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# Effects of Extra Food on *Peromyscus* and *Clethrionomys* Populations in the Southern Yukon*

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**Summary.** If food supply limits density in rodent populations, the addition of supplemental food ought to increase population size. From May to September we added food on 2-hectare areas of white spruce forest in the southern Yukon. In 1977, we used oats with no measurable impact. In 1978 and 1979 we used sunflower seeds and doubled or tripled the population densities of *Peromyscus maniculatus* and *Clethrionomys rutilus*. Supplemental feeding with sunflower seeds increased juvenile production in both species, probably by increasing early juvenile survival. The breeding season ended at the same time on experimental and control areas, and the onset of maturity in juveniles was not affected by feeding. Survival of adult rodents was not improved by feeding. Immigration into sunflower seed areas was very high, and was the major factor producing the increase in population density. Body weight was not changed by feeding. Food supply is thus one factor limiting population density in these subarctic small mammals, but we do not know why supplemental food produces no more than a 2- to 3-fold effect on densities.

## Introduction

Food supply is a limiting factor for temperate deer mouse (*Peromyscus maniculatus*) populations because where extra food is provided, deer mice grow and breed throughout the winter and double in density (Taitt 1981). In this study we attempted to determine whether food limitation also operates on northern populations of deer mice and voles. Deer mice are near the northern limit of their geographical range in the Kluane region of the Yukon Territory (Krebs and Wingate 1976). White spruce forests in this region are dominated by two rodents – *Peromyscus maniculatus* and *Clethrionomys rutilus*. Both species occur at low densities (<10/a) on average, and in this experiment we tried to increase average densities by providing supplemental food during the snow-free season.

We attempt in this paper to test three hypotheses which were suggested by earlier work (Taitt 1981):

(1) Food addition will produce a 2- to 3-fold increase in population density, and the density increase will result largely from immigration.

(2) Food addition will extend the breeding season and increase the growth rates of individual animals.

(3) Food addition will not reduce the loss rate from the breeding population.

## Methods

The study area was located in the southwestern Yukon, two miles south of Kluane Lake (61°N, 138°W, north latitude), in the boreal forest. A white spruce forest (*Picea glauca*) covered the study area, and the local substrate was composed of glacial and alluvial till. The forest had a dense shrub layer consisting of soapberry (*Shepherdia canadensis*), willows (*Salix glauca* and *S. alaxensis*), and silverberry (*Elaeagnus commutata*). The vegetative ground cover was sparse in many areas and usually consisted of licorice root (*Hedysarum boreale*), bearberry (*Arctostaphylos uva-ursi*, and *A. rubra*), bryophytes, and lichens. According to the vegetation classification of Douglas (1974), the study area was a *Picea glauca* – *Shepherdia canadensis* (closed phase) community.

Two grids (H and I), approximately 430 m apart, were established in June 1976, and in 1979 a third grid (J) was set out across a creek 400 m from grid H (Fig. 1). Each grid (2.3 ha) was divided into a 10 by 10 network of stations with 15.2 m between stations. A single Longworth trap was placed at each station, except in 1978, when 20 stations on grid H were each trapped with two Longworth traps. Trap disturbance by red squirrels was occasionally severe, and in 1979, twenty No. 103

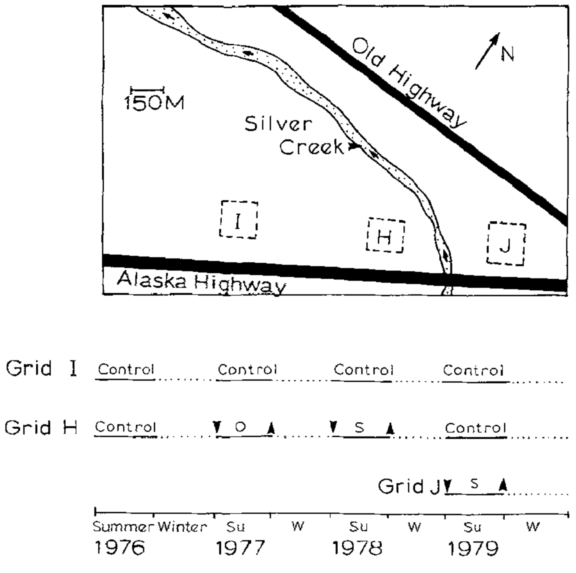

**Fig. 1.** Map of study area on the south side of Kluane Lake, Yukon Territory, and the experimental design. S = sunflower seeds supplied, O = oats supplied

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* Dedicated to Dr. Springer and Prof. Evenari

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National live-traps were used on each grid to protect individual Longworth traps. Mice were able to pass freely between the mesh of the National live-trap and enter the Longworth trap.

