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UNIVERSITY OF ALBERTA

# POPULATION DYNAMICS OF REDBACKED AND SINGING VOLES: RESPONSES TO WINTER FOOD ADDITION

BY

SABINE SCHWEIGER

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of M. Sc.

DEPARTMENT OF ZOOLOGY

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UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled "Population dynamics of redbacked and singing voles: responses to winter food addition" submitted by Sabine Schweiger in partial fulfillment of the requirements for the degree of M.Sc.

Stan Boutin

S.A. Boutin, Supervisor

Jan O Murie

J.O. Murie, Committee member

Mark R. T. Dale

M.R.T. Dale, Committee member

Richard C. Fox

R.C. Fox, Committee Chairman

1992/07/31

# ABSTRACT

Populations of redbacked voles (*Clethrionomys rutilus*) in the southwestern Yukon fluctuate in density over several years. Over-winter survival varies between years, and peak fall densities are associated with high survival over the previous winter. Variable winter food and/or changes in predation have been suggested to be two factors controlling over-winter survival.

I supplemented two populations of redbacked voles with winter food from 1987 to 1989, to test the hypothesis that increased winter food increases over-winter survival. I compared the food supplemented grids with two control grids. Over-winter survival was increased in resident females, but not males. I also examined the effect of winter food supplementation on other population dynamics that affect density. Immigration and emigration of adults over the winter were higher on the food addition grids and males and females initiated breeding earlier. Overall, densities declined during the study. I concluded that winter food is necessary for high over-winter survival, but does not ensure a population peak in the fall.

I also compared the responses of singing voles (*Microtus miurus*) to winter food supplementation on one grid with those of a control grid. The addition of food did not increase density through immigration, nor increase over-winter survival. Although initiation of breeding was earlier on the food grid, juvenile recruitment was poorer. Reproduction was not enhanced. These results are contrary to most other food addition studies. Since the data suggested that density of singing voles and redbacked voles was inversely related on the two grids, I examined the possibility of competition. They overlapped both spatially and temporally at trapping stations in the field, but singing voles initiated and won most encounters in arena behaviour trials against redbacked voles. Since singing vole juvenile recruitment was extremely low on the food supplemented grid despite earlier breeding, the possibility exists that the critical level of competition was at the early juvenile stage.

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# CHAPTER 1

## INTRODUCTION

Ecology has been dubbed the 'Economy of Nature' by Ricklefs (1983). Economics brings balance sheets and accountants to mind, totaling credits and debits in columns, and obtaining a final value that reflects the health, vitality and size of the account. Ecologists, in the simplest analogy, use a similar balance sheet, changing credits to immigration and births, debits to deaths and emigration, to monitor the change in the total population density. Ecologists, however, usually obtain the total without having the parts, and ask which of the debts and credits can account for the changes in the total. Other components have been added to the equation, as well as the realization that the components are not necessarily independent. Components can both affect and be affected by virtually every other variable in the equation. Natural systems are very complex, each population in the system having its own balance sheet that is not independent from all others. Add to this, changing environmental conditions, and it is little wonder that ecologists have remained interested in the balance of nature.

Ecologists, by definition, seek the knowledge to understand why populations of animals are distributed in space, time and number (Krebs 1985), striving to determine if there are general principles regulating population densities, or if each population comes with its own unique set of rules governing its population dynamics. Elton (1927) described populations of lemmings in northern Scandinavia that underwent great changes in density, naming the phenomenon 'population cycles'. Since then, there has been considerable interest in trying to explain the causation of these cycles across species and continents.

Although many studies address the problem of cyclic populations, the results to date are at times confusing and hard to assemble into a coherent, comprehensive package. Researchers have, understandably, been interested in testing different hypotheses, and have therefore carried out their work with different approaches, altering grid sizes, species composition (Flowerdew and Gardner 1978, Ylönen 1989) and trapping regimes (Krebs and Wingate 1985). Some studies have been experimental manipulations (Gilbert 1987), while others have been descriptive studies (Korpimäki and Norrdahl 1989). The proximity to removal areas (Schieck and Millar 1986) has been examined. Some work has been conducted on islands (Bujalska 1985), some within exclosures (Saitoh 1989) and still others in laboratories (Ims 1987). No one has been able to answer the question: What makes populations cycle?

Since most populations change in density over time, it is important to define a cyclic population. I will limit the discussion only to cycles of voles. Cyclic populations have a three to five year periodicity, during which t the population is almost extinct for one or two years, and then erupts, changing in density by many-fold (Henttonen *et al.* 1985). Lewontin (1966) developed a mathematical expression to test whether a population is truly cyclic, or merely fluctuates seasonally or irregularly. He called it *s* and is given by the formula

$$s=\sqrt{\frac{\Sigma(\log N_i-\overline{\log N_i})^2}{n-1}}$$

where Ni equals population density at time i, n equals number of years between peak densities. High *s* values indicate cyclic species. Hansson and Henttonen (1985) indicate that the spring crash typical of cyclic populations continues through the summer, resulting in very low autumn densities. This is an important characteristic that separates cyclic from non-cyclic populations.

At a symposium in Finland in 1985 dedicated solely to *Clethrionomys* species, researchers were urged to examine the differences in population dynamics between cyclic populations in northern Scandinavia and the non-cyclic ones in the south, as well as to examine the apparent lack of cyclicity in North American species (Hansson and Henttonen 1985). Gilbert (1987) has provided evidence for at least one population of redbacked voles (*Clethrionomys rutilus*) in North America exhibiting the properties characteristic of cyclic populations. His data pertain only to the four snow-free months of the year. Gilbert found a positive correlation between over-winter survival and subsequent fall density. When survival was high, the population peaked. The natural progression from this work is to examine the factors that could create differential over-winter survival on a large scale.

Two researchers, Saitoh (1989 (*Clethrionomys rufocanus*) and Ylönen (1989 (*C. glareolus*)) have worked year-round trying to understand the population dynamics of cyclic species. Their studies added food in small enclosures, and suggested that differential reproductive output and social system are important in the ability of a population to increase. Neither study was able to explain the differential over-winter survival reported by Gilbert.

In Chapter 2 I present the results from an experiment, in which I supplemented food during winter to two redbacked vole populations to test the hypothesis that food levels influence over-winter survival. I predicted that survival over-winter would increase with supplemental food.

Few studies have examined more than one species of microtine at the same time (Flowerdew and Gardner 1978, (*Apodemus sylvaticus* and *C. glareolus*), Ylonen 1989, (*C. glareolus* and *Micromys minutus*)). They report different responses various species to food addition. I supplemented food to one area that had populations of both *Clethrionomys rutilus* and *Microtus miurus*. In Chapter 3, I examine the results to establish if a food addition had the same responses in these two species. I also examine any evidence of competition between the species.

Overall, I am interested in looking at the balance sheet for these two species in this study area, to see if I can determine which aspects of births and immigration, deaths and emigration can account for changes in density.

## LITERATURE CITED

Bujalska, G. 1985. Regulation of female maturation in *Clethrionomys* species, with a special reference to an island population of *C. glareolus*. Ann.Zool.Fennici 22:331-342.

Elton, C.S. 1927. Animal Ecology. London.

Flowerdew, J.R., and G. Gardner. 1978. Small rodent populations and food supply in a Derbyshire ashwood. J.Anim.Ecol. 47:725-740.

Gilbert, B.S. 1987. Factors limiting growth of sympatric *Peromyscus* and *Clethrionomys* populations in Northern Canada. Thesis, Department of Ecology, Animal Ecology, University of Lund, Sweden.

Hansson, L, and H. Henttonen. 1985. Regional differences in cyclicity and reproduction in *Clethrionomys spp.*: are they related? Ann.Zool.Fennici 22:277-288.

Henttonen, H., A.D. McGuire, and L. Hansson. 1985. Comparisons of amplitudes and frequencies (spectral analysis) of density variations in long-term data sets of *Clethrionomys* species. Ann.Zool.Fennici 22:221-227.

Korpimäki, E., and K. Norrdahl. 1989. Predation of Tengmalm's owls: numerical responses, functional responses and dampening impact on population fluctuations of microtines. Oikos 45:154-164.

Krebs, C.J. 1985. Ecology: The Experimental Analysis of Distribution and Abundance, Third Edition. Harper & Row, Publishers, Inc., New York, New York 10022.

Krebs C.J., and I. Wingate. 1985. Population fluctuations in small mammals of the Kluane Region, Yukon Territory. Can.Field Nat. 99:51-61.

Ims, R.A. 1987. Determinants of competitive success in *Clethrionomys rufocanus*. Ecology 68:1812-1818.

Lewontin, R.C. 1966. On the measurement of relative variability. Syst.Zool. 15:141-142.

Ricklefs, R.E. 1983. The Economy of Nature. Charion Press, Incorporated, New York, New York 10025.

Saitoh, T. 1989. Effects of added food on some attributes of an enclosed vole population. J.Mamm. 70:772-782.

Schieck, J.O., and J.S. Millar. 1986. Can removal areas be used to assess dispersal of red-backed voles? Can.J.Zool. 65:2578-2587.

Ylönen, H. 1989. Temporal variation of behavioural and demographic processes in cyclic *Clethrionomys* populations. Biological research reports from the University of Jyväskylä 16.

# CHAPTER 2

## The effect of winter food supplementation on the population dynamics of *Clethrionomys rutilus*

### INTRODUCTION

While some populations of microtines undergo multi-annual population fluctuations (Elton 1927), others remain relatively stable from year to year and only fluctuate seasonally (Taitt and Krebs 1981). No one has demonstrated unequivocally any one factor or combination of factors that can adequately account for population fluctuations and cycles in a single species, or across species. Researchers have focused on extrinsic factors such as food (Gilbert 1987, Flowerdew and Gardner 1978, Ylönen and Viitala 1989) and predation (Korpimäki and Norrdahl 1989), as well as intrinsic ones such as spacing behaviour (Ylönen 1989) and competition (Turner *et al.* 1974). Batzli (1988) argues that although the cause may be multi-factorial, our comprehension of the effects of single factors is incomplete, and therefore single factor experiments are valuable.

Research on *Clethrionomys* species has increased over the past 15 years, particularly in Scandinavia and northern Europe. Of particular interest is a geographic split which divides the same species into cyclic northern populations and non-cyclic southern populations (see Hansson and Henttonen, 1985 for review). Northern populations are protected from most predators by continuous snow cover for seven months of the year. Populations are thought to be limited by food and reduced by specialist predators that fluctuate with a lag period (Henttonen 1985). Populations in the south are thought to be controlled by density-dependent predation, resulting in seasonal fluctuations below the level of food limitation (Erlinge *et al.* 1983). In North America, *Clethrionomys* has not been studied as extensively as Old World species (Grant 1976; Mihok and Fuller 1981; West 1977, 1982; Whitney and Feist 1984; Fuller 1985; Gilbert *et al.* 1986), and never with the same north-south comparison.

In the southwestern Yukon, Gilbert *et al.* (1986) studied a fluctuating population of red backed voles during the snow-free period for seven years, and concluded that high winter survival led to a population eruption the following autumn. They suggested that the two factors most likely to contribute to this differential winter survival were food supply and predation. Few experimental manipulations have been conducted during the non-breeding season to test either of these two hypotheses (Saitoh 1989).

In the past decade, the addition of food to a population has been a popular single-factor experiment (Boutin 1990). In *Microtus* species, food supplied during the reproductive season can increase density through increased reproductive output and immigration, but it does not prevent a population decline (Batzli 1986; Cole and Batzli 1978; Ford and Pitelka 1984; Taitt *et al.* 1981). Flowerdew and Gardner (1978) found a positive correlation of winter survival with a natural seed crop fluctuation in wood mice (*Apodemus spp.*), but they were not able to make any quantitative comparisons with controls. Andrzejewski (1975) and Saitoh (1989), in their respective food-supplemented populations of *Clethrionomys spp.*, found no increase in survival. Ylönen (1989) has conducted the most recent, comprehensive, year-round food-addition study on the population dynamics of *Clethrionomys glareolus* and *C. rufocanus*. His conclusions suggest that the social structure of microtines is flexible, being determined by habitat patchiness, food distribution and above all, food quantity. Increased food may promote congregations of individuals over the winter, allowing individuals to become familiar with one another and decreasing social strife in the following breeding season. Kin selection may enhance juvenile recruitment and survival in *Microtus spp.* (Boonstra 1984), which may lead to a population increase. Both Gilbert *et al.* (1986) and Ylönen (1989) suggest that winter food plays an important role in the population cycles of *Clethrionomys spp.* by simply increasing survival or through social changes.

In this paper, I present the results of an experiment in which I supplemented the food of *Clethrionomys rutilus* populations during the periods of snow cover, 1987-1989. I tested the hypothesis that survival during winter was determined by winter food and that high over-winter survival could lead to a fall peak density.

## METHODS

### *Study area*

This study was conducted in the Shakwak Trench of the southwestern Yukon, Canada, (61°N, 138°W). Kluane Lake is prominent at the north end of the valley, at an elevation of approximately 1000 m. The habitat is open boreal forest (10-50% cover: Nams, pers. comm) as described by Douglas (1974), with white spruce (*Picea glauca*) providing the dominant canopy cover. Moss was the predominant ground cover on the study areas, with bearberry (*Arctostaphylos spp*), lupine (*Lupinus arcticus*), horsetail (*Equisetum spp.*) and grass (*Festuca altaica*) being the predominant herbaceous layer. All areas had standing dead spruce trees and an estimated 10% of the ground covered by deadfall.

### *Experimental design and trapping regime*

I used four trapping grids, each 1.8 ha in size. The grids are denoted as "F" for food supplemented, and "C" for control, followed by a numeric corresponding to the replicate number. R1 grids (F1 and C1) were located 7 km east of Kluane lake, adjacent to the north side of the Alaska Highway (Figure 2.1), and were established in 1984 (Gilbert *et al.*). They were approximately 102 m apart at the closest point, with no similar habitat between them. R2 grids were established 1 km east of Kluane Lake on the south side of the Alaska Highway. F2 was surveyed in 1984 and trapped for one summer. C2 was surveyed in July of 1987. The grids were 129 m apart at the closest point. The habitat between the grids was not continuous forest. An old pipeline with a 36 m wide strip of predominantly grasses separated the two grids. The most apparent difference between the two areas was the greater abundance of willow (*Salix spp.*) on R1. As well, R1 was approximately 90 m higher than R2.

Each grid was laid out in a 10X10 pattern with stations 15 m apart. A Longworth trap, baited with whole oats and apple and supplied with cotton for nesting, was placed at every other trapping station. A trapping session consisted of setting all the traps on the grid in the evening before sunset, checking all traps for two to five consecutive mornings and evenings, and locking the doors open on the final morning. Each animal that was captured was tagged with a fingerling fish tag. Sex, weight, species, location, and reproductive status were recorded for each capture. Males were scored as abdominal if their testes could not be detected, and scrotal (indicating reproductively active) if they could. For each female, I scored vaginal opening: perforate (initial sign of the onset of reproduction or having just given birth) or non-perforate (non-reproductive or between litters); nipple condition: small (non-reproductive), medium, and lactating; pubic symphysis: closed (no recent birth) or open (litter recently born); and obviously pregnant or not pregnant. All animals were released at the site of capture.

Grids were initially trapped in late August-early September, 1987. I then established 25 winter trapping stations per grid at stations where females were repeatedly captured. Each of these stations consisted of a plywood box containing two Longworth traps. The box had two holes at ground level with tunnel extensions that linked the box to surrounding deadfall. These trapping stations also served as feeders on F1 and F2. Unshelled sunflower seeds were supplied *ad libitum* from 1 September (post-reproductive) until snow melt the following spring. Sunflower seed was added to the two food grids after each trapping session during the snow-cover period, and any remaining seed was scooped out before a trapping session was initiated. In the second winter, I increased the number of trapping stations on each grid to 50 with the addition of 25 plastic buckets, each of which contained one Longworth trap. These were used strictly as trapping stations, and received no sunflower seed on the food addition grids.

Trapping sessions were conducted year round, from August 1987 to August 1989. During the snow-free periods, grids were trapped biweekly for two consecutive mornings. During the snow-cover periods, I trapped voles for five consecutive mornings every month.

### *Classification of individuals*

I divided individuals into two categories for analysis. Animals caught during a single trapping session were classified as transients and animals caught in more than one session were termed residents.

