in Peromyscus: an experimental approach. Ph. D. Thesis, University of B. C., Vancouver, B. C.

Flowerdew, J. R. 1976. The effect of a local increase in food supply on the distribution of woodland mice and voles. J. Zool. Lond. 180:509-513.

Flowerdew, J.R. 1973. The effect of natural and artificial changes in food supply on breeding woodland mice and voles. J. Reprod. Fert. Suppl. 19:259-260.

Flowerdew, J. R. 1972 the effect of supplementary food on a population of wood mice (Apodemus sylvaticus). J. Anim. Ecol. 41:553-566.

Fordham, R. A. 1971. Field populations of deermice with supplemental food. Ecology 52:138-146.

Fuller, W. A. 1969. Changes in numbers of three species of small rodent near Great Slave Lake, N.W.T., canada, 1964-1967, and their significance for general population theory. Ann. Zool. Fenn. 6:113-144.

Gaines, M. S., and R. K. Rose. 1976. Population dynamics of Microtus ochrogaster in eastern Kansas. Ecology 57:1145-1161.

Grant, P. R. 1974. Population performance of Microtus pennsylvanicus confined to woodland habitat and a model of habitat occupancy. Can. J. Zool. 53:1447-1465.

Hansson, L. 1971. Small rodent food, feeding and population dynamics. Oikos 22:183-198.

Healey, M. C. 1967. Aggression and self-regulation of population size in deermice. Ecology 48:377-392.

Hilborn, R., J. J. Redfield, and C. J. Krebs. 1976. On the reliability of enumeration for mark and recapture census of voles. Can. J. Zool. 54:1019-1024.

Iverson, S. L., and B. N. Turner. 1974. Winter weight dynamics in Microtus pennsylvanicus. Ecology 55:1030-1041.

Jameson, E. W. 1955. Some factors affecting fluctuations of Mictotus and Peromyscus. J. Mamm. 36:206-209.

Jameson, E. W. 1953. Reproduction of deer mice (Peromyscus maniculatus and P. boylei) in the Sierra Nevada, California. J. Mamm. 34:44-58.

King, J. A. 1973. The ecology of aggressive behaviour. Ann. Rev. Ecol. System. 4:117-138.

Koeppl, J. W., N. A. Slade, and R. S. Hoffmann. 1975. A bivariate home range model with possible application to ethological data analysis. J. Mamm. 56:81-90.

Krajina, V. J. 1969. Biogeoclimatic zones and classification of British Columbia. Ecol. West. N. Amer. 1:1-17.

Krebs, C. J., I. Wingate, J. LeDuc, J. A. Redfield, M. Taitt, and R. Hilborn. 1976. *Microtus* population biology: dispersal in fluctuating populations of *M. townsendii*. Can. J. Zool. 54:79-95.

Krebs, C. J., and J. H. Myers. 1974. Population cycles in small mammals. Adv. Ecol. Res. 8:267-399.

Krebs, C. J., B. L. Keller, and R. H. Tamarin. 1969. *Microtus* population biology: demographic changes in fluctuating populations of *Microtus ochrogaster* and *Microtus pennsylvanicus* in southern Indiana. Ecology 50:587-607.

Krebs, C.J. 1966. Demographic changes in fluctuating populations of *Microtus californicus*. Ecol. Monogr. 36:239-273.

Krebs, C. J., and K. T. Delong. 1965. A *Microtus* population with supplemental food. J. Mamm. 46:566-573.

LeDuc, J., and C.J. Krebs. 1975. Demographic consequences of artifical selection at the LAP locus in voles (*Microtus townsendii*). Can. J. Zool. 53:1825-1840.

Leslie, P. H., J. S. Perry, and J. S. Watson. 1945. The determination of the median body-weight at which female rats reach maturity. Proc. zool. Soc. Lond. 115:473-488.

Mares, M. A., M. D. Watson, and T. E. Lacher. 1976. Home range perturbations in *Tamias striatus*. Oecologia 25:1-12.

McCabe, T. T. and B. D. Blanchard. 1950. Three species of *Peromyscus*. Rood Assoc., Santa Barbara.

McNab. B. K. 1963. Bioenergetics and the determination of home range size. Am. Nat. 47:133-140.

Metzgar, L. H. 1973. Exploratory and feeding home ranges in *Peromyscus*. J. Mamm. 54:760-763.

Millar, J. S. 1975. Tactics of energy partitioning in breeding *Peromyscus*. Can. J. Zool. 53:967-976.

Myers, J. H., and C.J. Krebs. 1971. Genetic, behavioral, and reproductive attributes of dispersing field voles *Microtus pennsylvanicus* and *Microtus ochrogaster*. Ecol. Monogr. 41:53-78.