Trapping was started as soon as snow melted in late April or early May and continued at approximately bi-weekly intervals until late September. On the first evening of a trapping session, the traps were supplied with cotton bedding and baited with fresh oats. A mixture of oats and sunflower seeds was used to bait traps on grid H in 1978 and grid J in 1979. The traps were checked the next morning and afternoon, and on the second morning, the traps were checked and locked open to pre-bait. Each animal that was caught for the first time was tagged on the right ear with a numbered fingerling fish tag. The following information was obtained for each animal captured: tag number, capture location, sex, weight, and reproductive condition. Pesola spring scales were used to weigh animals to the nearest gram. The position of testes in males was described as either scrotal or abdominal. Three external signs of females' reproductive condition were noted:

(i) vagina (perforate or imperforate),
(ii) nipples (small, medium, or large), and
(iii) pregnancy (only obviously pregnant females were scored).

The experimental design is shown in Fig. 1. In 1977, whole oats was used as a supplemental food on grid H; in 1978 and 1979, sunflower seeds were used because of their greater energy value [6.82 kcal/g for sunflower seeds, 2.87 kcal/g for oats (Kent-Jones and Amos 1967)]. The supplemental food was placed in weatherproof containers (either opaque plastic containers, or 1.4-l tin cans) at approximately fifty different trapping stations. Throughout the study, the feeding stations were checked and refilled during each trapping session from May until September.

We used the weight of an animal as an index of its age and defined adult *Clethrionomys* as animals weighing 21 g or more; subadults weighed 15–20 g, and juveniles less than 15 g. We did not distinguish *Peromyscus* subadults; adults weighed 20 g or more and juveniles weighed less than 20 g.

## Results

### *Density*

The minimum number of *P. maniculatus* known to be alive on each grid is plotted in Fig. 2. Changes in numbers of *P. maniculatus* show an annual cycle on the control grid. The adult population in the spring, averaging seven animals, declines gradually during May and June until juveniles begin to enter traps. Numbers usually peak in late July and then decline to an autumn level of approximately 12. There is no evidence of a spring decline, although male breeding activity was usually under way when trapping began in the spring, so a reorganization (Fairbairn 1977) may occur earlier under snow cover. Three supplemental feeding experiments were conducted, and numbers increased significantly in two of these. In 1977, supplemental oats was supplied to grid H but had no noticeable effect on numbers. In 1978, when sunflower seeds were used as a supplemental food, numbers became as much as three times higher on grid H, and twice as high on grid J when the experiment was repeated in 1979. Numbers on these grids increased as a result of juvenile recruitment from mid-July until September, when numbers were two to three times higher than average control densities. In 1979 we monitored the *Peromyscus* population on grid H, where exceptionally high numbers in spring 1979 were probably due to supplemental feeding during the previous year. The breeding population on grid H in May 1979 was 2.5 times that of the control grid, and since no food was provided to grid H in 1979, we expected it to decay in numbers back to the control level. Numbers reached a peak of 42 in mid-July and then declined steadily at the rate of 17% per week until September, when numbers reached the average autumn level (14–15) on grid H.

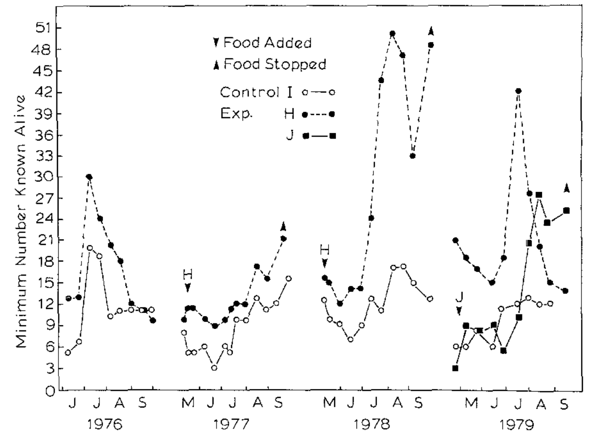

**Fig. 2.** Population sizes (minimum number alive) for *Peromyscus maniculatus* for the control and experimental grids, 1976–1979. Both sexes are combined because they behaved similarly. ▼ Food added, ▲ food addition stopped

