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Source: *Journal of Mammalogy*, Nov., 1978, Vol. 59, No. 4 (Nov., 1978), pp. 809-819

Published by: American Society of Mammalogists

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INFLUENCE OF SUPPLEMENTAL FEEDING ON A VOLE POPULATION

F. RUSSELL COLE AND GEORGE O. BATZLI

ABSTRACT.—Densities and demography of prairie voles (*Microtus ochrogaster*) vary widely in different habitats, and dramatic, cyclical changes in population densities occur. We provided high quality supplemental food (rabbit pellets) to a population in relatively unfavorable habitat (an old bluegrass pasture) to test the hypothesis that differences in food quality can account for those trends. Throughout the winter the experimental population showed higher breeding intensity, better adult survival, and higher body growth rates than the control population. As a result, the supplemental population reached densities (135/ha) 50% higher than those of the control population (90/ha). Moreover, body growth, litter size, and density remained higher in the supplemental population during the following spring and summer. However, supplemental feeding did not prevent or delay declining densities that occurred in late summer and autumn in both populations. We conclude that quality of available food influences the amplitude of population fluctuations of the prairie vole, but some other factor(s) must initiate the periodic declines.

The importance of food quality to domestic animals is well documented (Maynard and Loosli, 1969), but little is known about the influence of nutritional factors on natural populations of herbivores. Herbivorous mammals appear to have abundant food resources throughout the year (Golley, 1960; Grodzinski et al., 1966; Chitty et al., 1968), and similar observations led Hairston et al. (1960) to hypothesize that numbers of herbivores are limited by predation rather than food supply. This view has been the subject of lively debate (Murdoch, 1966; Erhlich and Birch, 1967; Slobodkin et al., 1967), and recent evidence indicates that changes in the quality of food supply influence herbivore populations.

Ungulates grazing in African grasslands appear to be limited during the dry season not because of insufficient amount of forage but because of the low quality of available forage (Sinclair, 1975). A similar situation may exist for microtine rodents. Batzli and Pitelka (1971) correlated the cessation of breeding of California voles, *Microtus californicus*, at the beginning of the dry season with a shift in diet from green grass stems and leaves to seeds, and subsequent laboratory work (to be published separately) has shown that grass seeds will not support reproduction. Other studies suggested that low body weights and lack of reproduction by voles during cold winters are caused by poor quality of available food, although the evidence was not conclusive (Hansson, 1971; Tast, 1972; Evans, 1973; Tast and Kaikusalo, 1976). Negus and Berger (1977) have shown recently that small amounts of green forage can start reproductive activity in nonreproductive winter populations of *M. montanus*.

Microtine rodents are well known for their periodic increases to high densities followed by rapid declines to low densities (Krebs and Myers, 1974), and some investigators have linked these cycles in abundance to changes in availability and quality of food supply (Pitelka, 1957; Schultz, 1964, 1969). Several experiments have been conducted to test the hypothesis that forage quality affects the density of grazing microtines, either by fertilization of forage (Hoffmann, 1958; Schultz, 1969) or by addition of fertilizer and food (Krebs and DeLong, 1965). In the latter study, fertilizing the vegetation and providing a food supplement to a population of *Microtus californicus* resulted in high body growth rates and good reproductive rates. Nevertheless, the supplemented population declined during the breeding season and demonstrated lower survival rates than the control population. These studies unfortunately produced

equivocal results, partly because the changes in available food (natural diet and food supplement) could not be related to the nutritional requirements of microtines.

Studies conducted on the prairie vole, *M. ochrogaster*, in central Illinois showed strong correlations between forage quality and demographic characteristics (Cole, 1977). Prairie vole populations living in habitats with high forage quality had higher densities, better reproductive performance, higher survival rates, and higher body weights than populations living in habitats with poor forage quality. This paper reports the results of an experiment conducted to test the hypothesis that availability of high quality food accounts for the differences observed in these populations. We added high quality supplemental food to a population in relatively poor habitat during the increase and decline phases of a population cycle. We predicted that the supplemental population would have higher densities, better reproductive performance, higher survival rates, and higher mean body weights than the control population. In addition, we expected to prolong the increase phase and at least delay, if not prevent, the decline phase of the cycle.