## RESULTS

### *Density estimates*

For all density estimates, I used 2.3 hectares as the effective area trapped. This was determined by including a band width of 7.5 m (1/2 the distance between traps) around the perimeter of the grid (Stenseth and Hansson 1979). I used the program Capture (White *et al.* 1982) to estimate the number of voles on the grid during each trapping session. The estimated number of voles (with 95% confidence limits) on each of the four grids over the two year study is shown in Figure 2.2 for R1 and Figure 2.3 for R2. As MNA (minimum number alive) is most commonly used in microtine studies, I compared Capture estimates with MNA estimates. Capture estimates were lower than MNA, with the food addition replicates being on average 14.2% and 17.8% lower, and the two controls being on average 5.8% and 6.7% lower.

### *Density Changes*

Densities on the food addition grids were not initially different from the controls, but increased immediately with the addition of food in late August, to a maximum difference in February 1988 of 4.8-fold on F2 and 4.6-fold on F1. Both F2 and F1 declined during the spring and summer 1988 to the point that densities were no longer different between control and experimental grids. With the addition of food in early September 1988, the food grids increased again.

The control grids decreased on average more than 50% from 1 September 1987 to 1 May 1988. In the same time period, F1 decreased only 10% while F2 increased 74%. All grids, however, decreased between 50% and 60% from September 1987 to September 1988. During the winter of 1988-89, both control grids declined again by almost 50%, while both food grids showed a net increase of 14% and 56% on F1 and F2 respectively. The overall pattern of density change on the control grids was one of decline; C1 decreased 86% while C2 decreased 53%. F1 had the same overall pattern, declining 74%. Only F2 was different, having an overall increase in density of 47% from September 1987 to August 1989. The addition of food altered the pattern of density change on only one of the replicates when compared to the control grids.

## *Causes of Population Change*

### *Recruitment*

Animals that weighed 20 g or less and had a juvenile pelage when first captured were classed as juveniles (Gilbert and Krebs 1986). Juveniles were trapped on the food addition grids earlier than on the control grids in both years of the study (Figure 2.4). In the second winter the difference was particularly pronounced, with a juvenile appearing on each of F1 and F2 in the first week of April 1989. The first juveniles caught on both C1 and C2 were juveniles that had been tagged previously on food grids. The first untagged juvenile was caught 20 June 1989 on C2, a full 12 weeks later than on F2.

Fewer juveniles were caught on the two control grids than their food addition counterparts. In 1988, 18 juveniles were caught on C1 and 12 on C2, compared with 46 on F1 and 37 on F2. In 1989, these totals were two, five, 21 and 46 respectively. The totals for the second summer are likely an underestimate, as the last trapping session was 15 August 1989, at which time many females were still reproductive. In 1988, juveniles on F1 and F2 were caught well into the fall and early winter (Figure 2.4).

### *Immigration*

An adult animal was classified as an immigrant if it was new to a grid at any time after the initial August 1987 trapping period. I examined the effects of year (1987-88, 1988-89), time period (fall, winter, spring) and treatment (food addition, control) on number of immigrants by a three-way ANOVA. The food addition grids consistently had more immigrants than the controls (Figure 2.5) ($P<0.001$, $F=27.064$, $df=1,12$). Fewer immigrants were caught during the second year of the study, regardless of treatment ($P<0.001$, $F=17.321$, $df=1,12$).

### *Disappearance of Individuals*

An animal was classified as having disappeared from a grid if it was never caught on that grid again. The total number of animals disappearing in a given time period was compared between treatment and year (Figure 2.6). A three-way ANOVA, with year, time and treatment as main effects, revealed that fewer animals disappeared on the control grids than on the food addition grids ($P<0.001$, $F=27.518$, $df=1,12$), as well as on both types of grids during the second year of the study ($P<0.001$, $F=29.976$, $df=1,12$). When these results are coupled with the immigration results (Figure 2.5), it is evident that the turnover of individuals on food grids was higher than that on control grids.

### *Survival*

I defined over-winter survival as the proportion of animals remaining in the spring that were caught during the snow-cover period. There was no difference in winter survival between any of the treatments when all individuals were considered. However, if transients are excluded, I found that females survived better in both years on the food addition grids than on the controls (P=0.027, F=11.626, df=1,4), whereas males survived equally well on food addition grids and control grids (P=0.407, F=0.858, df=1,4)(Table 2.1).

### *Population Dynamics of Residents*

Despite the differences in survival between transients and residents, the pattern of density change when only residents were considered did not change from that of the entire population (Figure 2.7). Since the number of animals decreased when considering only residents, I used the MNA estimates to compare the patterns of density change between the entire population and the residents. The most noteworthy difference was on R1 in the fall of 1989. When the entire population was considered, both control and food addition grids showed parallel population increases, while the MNA of residents showed a parallel decrease over the same time period. This suggests that a large cohort of animals appeared on the grid for a single session, and were thus included in the total population estimate. The timing of this influx corresponds to when a large number of juveniles were trapped on the grids late in the second summer (Figure 2.4), and may explain why no population peak was realized. The animals either did not survive or else did not remain on the grid.

The ratio (food addition:control) of residents produced results similar to those obtained for the entire population, with a maximum difference in the winter of 1987-88 of 6.5-fold on R2 and 4.8 on R1. The minimum ratio for both pairs of grids was one at the start of the study as well as in the following fall and both springs.

### *Initiation Of Breeding*

I examined the reproductive condition of individuals to determine the initiation of breeding. Males were scrotal when breeding started, and females were perforate, followed by obvious pregnancy and lactational tissue in subsequent trapping sessions. I did not trap any of the grids between 22 February and 1 April 1988, and therefore missed the initiation of breeding in males. On 1 April 1988, all of the males on F1 (n=14) and F2 (n=17) were already scrotal, whereas on C1, 77% (n=13) were reproductive. None of the males on C2 were scrotal (n=11), but all males on all grids were scrotal in the next week.

All males were known to be [illegible] abdominal in early December of 1988. On 24 Decembe[illegible]% of males on F2 were already scrotal (n=9). By 1 February 1989, 89% of males on F2 (n=9) and 67% on F1 (n=3) were scrotal. Two scrotal males were caught on C1 during the same trapping session, but were known to have spent the winter on F1 up to that time. The first male that over-wintered on C1 became scrotal 15 March 1989 (n=5). It was not until 15 April that all males on C1 were scrotal. The first scrotal male to be caught on C2 spent the winter on F2 (10 March 1989). At this time, all other males on C2 were still abdominal (n=3), with the first C2 scrotal males caught on 1 April (100% scrotal, n=3). Male initiation of breeding was advanced on the food addition grids.

Females initiated breeding earlier on the food addition grids. On 1 April 1988, 89% (n=9) and 93% (n=14) of females caught on F1 and F2 respectively were perforate, compared with 17% (n=6) and 0% (n=4) on C1 and C2. However, all females were noticeably pregnant within three weeks. In 1989, no females were breeding in December (compare with males on F2). Females on F2 were not caught again until 10 March 1989, at which time all (n=4) females were already lactating, indicating that they already were nursing young. No females on F1 were caught for comparison. On C2, the one female was still non-reproductive. The first pregnant female on a control was caught 1 May 1989.

### *Estimated Juvenile recruitment*

I scored each female as having had a litter based on weight gain and sudden decreases, as well as presence of lactational tissue. Using an average litter size of 6.25 (Krebs and Wingate 1985), I calculated the potential number of juveniles born on each of the grids. In the summer of 1988, C1 had seven litters, for a total of 43 juveniles. F1 had 20 litters, giving rise to 125 potential juveniles, C2 nine litters and 56 juveniles and F2 25 litters for a potential 156 juveniles. The estimated number of recruits per litter was poor, never exceeding 2.7 (Table 2.2).

### *Inter-Grid Movements*

Over the course of the two-year study, a total of 43 individuals were caught on a grid different from their grid of initial capture. Twenty-five animals were not caught on their original grid again, and are therefore considered "one-way movers". Of the 16 males that were "one-way movers", 56% (n=9) moved from food addition grids (high density) to control grids (low density). Most of the movement occurred in the spring (50%, n=8) and early summer (31%, n=5), with no males moving during the winter. Fifty percent of the "movers" were born on the grid, of which 63% (n=5) were classified as residents before leaving. In total, 50% (n=8) of individuals were classified as residents on their original grid. None of these became residents on the second grid, whereas all the non-residents on the first grid established themselves on the second grid.

Nine females moved in one direction, with 67% (n=6) moving from high to low density. The majority moved in the spring (33%) and early summer (44%), with one individual moving in each of fall and winter. Of the six (67%) born on their original grid, only one was resident before "moving". A total of six (66%) became residents on the second grid, none having been residents on the original grid. Of the juvenile females that stayed on the food grid where they were born (n=23), only 25% reproduced in their first summer, whereas 100% of the juvenile females "moving" to a control grid (n=5) bred in their first summer.

## DISCUSSION

I increased over-winter survival of resident female *Clethrionomys rutilus* in two consecutive years by supplemental feeding. Fed populations achieved over-winter survival similar to that found by Gilbert (1987) in the winter preceding peak densities. Saitoh (1989) and Jensen (1982) found no difference in over-winter survival of food supplemented populations of *C. rufocanus bedfordiae* and *C. glareolus*. Flowerdew and Gardner (1978) noted increased survival of *C. glareolus* but not of *Apodemus sylvaticus* in the same natural food addition. Those studies did not distinguish between residents and non-residents, which was important in this study.

I was not able to increase survival of male *C. rutilus*. The populations on all grids declined by at least 50% after the snow had disappeared. The initiation of reproduction in the control populations occurred shortly before this event. Of the individuals that were known to move from grid to grid, most were males, and the predominant time for movement was in the spring. Survival of individuals therefore can be underestimated if animals simply disappear from grids, and are not trapped elsewhere. Thus emigration could explain why the survival of males was not increased in this study. Flowerdew and Gardner (1978) reported the same differential over-winter survival between the sexes in *A. sylvaticus*.

The addition of winter food increased the winter density of *Clethrionomys* up to six fold through immigration, and advanced onset of breeding. These two results are the most common response to food addition in small mammals (Boutin 1990). The density of *Clethrionomys* on the food addition grids was not maintained over the course of the summer, however, and all grids declined in density.

The movement of individuals to surrounding areas may account for the apparent decline and introduces another factor, that of scale, could be central to understanding how and when populations erupt. Population fluctuations occur over large areas, and not on the small scale of my experiments. The surrounding population density is therefore important to consider in such an experiment. I created a density gradient similar to that created by experimental removal, and my results support the arguments of Schieck and Millar (1986) that dispersal sinks are not a good measure of the number and age-sex structure of animals, as the density gradient draws animals away from the higher density area. I propose that the food addition grids were artificial source populations that then populated the surrounding areas. Although the data presented here on the movement and success of individuals that leave a grid are not conclusive, they do give evidence to refute the assumption that animals that disappear from a study site do not survive, and can therefore be disregarded in terms of population dynamics. An effort must be made to determine the importance of movement in a population with a heterogeneous dispersion of individuals. My results emphasize the need for continuing research on the dispersal of small mammals as a factor leading to population stabilization or fluctuation.

It may be relevant that winter breeding in the populations of the southwestern Yukon has not been reported (Gilbert 1987). Although winter food may be important to winter survival, it is either not naturally abundant enough or available enough to enhance breeding significantly. My experiment demonstrates that voles in this population are capable of winter breeding. The differences observed in breeding between my manipulated populations and naturally occurring ones may be a function of the manner in which the seed was distributed. Food was added in a clumped manner at food stations. Naturally, the seed from spruce trees is dispersed over time, starting in the fall, and continuing over several months. The seed is therefore dispersed in a three dimensional fashion - thinly over a large area and embedded in successive layers of snow. I would predict that foraging costs associated with obtaining food would be higher than in my experiment. Voles are able to increase their energy enough to increase survival in peak cone years, but not enough to breed earlier. This assumes that there is an energy threshold that must be attained before an animal can become reproductive. In the winter of 1987-88, the onset of breeding was not greatly enhanced over the control areas, whereas in the winter of 1988-89, it was. As densities on grids were higher in the first winter, it is probable that the minimum energy threshold was not attained as early as in the next winter.

Populations on the food addition grids resembled the increase phase of a cycle before the peak. Winter survival of females was high, breeding was initiated in the winter, and juveniles recruited to the population during the snow cover period. Only a small proportion of juvenile females recruiting to the manipulated populations bred in their first year. The population did not, however, reach peak numbers, because, I contend, of the heterogeneity in density of surrounding areas. Juveniles should breed in the year of their birth, as the probability of surviving to the following summer is low (Gilbert *et al.* 1986), but females need to find an empty territory to do so (Bujalska 1985). The only way that a female knows that she has been born into a peak year is to make forays into the surrounding areas. In years of high density, the juveniles would soon discover high densities of hostile, territorial females everywhere, and the best strategy may well be to return home and live with kin (Ylönen 1989). Apparent juvenile recruitment to the population could therefore be higher, as well as juvenile survival. Dispersal would be low.

Enclosure experiments, such as those of Saitoh (1989) and Ylönen (1989), may have underestimated the importance of dispersal of *Clethrionomys* at high density, as they reported no adverse effects on the population with increasing density. This may simply be a case of frustrated dispersal (Lidicker 1975), with kin aggression being low.

Populations in North America are not thought to cycle in the same manner as the northern Scandinavian populations (Hansson and Henttonen 1985), despite experiencing similar environmental factors, including variable seed mast years, snow cover over long periods of the year, and varying numbers of specialist predators. The presence of these three factors only in northern Scandinavia is used to explain why populations in the north cycle, while in the south they are stable (Erlinge *et al.* 1983). It is not clear to me why populations in North America do not cycle. Populations in southern Scandinavia are not thought to be food limited; rather they are regulated by generalist predators that switch between species (Erlinge *et al.* 1983). A characteristic of southern populations is their constant, but low over-winter survival. In a study by Flowerdew and Gardner (1978), massive cone crops increased density and survival significantly and produced a fall peak. This suggests to me that southern populations are also food-limited over the winter. This should raise critical comment on the hypotheses thought to control the cycles in Scandinavia.

I propose that abundant winter food is the first step necessary for a population peak. High winter food does not guarantee that a population peak will ensue. Sporadic disease, early thaws or low snow pack may prevent a peak from being realized. Localized food abundances do not result in wide-spread population increases, as other factors such as spacing behaviour and dispersal dilute any effects of increased density. Only with widespread abundant food supply is habitat saturation realized. Juveniles stay at home, minimizing social antagonism from strangers and do not breed in their first year. In most cases, populations then decline. The cause for the decline is not known. There may be several reasons for the decline, two of which are food limitation and predation. If the voles are food-limited after the peak, then adding food over very large areas should keep the populations high. An alternative test of this idea is to find areas where the food has remained high for more than one year and see if the population has remained high. Conversely, one could find areas where populations have remained high or have not followed the typical, dramatic crash, and ask why not? Past experiments (including this one) that have added food, yet have not been able to prevent the decline, are not conclusive proof that food is not critical during this period, as food has been added over much too small an area to mimic natural, widespread food abundance.

An alternative to the food limitation hypothesis is that specialized predators increase in density with a lag phase to the voles, and are able to cause the decline. If that is the case, then widespread food additions will not prevent a decline. Any localized populations erupting during the decline phase may attract predators (prey "hot spots"), preventing these populations from "seeding" the rest of the area. Only after the predators decline can the vole populations increase again. The definitive test of this predator hypothesis would be large scale winter food addition after the predators have declined, and in a year where natural winter food is not abundant.

I predict that when food is naturally abundant, it will be found over a large area, leading to an increase in winter survival and body condition of residents, which in turn will give rise to a peak in the fall population due to habitat saturation. The mechanisms causing the populations to cycle with a defined periodicity in northern Scandinavia still need to be determined. Larger scale, manipulative research that compares north with south in both Scandinavia and North America might shed light on to the mechanisms.

We need to quantify natural food abundance, so comparisons can be made between areas. Long-term studies will help eliminate conclusions based on chance happenings. Although voles are small creatures, I think that it is about time that we started to "think big", both in terms of the size of the area manipulated and monitored when trying to determine what causes the populations to fluctuate and over a several year span.

## LITERATURE CITED

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

Batzli, G.O. 1986. Nutritional ecology of the California vole: influences of food quality on reproduction. Ecology 67:486-412.

Batzli, G.O. 1988. The role of nutrition and carrying capacity in models of small rodent population dynamics. Oikos 52:224-226.

Boonstra, R. 1984. Aggressive behaviour of adult meadow voles (*Microtus pennsylvanicus*) towards young. Oecologia 62:126-131.