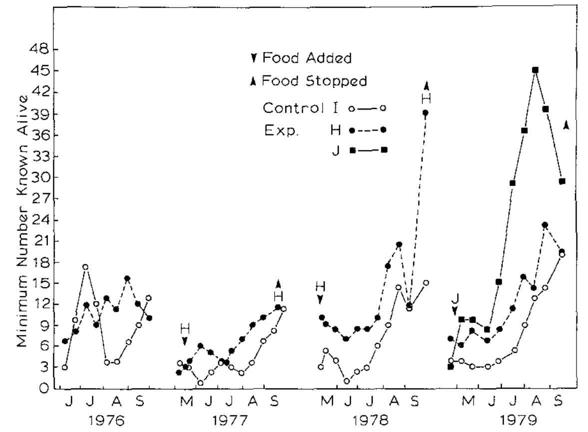

**Fig. 3.** Population sizes (minimum number alive) for *Clethrionomys rutilus* for control and experimental grids, 1976–1979. Both sexes are combined because they responded similarly. ▼ Food added, ▲ food addition stopped

The spring population density of *C. rutilus* was always about half that of *P. maniculatus* on the control grid (Fig. 3). Autumn numbers on the control grid varied greatly between years; in 1976 and 1978, the numbers of both species were similar; in 1977, *P. maniculatus* numbers were higher and in 1979, *C. rutilus* numbers were higher. *C. rutilus* on grid H did not respond numerically to the addition of oats in 1977; however, autumn population size was increased in both years when sunflower seeds were added. In 1978, the autumn population on grid H was 2.6 times that on the control, and in 1979 in a replicate experiment on grid J, numbers were 2.7 times higher than on the control grid during August and September. Supplemental food was no longer available on grid H in 1979 and numbers remained only slightly greater (1.3 times) than on the control.

To summarize: supplemental feeding with oats had no effect on numbers of *Peromyscus* or *Clethrionomys* in 1977, but when sunflower seeds were used in 1978 and 1979, numbers of both

**Table 1.** *Peromyscus* reproduction data for 1976–1979. Values in boldface are from sunflower seed experimental areas

| | | 1976 | 1977 | 1978 | 1979 |
|---|---|---|---|---|---|
| End of male breeding season[a] | | July 7 | June 19 | July 11 | June 24 |
| Juveniles first trapped | | July 7 | July 3 | June 29 | June 24 |
| End female lactation[a] | | Aug. 18 | Aug. 16 | Aug. 7 | July 15 |
| Estimated No. litters (Number of females) | I | 9 (5) | 2 (2) | 6 (4) | 6 (4) |
| | H | 18 (10) | 8 (5) | **11 (7)** | 13 (12) |
| | J | | | | **6 (4)** |
| No. juvenile recruits | I | 20 | 22 | 23 | 22 |
| | H | 34 | 18 | **69** | 41 |
| | J | | | | **30** |
| Juvenile productivity | I | 2.2 | 11.0 | 3.8 | 3.7 |
| | H | 1.8 | 2.3 | **6.3** | 3.2 |
| | J | | | | **5.0** |

[a] Less than 50% adults in breeding condition

**Table 2.** *Clethrionomys* reproduction data for 1976–1979. Values in bold face are from sunflower seed experimental areas

| | | 1976 | 1977 | 1978 | 1979 |
|---|---|---|---|---|---|
| End male breeding season | | Sept. 1 | Sept. 2 | Aug. 22 | Aug. 13 |
| Juvenile first trapped | | June 20 | June 5 | June 14 | June 25 |
| No. juvenile recruits | I | 31 | 12 | 31 | 18 |
| | H | 22 | 23 | **71** | 34 |
| | J | | | | **76** |

rodent species increased 2- to 3-fold over the summer breeding period.

### *Reproduction*

The density increase achieved by supplemental feeding must be produced by increased reproduction, reduced losses, or immigration. We consider first reproduction.