Negus, N.C., and P. J. Berger. 1977. Reproductive strategy of *Microtus montanus*. J. Mamm. 58:347-353.

Petticrew, B. G., and R. M. F. S. Sadleir. 1974. The ecology of the deermouse *Peromyscus maniculatus* in a coastal forest: I. Population dynamics. Can. J. Zool. 52:107-118.

Redfield, J. A., M. J. Taitt, and C. J. Krebs. 1978. Experimental alteration of sex-ratios in populations of *Microtus townsendii* , a field vole. Can. J. Zool. 56:17-27.

Redfield, J. A., C. J. Krebs, and M. J. Taitt. 1977. Competition between *Peromyscus maniculatus* and *Microtus townsendii* in grasslands of coastal B. C. J. Anim. Ecol. 46:607-616.

Rowley, M. H., and J. J. Christian. 1976. Intraspecific aggression of *peromyscus leucopus*. Behav. Biol. 17:249-253.

Sadleir, R. M. F. S. 1974. The ecology of the deermouse *Peromyscus maniculatus* in a coastal forest: II. Reproduction. Can. J. Zool. 52:119-131.

Sadleir, R. M. F. S., K. D. Casperson, and J. Harling. 1973. Intake and requirements of energy and protein for the breeding of wild deermice, *Peromyscus maniculatus*. J. Reprod. Fert. Suppl. 19:237-252.

Sadleir, R. M. F. S. 1970. Population dynamics and breeding of the deermouse *Peromyscus maniculatus* on Burnaby Mountain, B. C. Syesis. 3:67-74.

Sadleir, R. M. F. S. 1965. The relationship between agonistic behaviour and population changes in the deermouse, *Peromyscus maniculatus* (Wagner). J. Anim. Ecol. 34:331-352.

Savidge, I. R. 1974. Social factors in dispersal of deer mice (*Peromyscus maniculatus bairdi*). From their natal site. Am. Midl. Nat. 91:395-405.

Simon, C. A. 1975. The influence of food abundance on territory size in the iguanid lizard *Sceloporus jarrovi*. Ecology, 56:993-998.

Smith, M. H. 1971. Food as a limiting factor in the population ecology of *Peromyscus*. Ann. Zool. Fennici. 5:109-112.

Smyth, M. Breeding in woodland mice, *Apodemus sylvaticus* and voles *Clethrionomys glareolus* and *Microtus agrestis*, near Oxford. J. Anim. Ecol. 35:471-485.

Stebbins, L. L. 1978. Some aspects of overwintering in *Peromyscus maniculatus*. Can. J. Zool. 56:386-390.

Stickel, L. F. 1968. Home range and travels, p. 373-411 In J. A. king (ed.) Biology of *Peromyscus* (Rodentia). Spec. Publ. No. 2 Amer. Soc. Mammal.

Sullivan, T. P. 1976. Demography and dispersal in island and mainland populations of the deermouse, *Peromyscus maniculatus*. M. Sc. Thesis, University of B. C., Vancouver, B. C.

Terman, C. R. 1968. Population dynamics, p. 412-450 In J. A. King (ed.) Biology of *Peromyscus* (Rodentia). Spec. Publ. No. 2 Amer. Soc. Mammal.

Turner, B. N., and S. L. Iverson. 1973. The annual cycle of aggression in male *Microtus pennsylvanicus*, and its relation to population parameters. Ecology 54:967-981.

Watson, A., and R. Moss. 1970. Dominance, spacing behavior, and aggression in relation to population limitation in vertebrates, p. 167-218 In Animal populations in relation to their food resources. Edited by A. Watson. Blackwell, Oxford.

Watts, C.H.S. 1970. Effect of supplementary food on breeding in woodland rodents. J. Mamm. 51:169-171.

Watts, C. H. S. 1969. The regulation of wood mouse (*Apodemus sylvaticus*) numbers in Wytham Woods, Berkshire. J. Anim. Ecol. 38:285-304.

Wynne-Edwards, V. C. 1962. Animal dispersion in relation to social behaviour. Oliver and Boyd, Edinburgh.

Wynne-Edwards, V. C. 1965. Self-regulating systems in populations of animals. Science, 147:1543-1548.

Zach, R., and J. B. Falls. 1975. Response of the ovenbird to an outbreak of spruce budworm. Can. J. Zool. 53:1669-1672.