Boutin, S. 1990. Food supplementation experiments with terrestrial vertebrates: patterns, problems and the future. Can.J.Zool. 68:203-220.

Bujalska, G. 1985. Fluctuations in an island bank vole population in the light of the study on its organization. Acta Theriol. 30: 3-49.

Cole, F.R., and G.O. Batzli. 1978. Influence of supplemental feeding on a vole population. J.Mammal. 59:809-819.

Douglas, G.W. 1974. Montane zone vegetation of the Alsek River region, southwestern Yukon. Can.J.Bot. 52:2505-2532.

Elton, C.S. 1927. Animal Ecology. London.

Erlinge, S., G. Göranson, L. hansson, G. Högstedt, O. Liberg, I.N. Nilsson, T. Nilsson, T. van Schantz and M. Sylven. 1983. Predation as a regulating factor on small rodent populations in southern Sweden. Oikos 40:36-52.

Flowerdew, J.R., and G. Gardner. 1978. Small rodent populations and food supply in a Derbyshire ashwood. J.Anim.Ecology. 47:725-740.

Ford, R.G., and F.A. Pitelka. 1984. Resource limitation in populations of the California vole. Ecology 65(1):122-136.

Fuller, W.A. 1985. Demography of *Clethrionomys gapperi*, parapatric *C. rutilus*, and sympatric *Peromyscus maniculatus* in northern Canada. Ann. Zool. Fennici. 22:229-241.

Gilbert, B.S. 1987. Factors limiting growth of sympatric *Peromyscus* and *Clethrionomys* populations in northern Canada. Thesis, Department of Ecology, Animal Ecology, University of Lund, Sweden.

Gilbert, B.S. and C.J. Krebs. 1986. Effects of extra food on *Peromyscus* and *Clethrionomys* populations in the southern Yukon. Oecologia 51:326-331.

Gilbert, B.S., C.J. Krebs, D. Talarico and D.B. Cichowski. 1986. Do *Clethrionomys rutilus* females suppress maturation of juvenile females? J.Anim.Ecol. 55:543-552.

Grant, P.R. 1976. An 11 year study of small mammal populations at Mont St. Hilaire, Quebec. C.J.Zool. 54:2156-2173.

Hansson, L., and H. Henttonen. 1985. Gradients in density variations of small rodents: the importance of latitude and snow cover. Oecologia 67:394-402.

Henttonen, H. 1985. Predation causing extended low densities in microtine cycles: further evidence from shrew dynamics. Oikos 44:156-157.

Jensen, T.S. 1982. Seed production and outbreaks of non-cyclic rodent populations in deciduous forests. Oecologia 54:184-192.

Korpimäki, E. and K. Norrdahl. 1989. Predation of Tengmalm's owls: numerical responses, functional responses and dampening impact on population fluctuations of microtines. Oikos 54:154-164.

Lidicker, W.Z.,Jr. 1975. The role of dispersal in the demography of small mammals. Pp. 103-128, in Small mammals: their productivity and population dynamics (F.B. Golley, K. Petrusewicz, ans L. Ryszkowski,eds.). Cambridge Univ. Press, London, 451 pp.

Mihok, S. 1979. Behavioural structure and demography of subarctic *Clethrionomys gapperi* and *Peromyscus maniculatus*. Can.J.Zool. 57:1520-1535.

Saitoh, T. 1989. Effects of added food on some attributes of an enclosed vole population. J.Mammal. 70(4):772-782.

Schieck, J.O. and J.S. Millar. 1986. Can removal areas be used to access dispersal of red-backed voles? Can.J.Zool. 65:2575-2578.

Stenseth, N.C. and L. Hansson. 1979. Correcting for the edge effect in density estimation: explorations around a new method. Oikos 32:337-348.

Taitt, M.J., and C.J. Krebs. 1981. The effect of extra food on small rodent populations: II. voles (*Microtus townsendii*). J.Anim.Ecology 50:125-137.

Turner, B.N., M.R. Perrin, and S.L.Iverson. 1974. Winter coexistence of voles in spruce forest: relevance of seasonal changes in aggression. Can.J.Zool. 53:1004-1011.

West, D.S. 1977. Midwinter aggregation in the northern red-backed vole, *Cletnrionomys rutilus*. Can. J. Zool. 55:1404-1409.

West, D.S. 1982. Dynamics of colonization and abundance in central Alaskan populations of the northern red-backed vole, *Clethrionomys rutilus*. J. Mammal. 63:128-143.

White, G.C., D.R. Anderson, K.P. Burnham and D.L. Otis. 1982. Capture - recapture and removal methods for sampling closed populations. Los Alamos National Laboratory, LA 8787-NERP, Los Alamos, New Mexico, U.S.

Whitney, P. and D. Feist. 1984. Abundance and survival of *Clethrionomys rutilus* in relation to snow cover in a forested habitat near College, Alaska. In Merritt, J.F. (Ed) Winter Ecology of Small Mammals. Carnegie Museum of Nat. Hist. Spec. Publ. 10:113-119.

Ylönen, H. 1989. Temporal variation of behavioural and demographical processes in cyclic *Clethrionomys* populations. Biological Research Reports from the University of Jyväskylä 16.

Ylönen, H., T. Mappes, and J.Viitala. 1990. Different demography of friends and strangers: an experiment on the impact of kinship and familiarity in *Clethrionomys glareolus*. Oecologia 83:333-337.

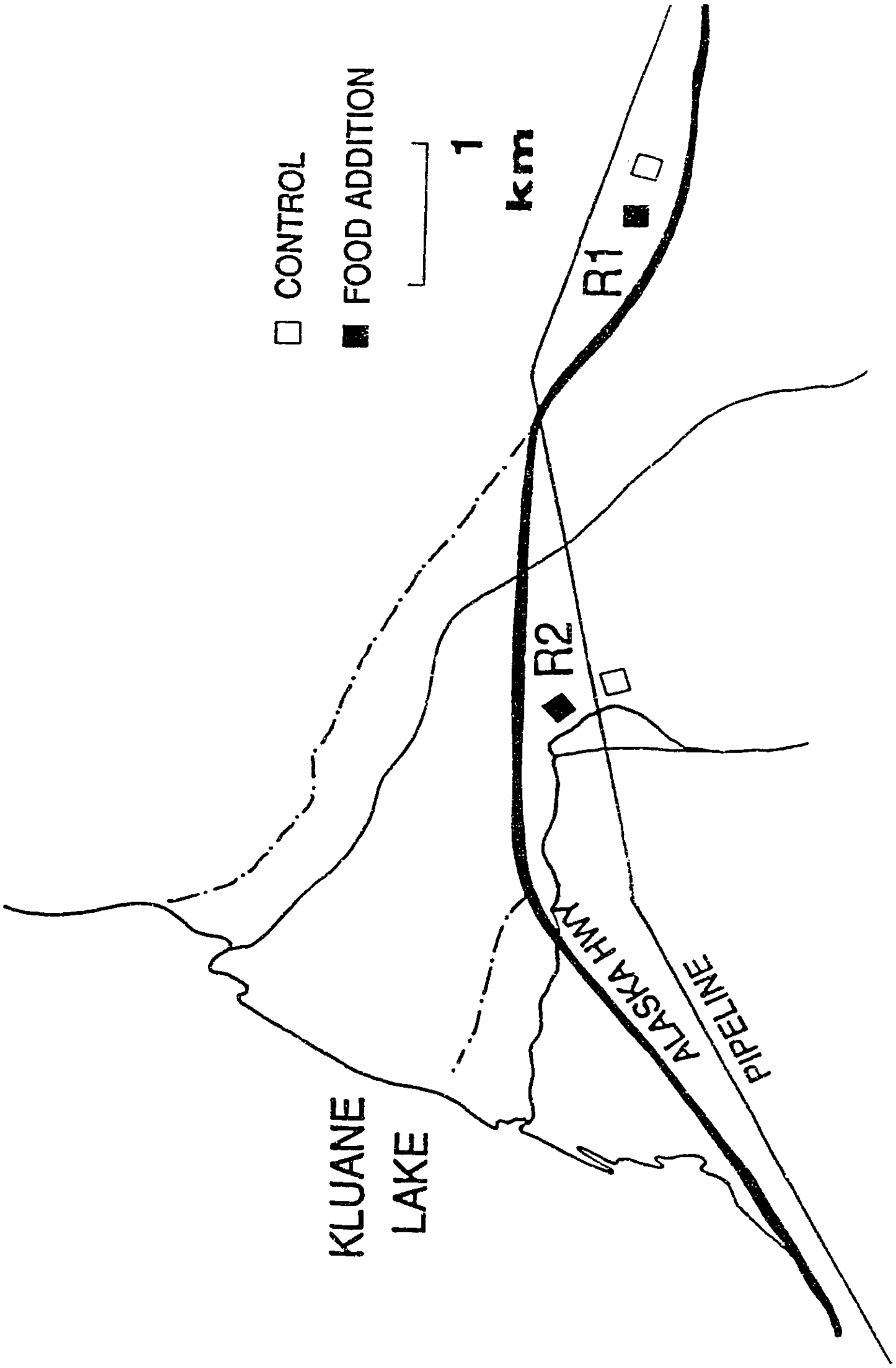


**Figure 2.1** Map of study area, near Kluane Lake, Yukon. R1 (C1=control 1, F1=food addition 1). R2 (C2=control 2, F2=food addition 2).

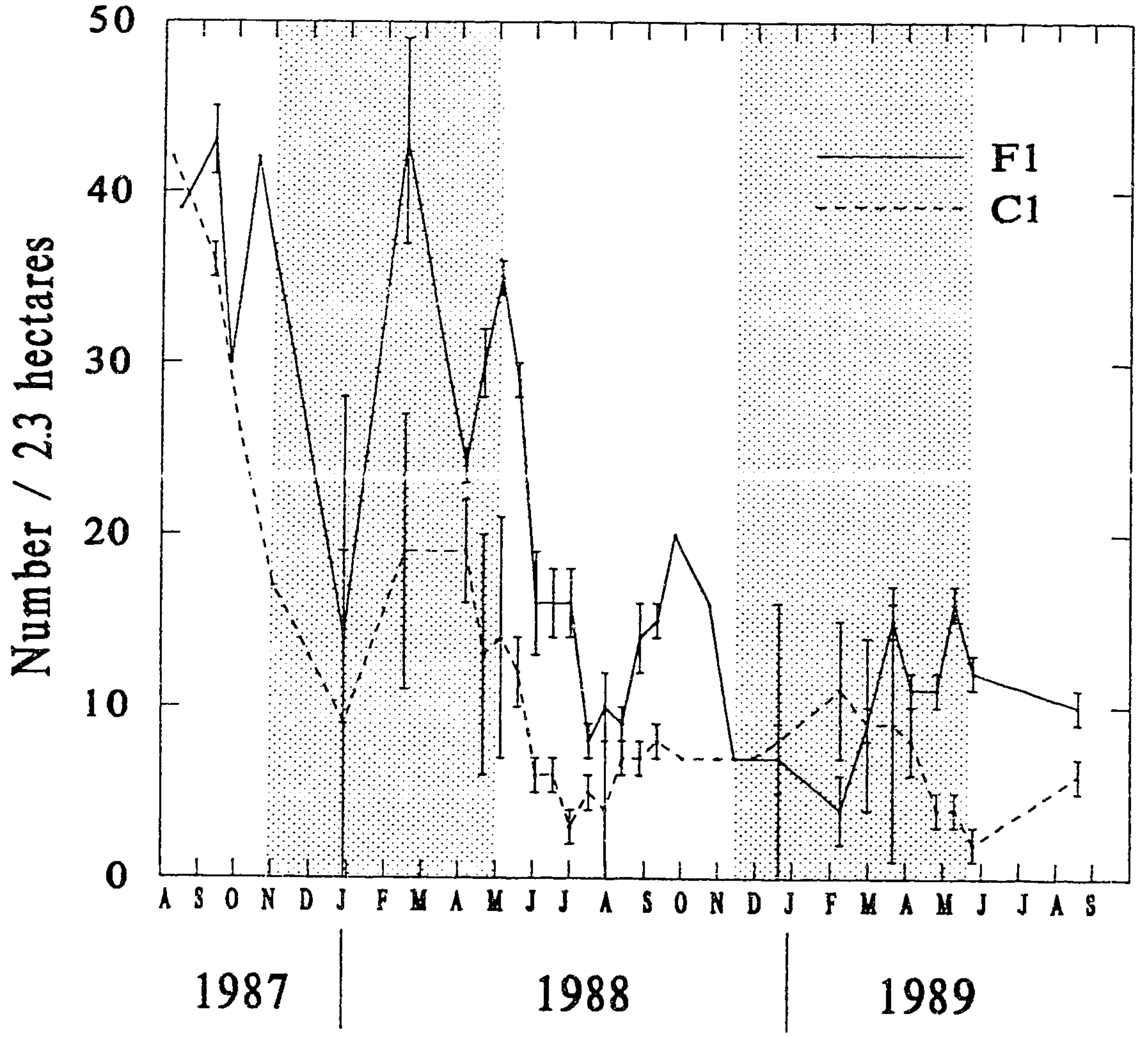


**Figure 2.2** Population estimates of *Clethrionomys rutilus* on R1 from August 1987 to August 1989. Snow cover period indicated by stippled area. Food addition started on 1 September each year and ended with disappearance of snow cover. Bars = 95% confidence limits. Estimates obtained from Capture (White *et al.* 1982).

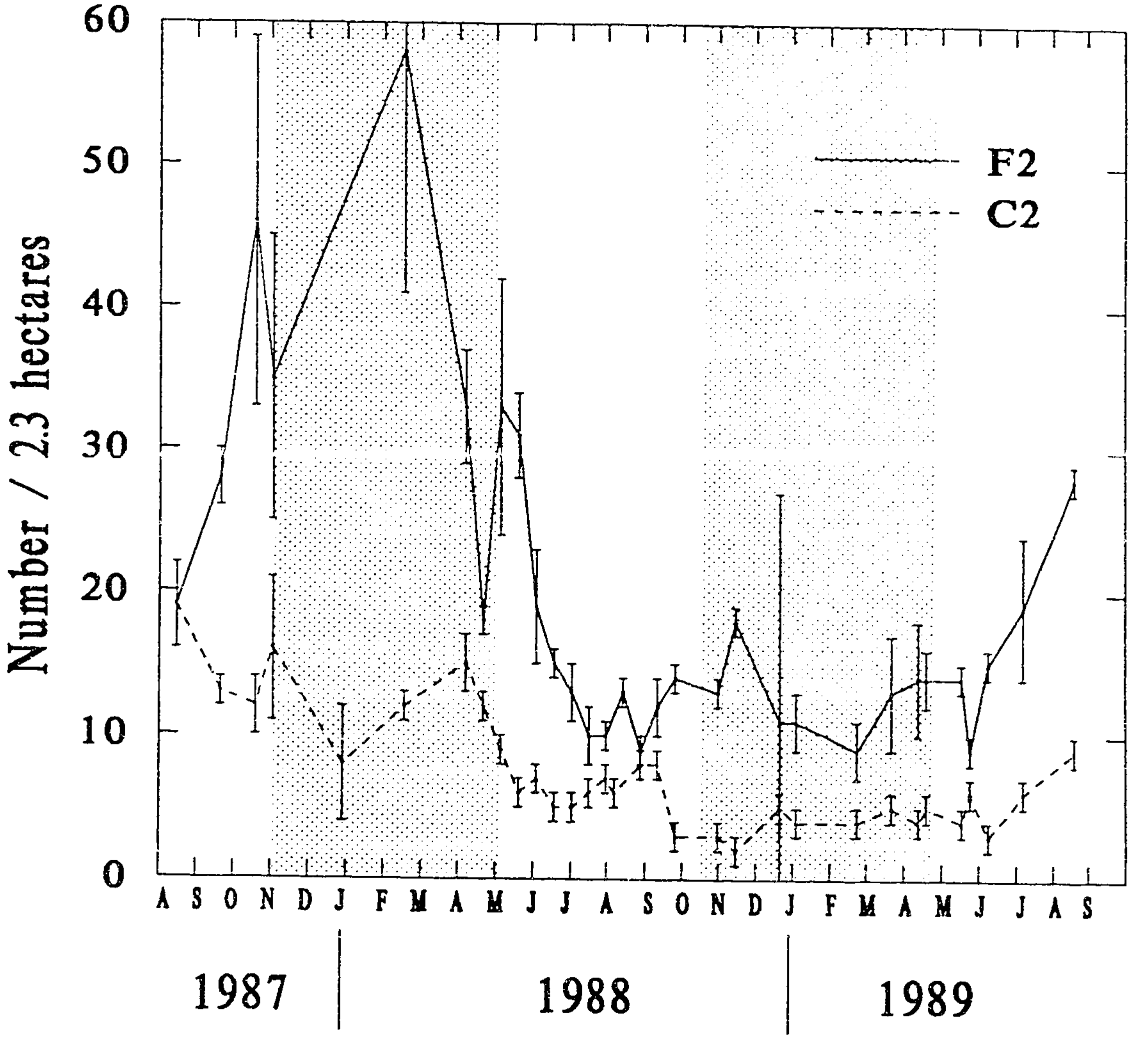


**Figure 2.3** Population estimates of *Clethrionomys rutilus* on R2 from August 1987 to August 1989. Snow cover period indicated by stippled area. Food addition started on 1 September each year and ended with disappearance of snow cover. Bars = 95% confidence limits. Estimates obtained from Capture (White *et al.* 1982).