*Peromyscus maniculatus* in this study seldom bred until they were one year old – we recorded only two juveniles breeding in the summer of their birth. All individuals present in the spring reached breeding condition.

The analysis of *Peromyscus* reproduction and juvenile recruitment is given in Table 1. Did the provision of additional food cause an increase in the reproductive rate of *Peromyscus*? Juvenile production is affected by three aspects of female reproduction: the duration of the breeding season, the litter size, and the number of recruits per litter (a measure of early juvenile survival). Data on the male breeding season are very limited because most males were already in breeding condition when trapping began in the spring, and the number of adult males on each grid was usually very low (less than six). The length of the male breeding season seemed to be similar on all grids for any particular year. We recorded no cases of female *P. maniculatus* littering in traps and therefore have no measure of litter size on grids supplied with additional food. We use the date that small juveniles first appeared in traps as a crude index of the date of the first litter and the start of the female breeding season. The date of the appearance of young was synchronous between the control and experimental grids for any given year. The end of the female breeding season was also synchronous between the grids, although the 1977 comparison is hindered by a sample size of one on the control grid. Thus, for *Peromyscus* we could find no evidence of changes in the length of the breeding season caused by supplemental feeding.

To estimate the number of *Peromyscus* litters produced on each grid, we used the records of each individual female's breeding condition during the year. Our definition of juvenile production is the number of juvenile recruits that were tagged during the season divided by the estimated number of litters raised on that grid. There is an indication that the number of litters per female may be increased by supplemental feeding. Five of the 11 females had two litters on grid H in 1978 when sunflower seeds were provided, whereas none of 12 females had two litters in 1979 when no seeds were given. Juvenile production was also enhanced 35–66% in the two sunflower feeding experiments (Table 1). The high density population on grid H in 1979 showed a decrease in the number of litters produced per female, although juvenile productivity remained at the control level, representing a 50% decrease in juvenile production from the previous year.

Data on *Clethrionomys* reproduction and juvenile recruitment are given in Table 2. Because of smaller sample sizes, we were unable to do a fine scale analysis of the components of reproduction in *Clethrionomys*. Male *Clethrionomys* began breeding by early May in each year on all grids. The end of the male breeding season in late August and early September was also similar on all grids and thus not affected by food addition. Small juveniles appeared in the traps for the first time consistently two weeks later on the control grid than on the food supplemented grids in each year. This minor difference could be an artifact of trapping, but its consistency suggests that female reproduction may have begun 1–2 weeks earlier on the food grids than on the control. The end of the female breeding season was never later on the experimental grids than on the control, and breeding was over by mid-September on all areas. Because of the small number of adult females caught, we were unable to estimate the number of litters produced on each grid. Juvenile recruitment was much higher on all the food grids. In 1977, twice as many juveniles were caught on the grid provided with oats, and in 1978 and 1979, 2–4 times as many juveniles were caught on the sunflower seed grids.

In contrast to *Peromyscus*, juvenile *Clethrionomys* were often able to mature and breed during their first summer. On control grid I, 50% of the females and 23% of the males bred during their first summer. On the grids provided with extra food, only 21% of the females and 27% of the males bred during their first summer. There is thus no indication that extra food allowed more young of the year to mature.

Thus, supplemental feeding with sunflower seeds increased juvenile production in both species, probably by increasing early juvenile survival. Extra food did not change the length of the breeding season. Nor was the onset of sexual maturity changed in the juveniles of either species.

### *Survival*

A higher density on the food-supplemented areas might be caused by better survival. In this section we examine the survival rates of the trappable populations. Survival is equated with remaining alive on the trapping area, and thus losses may involve deaths or migration. We will consider survival in three parts: (1) adult survival during spring and summer; (2) juvenile survival during the summer, and (3) overwinter survival.