Appendix 1

Possible Experimental Problems

Grid 1

I was not satisfied with the Sherman traps which Daphne Fairbairn had been using on this grid. The nature of the trap prohibits one from putting what I consider is sufficient cotton batting and food to keep mice warm and fed over a cold night in winter. The system with the Sherman trap was to use a small piece of artificial cotton and a piece of mouse chow attached to the side of the trap by peanut butter. I used this method for the two trapping periods in November, 1974. During these trapping periods two mice died from having insufficient food and insulation. Two more mice were extremely weak; they had eaten the peanut butter but little of the chow. Neither of the latter two were present on the grid again. A fifth mouse had attempted to chew on the grill at the rear of the trap, its teeth had become stuck in the wire and it was dead. In addition, I regularly caught _Microtus oregoni_ in my Longworth live traps, whereas Daphne Fairbairn caught only dead ones in her Sherman traps. Since I had not lost any mice up to this point in my study, I abandoned the use of Sherman traps and used Longworths from December 1974 onwards. The grid was not trapped on January 8 - 10th, 1975 because of a warning of heavy snowfall. There was an immigration of _M. oregoni_ during the summer of 1975.

Grid 2

This grid was not trapped during the first period in September, 1974. Unfortunately, all the food stations were depleted over this period. The third trapping period in October, 1974 was disrupted by an invasion of a raccoon. The raccoon was seen on the grid, most of the traps were disturbed, and some had blood on them. The second check was not run on January 9th, 1975 because of a snow warning. The catch during the first trapping period in February was reduced because many traps froze. Raccoons or possibly a feral cat were a problem on March 5th, April 17th, May 1st, and June 27 in 1975. This, combined with the large influx of M. oregoni, caused me to abandon this grid a month earlier than I had intended.

Grid 3

I set up this grid at the same time as grid 2, intending to feed it at a lower food level. It became apparent that the populations were not comparable: grid 3 had only half the population of Grid 2. I think that because of its location this grid was similar to Sadleir's Grid B (Sadleir, 1965). His grid was in a small 'island' of forest, and the P. maniculatus population became extinct during his study. Apart from a large influx of M. oregoni after I removed the food stations from this grid, nothing else untoward happened.

Grid 4

The second check on January 9th was abandoned because of snow warnings, and in February many traps were frozen in the first trapping period, which reduced the catch. Raccoons or a cat disturbed the traps on March 20th and 21st and again on April 4 to 5th and May 15th. M. oregoni immigrated onto this grid in late winter and spring.

Grid 5

Again I was not satisfied with the Sherman traps on this grid so I replaced them with Longworths on December 11th, 1974. No trapping was done because of the snow warning in January 1975. After the first removal of food from this grid there was an influx of M. oregoni, which maintained high numbers for the rest of the study.

Appendix 2

Peromyscus: Trappability Of Males (ML) And Females (FM)

Date		Grid 1		Grid 2		Grid 3		Grid 4		Grid 5	
		ML	FM	ML	FM	ML	FM	ML	FM	ML	FM
Nov.	1973	79	82	94	80	100	75			88	70
Dec.	"	88	84	89	82	84	79			97	71
Jan.	1974	51	45	85	71	61	77			79	42
Feb.	"	86	73	80	71	91	99			86	59
Mar.	"	85	60	60	51	82	86			100	68
Apr.	"	100	81	68	71	67	91			77	84
May.	"	89	84	71	61	54	80			94	94
Jun.	"	94	69	89	64	78	100			100	91
Jul.	"	92	70	67	64	100	71	88	85	100	69
Aug.	"	79	91	69	70	100	71	65	83	100	67
Sep.	"	68	75	50	65	80	100	69	50	57	64
Oct.	"	57	67	45	48	92	93	67	59	82	60
Nov.	"	33	67	81	76			75	64	58	62
Dec.	"	86	70	69	82			73	81	50	96
Jan.	1975	89	67	63	74			61	72	78	75
Feb.	"	74	67	59	78			55	64	63	79
Mar.	"	72	82	53	73			60	72	76	78
Apr.	"	73	79	60	68			54	62	79	73
May.	"	75	76	44	68			75	83	93	67
Jun.	"	89	89	41	43					85	63
Jul.	"	64	76	56	100					76	68
Aug.	"	57	70							75	50

Appendix 3

Peromyscus: Minimum Number Alive Males (ML) And Females (FM)