STUDY AREA

The 1.5-ha study area was an abandoned bluegrass pasture located at the University of Illinois Biological Research Area (Phillips Tract) 5 km E Urbana, Illinois. The pasture had been released from grazing for 2 years and was surrounded by habitat unfavorable for prairie voles—farmyard, forest, grazed pasture, plowed field, and old field with sparse cover. Performance of prairie voles in bluegrass habitats is generally poorer than in old fields dominated by alfalfa (Cole, 1977), so addition of food to bluegrass habitat provided a suitable test of our hypothesis. All favorable vole habitat in the general area (five hectares) was regularly live-trapped as part of another study, and because all voles were marked by toeclipping, the origin of those moving on or off the site could be determined.

A mowed strip 10 m wide divided the study plot into two live-trapping grids of 0.80 ha and 0.55 ha. This artificial barrier effectively limited movement of voles between the grids and allowed placement of the grids in close proximity (see Cole, 1978 for map and analysis of movement).

Vegetation on both grids was dominated by bluegrass, *Poa pratensis*, which comprised more than 75% of the cover. *Phleum pratense* and *Bromus* spp. comprised most of the other monocots present (5% of the cover). Broad-leaved herbs formed approximately 20% of the cover during the growing season. *Taraxacum officinale*, *Trifolium repens*, *T. pratense*, and *Solidago altissima* were common on both grids, although slightly more common on the 0.80-ha grid. Dicots are preferred forage for the prairie vole (Zimmerman, 1965; Fleharty and Olson, 1969; Cole, 1977) and, because they were less abundant on the 0.55-ha grid, it was designated the experimental grid and received the food supplement.

Some meadow voles (*M. pennsylvanicus*) were captured on the control grid, but they were never common (0–7/ha). We removed all captured meadow voles from the study area to prevent competitive interactions with the prairie vole. Short-tailed shrews (*Blarina brevicauda*) and western harvest mice (*Reithrodontomys megalotis*) occurred throughout both grids, the latter only sporadically. House mice (*Mus musculus*) and Norway rats (*Rattus norvegicus*) occurred only at the north end of the supplemental grid near abandoned farm buildings.

Vertebrate predators were common throughout the study. Fecal droppings indicated that raccoons and feral cats regularly used the area. A majority of the scats (80%) were found on the supplemental grid. Least weasels (*Mustela nivalis*) occurred commonly on both study areas, and during one trapping session seven weasels were captured. Long-tailed weasels (*Mustela frenata*), striped skunks (*Mephitis mephitis*), red foxes (*Vulpes vulpes*), and fox snakes (*Elaphe vulpina*) also were observed in the area. Avian predators included red-tailed hawks (*Buteo jamaicensis*) and great horned owls (*Bubo virginianus*).

METHODS

Wooden multiple catch traps (Burt, 1940) were set one trap per station at 10-m intervals. The control grid consisted of 72 stations and the experimental grid had 60 stations. We set traps in

runways or next to holes within 2 m of the station marker and moved them frequently to increase the probability of capturing all resident voles.

Live-trapping began May 1975 on the supplemental grid; but, because there were few signs of voles, the control grid was not trapped until August 1975. Trapping sessions, conducted every 3 weeks, consisted of 2 days prebaiting with a small amount of cracked corn and 3 days of trapping. This procedure generally produced recapture rates greater than 80% for the last trap check. To reduce mortality, cotton was supplied as nesting material in the winter, traps were covered with vegetation during the summer, and traps were checked twice a day. Only five voles died in traps during the study.

After recording animal number, sex, reproductive condition, weight, and location of capture, voles were released at the point of capture. Embryos could be detected by palpation 10–12 days after conception in the laboratory, although it was difficult to determine litter size this early. Enlarged teats or teats red at the tips indicated lactation. If a lactating vole had not been detected as pregnant three weeks earlier, the pregnancy rate for the earlier date was corrected to include these animals. Scrotal testes, taken as a sign of reproductive activity in males, may not be reliable (Batzli and Pitelka, 1971), and results obtained using this characteristic should be evaluated with caution.

Prairie voles exhibit high growth rates and high reproductive performance (numbers of litters and litter size) when fed rabbit pellets (Purina #5321) in the laboratory (Cole, 1977). Moreover, the rabbit pellet diet approximates the nutritive value of their preferred natural diet (dicots, particularly legumes) (Cole, unpublished data). Therefore, rabbit pellets were used as the supplemental food. The 210 feeding stations consisted of small bottles (200 ml) filled with rabbit pellets and were placed in vole runways every 5 m throughout the supplemental area. The large number of feeding stations reduced the possibility that socially dominant voles could monopolize them. Bottles were refilled as often as necessary to keep food available, which was about every 4 days in the winter and every 12 days in the summer, but more frequently if disturbed by rain or predators.