**Table 3.** Juvenile minimum 2-week survival rates averaged over the entire summer for young-of-the-year *Peromyscus* and *Clethrionomys*. Sexes pooled. Values in bold face are from food supplement experiments. Sample size in parentheses

| | Control I | Exp. H | Exp. J |
|---|---|---|---|
| *Peromyscus* | | | |
| 1976 | 0.77<br>(44) | 0.49<br>(53) | |
| 1977 | 0.70<br>(30) | 0.82<br>(29) | |
| 1978 | 0.79<br>(47) | **0.71**<br>(105) | |
| 1979 | 0.50<br>(34) | 0.57<br>(67) | **0.93**<br>(43) |
| *Clethrionomys* | | | |
| 1976 | 0.63<br>(30) | 0.63<br>(41) | |
| 1977 | 0.80<br>(15) | 0.62<br>(26) | |
| 1978 | 0.58<br>(38) | **0.47**<br>(73) | |
| 1979 | 0.70<br>(27) | 0.50<br>(38) | **0.59**<br>(118) |

In *Peromyscus*, adult survival was analyzed in two periods – *spring*, including May and June before any young had appeared, and *summer*, including July and August, after young were present in the trappable population. We could find no significant changes in *Peromyscus* adult survival in this experiment during either period. For example, in spring, females on the control averaged 0.84 survival rate per 2 weeks, while females on the food grids averaged 0.82. During summer, the corresponding figures were 0.85 and 0.82. In *Clethrionomys* we also found no changes in summer adult survival associated with the feeding experiment. Thus, adult survival seems unaffected by food additions.

Juvenile survival ought to be especially sensitive to the food supply. Table 3 gives the minimum survival rates for juveniles caught in live traps during their first summer of life. Juvenile survival fluctuates between years, but there are no systematic effects of food addition on juvenile survival in either species. For *Peromyscus*, juvenile survival appears to be improved on the food grid in 1979, but not in 1978. For *Clethrionomys*, juvenile survival seems if anything to be slightly worse on the food grids. We conclude that food supplementation does not improve juvenile survival during the summer in either species.

Overwinter survival was determined from the capture of tagged individuals in spring. Table 4 presents these data for three winters for *Peromyscus* and *Clethrionomys*. Survival overwinter seems to be improved in only one instance – *Peromyscus* in 1977–78 after the oats supplementation on grid H. There is no apparent impact the following winter after the sunflower seeds were used on grid H, nor is there any detectable effect in *Clethrionomys* for either year. The single positive result may be a chance effect, and the majority of the evidence suggests that food supplementation does not improve overwinter survival.

Thus we are unable to show any improvement in survival of either adults or juveniles during summer or winter in response to food supplementation. Increased density on the food grids did not result from changes in survival within the trappable population.

**Table 4.** Overwinter survival rates standardized to 8-month periods for *Peromyscus* and *Clethrionomys*. Sexes pooled. Sample size in parentheses

| | 1976–1977 | 1977–1978 | 1978–1979 |
|---|---|---|---|
| *Peromyscus* | | | |
| Control Grid I | 0.44<br>(9) | 0.21<br>(14) | 0.26<br>(15) |
| Exp. Grid H | 0.33<br>(3) | 0.59<br>(19) | 0.27<br>(53) |
| *Clethrionomys* | | | |
| Control Grid I | 0.07<br>(14) | 0.33<br>(12) | 0.05<br>(18) |
| Exp. Grid H | 0.13<br>(15) | 0.36<br>(17) | 0.11<br>(52) |

**Table 5.** Number of adult immigrants for *Peromyscus* and *Clethrionomys* for 1977–1979. Adult immigrants are untagged individuals of adult size

| Month | Control Grid I | | Exp. Grid H | | Exp. Grid J | |
|---|---|---|---|---|---|---|
| | ♂ | ♀ | ♂ | ♀ | ♂ | ♀ |
| *Peromyscus* | | | | | | |
| June 1977 | 5 | 0 | 0 | 2 | – | – |
| July | 1 | 0 | 1 | 0 | – | – |
| August | 1 | 0 | 1 | 0 | – | – |
| June 1978 | 0 | 0 | 1 | 2 | – | – |
| July | 0 | 0 | 3 | 2 | – | – |
| August | 0 | 2 | 2 | 1 | – | – |
| June 1979 | 0 | 1 | 0 | 1 | 3 | 1 |
| July | 1 | 1 | 0 | 3 | 0 | 0 |
| August | 1 | 1 | 3 | 0 | 3 | 3 |
| *Clethrionomys* | | | | | | |
| June–Sept. 1977 | 1 | 0 | 0 | 1 | – | – |
| June–Sept. 1978 | 1 | 0 | 3 | 3 | – | – |
| June–Sept. 1979 | 2 | 5 | 2 | 4 | 2 | 3 |