Date	Grid 1 ML	FM	Grid 2 ML	FM	Grid 3 ML	FM	Grid 4 ML	FM	Grid 5 ML	FM
Nov. 1973	12	12	11	11	14	07			12	20
	21	13	17	15	12	07			14	19
Dec. "	25	14	19	18	11	06			16	22
	21	14	20	20	09	07			15	21
	20	16	19	23	09	07			14	18
Jan. 1974	21*	15*	21	23	09*	07			10	13*
	21*	16*	23	30	09*	10			10	13*
Feb. "	18	17	24	30	12	14			09	14*
	16	16	29	37	18	15			09	13*
Mar. "	16	17*	28*	33*	16	13			08	11
	16	16*	31*	34*	13	16			08	13
Apr. "	13	16	31	30	11	20			08	12
	14	14	33	36	10	19			07	10
May. "	15	15	28	27*	09*	16			08	11
	15	16	27	33*	10*	13			09	12
	14	17	26	28*	15*	10			07	11
Jun. "	12	16	18	19*	09	08			07	11
	12	16	20	16*	09	09	06	03	06	12
Jul. "	10	17	22	15*	08	09	15	09	09	11
	11	17	21	17*	07	07	13	12	06	08
Aug. "	09	13	17	16	08	08	15*	12	08	09
	09	14	18	17	07	08	19*	18	06	07
Sep. "	09	15	--	--	--	--	--	--	07*	08*
	12	15	18*	18*	11	07	18	20*	11*	10*
Oct. "	12*	13	19	20	13	11	21	19*	13	10*
	12*	14	20	22	14	10	23	21*	14	12*
	09*	12	14	15	11	07	22	21*	15	12*
Nov. "	07	12	16	19	11	05	20	19	11*	13*
	05	12	16	14			23	13	13*	12*
Dec. "	12	10	16	13			26	17	09	13
	14	10	20	14			27	18	12	14
Jan. 1975	--	--	14*	11			23*	15	--	--
	10	11	16*	11			24*	16	14	16
Feb. "	11	11	19*	15			24*	17*	15*	15
	12	11	22*	17			23*	16*	16*	19
Mar. "	15	15	20*	18			22*	17	15	19
	16	18	20*	22			19*	14	19	21
Apr. "	16	16	22*	20			19*	09*	16	18
	18	14	19*	19			19*	12*	17	18
May. "	18	16	15*	11			16	14	19	19
	18	17	18*	16			16	10	18	19
	21	19	16*	20			11	08	17	18
Jun. "	17	15	17*	20*					15	18*
	14	16	13*	20*					14	16*
Jul. "	08*	14	10*	09					11	15
	08*	12	18*	06					11	14
Aug. "	09*	11							10	13*
	16*	16							20	15*

Appendix 4

Peromyscus Age Classes

Female weights are confounded by the increase in weight associated with pregnancy, so I have considered males only. Taking the data for both breeding seasons for the control grid, I calculated the percentage of males which had scrotal testes in each weight class:-

Weight Class(g)	Number of Males	% of Males Scrotal
10	3	0
11	8	0
12	6	0
13	17	0
14	18	11
15	30	13
16	32	19
17	61	33
18	64	45
19	72	57

The percentage of mice that are sexually mature changes abruptly from 19% to 33% at 17 g. Also the actual number of sexually mature males changes from 6 mice to 20 mice. Therefore, I consider that mice of 17g and heavier are adults. No mice weighing 13g or lower were ever found with scrotal testes, I consider all these mice to be juveniles. Subadults are mice weighing between 14g and 16g. Other workers on P. maniculatus have used the following cutoffs:-

Fairbairn (1976): "All mice weighing at least 15 g were considered to be adult."

Sadleir (1965): Mice "weighing less than 16 g were considered juvenile unless they had either perforate vagina or descended testes."

Sullivan (1977): all mice weighing 17 g or more were adults. Sub-adults weighed from 13 to 16 g and juveniles weighed 12 g or less.

Appendix 5

Peromyscus: Percentage Of Adult Males And Females Breeding.