Several observations indicated that voles utilized the supplemental food. Voles deposited feces in the bottles, and these feces contained particles similar to those in rabbit pellets. In addition, the rate of rabbit pellet removal from the bottles correlated well with the number of voles known to be alive on the supplemental grid.

RESULTS

Population Dynamics

Densities on the supplemental grid reached higher levels than those on the control grid (Fig. 1). The control population increased from an initial density of 28/ha in August at a mean rate of 18%/week to a peak density of 90/ha in October 1975. The population then declined during the winter months (mean rate -8%/week). The onset of the growing season coincided with a gradual recovery in density to the level of 65/ha in June. Densities remained at approximately these levels for 10 weeks. A rapid decline (mean rate of -24%/week) followed until low densities (5/ha) were reached in late October 1976. Similar fluctuations occurred in nearby bluegrass fields.

A different pattern occurred on the supplemental grid. This population increased at a mean rate of 25%/week until reaching a density of 80/ha in late September 1975. Then, unlike the control population, violent fluctuations in density occurred, increasing in amplitude and culminating in a peak density of 135/ha in April 1976. Two more fluctuations of decreasing amplitude occurred, then a rapid decline (mean rate of -36%/week) began in early August and ended in late October 1976 when densities reached 1/ha. Peak density in the supplemental population was almost 50% higher than in the control population and was higher than any other *M. ochrogaster* population in nearby habitats.

The accuracy of these enumerations depends upon probability of capture of prairie voles (Hilborn et al., 1976). Krebs et al. (1969) found trappabilities (the percentage of voles captured relative to the total number of voles known to be alive during a trapping

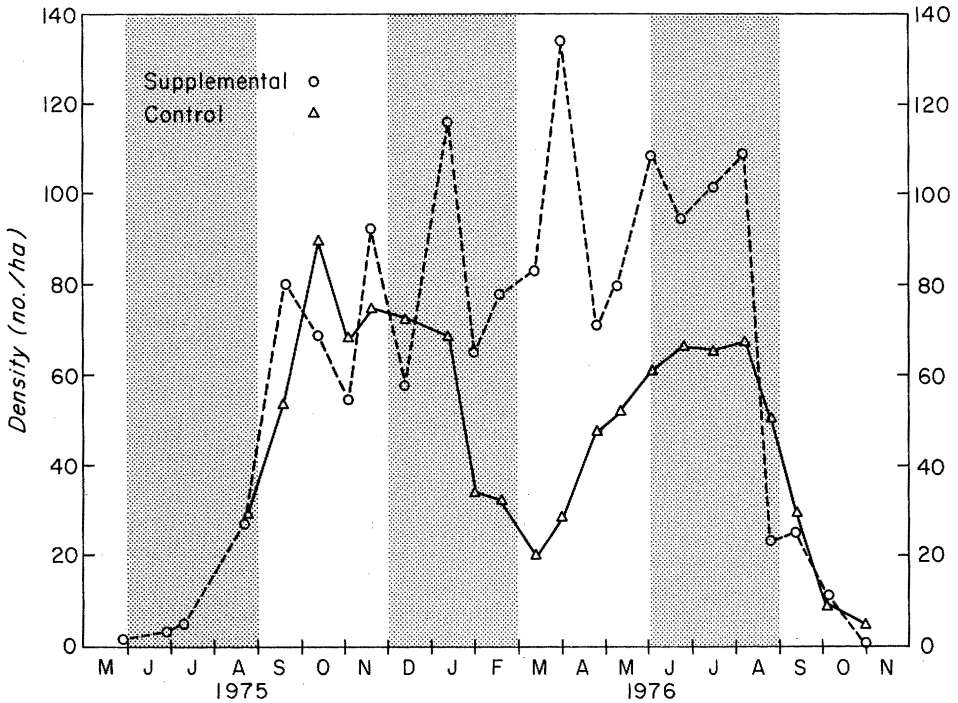


FIG. 1.—Minimum number of *Microtus ochrogaster* on grid with supplemental food and on control grid. Summer and winter months are shaded.

session) to be greater than 90% for prairie voles in southern Indiana, although Gaines and Rose (1976), studying prairie voles in Kansas, observed somewhat lower trappabilities (>75%). In the present study, the trappability of voles remained high (>90%) throughout the study on the control grid but was considerably lower on the supplemental grid where trappability reached 53% in February, probably as a result of reduced effectiveness of bait in the traps. Differences were significant during the winter and spring (Chi-square, $P < .05$) but not during the fall or summer. Thus enumerations obtained during winter and spring on the supplemental grid probably underestimated actual prairie vole densities, but any bias in that direction would reinforce our conclusions.