### *Dispersal*

Some of the population increase on the food-supplemented areas might have come from migration of individuals. We recognize two components of migration: (1) adult immigration, defined as untagged adult animals appearing in live traps, and (2) juvenile immigration, defined as the known movements of tagged juveniles during their first summer. We assume in this analysis that all new adults captured are immigrants as opposed to being residents that have avoided capture for some time. We omitted the May samples from this analysis because a new adult captured in May could possible be an overwintered resident not caught the previous autumn. Juveniles' movements are harder to measure, since all juveniles are new at first capture and we have no way of knowing if they are resident juveniles or immigrants that moved just after weaning. For these reasons, we can obtain only a partial picture of the role of dispersal in these experiments.

Table 5 gives the numbers of adult immigrants for *Peromyscus*. Immigration of adults is greater into the food grids supplemented with sunflower seeds. Six times as many male *Peromyscus* immigrated into the sunflower seed areas in 1978 and 1979, and twice as many females, compared with the control area.

In *Clethrionomys*, the same result was observed in 1978 but not in 1979.

The movement of tagged individuals between trapping areas was quite rare during 1976–1978. Only five *Peromyscus* per year moved between grids H and I and these movements were reciprocal. Even fewer tagged *Clethrionomys* moved between trapping grids. But in 1979, much more dispersal was observed. Sixteen *Peromyscus* tagged on grid H moved 400 m to grid J during the summer of 1979. Eleven of these were juveniles. Dispersal in *Clethrionomys* was also common in 1979 (Table 5) but was not apparently oriented toward the food grid J.

Thus, in one case out of four (*Peromyscus* on grid J in 1979), a significant fraction (44%) of the population increase can be explained by observed immigration. In the other three cases, immigration could have occurred without being detected because of a lack of tagged individuals in the source areas.

### *Body Weight and Growth*

Body size might be changed by the provision of supplemental food. We looked at three aspects of size: (1) adult body weights in spring (May–June); (2) juvenile body weights in autumn (September), and (3) juvenile growth rates during summer.

Spring adult body weights were unaffected by food supplementation. For example, male *Peromyscus* on the control grid averaged 27.3 g on June 14, 1978 and 25.3 g on food grid H. The same result was obtained for *Clethrionomys*.

Juvenile *Peromyscus* increase in weight over the summer and reach an asymptotic overwintering weight of 18–21 g during September. We analyzed the average body weights for September and were unable to detect any difference between control and food-supplemented grids. The same result was found for *Clethrionomys*, which overwinter at slightly lower weights than *Peromyscus*.

Juvenile growth rates were compared by an analysis of covariance among treatments with instantaneous relative growth rate as the variate and body weight as the covariate. A significant effect of feeding on juvenile growth was detected only in 1977 in both *Peromyscus* and *Clethrionomys* when growth rates were higher on food grid H. In 1978 and 1979, when we fed sunflower seeds, there were no significant differences in growth rates between the food and control grids. One possible explanation for these negative findings in 1978 and 1979 is that we failed to trap many of the experimental mice until they were nearly full grown. For example, the average weight at first capture for *Peromyscus* was 13.9 g on the control grid in 1979 but 17.6 g on food grid J. Growth rates could have been augmented during the critical interval from weaning to first trap capture and we have no way to measure that effect in this study.

Thus, supplemental feeding did not increase adult body size or juvenile weights in autumn, but may have increased juvenile growth rates in summer for *Peromyscus* and *Clethrionomys*.

## Discussion

Small mammal populations can be said to be food limited if the addition of supplemental food causes the average density to rise. There is a growing body of experimental evidence that shows food limitation in small mammals. Flowerdew (1972) showed that supplemental wheat increased the density of *Apodemus sylvaticus*. Smith (1971) found that supplemental food approximately doubled the density of *Peromyscus polionotus*. Cole and Batzli (1978) fed rabbit pellets to a *Microtus ochrogaster* population and increased density 50% above the control population. Andrzejewski (1975) supplied oats to a *Clethrionomys glareolus* population for two years and found a 2- to 4-fold increase in density. Taitt (1981) provided oats to a *Peromyscus maniculatus* population for two years and observed a doubling in population. Taitt and Krebs (1981) provided extra food to *Microtus townsendii* populations and produced a 2- to 5-fold increase in peak densities.