Date	Grid 1 ML	Grid 1 FM	Grid 2 ML	Grid 2 FM	Grid 3 ML	Grid 3 FM	Grid 4 ML	Grid 4 FM	Grid 5 ML	Grid 5 FM
Nov. 1973	0(5)	75(4)	0(3)	0(1)	0(0)	0(2)			0(2)	67(3)
Dec. "	0(4)	50(5)	0(2)	0(2)	0(1)	0(3)			0(3)	100(1)
Jan. 1974	0(6)	0(5)	0(4)	0(3)	0(2)	0(2)			0(4)	0(2)
Feb.	0(6)	0(3)	0(10)	0(1)	0(3)	0(2)			0(1)	0(0)
"	0(5)	0(3)	0(7)	0(2)	0(3)	0(1)			0(1)	0(1)
Mar.	0(3)	0(1)	26(19)	25(4)	0(5)	0(2)			0(3)	0(0)
"	0(8)	0(3)	73(15)	13(8)	69(16)	0(4)			0(1)	0(1)
Apr.	0(5)	0(4)	78(27)	23(22)	50(15)	10(10)			0(3)	0(3)
"	11(9)	0(2)	89(18)	45(11)	60(10)	38(13)	40(5)	0(2)	25(4)	0(3)
May.	0(11)	20(5)	61(16)	50(24)	50(10)	50(16)	43(14)	25(3)	50(2)	0(3)
Jun.	20(10)	0(2)	100(21)	52(21)	60(10)	46(13)	30(10)	38(3)	50(2)	25(4)
"	20(10)	0(3)	92(24)	82(22)	83(6)	82(11)	10(10)	43(7)	50(2)	17(6)
Jul.	25(5)	0(5)	100(19)	55(20)	100(5)	63(8)	0(9)	82(11)	50(2)	14(7)
"	44(9)	0(9)	86(14)	61(13)	75(4)	50(6)			33(6)	0(1)
Aug.	20(10)	0(10)	89(18)	71(17)	88(8)	67(6)	40(5)	40(5)	50(4)	67(3)
"	36(11)	0(7)	71(14)	60(12)	75(4)	60(5)	0(5)	0(4)	50(2)	43(7)
Sep.	67(9)	0(1)	55(11)	78(9)	60(5)	33(6)	33(9)	0(4)	0(2)	100(5)
"	88(8)	0(8)	73(15)	67(9)	100(4)	29(7)	14(7)	14(7)	67(6)	100(7)
Oct.	67(9)	38(13)	55(11)	89(9)	67(3)	40(5)	0(8)	33(3)	0(0)	67(3)
Nov.	63(8)	83(12)	80(5)	57(7)	80(5)	40(5)	0(11)	50(2)	40(5)	100(1)
"	57(7)	100(9)	25(8)	—	100(4)	—	0(11)	0(4)	25(4)	100(1)
Dec.	0(5)	33(8)	0(3)	0(1)	0(1)	50(2)	0(16)	0(0)	0(0)	0(2)
Jan. 1975	0(4)	29(7)	40(5)	0(0)	0(0)	0(2)	0(11)	0(0)	0(0)	0(2)
Feb.	0(3)	22(9)	29(7)	0(4)	0(3)	0(2)	17(13)	0(4)	0(4)	0(2)
"	50(2)	0(3)	75(4)	15(13)	0(2)	0(2)	42(12)	13(8)	0(0)	0(6)
Mar.	0(1)	0(6)	58(7)	50(8)			39(16)	40(5)	0(6)	0(3)
"	0(2)	0(5)	70(10)	50(8)			57(14)	25(12)	28(8)	0(9)
Apr.	0(2)	0(6)	39(13)	14(7)			64(11)	60(10)	33(6)	46(6)
"	0(5)	0(5)	25(9)	29(7)			70(7)	25(8)	50(4)	—
May.	33(12)	—	14(7)	56(9)			83(12)	33(3)	—	80(10)
Jun.	14(7)	0(3)	20(7)	67(6)			73(11)	67(6)	50(3)	60(5)
"	22(9)	29(7)	27(11)	91(11)			90(11)	75(8)	103(4)	64(11)
Jul.	63(8)	50(6)	78(9)	64(11)			83(8)	50(6)	44(9)	67(12)
"	78(9)	78(9)	67(6)	89(9)				80(5)	75(12)	73(11)
Aug.	100(6)	63(8)	92(12)	83(12)					70(10)	40(10)

Appendix 6

Weather Summary For Nov. 1973 To August 1974

Date	Mean Temp.(F)	Precipit.(ins.)	Sunshine(hrs.)
Nov. 1973	39.6 (-3.3)	7.24 (+1.68)	54.5 (-15.1)
Dec. "	41.5 (+2.6)	9.22 (+2.71)	39.1 (-5.3)
Jan. 1974	36.7 (+0.4)	7.05 (+1.25)	83.8 (+28.5)
Feb. "	40.3 (+0.3)	4.30 (-0.29)	62.9 (-29.6)
Mar. "	43.0 (+0.5)	7.34 (+3.65)	117.1 (-12.4)
Apr. "	48.2 (-0.1)	3.96 (+1.57)	131.0 (-49.0)
May. "	51.0 (-3.3)	4.64 (+2.77)	211.6 (-41.4)
Jun. "	58.2 (-1.4)	0.79 (-0.99)	260.7 (+17.2)
Jul. "	60.6 (-2.8)	2.97 (+1.8)	254.8 (-49.7)
Aug. "	63.2 (+0.5)	0.13 (-1.33)	305.1 (+50.1)
Sep. "	60.3 (+2.7)	0.93 (-1.48)	252.5 (+64.6)
Oct. "	50.5 (+0.4)	2.01 (-2.8)	179.0 (+63.2)
Nov. "	43.6 (+0.7)	7.60 (+2.04)	63.7 (-5.9)
Dec. "	41.6 (+2.7)	7.40 (+0.89)	49.8 (+5.4)
Jan. 1975	36.3 (0.0)	6.80 (+1.0)	57.5 (+2.3)
Feb. "	36.7 (-3.2)	5.22 (+0.63)	69.0 (-23.5)
Mar. "	41.2 (-1.3)	3.80 (+0.11)	173.2 (+43.7)
Apr. "	45.0 (-3.1)	0.93 (-1.46)	177.7 (-2.3)
May. "	53.1 (-1.3)	1.73 (-0.14)	258.4 (+5.4)
Jun. "	57.7 (-1.8)	0.97 (-0.81)	218.0 (-25.5)
Jul. "	64.4 (+1.0)	0.47 (-0.7)	333.5 (+29.0)
Aug. "	60.4 (-2.0)	3.98 (+2.52)	145.7 (-109.3)