Supplemental feeding also affected the structure of the trappable population. Three age classes were used in this analysis: juveniles (<20 g for males and females), subadults (20–30 g for males and 20–28 g for females), and adults (>30 g for males and >28 g for females). These weight intervals were derived from molting patterns and growth rates of voles raised in the laboratory and fed a natural forage diet. Adult voles were the most abundant age class throughout the study (41–96% in the control population and 55–92% in the supplemental population). Subadults were more abundant in the control population, particularly during the winter and spring (12–29% of the population) than in the supplemental population (4–18% of the population). The higher proportion of subadults in the control population reflects the slower growth of young voles and poorer survival of adults at this time (see below). The proportion of juveniles in both populations reached highest levels in summer and fall during population growth and at peak density, but during the winter months juveniles comprised 3 to 33% of the supplemental population and none of the control population.

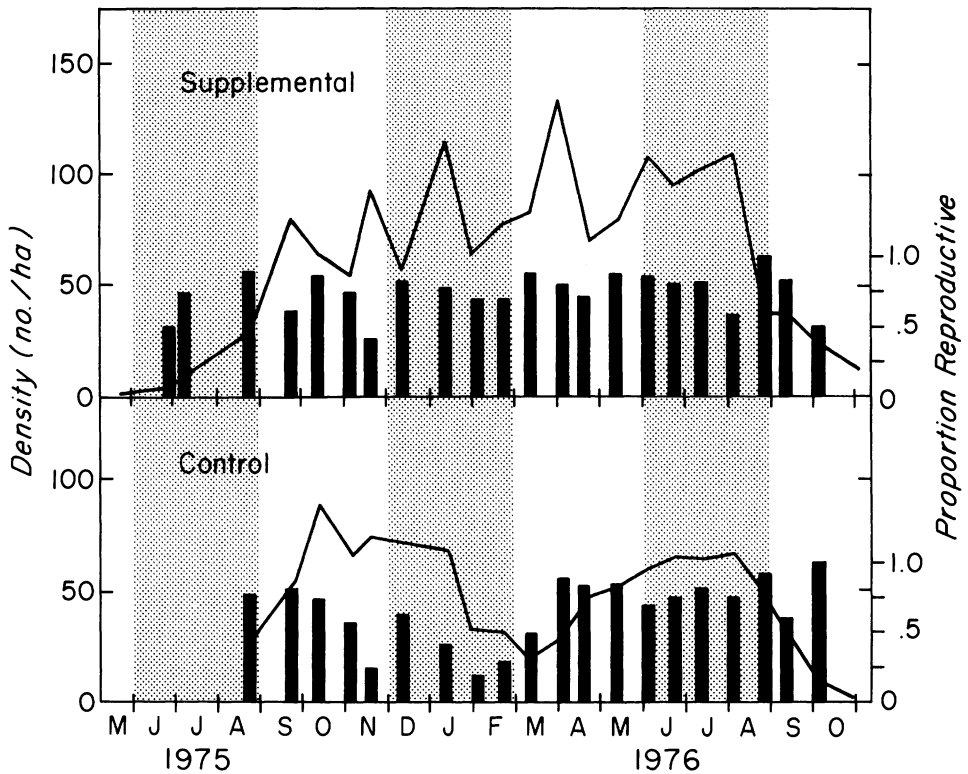


FIG. 2.—Proportion of reproductive female voles in the supplemental and control populations (bar graphs) in relation to population densities (line graph).

Reproduction

Population growth depends, in part, upon the intensity of breeding, length of the breeding season, and litter size. Reproductive activity in the supplemental population, as measured by proportion of reproductive females (proportion pregnant plus proportion lactating), remained at high levels ($\geq .5$) throughout the study whereas breeding activity was depressed in the control population during the winter (Fig. 2). Data on reproductive activity pooled for each season indicated that the proportion of scrotal males and the proportion of pregnant females were significantly higher in the experimental population only during winter (Chi-square, $P \sim .05$ and $P < .001$, respectively).