Increased populations on the food grids could be a product of either increased densities or increased movements. If mice and voles move more to utilize the extra food, the effective grid area will increase and thus the number of animals caught. Our data suggest that this is not what happens. Voles and mice seem to move less, not more, when extra food is present. We conclude that increased numbers resulted from increased *densities* of *Peromyscus* and *Clethrionomys*, and not from a change in effective area trapped.

The results of our experiments are consistent with the pattern observed in other food addition experiments, and suggest this generalization: *providing extra food to a small mammal population will cause numbers to double.* Future experiments with supplemental food should adopt this as a null hypothesis, and we need therefore to search for instances in which this experiment produces no effect on numbers or a much larger effect. Food supply is thus one important variable producing differences in average density between populations.

Why, we need to ask, should food supplementation only allow numbers to double? Almost no experiments of a dose-response type have been done on small rodents. Taitt and Krebs (1981) supplemented *Microtus townsendii* populations at two levels of food and found larger increases under high-food than under low-food. But the results were within the 2- to 5-fold range of increase over the control numbers. We do not know why numbers should not increase ten-fold or a hundred-fold when we provide food ad lib.

The mechanics of the demographic response to food supplementation are similar in many small mammals. Winter breeding is a common response (Cole and Batzli 1978; Andrzejewski 1975; Taitt 1981), but we did not see it in this study. One possible explanation is that we could not get the food out early enough in the spring. We could not provide food over the winter under the snow, and so we began putting out food only in late April.

Immigration into the food-supplement area is a second common response (Flowerdew 1972; Taitt 1981; Taitt and Krebs 1981), and is probably the most immediate response to food addition. In this study, immigration of both adults and juveniles was responsible for a large portion of the density responses. Individuals must search large areas in order to locate sites where food is provided.

By contrast, survival rates do not necessarily improve with extra food (Taitt and Krebs 1981). Some studies have shown improvement in survival in food-supplemental populations (Cole and Batzli 1978; Flowerdew 1972; Taitt 1981). Part of the problem is that survival in live-trapping studies is the remainder from two processes – death and emigration, and we have no way of separating death and emigration. Equal survival rates in experimental and control populations could result from the addition of two unequal rates of death and emigration.

It is important to remember that once the food supplemented population has doubled in size, demographic equilibrium must again prevail so that in the long run:

births + immigration = deaths + emigration.

Thus if extra food allows a permanently higher birth rate (e.g., winter breeding), either immigration must decline or deaths and emigration must increase to maintain the equilibrium. The evidence available so far suggests that emigration and immigration are the independent variables which balance the equation.

The failure of our 1977 feeding experiment in which oats was used can be explained either as an unlucky single sample or perhaps as a result of the lower energy value of oats compared with sunflower seeds. Little work has been done with different types of supplemental food in field populations. Getz et al. (1979) showed elegantly that *Microtus ochrogaster* and *M. pennsylvanicus* reach different peak densities in bluegrass, prairie, and alfalfa habitats. We presume that different food quality will produce different population responses in other small rodents.

The density carry-over which occurred on grid H in the year following the feeding experiment can be explained most simply on the basis of food caches. We suspect that mice and voles, as well as chipmunks and red squirrels, were caching sunflower seeds for use during the following winter. Certainly far more seeds disappeared than could possibly have been eaten by the animals present during the summer months. Abbott and Quink (1970) found that *Peromyscus leucopus* and *Clethrionomys gapperi* cached large quantities of white pine seeds.

Even though food supply seems to limit populations of small rodents in our study areas, we could find no evidence of starvation. Neither body weights nor growth rates seemed to change when food was added. Food limitation is apparently achieved by alterations in spacing behaviour rather than directly through nutritional deficiencies.

Two experimental designs can be suggested for future food supplement experiments. A replicated experiment with at least five levels of food addition would permit one to evaluate the shape of the response curve in detail and in particular to determine if there is an upper limit to raising the density. Alternatively one could hold density constant in a cropping experiment with several levels of food supplementation to look in more detail at the demographic responses in the absence of density effects.

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