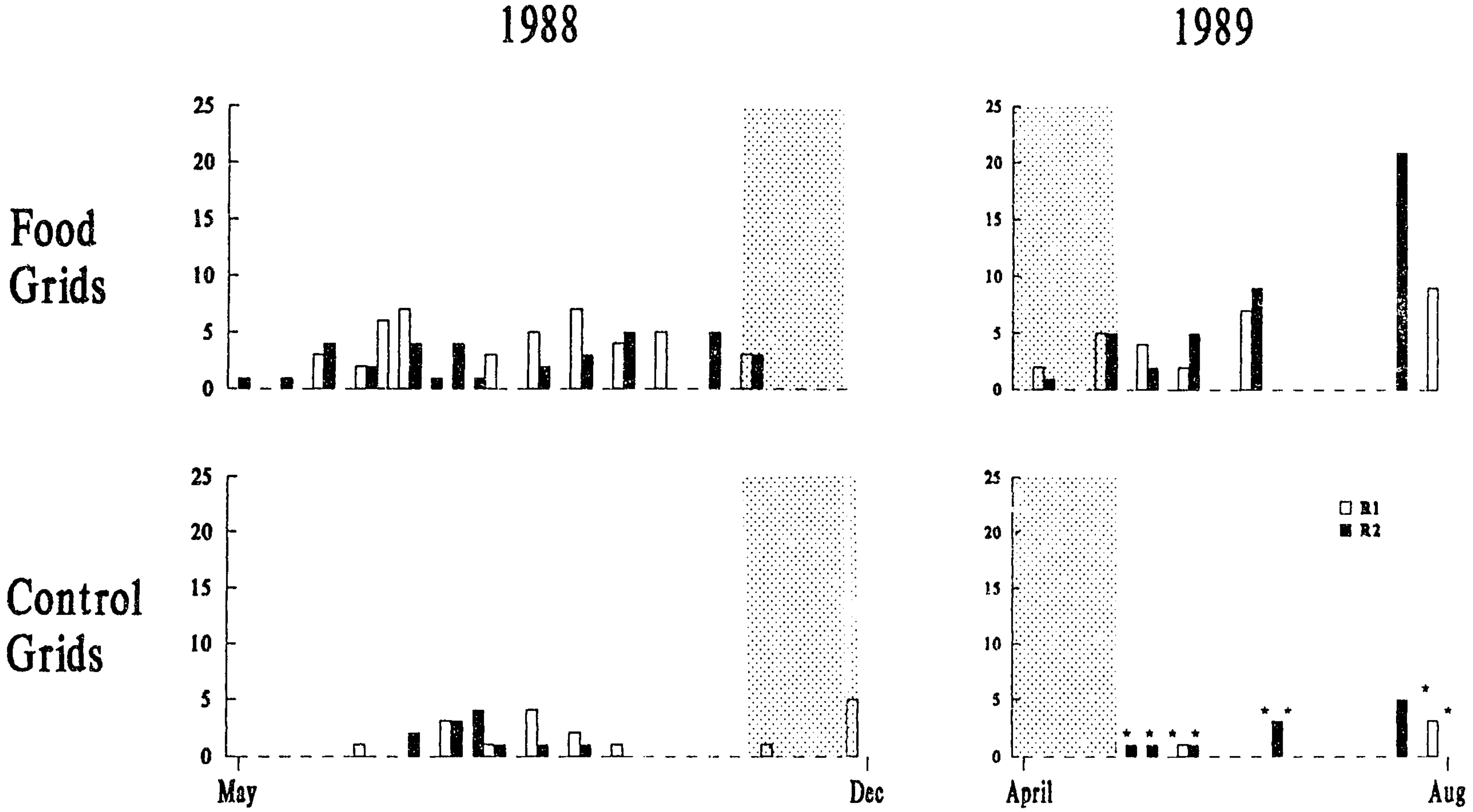


**Figure 2.4** Number and timing of juvenile recruitment on the four grids for each year. Data are pooled for the sexes. Stippled area corresponds with snow cover period. Food was still being added at this time on food addition grids. Number of *'s corresponds to number of juveniles that were tagged on another grid prior to being caught on the second grid.

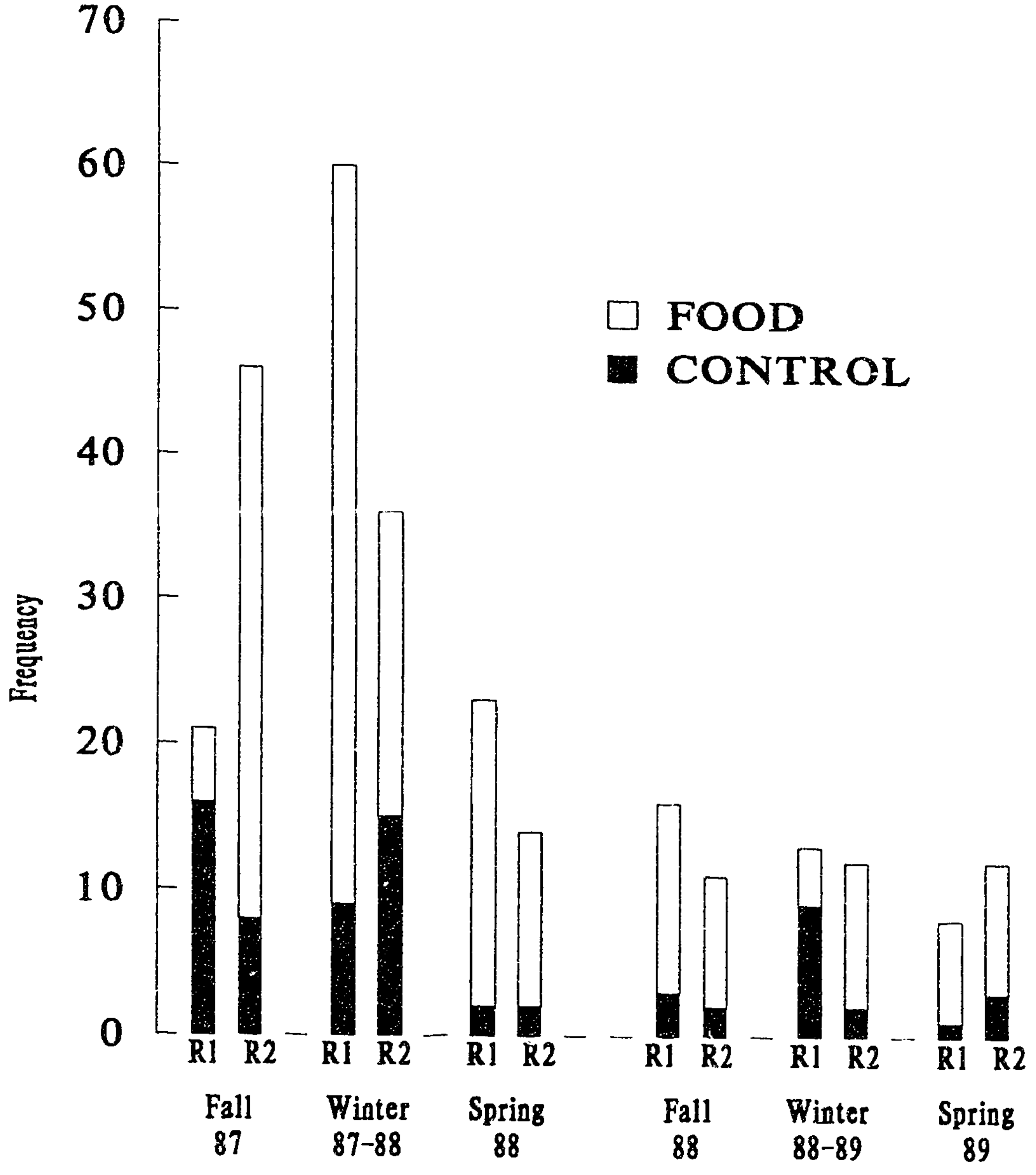


**Figure 2.5** Total number of new adults tagged on the grids during each time period: fall = post reproductive to snow cover, winter = snow cover period, spring = post snow cover to juvenile emergence on the control areas (read total height of bar to determine the number of new adults on the food grids).

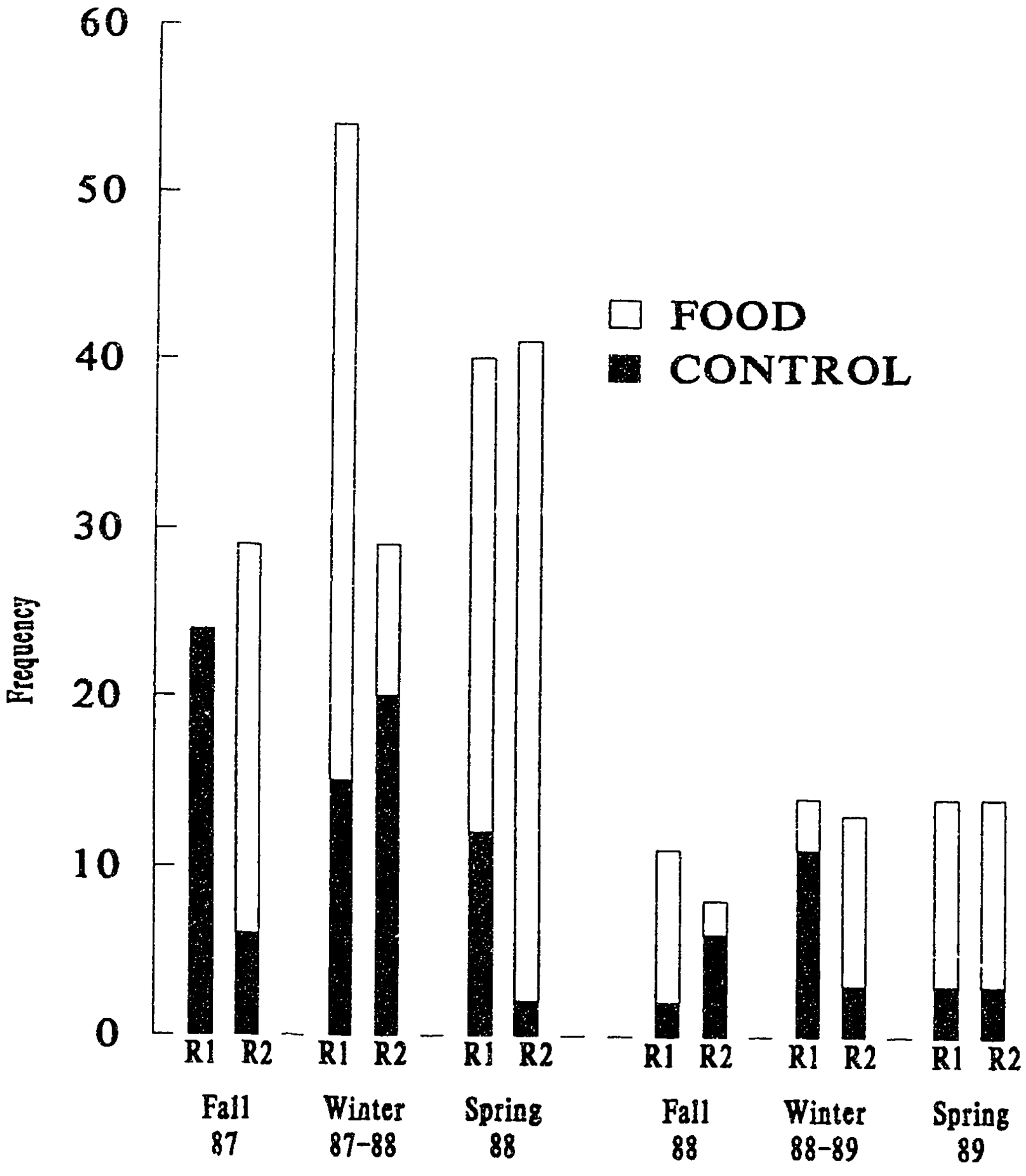


**Figure 2.6** Total number of individuals disappearing from the grids during each time period: fall = post reproductive to snow cover, winter = snow cover period, spring = post snow cover to juvenile emergence on the control areas (read total height of bar to determine the number disappearing from food grids). In the fall of 1987, F1=C1.

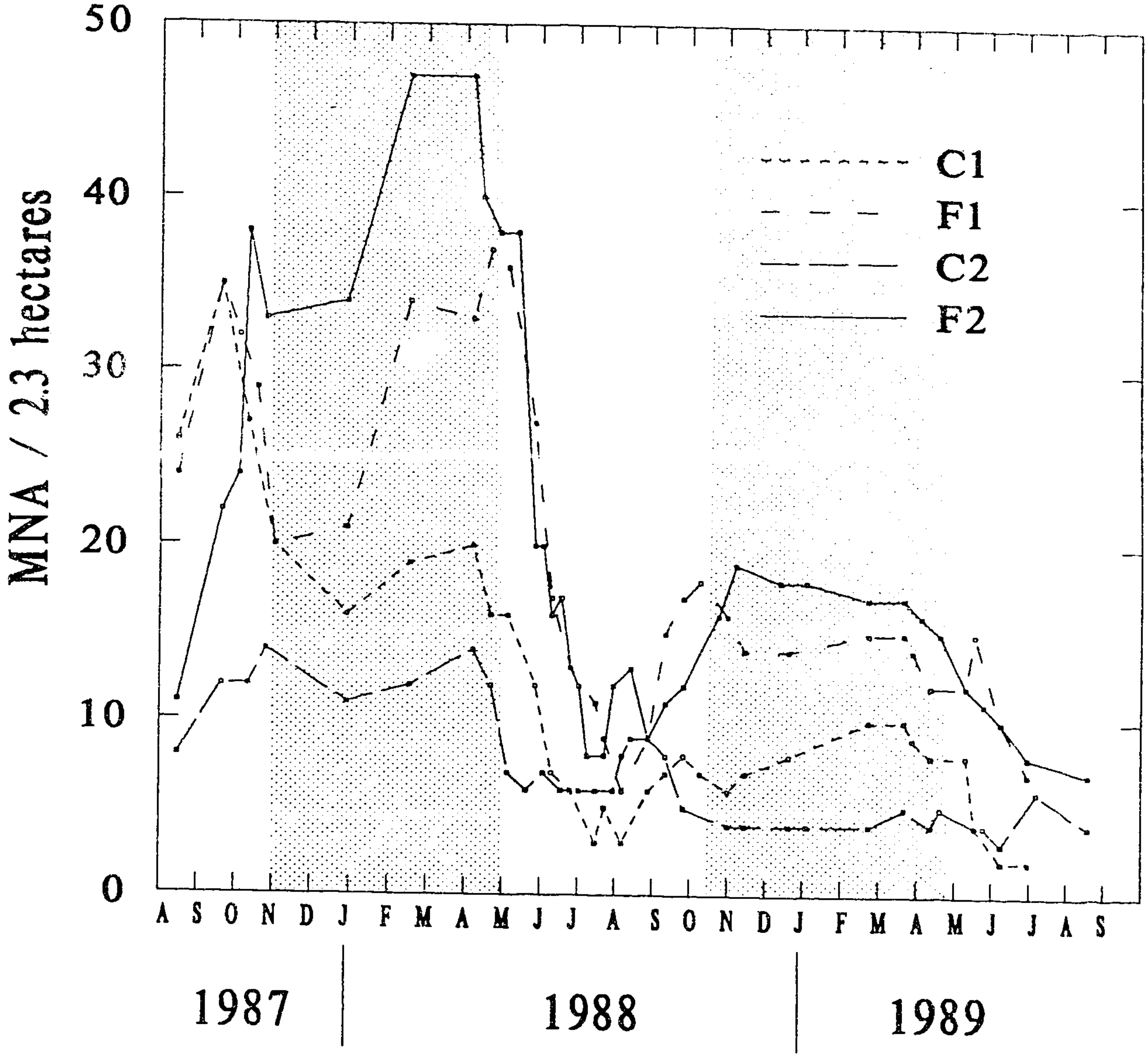


**Figure 2.7** Minimum number alive of resident *Clethrionomys rutilus* on food addition grids (F1 and F2) and controls (C1 and C2). Stippled area represents periods of snow cover.