The deviation from the 'Normal Monthly Mean' is given in parenthses. These records are from the Vancouver International Airport Atmospheric Station of Environment Canada.

Appendix 7

Peromyscus: Mean Weight Of Males And Females In Each Trapping Period. ML=males And FM=females.

Date	Grid 1 ML	Grid 1 FM	Grid 2 ML	Grid 2 FM	Grid 3 ML	Grid 3 FM	Grid 4 ML	Grid 4 FM	Grid 5 ML	Grid 5 FM
Nov. 1973	16.0	15.6	15.2	13.1	14.4	15.4			15.4	14.6
	14.9	15.7	14.4	14.0	14.2	15.4			15.2	13.8
Dec. "	15.7	15.2	15.1	14.0	14.4	16.7			15.4	14.6
	15.9	15.4	16.1	13.9	15.1	15.2			15.0	14.1
	15.5	14.5	15.8	13.4	15.1	15.4			14.9	13.9
Jan. 1974	16.2	--	16.6	14.5	17.0	15.0			15.2	14.5
	16.8	14.8	18.2	14.9	16.9	14.7			15.5	13.3
Feb. "	16.8	15.7	18.2	16.0	16.4	15.4			15.9	14.0
	17.3	14.8	19.8	17.5	19.0	18.3			15.9	14.8
Mar. "	17.2	15.5	21.2	19.7	19.1	18.6			16.5	15.1
	17.2	15.6	18.6	18.0	18.3	19.6			16.5	14.4
Apr. "	18.3	16.1	20.1	20.3	19.8	19.4			16.5	15.5
	16.8	15.9	19.0	17.9	18.1	16.7			16.3	15.5
May. "	17.1	16.2	18.7	18.5	17.4	18.8			16.0	15.6
	18.1	16.6	18.9	18.2	15.0	17.4			17.2	16.5
	18.1	17.2	18.9	19.6	16.6	17.9			17.6	16.7
Jun. "	17.7	14.8	19.1	18.1	16.8	18.6			15.3	14.8
	17.4	16.8	18.6	17.3	17.0	15.7	17.8	17.0	16.5	15.7
Jul. "	19.9	18.3	19.2	19.4	17.3	18.4	18.3	17.2	17.7	19.3
	18.5	19.1	16.7	17.6	16.0	19.6	18.2	18.8	15.7	19.8
Aug. "	17.9	18.6	16.3	18.3	16.5	17.1	17.1	18.7	16.8	18.7
	16.9	18.0	15.9	15.8	17.0	18.0	17.1	17.8	17.2	16.2
Sep. "	17.0	16.1	--	--	--	--	--	--	12.8	14.5
	16.1	16.6	15.4	14.1	14.5	16.7	15.9	15.2	12.6	13.9
Oct. "	17.7	17.1	16.0	14.3	14.6	14.4	16.4	15.9	15.5	14.6
	16.0	15.4	16.3	15.0	15.3	14.9	16.4	15.2	14.7	13.6
	15.9	16.8	17.2	16.3	15.3	15.1	16.3	16.0	15.5	15.3
Nov. "	16.7	16.7	18.1	17.6	15.3	15.6	16.8	15.2	17.6	17.1
	16.7	17.1	17.9	18.1			16.9	15.8	17.1	16.8
Dec. "	16.3	16.9	17.9	17.9			17.1	15.6	18.0	17.6
	17.8	18.5	17.5	17.7			17.5	15.9	18.7	19.9
Jan. 1975	--	--	17.6	20.1			18.9	17.0	--	--
	18.4	21.1	17.4	19.8			19.4	16.5	16.6	18.0
Feb. "	19.6	20.6	17.1	16.8			19.5	16.6	16.7	17.8
	19.4	21.8	18.0	18.8			20.0	17.1	17.8	16.9
Mar. "	17.0	18.8	18.2	18.5			20.4	16.6	17.9	18.5
	17.1	16.9	17.6	17.4			19.2	17.5	17.7	18.4
Apr. "	17.3	15.9	17.6	18.8			20.4	19.3	15.2	18.0
	17.9	18.6	18.5	18.2			19.0	17.2	16.1	16.4
May. "	18.1	16.9	19.2	21.0			19.3	17.7	16.5	15.4
	18.8	17.0	18.2	18.5			19.3	18.2	16.6	16.6
	18.7	17.2	18.8	19.1			19.3	16.6	17.4	17.3
Jun. "	18.9	18.9	17.7	20.1					17.6	17.9
	19.4	19.0	18.3	17.6					20.0	19.6
Jul. "	18.5	19.7	17.3	20.2					19.6	17.5
	18.3	20.7	15.9	20.0					17.7	19.3
Aug. "	18.3	20.3							17.5	18.5
	15.1	17.1							14.6	15.2