During spring and summer of 1976 females in advanced pregnancy were held in captivity until parturition to determine litter sizes. Mean (± 1 SE) litter size in the population receiving supplemental food ($5.11 \pm .35$, $N = 19$) was larger than that in the control population ($4.25 \pm .23$, $N = 28$); although small, the difference is significant (t-test; $P < .001$). Both values are higher than those reported for the prairie vole by Martin (1956) $3.18 \pm .24$, by Fitch (1957) $3.4 \pm .1$, and by Keller and Krebs (1970) $3.06 \pm .19$ to $3.53 \pm .24$.

Survival

Losses from the trappable population include both mortality and emigration. Emigration from the study area was low; only 36 emigrants (5% of the total) were captured by intensive live-trapping of all nearby suitable habitats; these habitats were trapped

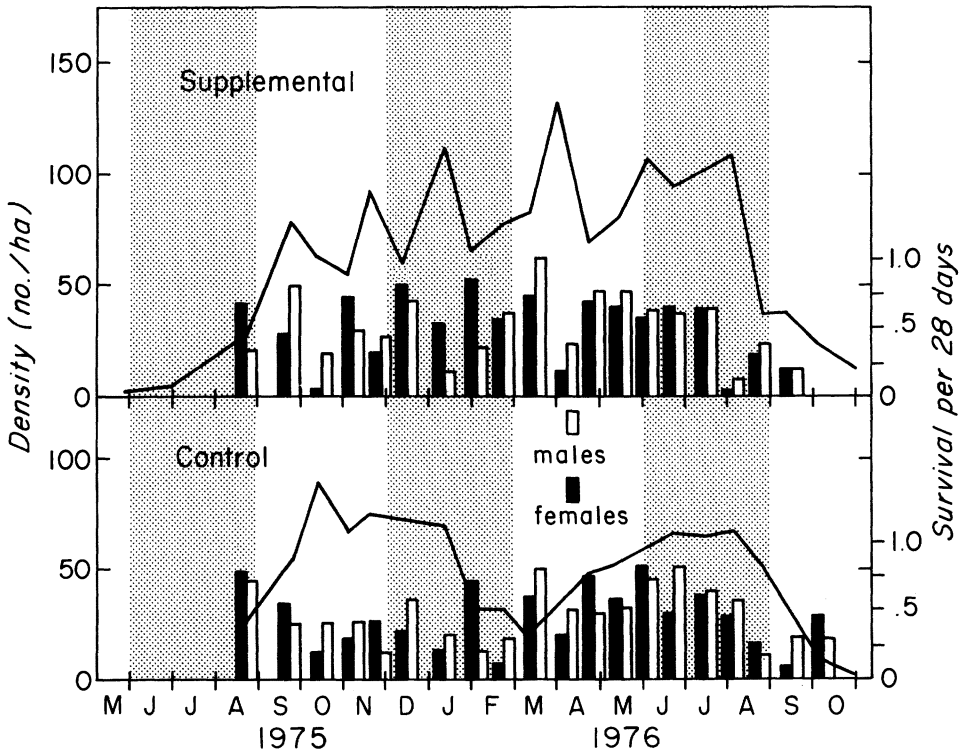


FIG. 3.—Survival rates per 28 days for adult male and female voles in the supplemental and control populations (bar graphs) in relation to population density (line graph).

at three-week intervals throughout the duration of the study. Therefore, our estimates are thought to be an accurate reflection of survival in the two populations.

Adult survival per 28 days was highly variable, particularly in the supplemental population (Fig. 3). Periods of low adult survival corresponded with the abrupt declines in density and may reflect heavy predation pressure. Nevertheless, survival of male and female voles was generally higher during the fall and winter on the experimental grid than on the control grid, although only adult female survival was significantly different between populations (Chi-square, $P < .001$). Both populations had low survival during the late summer decline in 1976. No difference in juvenile and subadult survival per 28 days occurred during the winter in the two populations, probably due to small sample sizes. Survival of young voles on both grids increased in spring after onset of vegetational growth.