**Table 2.1** Percentage over-winter survival of resident adult *Clethrionomys rutilus* from the fall to the disappearance of snow in each year. Sample size in parentheses.

| | | | SURVIVAL ON: | |
|---|---|---|---|---|
| YEAR | REPLICATE | SEX | CONTROL | FOOD ADDITION |
| 1988 | 1 | M | 27.3 (22) | 54.1 (41) |
| | | F | 18.2 (29) | 46.9 (29) |
| | 2 | M | 31.2 (11) | 29.3 (37) |
| | | F | 27.8 (11) | 48.3 (32) |
| 1989 | 1 | M | 33.3 (10) | 28.6 (14) |
| | | F | 0 ( 5) | 60.0 (13) |
| | 2 | M | 30.0 ( 9) | 42.9 (14) |
| | | F | 20.0 ( 3) | 46.2 (10) |

**Males**: no difference (P=0.407, F=0.858, df=1,4) in over-winter survival between grids.
**Females**: significantly (P=0.027, F=11.626, df=1,4) higher survival on food grids.

**Table 2.2** Estimated production of *Clethrionomys rutilus* on the four grids.

**1988**

|  | GRID |  |  |  |
|---|---|---|---|---|
|  | C1 | F1 | C2 | F2 |
| NUMBER OF JUVENILES CAUGHT | 18 | 46 | 12 | 37 |
| ESTIMATED # OF LITTERS | 7 | 20 | 9 | 25 |
| JUVENILE PRODUCTION/LITTER | 2.6 | 2.3 | 1.3 | 1.5 |

**1989**

|  | GRID |  |  |  |
|---|---|---|---|---|
|  | C1 | F1 | C2 | F2 |
| NUMBER OF JUVENILES CAUGHT | 2 | 21 | 5 | 46 |
| ESTIMATED # OF LITTERS | 2 | 10 | 3 | 17 |
| JUVENILE PRODUCTION/LITTER | 1.0 | 2.1 | 1.7 | 2.7 |

# CHAPTER 3

## An overwinter food addition to *Microtus miurus*: population dynamics and interspecific competition

### INTRODUCTION

The singing vole, *Microtus miurus* is a medium-sized vole inhabiting tundra and mossy areas of the boreal forest (Krebs and Wingate 1976). It is conspicuous because of its behaviour, "singing" when an intruder passes through its habitat. This singing is a monotone, single note chirp, emitted with the animal standing on its hind legs, very similar to the alarm call of a ground squirrel. The function of the singing is unknown. Murie (1948) described *M. miurus* as "the mysterious mouse", documenting for the first time field observations of the species in Alaska. Little else is known about the species, as its northern distribution and scarcity make it an animal that is difficult to work with.

In the southwestern Yukon, there are reports of periodic high numbers of singing voles (Gilbert, unpublished), indicating that this species fluctuates. However, it has not been documented whether the fluctuations coincide with other cyclic species in the area. Batzli and Henttonen (1990) report that fluctuations of *M. miurus* in Alaska coincide with fluctuations of *M. oeconomus*.

In 1987-88, the number of singing voles in the southwestern Yukon was at a peak, coinciding with peak *Clethrionomys rutilus* populations (Gilbert, unpublished). During that period, I was conducting a winter food addition experiment on *C. rutilus* populations to test the hypothesis that winter survival could be enhanced with the addition of winter food, and whether this would translate into a population peak. One set of grids (R2) had relatively high *M. miurus* populations which allowed me to address the questions of whether winter food affected the winter survival of this species, whether food addition affected the population dynamics of this species, and whether *C. rutilus* and *M. miurus* showed a similar response to food addition.

In this paper, I document, by live trapping, the population dynamics of *M. miurus* over two years and compare them with those of *C. rutilus*. The second component of this paper evaluates the effect of winter food on the population dynamics of *M. miurus*. Food addition studies on other species of small mammals have shown the following responses, increased density through immigration, advanced initiation of breeding, and earlier breeding by juveniles (see Boutin 1990 for a review). The third aspect deals with assessing competition between *Clethrionomys* and *Microtus*. I use trapping data (locations and time of capture) to evaluate spatial and temporal overlap. Finally, I conducted arena trials between *M. miurus* and *C. rutilus* to examine "competition" directly.

## METHODS

### *Experimental Design and Trapping Regime*

This study was conducted in the boreal forest of the southwestern Yukon, southeast of Kluane Lake (61°N, 138°W). I established four trapping grids (see Chapter 2), only two of which had populations of both *Clethrionomys rutilus* and *Microtus miurus*. The grids are referred to as F2 (received supplemental food for two consecutive winters), and C2 (control grid) (Figure 3.1). The data presented in this paper are results obtained from only these two grids.

Each grid was 1.8 ha in size, with stations 15 m apart in a 10X10 pattern. Every other station was trapped, resulting in 50 trapping stations per grid. A Longworth trap baited with whole oats and apple and supplied with cotton for nesting, was placed at every trapping station. The food addition grid had whole sunflower seed supplied *ad libitum* throughout the snow cover period, while the other grid served as the control. Both grids were trapped every other week during the snow-free periods, and monthly during the winter. A trapping session consisted of setting all the traps on the grid in the evening before sunset, checking all traps for two to five consecutive mornings and evenings, and locking the traps open on the final morning. Each animal that was captured was tagged with a fingerling fish tag bearing a unique number, sexed, weighed, and the species, location, and reproductive status recorded. Males were scored as abdominal if their testes could not be detected, and scrotal (indicating reproductively active) if they could. Females were examined for five characteristics: perforate (initial sign of the onset of reproduction or having just given birth) or non-perforate (non-reproductive or between litters); nipple condition-small (non-reproductive), medium and lactating (indicating reproductive activity); pubic symphysis closed (no recent birth) or open (litter recently born); pregnant or not pregnant; and litter size in trap, where applicable. All animals were released at the site of capture, and traps reset.

The grids were trapped year-round, from August 1987 to August 1989. Sunflower seed was added to the food grid after each trapping session during the snow-cover period, and any remaining seed was scooped out before a trapping session was initiated.

I used the program Capture (White *et al.* 1982) to estimate the number of voles present on the study area during each trapping session. I also classified animals as residents (caught in at least two trapping sessions) or transients (caught in only one session). I used MNA (minimum number alive) to compare relative densities of residents of both species over time.

### *Assessment of Competition*

#### *Spatial Overlap*

Within a trapping session, I looked at the number of trapping stations that caught single animals of either species, multiple animals of the same species, and multiple species to evaluate whether the two species were separated spatially from each other. I calculated the mean number of stations in each category for four time periods of both years - fall, winter, spring and summer (Chapter 2).

#### *Temporal Overlap*

For each trapping session, I tabulated the frequency of capture in the morning and evening checks for each species to evaluate whether activity of *C. rutilus* and *M. miurus* was temporally separated.

#### *Behaviour Trials*

In August of 1989, I conducted arena behaviour trials between pairs of *Clethrionomys rutilus* and *Microtus miurus*. The arena was constructed of clear Plexiglass, measuring 60 cm X 30 cm by 50 cm high. A removable, opaque piece of Plexiglass divided the arena in half. The arena had no bottom, and was placed directly on the ground, which was covered by moss. All trials were conducted well off the home ranges of the contestants. Two animals were randomly selected for each trial and placed on opposite sides of the arena with the divider in place. The animals were allowed to habituate to the arena for five minutes, at which time the divider was removed. All activity was recorded for a ten minute period, or until one animal repeatedly attacked the other. The outcome from every encounter was classified as to which animal initiated the event, and which animal 'won' the encounter. An individual won if the opponent retreated as a result of the encounter. A neutral encounter was one in which neither animal avoided the contact. At the end of the 10 minute period, animals were returned to the location at which they were trapped, and the arena was moved to a new location for the next trial. An animal was not used more than once per day.

Although the main target of these trials was adults of the two species, I attempted some trials with adults and juveniles in various combinations, as well as trials with conspecifics.

## RESULTS

### *Density Changes of Microtus miurus*

For all density estimates, I used 2.3 hectares as the effective area trapped. This was determined by including a band width of 7.5 m (1/2 the distance between traps) around the perimeter of the grid (Stenseth and Hansson 1979). Both the control and food addition grid had similar densities throughout the study (Figure 3.2) with the exception of two periods. C2 had significantly higher densities than F2 in April and May 1988 (approximately three-fold higher) and again from October 1988 to March 1989 (an average of two-fold higher). Overall, the pattern of density change was one of decline, with both grids decreasing approximately three-fold over the two year study.

I also calculated MNA estimates for resident *Clethrionomys* and *Microtus* (Figure 3.3). The overall pattern of change in *M. miurus* resident densities was similar to that obtained by program Capture. The salient point to note in Figure 3.3 is the relative densities of the different species on the two grids. *C. rutilus* had the highest overall density on F2, yet the lowest density on C2. *M. miurus* densities were higher on C2 than on F2, and were intermediate to *C. rutilus* densities. In summary, the overall pattern was one of declining density over the two years for both species on both grids. Higher *C. rutilus* densities on F2 were associated with low *M. miurus* densities, and relatively low *C. rutilus* densities were associated with higher *M. miurus* densities on C2. *M. miurus* never showed higher densities than *C. rutilus* on F2.

### *Overwinter Survival*

I defined overwinter survival as the proportion of individuals alive at snow melt that were originally caught between August of the previous year and snow melt. Survival was compared by sex and treatment (Table 3.1). There was no difference in survival between treatments or sexes.

### *Reproduction*

#### *Males*

I compared the timing of initiation of breeding between the two treatment grids to determine if food advanced breeding. On 1 April 1988, snow-cover was still complete but five of the seven males caught on F2 were already scrotal. At the same time, the males caught (10) on C2 were all still abdominal. Within two weeks the majority of males were scrotal on both grids. I could not determine the exact date that males became scrotal on F2 because I did not trap between 27 February and 1 April 1988. The length of the breeding season was not extended on F2. All males on both grids were abdominal by mid-August. In 1989, the single over-wintering *M. miurus* male on F2 was scrotal on 6 February, a full seven weeks prior to the first C2 males becoming scrotal (two out of seven). Males on both grids were still in breeding condition at the end of the study in mid-August of 1989. Although the sample size is small, breeding by males in 1989 was advanced on F2.

*Females*

There was no noticeable difference in the initiation of reproduction of females in the spring of 1988. In 1989, the two females on F2 were known to be pregnant in early February, and lactating by 6 March, whereas the female on C2 was first lactating on 22 May, a difference of almost nine weeks. The addition of food appears to have significantly advanced the onset of breeding in at least one year in both males and females.

## *Recruitment*

*Weight at first capture*

I identified recruits as any untagged animal appearing on the grid. Figure 3.4 summarizes the frequency of weight at first capture for males and females on the two grids. Females were generally lighter than males, with few individuals weighing more than 30 g at first capture. However, males ranged in weight from seven to 50 g. It was difficult to separate juveniles from adults using a weight criterion, as most individuals were first captured at weights close to those of adults. Individuals of both sexes that entered the population in late summer and early fall did not appear to gain weight as winter approached (Figure 3.5), and in fact, adults from the summer lost significant weight (30% body weight) going into the winter.

*Timing of recruitment*

On C2, new individuals were recruited throughout the study (Figure 3.6). The largest influx occurred in late March to late April of 1988. This influx created a significant difference in density between C2 and F2 (Figure 3.2). The average weights of the new animals (Figure 3.6) appearing before July were similar to masses of known adults from C2 (Figure 3.5), and are most likely over-wintered animals. Smaller individuals (young of the year?) did not recruit until August of 1988, despite the fact that females were lactating in May.

Recruitment on F2 was higher than C2 for only one time period: the fall of 1987, when food was first added (Figure 3.7). Few light-weight animals appeared in the population at any time. There were fewer recruits on F2 than C2, with virtually no recruitment on F2 after November 1988. This is despite females and males being reproductive on F2 in early February. It does not appear as though the early breeding produced any juveniles that entered the F2 population.

*Potential juvenile recruitment*

I tabulated the number of potential young produced on each grid for the summer of 1988 by estimating the number of litters born (based on trapping observations of females lactating combined with a decrease in weight) multiplied by a litter size of six (based on personal observations from a female that gave birth in a trap and from locating two nests of radio collared females: all litters had six young). On F2, I identified 19 potential litters which should have resulted in 114 juveniles. Fifty-one new individuals were caught after 6 June 1988. If all of these young were considered to be juveniles, the proportion recruiting was 45%. On C2, 16 potential litters were identified, resulting in 96 potential juveniles, of which 69 were caught. Juvenile recruitment on C2 is therefore estimated at 72%. These are likely overestimates of the proportion of young recruiting to the population. However, the estimates suggest that the proportion recruiting was higher on C2 than F2.

### *Sex ratio of recruits*

On F2, 30 of the 51 new animals caught after 6 June 1988 were females. On C2, 41 of the 69 were female. Although there were more females caught on both grids, the difference is not significantly different from 1:1 (C2: $X^2$=2.5, df=1,P=0.118. F2: $X^2$=1.6, df=1,P=0.208).

## *Assessment of Competition*

### *Time of Capture*

For each trapping session, I separated captures of residents into two time periods, morning and evening. The proportion of animals caught in a time period per trapping session was used to compare the time of use of trapping stations between species and grids. Residents of both species used the trapping stations slightly more in the mornings (Table 3.2) with no apparent differences between grids or species.

### *Spatial Overlap*

For each trapping session, I classified stations according to whether single individuals, single species, or multiple species were trapped there. I examined four time periods per year: fall, winter, spring and summer, and calculated a mean for each category based on the trapping sessions in each period. If the two species were separated spatially, the number of stations catching both species should be rare. This was not the case (Figures 3.8 and 3.9). In all cases, *M. miurus* was as likely to be caught in traps used by *C. rutilus* as in traps where conspecifics were caught. The same was true for *C. rutilus* in most time periods.

### *Behaviour Trials*

Data were obtained from 41 trials; 31 interspecific and 10 intraspecific. The data are presented in Table 3.3. In the eight *Clethrionomys / Clethrionomys* trials, 41 approaches ($\overline{x}$=5.1) resulted in 17 wins and 24 neutral outcomes. Unfortunately, I was able to conduct only two *Microtus / Microtus* trials. The all-male trial had to be terminated as the contestants were locked in a fight from the moment the partition was raised. In the female / female trial, one of the females appeared to be dominant, winning four of the six encounters, while the other two encounters resulted in a neutral outcome.

Thirty-one trials were conducted using *Clethrionomys / Microtus* of varying sex and age. *Microtus* approached *Clethrionomys* more often than the reverse ($t=6.3$, $df=30$, $P<0.001$), and won more of the encounters ($t=4.3$, $df=30$, $P<0.001$), regardless of whether it was the instigator. The same outcome was true when juvenile *M. miurus* were paired with adult *C. rutilus*. The average number of *Clethrionomys* approaches was higher in the all *Clethrionomys* trials than in those between species, indicating that *Clethrionomys* were behaving differently in the presence of *Microtus*. With the one *Microtus / Microtus* trial that was allowed to continue for the 10 min duration, the number of encounters ($n=6$) was equal to the mean number of times in which a *Microtus* approached a *Clethrionomys* during mixed species trials. No conclusion can be made about the activity level of *M. miurus* based on this one sample. The number of neutral outcomes was highest in the *Clethrionomys / Clethrionomys* trials involving juveniles of the same age.