Peromyscus: Instantaneous Relative Growth Rates Of Mice On Grids 1 And 2.

	Grid 1(control)						Grid 2(food)					
	Ad		Sa		Ju		Ad		Sa		Ju	
November 1973	60	-134	127	203	193	539	129	-120	180	-12	231	96
	-136	-149	-15	-281	107	-412	164	-224	188	-126	213	-27
January 1974	396	-25	464	145	532	-66	524	400	652	476	779	551
	13	185	215	82	418	-21	416	753	461	655	506	553
March "	-10	-49	44	107	97	264	238	481	473	741	708	1002
	-84	63	-200	37	-316	12	501	525	1020	940	1540	1352
May "	460	365	-52	285	-564	204	559	487	1085	852	1612	1216
	-63	-367	464	-658	931	-948	204	536	469	742	734	948
	214	1048	-413	1009	-1040	971	359	789	462	1434	565	2078
July "	-405	-7	-474	36	-543	79	-107	639	425	1368	95	2098
	-229	-315	-131	-256	-33	-196	288	-228	543	356	797	941
September "	317	146	-68	387	-453	627	-147	-935	313	9	774	952
	-441	-196	-51	289	338	775	276	877	897	403	1518	-72
November "	-149	5	399	-236	947	-476	264	160	251	574	239	989
	709	227	344	196	-21	165	286	216	538	-50	790	-317
January 1975	115	404	-302	220	-720	36	236	497	951	940	1667	1382
	695	725	1618	1195	2541	1665	668	885	1233	1091	1799	1377
March "	245	622	739	1152	1232	1682	275	552	719	883	1163	1215
	332	272	823	517	1314	763	566	779	1432	1198	2298	1617
May "	98	24	-8	274	-114	524	194	957	252	1627	310	2296
	262	377	547	624	833	872	250	906	189	1080	127	1254
	254	483	411	577	568	671	267	149	358	227	449	305

Multiply each number by 10^{-5} (q)

Data are given for males and females in each age class:-

Ad = adults   Sa = sub-adults   Ju = juveniles

Appendix 9

Peromyscus And Microtus: Straight-line Home Range Calculation

I calculated home range sizes for each animal with all capture points in a straight line by multiplying the number of different capture locations (cap) it visited by the area of these circles:-

Grids 1,5 :   r=7.50m (half the distance between stakes)

Grids 2,3,4 :   r=7.62m (''   ''   ''   ''   ''   )

All vole grids: r=3.81m (''   ''   ''   ''   ''   )

Home Range Area (in square meters)

Grids	1 cap	2 cap	3 cap
1,5	176.7	353.4	530.1
2,3,4	182.4	364.8	547.2
All vole grids	45.6	91.2	136.8

Appendix 10

Microtus: Minimum Number Alive on Grids E, R, and T in Each Three-month Period.

Date	Grid E		Grid R		Grid T	
	ML	FM	ML	FM	ML	FM
Jul Sep 1972	16.3	14.3	20.0	24.9	23.9	23.0
Oct Dec "	22.2	25.0	27.7	37.8	39.5	50.5
Jan Mar 1973	22.0	23.3	34.7	48.9	52.6	71.4
Apr Jun "	26.3	23.0	46.7	58.8	54.7	84.3
Jul Sep "	29.4	26.9	58.3	54.1	77.4	91.3
Oct Dec "	23.8	22.7	46.8	46.5	109.8	109.8
Jan Mar 1974	25.9	21.1	42.3	50.7	86.9	109.1

ML = Males And FM = Females

Microtus: Immigration to Long-term Food Grids.