Nestling survival was estimated by an index dividing number of juveniles in the trappable population at time t by the number of lactating females caught at $t - 3$ weeks (Krebs, 1966). Indices calculated for each trapping session were combined by season and averaged to obtain a mean survival index. Nestling survival on the control grid was highest during the fall 1975 increase (2.85), declined through the winter (1.71), and remained low in the spring (.69) and summer (.73). The winter survival index is somewhat misleading for the control grid because only a small portion of the females were reproducing at that time and few juveniles were captured (none in late January and February). Survival of nestlings on the supplemental grid was moderate during fall 1975 (1.34), high during winter (3.23), and then declined during spring (.79) and summer (.40). The high nestling survival observed during the winter may

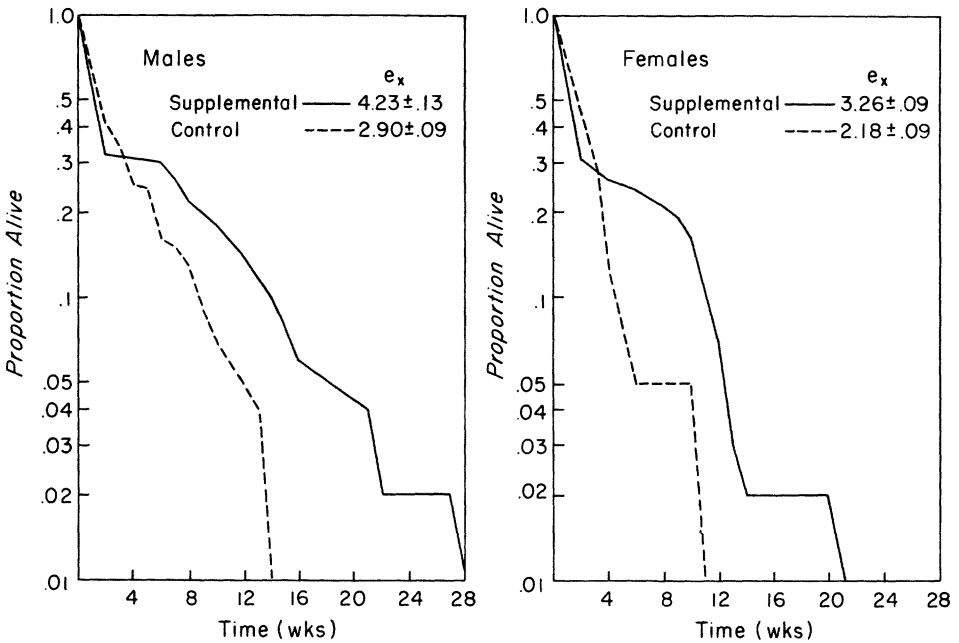


FIG. 4.—Survivorship curves for male and female voles in the supplemental and control populations after first capture as juveniles. Mean expectation to further life (± 1 SE) given for time at first capture.

reflect a possible response to the improved food supply. Juveniles in this population were caught throughout the winter, and the population continued to increase, also suggesting high juvenile survival. Lowest nestling survival in both populations occurred in late summer 1976, just before the decline. Observations on survival of toe-clipped nestlings from April to October 1976 indicated higher juvenile survival in the supplemental population, even during the decline.

Overall survival can be summarized by constructing survivorship curves for voles first caught as juveniles and followed until they disappeared from the population. Survivorship of both sexes improved on the supplemental grid (Fig. 4). The mean expectation to further life for voles first captured as juveniles, calculated using the method of Leslie et al. (1955), was significantly greater for both sexes in the supplemental population than in the control population (t -test, $P < .05$).

Sex ratios in both populations never differed significantly from 1:1, despite better male survival (Fig. 4). The adult sex ratio differed between populations only during spring 1976 (Chi-square, $P < .005$). At that time females were more abundant (57%) in the supplemental population (at peak densities) while males were more abundant (65%) in the control population (at moderate densities).

Body Growth

Growth rates were compared by instantaneous relative growth rates (% per day) and changes in mean body weight. Only males were used in this analysis because of the high variability in female growth rates resulting from pregnancies.