## DISCUSSION

I was not able to alter the pattern of density change in *Microtus miurus* by winter supplemental feeding. Most food augmented populations increase two-fold, due largely to immigration (Boutin 1990). In this study, however, the control grid had higher immigration, which is a reversal from most food addition studies. It is possible that the study area was generally sub-optimal for *M. miurus*. Potential source populations for immigration would therefore be low, but none-the-less would be equal for both control and food addition. Only one study (Krebs and Wingate 1976) has documented the distribution and abundance of *M. miurus* in different habitats during the same time period. *M. miurus* were found at low densities throughout the boreal forest and alpine tundra. Others report alpine tundra as the main habitat (Banfield 1974; Youngman 1985; Galindo and Krebs 1985; Batzli and Henttonen 1990). If environmental conditions in this study could be rated as poor, then I would have expected to see a greater response in magnitude to the food addition (Boutin 1990). However, I have no valid basis for assessing the quality of the habitat.

An alternative explanation as to why *M. miurus* failed to respond numerically to the food addition was the inappropriateness of the food. *M. miurus* eat dicotyledons and horsetails (Batzli and Henttonen 1990), but seed and fruit are found in trace quantities in stomach samples. I observed several instances of *M. miurus* eating sunflower seed in the trapping stations after being released. The fact that both sexes on the food addition grid bred earlier than on the control grid suggests that the food addition grid animals were in better condition than their control counterparts. Winter breeding is a common response to food supplied over the winter (Boutin 1990, Chapter 2), and I therefore attribute earlier breeding in this study to the addition of food. The possibility still remains, however, that the sunflower seed was not able to increase density of *M. miurus*, despite showing positive results with *C. rutilus*. Getz *et al.* (1979) were able to produce different densities in *M. ochrogaster* and *M. pennsylvanicus* by altering the food quality.

*C. rutilus* and *M. miurus* differed in their response to food addition in two respects: immigration and juvenile recruitment. Since these two species overlapped in habitat use, the possibility exists for competition contributing to these different responses. The observed inverse relationship in density suggests that this is the case. It is not clear which species was the dominant animal. If the food addition grid was naturally sub-optimal habitat for *M. miurus* and therefore did not attract large numbers of the species, their absence may have allowed *C. rutilus* to respond numerically. The low density of *C. rutilus* on the control grid may be explained by the higher numbers of *M. miurus*. The results from the arena trials would support this. However, the fact that the responses seen by *C. rutilus* on the two replicates were similar (Chapter 2) suggests that the dynamics of *C. rutilus* was not affected by the presence of *M. miurus*. I would have expected the density of *C. rutilus* on the grids with both species to have been lower, the survival poorer, or juvenile recruitment reduced, if *M. miurus* had a competitive effect on the population dynamics of *C. rutilus*.

It is difficult to answer whether *M. miurus* densities were suppressed by *C. rutilus*, as my design did not include any areas with only *M. miurus*. The two species were not segregated temporally or spatially on either grid. Gilbert *et al.* (1987) examined the activity patterns of these two species and also concluded that they were not temporally separated, at least to a time scale of two hours.

The results of the behaviour trials are the most direct measure of contact behaviour that I have. The data suggest that *M. miurus* is competitively superior to *C. rutilus*, as *M. miurus* "won" most of the outcomes. Whether this is a true reflection of what happens in an unconfined space is difficult to say.

At least one study supports that a *Microtus* species is competitively inferior to a *Clethrionomys* species. Turner *et al.* (1975) measured the aggression levels between *M. pennsylvanicus* and *C. gapperi*, and found that aggression varied with the breeding season. When individuals of both species were not reproductive, populations were sympatric in wooded areas, but with the onset of breeding, *M. pennsylvanicus* densities decreased due to increased aggression. I observed a decline in adult density of *M. miurus* over the entire study, rather than associated with any one season. The lack of juvenile recruitment on the food addition grid is perplexing. There is a discrepancy in juvenile recruitment between the two grids and between the two species with respect to the food addition. *C. rutilus* had increased juvenile recruitment with the addition of food. In *M. miurus*, however, advanced breeding on the food addition grid did not translate into greater recruitment. There was no suggestion that juveniles were leaving the food addition grid shortly after weaning as no movement of known individuals was detected between grids (compare with movement between grids of *C. rutilus*, Chapter 2). Higher juvenile recruitment on the control area which had a lower *C. rutilus* density suggests that *C. rutilus* may have affected early survival of *M. miurus* juveniles. A similar relationship between poor juvenile survival of *Peromyscus maniculatus* with increasing *C. rutilus* densities has been documented by Gilbert and Krebs (1984).

The data from this study add some interesting results to microtine studies. It is the first study to monitor *M. miurus* population dynamics over the snow-cover period, as well as being the first food addition to this species. It is an example of a food addition that did not increase density through immigration. Proper documentation on the abundance and distribution of the species throughout its range is needed before this study can be evaluated in terms of habitat quality. The social system of *Microtus miurus* still remains unknown. It is an appealing study animal, as it appears to be very social, and emits alarm calls when disturbed. The delayed emergence of juveniles suggests that either juvenile survival before entering the trappable population is very low, or the length of maternal care is greatly extended or the juveniles are dispersing at a very young age. Altering the trapping method to focus locally on juveniles is needed. The tantalizing thought of *C. rutilus* directly affecting juvenile survival of *M. miurus* begs to be explored. In future studies involving both *M. miurus* and *C. rutilus*, altering species composition should be included as an experimental treatment.

## LITERATURE CITED

Banfield, A.W.F. 1974. The mammals of Canada. Univ. of Toronto Press, Toronto.

Batzli, G.O., and H. Henttonen. 1990. Demography and resource use by microtine rodents near Toolik Lake, Alaska, U.S.A. Arctic Alpine Research 20:51-64.

Boutin, S. 1990. Food supplementation experiments with terrestrial vertebrates: patterns, problems, and the future. Can. J. Zool. 68:203-220.

Galindo, C. and C.J. Krebs. 1984. Habitat use by singing voles and tundra voles in the southern Yukon. Oecologia 66:430-436.

Getz, L.L., L. Verner, F.R. Cole, J.E. Hofmann, and D.E. Avalos. 1979. Comparisons of population demography of *Microtus ochrogaster* and *M. pennsylvanicus*. Acta Theriologica 24:319-349.

Gilbert, B.S., and C.J. Krebs. 1984. Competition between *Peromyscus maniculatus* and other small rodents in the boreal forest of the southern Yukon Territory. Acta Zool. Fennica 172:51-56.

Gilbert, B.S., D.B. Cichowski, D. Talarico, and C.J. Krebs. 1986. Summer activity patterns of three rodents in the southwestern Yukon. Arctic 39:204-207.

Krebs, C.J., and I. Wingate. 1976. Small mammal communities of the Kluane region, Yukon Territory. Can. Field Nat. 90:379-389.

Murie, A. 1948. The mysterious mouse. Audubon 50(4):202-210.

Stenseth, N.C. and L. Hansson. 1979. Correcting for the edge effect in density estimation: explorations around a new method. Oikos 32:337-348.

Turner, B.N., M.R. Perrin, and S.L. Iverson. 1975. Winter coexistence of voles in spruce forest: relevance of seasonal changes in aggression. Can.J.Zool. 53:1004-1011.

White, G.C., D.R. Anderson, K.P. Burnham and D.L. Otis. 1982. Capture - recapture and removal methods for sampling closed populations. Los Alamos National Laboratory, LA 8787-NERP, Los Alamos, New Mexico, U.S.

Youngman, P.M. 1985. Mammals of the Yukon territory. Natural Museums of Canada, Publs Zoology 10.

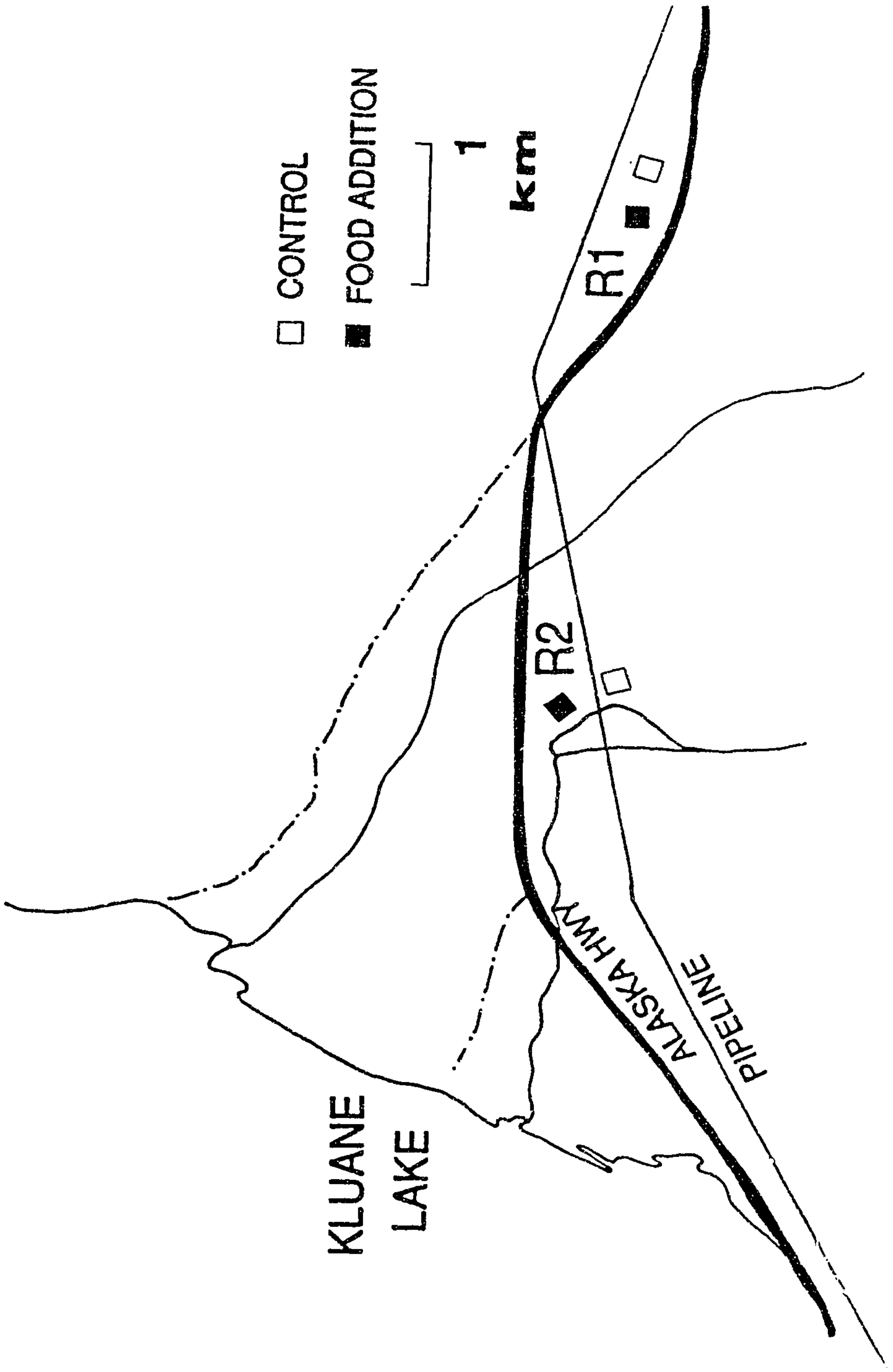


**Figure 3.1** Map of study area, at the south end of Kluane Lake, Yukon. R1 (C1=control 1, F1=food addition 1). R2 (C2=control 2, F2=food addition 2).

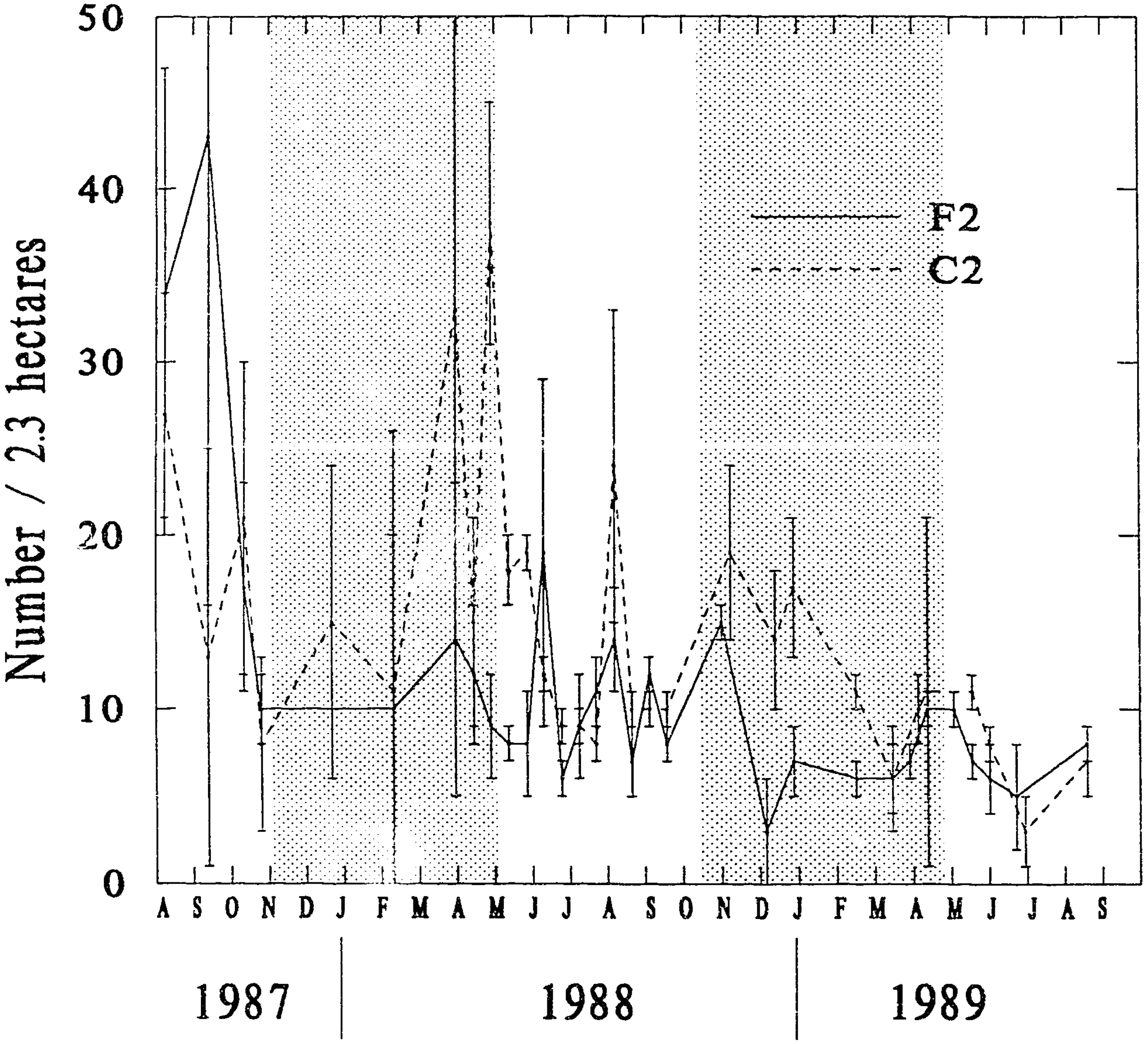


**Figure 3.2** Poulation estimates of *Microtus miurus* on R2 from August 1987 to August 1989. Snow cover period indicated by stippled area. Food addition started on 1 September each year, and ended with disappearance of snow cover. Bars = 95% confidence limits. Estimates obtained from Capture (White *et al.* 1982).