	Grid E			Grid R			Grid T			Grid M		
	Ad	Sa	Ju	Ad	Sa	Ju	Ad	Sa	Ju	Ad	Sa	ju
Jul Sep 1972	23:17	9:11	12:12	23:15	12:12	4:26	27:16	13:15	8:14	37:33	10:10	12:11
Oct Dec "	7:1	4:3	12:17	7:5	7:6	17:18	8:12	19:19	18:20			
Jan Mar "	10:1	2:7	4:4	12:5	6:9	4:8	22:6	11:12	5:17			
Apr Jun "	25:10	5:15	7:4	24:14	24:16	20:28	24:21	21:27	20:21			
Jul Sep "	10:3	13:9	8:9	7:1	27:8	22:27	9:5	53:37	23:29			
Oct Dec "	0:0	6:2	8:8	3:1	10:7	2:7	9:5	32:40	10:3			
Jan Mar 1973	13:0	4:4	2:6	15:3	7:9	2:3	30:12	7:15	0:5			
Oct Dec "	27:9	29:19	23:27							42:33	37:40	19:22
Jan Mar 1974	39:14	8:17	7:16							60:39	29:40	19:28
Apr Jun "	37:41	7:13	4:6							62:72	36:36	25:37

E = control, R = low-food, T = high-food, M = intermediate-food

Ratio = males:females, Ad = adults, Sa = sub-adults, Ju = juveniles

Microtus: Instantaneous Relative Growth Rates Of Voles On Grids E, R, And T.

	Grid E			Grid R			Grid T		
	Ad	Sa	Ju	Ad	Sa	Ju	Ad	Sa	Ju
Nov. 1972	498/ -61	604/ 148	709/ 358	80/ 93	298/ 145	516/ 197	105/-183	262/ -28	419/ 126
	355/ 298	528/ 364	700/ 431	490/ -75	762/ 62	1035/ 198	411/ -62	565/ 21	718/ 104
Jan. 1973	385/ 17	667/ 155	948/ 293	408/ 368	575/ 535	742/ 702	634/ 597	775/ 622	917/ 847
	358/ 534	440/ 587	522/ 639	141/ 347	129/ 241	116/ 135	246/ 185	361/ 377	475/ 569
Mar. 1973	124/ 100	89/ -34	53/-163	716/ 571	866/ 760	1016/ 948	1178/ 618	1415/ 884	1652/1151
	1768/ 263	2324/ 277	2879/ 292	579/ 227	713/ 251	847/ 275	332/ 739	406/1099	479/1460
May 1973	741/ 754	901/1173	1061/1593	859/1078	1066/1526	1274/1974	1051/ 612	1293/ 891	1535/1170
	635/ 477	842/ 653	1049/ 828	-67/-133	-21/ -40	25/ 53	830/ 251	1079/ 416	1327/ 582
Jul. 1973	341/ 214	467/ 504	592/ 793	39/-206	87/ -59	135/ 89	141/ -44	219/ 45	298/ 134
	63/-237	92/ -43	121/ 201	-258/-557	-142/-432	-27/-306	-289/-371	-213/-267	-146/-164
	-91/ 291	-64/ 251	-37/ 212	-95/-273	-33/-156	29/ -40	163/ 234	255/ 288	347/ 341
Sep. 1973	2/-274	125/ -79	248/ 105	72/ 137	70/ 71	69/ 6	156/ 120	156/ 145	156/ 170
	-215/ -54	-172/ 98	-128/ 251	-121/ -35	-44/ -2	32/ 31	100/ -27	33/ -64	-44/-102
Nov. 1973	-476/-340	-320/-318	-164/-298	256/ -52	235/ -20	214/ 11	87/ 13	195/ 13	303/ 11
	-96/ 125	231/ 149	557/ 173	557/ 439	501/ 339	446/ 333	436/-27	340/ -20	244/ -12
Jan. 1974	553/ 172	691/ 243	825/ 314	396/ 215	510/ 128	624/ 40	460/ 48	559/ 145	659/ 241
	797/ 500	931/ 705	1065/ 911	651/ 695	766/ 819	881/ 944	366/ 531	390/ 597	414/ 663
Mar. 1974	239/ 216	260/ 705	282/1194	188/ 450	172/1000	156/ 155	579/ 418	700/ 643	822/ 863
	207/ 537	208/ 847	209/1157	573/ 641	758/ 944	944/1248	637/ 292	852/ 574	1067/ 856

Multiply each number by 10^5 (q)

E = control, R = low-food, T = high-food

Data are given for males/females in each age class:-

Ad = adults   Sa = sub-adults   Ju = juveniles