A linear regression between the mean body weight and instantaneous relative growth rate was calculated for each season (Krebs, 1966) and growth rate was determined for a hypothetical 35 g prairie vole (Table 1). Most rapid growth occurred in

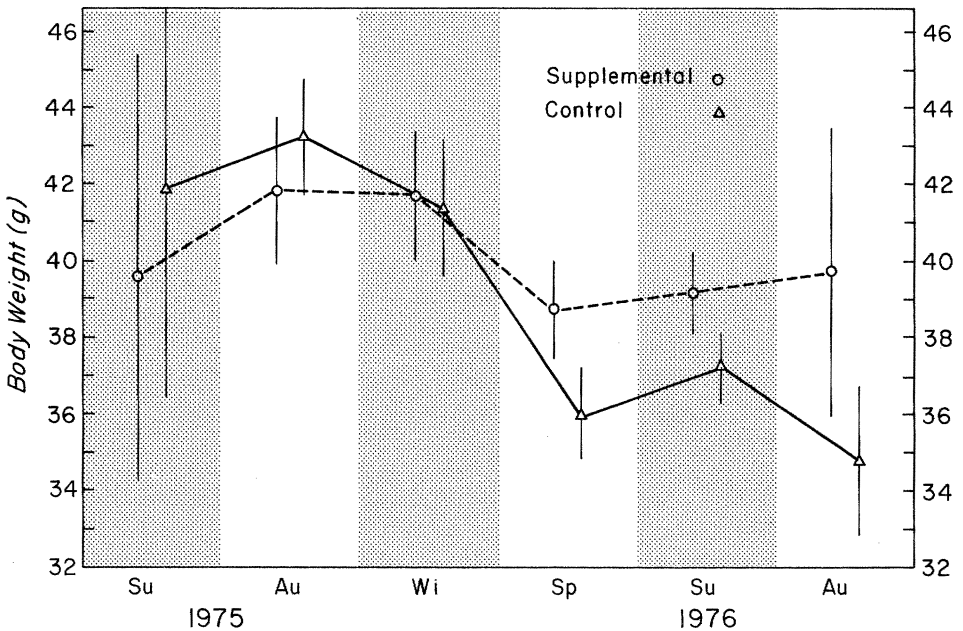


FIG. 5.—Mean body weight of male voles in the supplemental and control populations. Data pooled by seasons. Vertical lines represent 95% confidence limits.

the fall of 1975 in both populations. Growth rates of voles in the supplemental population were 15% lower than in the control population. Growth rates in the supplemental population almost doubled those in the control population during winter and remained higher (30%–50%) throughout the rest of the study. Mean instantaneous relative growth rates, however, were statistically higher for the supplemental population only during spring (t -test, $P \sim .05$).

Differences in mean body weight reflect changes in both growth and survival. Adult males weighed more in the control population during the summer and fall of 1975, but the difference was not significant (Fig. 5). Mean body weights dropped sharply on the control grid during the winter while weights of supplemented voles dropped less. By spring and throughout the following summer mean body weight of males remained significantly higher ($P < .05$) in the supplementally fed population.

DISCUSSION

Prairie vole populations have now been studied in detail in Kansas (Martin, 1956; Gaines and Rose, 1976), in southern Indiana (Krebs et al., 1969; Gaines and Krebs, 1971), and in central Illinois. The population cycles of prairie voles differ somewhat from the typical 3- to 4-year microtine cycle (Krebs and Myers, 1974). The peak phase lasts only a few months, and the entire cycle may last only 2 years.

In this study the presence of high quality food prevented a winter decline, thereby prolonging the population increase approximately 6 months, increased the amplitude of the cycle, but did not prevent or delay the cyclic decline. Two previous experiments using supplemental food also failed to prevent population declines. Krebs and DeLong (1965) provided supplemental food to a population of *M. californicus*, and Chitty and Phipps (1966) fed a population of *M. agrestis*. However, the food supplement in those studies was of unknown quality whereas the high nutritive value of rabbit pellets fed to *M. ochrogaster* in this study was established in laboratory experiments (Cole, 1977).

TABLE 1.—Mean instantaneous relative growth rates ($\pm 95\%$ confidence limits) expressed as %/day for male voles in the supplemental and control populations. Data were pooled by seasons and adjusted by regression to hypothetical 35 g vole. Values in parentheses indicate number of observations.

Population	Seasons 1975-1976			
	Autumn	Winter	Spring*	Summer
Supplemental	1.83 \pm .31 (28)	.78 \pm .47 (25)	.72 \pm .23 (42)	.85 \pm .28 (47)
Control	2.14 \pm .36 (48)	.44 \pm .32 (28)	.38 \pm .25 (39)	.59 \pm .18 (63)

* Means significantly different (t -test, $P \sim .05$).