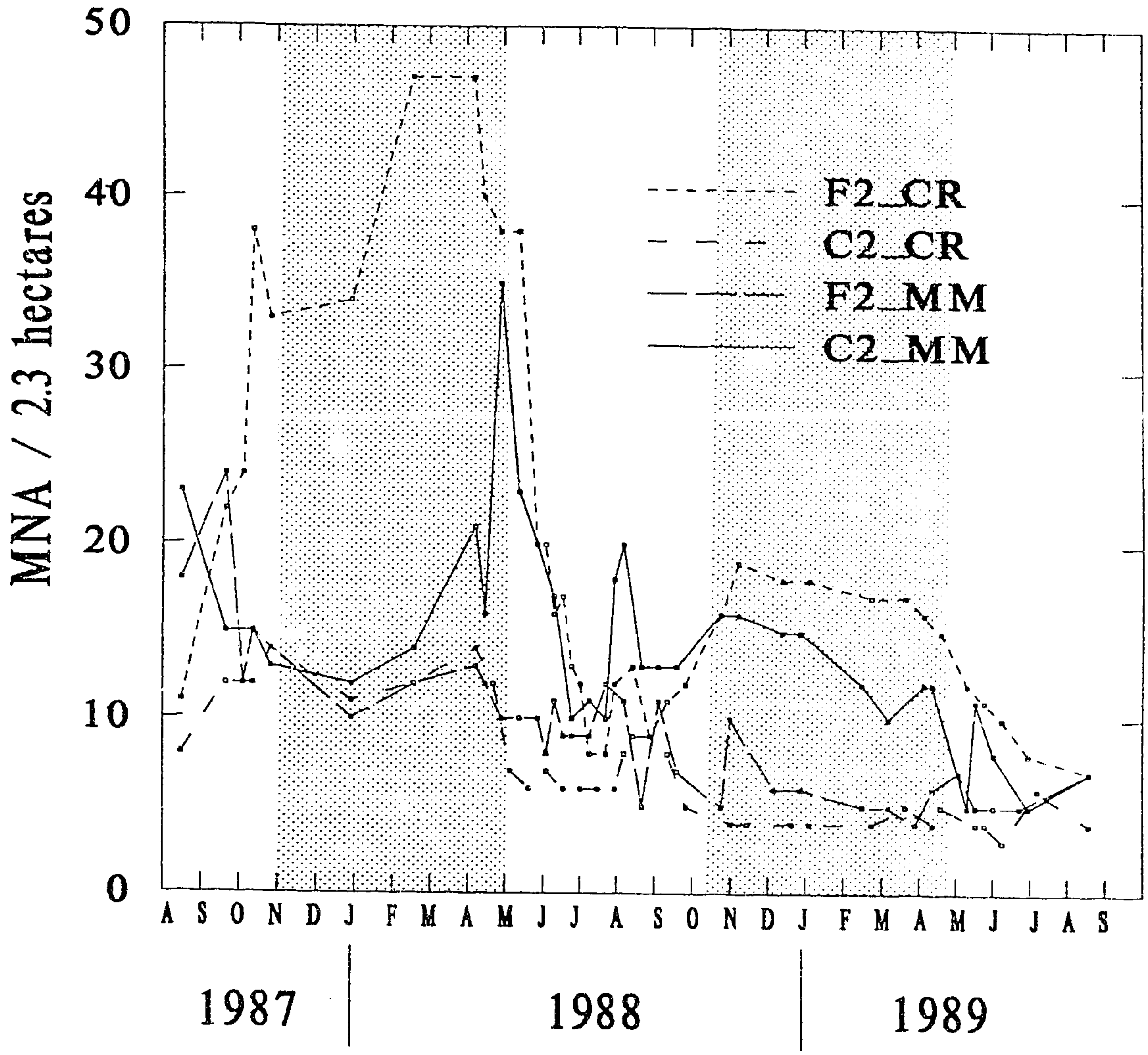


**Figure 3.3** Minimum number alive estimates of resident *Clethrionomys rutilus* and *Microtus miurus* on F2 and C2. Snow cover period indicated by stippled area. Food addition started on 1 September each year and ended with disappearance of snow cover.

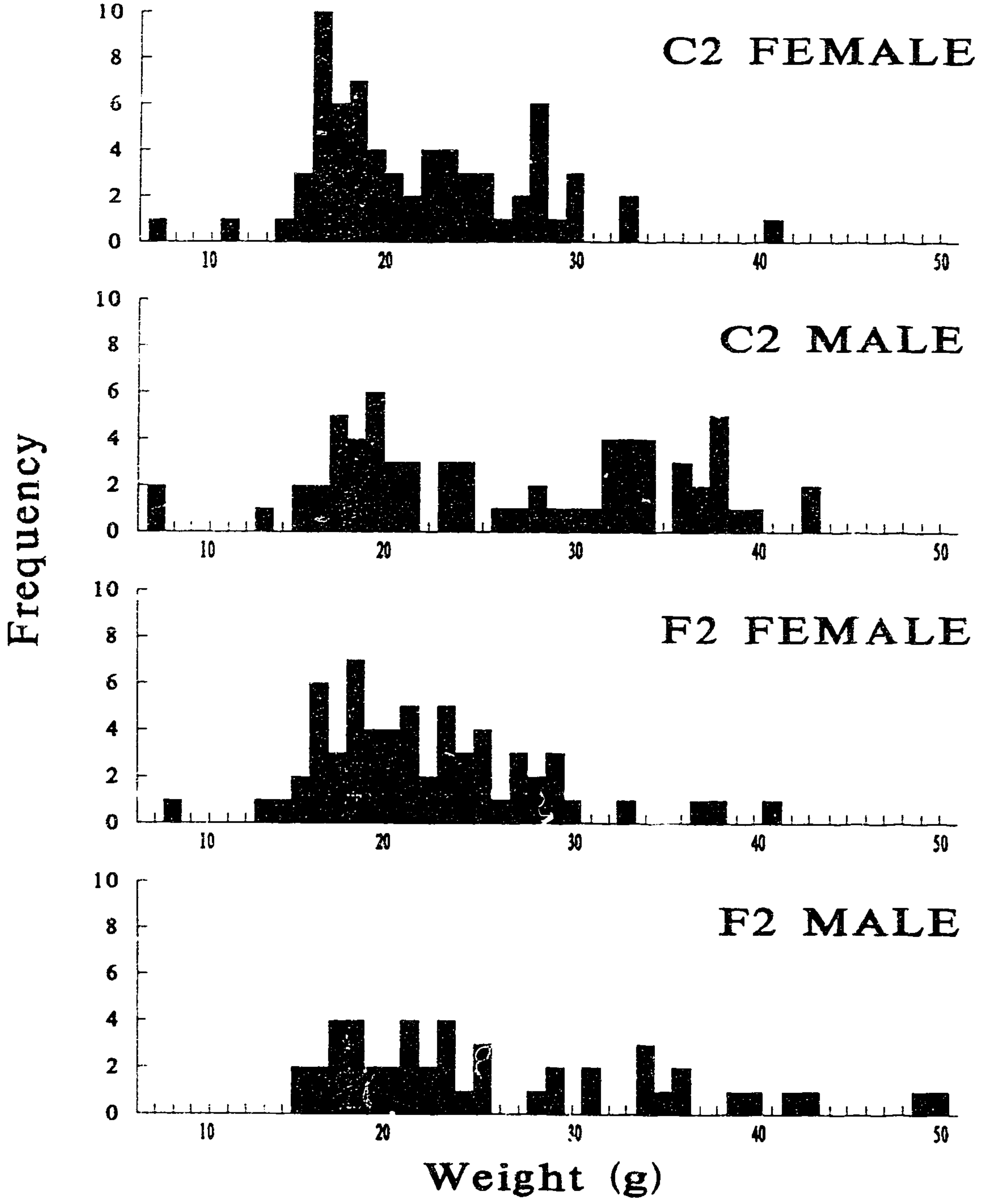


**Figure 3.4** Frequency distribution of weight at first capture for all male and female *Microtus miurus* caught on food (F) and control (C) grids.

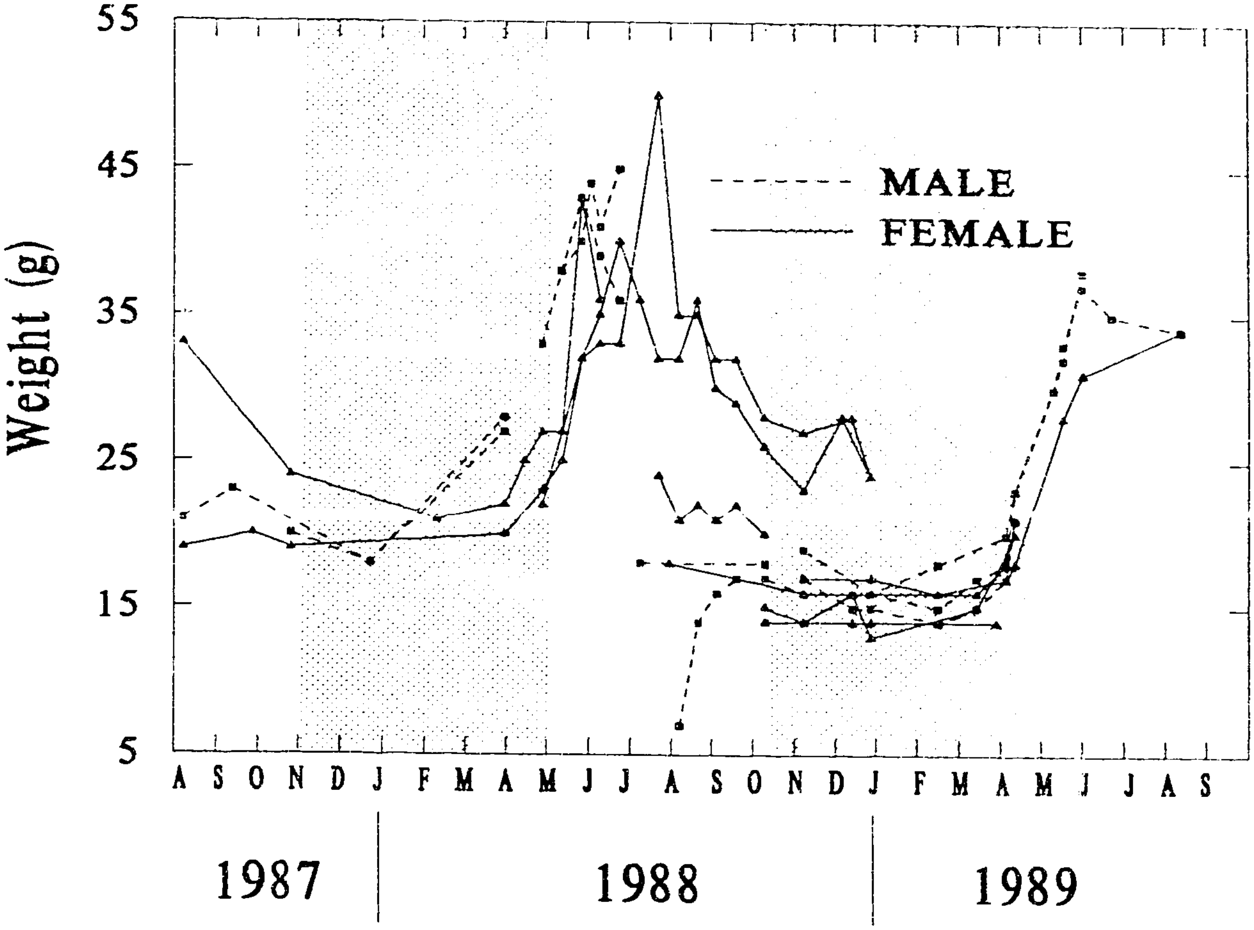


Figure 3.5 Weight change in individual *Microtus miurus* males and females from the control grid (C2). Snow cover period indicated by stippled area.

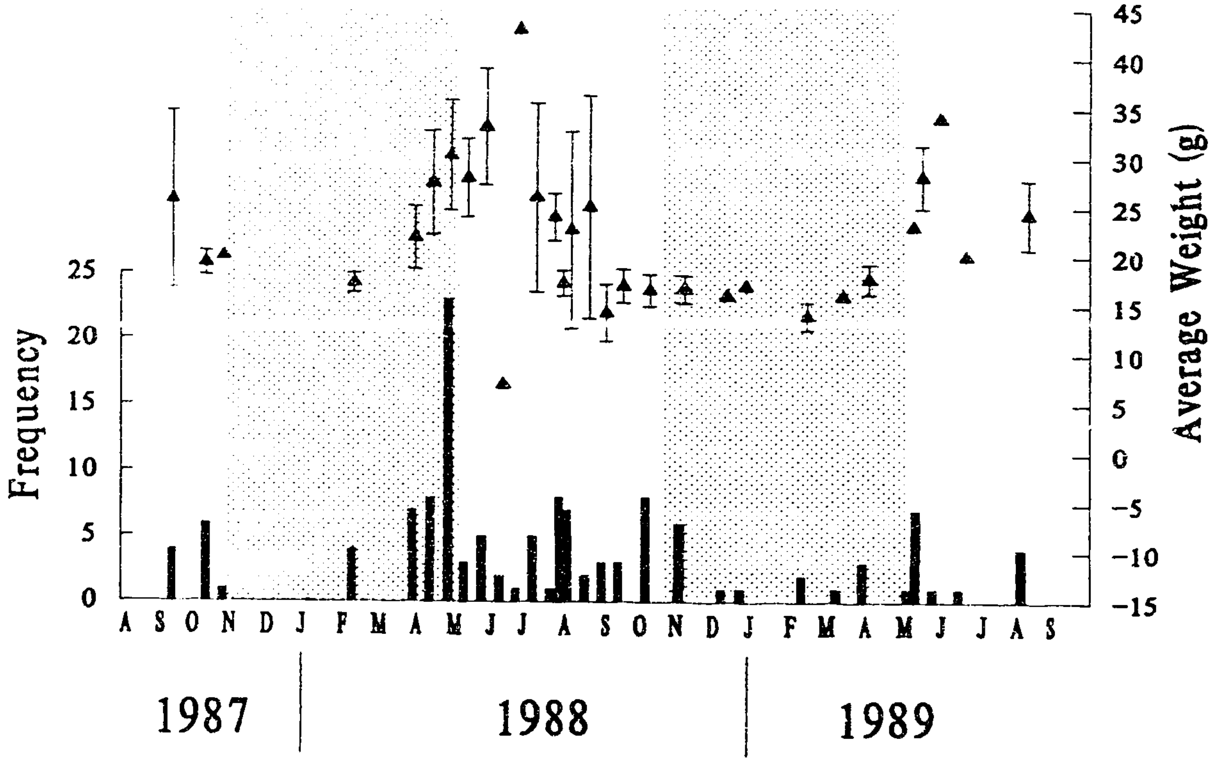


**Figure 3.6** Temporal distribution of the appearance of new *Microtus miurus* individuals on C2 (histogram), and the mean weight (+/- 1 SD) of those individuals. Sexes are pooled. Snow cover period indicated by stippled area.

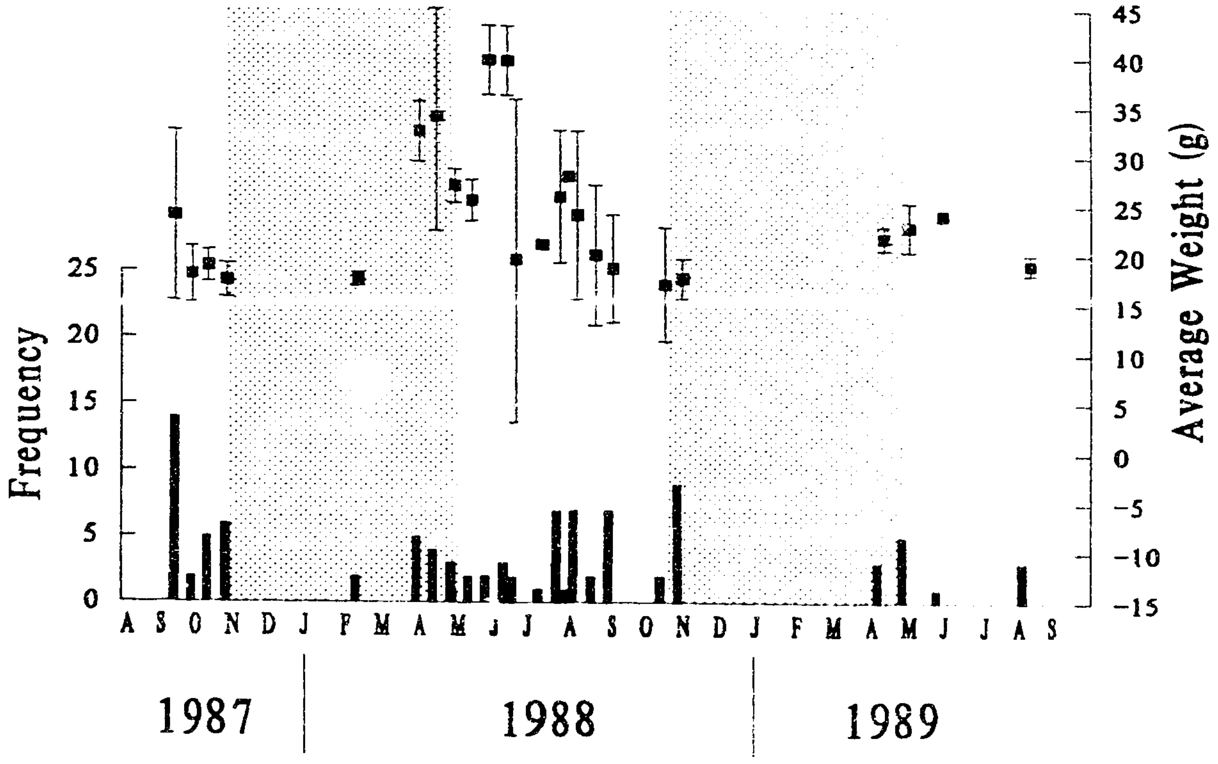


**Figure 3.7** Temporal distribution of the appearance of new *Microtus miurus* individuals on F2 (histogram), and the mean weight (+/- 1 SD) of those individuals. Sexes are pooled. Snow cover period indicated by stippled area.

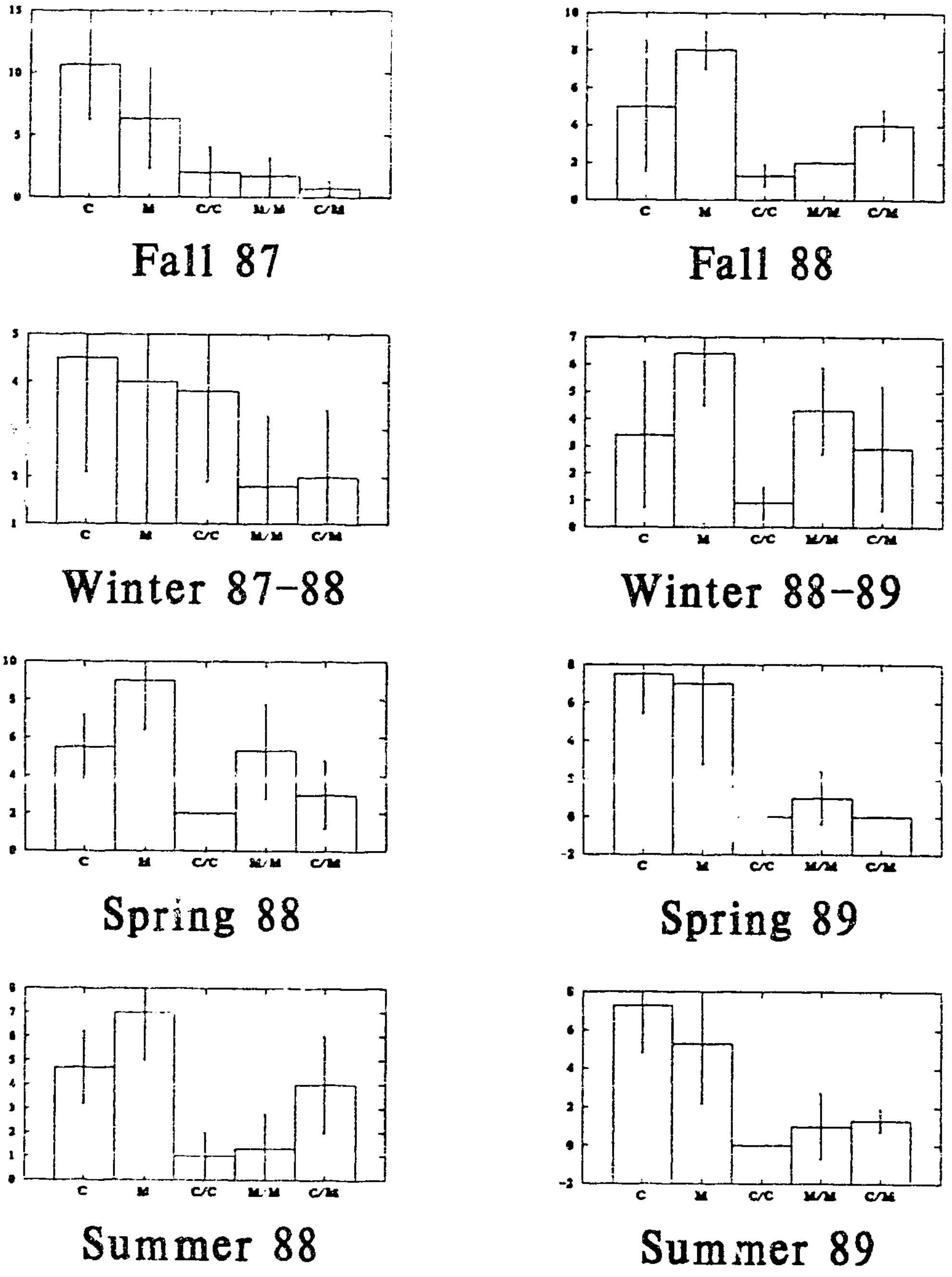
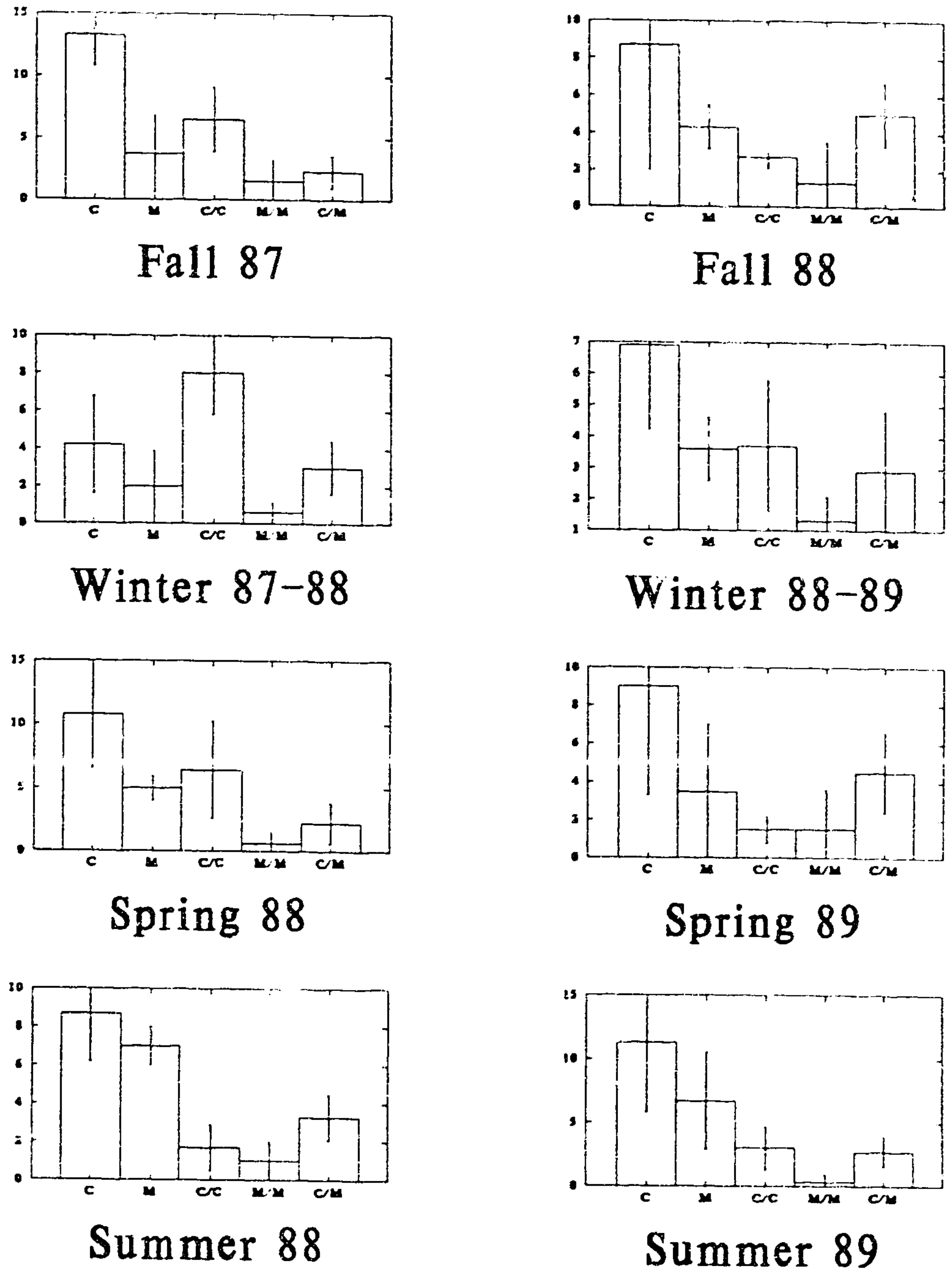


**Figure 3.8** The average number of trapping stations per trapping session that caught single *Clethrionomys*, single *Microtus*, multiple *Clethrionomys*, multiple *Microtus* and *Clethrionomys* and *Microtus* on C2. (Bars = +/- 1 SD).



Fall 87

Fall 88

Winter 87-88

Winter 88-89

Spring 88

Spring 89

Summer 88

Summer 89

**Figure 3.9** The average number of trapping stations per trapping session that caught single *Clethrionomys*, single *Microtus*, multiple *Clethrionomys*, multiple *Microtus* and *Clethrionomys* and *Microtus* on F2. (Bars = +/- 1 SD).

**Table 3.1** Percent over-winter survival of resident *Microtus miurus* on F2 and C2. Sample size in parentheses.

| YEAR | SEX | CONTROL | FOOD ADDITION |
|---|---|---|---|
| 88 | M | 38.89 (18) | 10.00 (10) |
| | F | 54.17 (24) | 53.85 (13) |
| 89 | M | 18.18 (11) | 16.67 (6) |
| | F | 11.76 (17) | 14.29 (7) |

**Table 3.2** Proportion of resident animals caught in the morning check (N = number of trapping sessions used in calculations).

| GRID | SPECIES | AVERAGE | SD | N |
|---|---|---|---|---|
| C2 | *M.m.* | 0.55 | 0.14 | 32 |
| | *C.r.* | 0.56 | 0.10 | 32 |
| F2 | *M.m.* | 0.50 | 0.08 | 35 |
| | *C.r.* | 0.52 | 0.09 | 35 |

**Table 3.3** Results of arena behavioural trails.
**SPECIES**: ***Clethrionomys rutilus* / *Microtus miurus*.**

| Sex | Age | *C. rutilus* approaches | Winner | | | *M. miurus* approaches | Winner | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | *C.r.* | *M.m.* | neutral | | *C.r.* | *M.m.* | neutral |
| F/F | A/A | | | | | 10 | | 10 | |
| | | 1 | | 1 | | 3 | 1 | | 2 |
| | | 1 | | 1 | | 5 | | 5 | |
| | | | | | | 3 | | 2 | 1 |
| | | | | | | 2 | | 1 | 1 |
| | | 1 | | 1 | | 1 | | | 1 |
| | | | | | | 13 | 1 | 11 | 1 |
| | | | | | | 3 | | 3 | |
| | | | | | | 6 | | 6 | |
| | | | | | | 6 | 4 | 1 | 1 |
| | | 1 | | 1 | | 3 | | 3 | |
| M/M | A/A | | | | | 8 | 5 | 3 | |
| | | | | | | 18 | | 17 | 1 |
| | | 1 | | 1 | | 6 | | 6 | |
| | | | | | | 13 | | 13 | |
| | | | | | | 10 | 8 | 1 | 1 |
| F/M | A/A | 1 | | 1 | | 5 | | 5 | |
| | | 4 | | 3 | 1 | 1 | | 1 | |
| M/F | A/A | 1 | | 1 | | 6 | | 5 | 1 |
| | | | | | | 6 | 2 | | 4 |
| | | 1 | | | 1 | 11 | | 11 | |
| F/F | A/J | 1 | | | 1 | | | | |
| | | 1 | 1 | | | 3 | 1 | | 2 |
| F/M | A/J | 2 | | 2 | | 5 | | 5 | |
| F/F | J/A | 1 | | 1 | | 4 | | 3 | 1 |
| | | 2 | | 1 | 1 | 5 | | 5 | |
| M/M | A/J | | | | | 10 | | 10 | |
| M/F | J/A | 2 | | 1 | 1 | 4 | | 4 | |
| F/M | J/A | 3 | | 2 | 1 | 3 | | 3 | |
| F/F | J/J | | | | | 9 | 3 | | 6 |
| | | | | | | 4 | | | 4 |
| | **TOTAL** | **24** | **1** | **17** | **6** | **186** | **25** | **134** | **27** |

**Table 3.3** (continued).

**SPECIES: *Clethrionomys rutilus / Clethrionomys rutilus***

| Sex | Age | *C. rutilus* approaches | Winner |  |  | *M. miurus* approaches | Winner |  |  |
|---|---|---|---|---|---|---|---|---|---|
|  |  |  | *C.r.* | *M.m.* | neutral |  | *C.r.* | *M.m.* | neutral |
| F/F | A/A | 0 |  |  |  |  |  |  |  |
|  |  | 8 | 6 | - | 2 |  |  |  |  |
|  |  | 4 | 2 | - | 2 |  |  |  |  |
| M/F | A/J | 2 | 2 | - |  |  |  |  |  |
| F/F | J/J | 15 |  | - | 15 |  |  |  |  |
|  |  | 5 | 4 | - | 1 |  |  |  |  |
| M/M | J/J | 3 |  | - | 3 |  |  |  |  |
|  |  | 4 | 3 | - | 1 |  |  |  |  |
|  | **TOTAL** | **41** | **17** | **-** | **24** |  |  |  |  |

**SPECIES: *Microtus miurus / Microtus miurus***

| Sex | Age | *C. rutilus* approaches | Winner |  |  | *M. miurus* approaches | Winner |  |  |
|---|---|---|---|---|---|---|---|---|---|
|  |  |  | *C.r.* | *M.m.* | neutral |  | *C.r.* | *M.m.* | neutral |
| F/F | A/A |  |  |  |  | 6 | - | 4 | 2 |
| M/M | A/A |  |  |  |  | TRIAL ENDED DUE TO CONTINUOUS FIGHTING |  |  |  |

# CHAPTER 4

## FUTURE DIRECTIONS

In this study of the population dynamics of *Clethrionomys rutilus,* I concluded that future manipulations of microtines 1) need to be maintained over a larger total area, and 2) an even larger area surrounding the manipulation needs to be monitored. I demonstrated that the area surrounding the manipulated area could not be ignored, that individuals leaving an area do not necessarily have zero survival, and are known to breed successfully. The arguments surrounding these recommendations are based on the premise that immigration and emigration are not trivial in the population dynamics of small mammals, and should not be assumed to be equal. Localized food additions are not able to inflate density infinitely. Social behaviour of the animals dictate different needs than those based solely on a food requirement.

Pulliam (1988) divides populations into source and sink sub-populations, noting that habitat is rarely homogeneous. Habitat that is optimal for a species is not usually widely distributed, being intermixed with less productive habitat. Reproductive output and survival rates are habitat specific. Immigration and emigration are partly contingent on density and social structure.

Researchers manipulating food supply to small mammals have been evaluating source populations for years, but without using the specific terminology that Pulliam uses. Food addition studies of microtines alter immigration, reproductive rates, and survival rates (Boutin 1990). Populations do not increase infinitely; in fact, most populations are only doubled with the addition of food. This upper limit can be controlled by social structure (Ylönen 1989). The components missing from Pulliam's model in the current literature are empirical data accounting for the losses from the population due to emigration versus death. My data nicely complement Pulliam's model in directing future studies towards evaluating population dynamics on a larger scale.

The premise that source population habitat varies between species might be a new focus for multi-species studies. In this study of *Microtus miurus* and *Clethrionomys rutilus,* responses to food were not identical. Although I addressed the question of habitat suitability to the 2 species, I was not able to make any conclusions indicating that in my study *Microtus miurus* was not in its source habitat, and other factors may have accounted for poor reproductive output. However, the basic requirement necessary to look at what constitutes a source habitat for a species is understanding the life history strategies of a species. Life history of *Microtus miurus* is still poorly understood. Studies that compare the four main population parameters, births and deaths, immigration and emigration, in various habitats are needed to evaluate source and sink habitats and populations.

## LITERATURE CITED

Boutin, S. 1990. Food supplementation experiments with terrestrial vertebrates: patterns, problems, and the future. Can. J. Zool. 68:203-220.

Pulliam, H.R. 1988. Sources, sinks, and population regulation. Am.Nat.132:652-661.

Ylönen, H. 1989. Temporal variation of behavioural and demographical processes in cyclic *Clethrionomys* populations. Biological Research Reports from the University of Jyväskylä 16.