Factors other than quality of the diet apparently were responsible for the population decline. There was no evidence of disease or parasitic infestations, and weather remained favorable. In addition, dispersal appeared low throughout the study and apparently had little influence on the dynamics of these populations. On the other hand, as the density of voles increased, feral cats from neighboring farms and raccoons living in an adjacent woodlot began frequenting the area. Cat and raccoon scats were common on the supplemental grid by early winter. An intensive search of the study area during this time produced 74 scats, 80% of which were found on the supplemental grid. Least weasels were common (4-6/ha) by late winter. The violent fluctuations in density observed in the supplemental population during the winter were probably due to episodes of heavy predation. After each decline there was a rapid increase to progressively higher density until peak densities were reached. Reproductive rates remained high throughout the study whereas periods of low survival corresponded with declines in density. Predators previously have been implicated in population declines of microtine populations (Pearson, 1964, 1966, 1971), and their numerical response was probably a factor preventing attainment of high densities of lemmings on a fertilized plot in tundra habitat (Schultz, 1969). If the decline in the summer of 1976 was caused by predators, they must have been much more efficient than those present during the winter. This leads us to the conclusion that other factors, perhaps those intrinsic to the population, must have been involved.

Patterns of breeding intensity reported for prairie voles are extremely variable. Martin (1956) indicated that prairie voles breed throughout winter only if food supplies and other environmental conditions are favorable. Gaines and Rose (1976) also observed breeding activity throughout the year in populations of *M. ochrogaster* in Kansas, although in some years a depression of breeding activity occurred in the winter. Reproductive activity may also be depressed during the summer, possibly because of drought (Fitch, 1957; Gaines and Rose, 1976). In southern Indiana, Krebs et al. (1969) observed a decline in reproduction during winter but not in summer, similar to our observations on the control grid. The maintenance of winter breeding when supplemental food was provided suggests that nutrition controls winter reproductive activity. A recent experiment by Negus and Berger (1977), wherein nonbreeding winter populations of *M. montanus* given small supplements of green wheat sprouts began breeding within 2 weeks supports this view.

Our results indicated that supplemental food can increase litter size as well as breeding intensity, and other studies also suggest an effect of food quality on litter size. Hoffmann (1958) reported a direct correlation between food quality (crude protein) and litter size for *M. montanus*, and Batzli and Pitelka (1971) found marked seasonal changes in litter size associated with different diets of *M. californicus*.

Supplemental feeding also increased female and nestling survival in our experiment, particularly during the winter, a time of deteriorating food quality and environmental stress. Previous studies of microtine rodents also identified female and juvenile survival as important determinants of population growth (Krebs, 1966; Krebs et al., 1969; Krebs and Myers, 1974).

Individual growth rates are linked to population growth rates by age at reproductive maturity. Voles with high growth rates reach maturity earlier and exert a greater effect on population growth than voles with low growth rates (Cole, 1954). In addition, litter size is correlated with female body size in the prairie vole (Jameson, 1947), suggesting that faster-growing females may produce larger litters. Our supplemental feeding enhanced the growth rate of voles, even during the growing season. Voles born in the fall remained subadults throughout the winter in the control population, then grew rapidly to maturity in the spring after the onset of the growing season. On the other hand, voles in the supplemental population continued to grow and reached maturity during the winter. Some of these voles reproduced during the winter.

Thus, it seems clear that quality of food supply strongly influences the density and demography of microtine rodents. Supplemental feeding produced higher reproductive activity, enhanced survival and growth rates, and resulted in higher densities. However, the availability of high quality food was not sufficient to prevent a cyclic decline in prairie vole populations, and the cause of this decline remains unknown.

ACKNOWLEDGMENTS

Diana Avalos-Dummitt, John Edgington, Glenn Guntenspergen, Lonnie Hansen, Joyce Hofmann, and Lou Verner all contributed to this work, and we are grateful for their help. We especially thank Dr. Lowell Getz for his advice, encouragement, and cooperation in planning and performing this research. Financial support for this project was provided in part by NIH Grant HD 09328 (to L. L. Getz), the School of Life Sciences of the University of Illinois, the Granite City Steel Foundation, the American Museum of Natural History, and a Grant-in-Aid of Research from Sigma Xi.

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