Condition and Diet of Cycling Populations of the California Vole, Microtus californicus
Author(s): George O. Batzli and Frank A. Pitelka
Source: *Journal of Mammalogy*, Vol. 52, No. 1 (Feb., 1971), pp. 141-163
Published by: American Society of Mammalogists
Stable URL: http://www.jstor.org/stable/1378438
Accessed: 16-11-2016 20:56 UTC

CONDITION AND DIET OF CYCLING POPULATIONS OF THE CALIFORNIA VOLE, *MICROTUS CALIFORNICUS*

George O. Batzli and Frank A. Pitelka

Abstract.—Populations of the California vole, *Microtus californicus*, were followed at two sites near San Francisco Bay in order to investigate changes in diet and condition of these cycling microtine rodents. Mark and recapture analyses provided information on condition during seasonal (season to season) and annual (year to year) fluctuations, and snap trapping provided stomach samples for dietary analyses and carcasses for determinations of reproductive condition and fat reserves.

Seasonal changes in condition were found to be correlated with dietary changes. The end of the breeding season in late spring was associated with low growth rates, low survival rates, and low fat reserves. At the same time the vegetation was drying, and the diet changed from one dominated by grass stems and leaves to one dominated by grass seeds. Breeding and adult growth sometimes began before the autumn rains while grass seeds were still the major dietary item, but occasional meals of green forbs and perennial grass were also taken at this time.

Three annual grasses, *Lolium multiflorum*, *Avena fatua*, and *Bromus rigidus*, were preferred foods and formed the bulk of the winter diet at both low and high populations. The standing crop and seed production of these grasses were severely reduced by high vole populations. Reduction in food availability and quality might have caused the delay in the start of the breeding season, the low fat reserves and the continued population decline that were observed after the peak population.

These results indicated that nutritive factors could be involved in microtine population cycles at low latitudes and point to the need for further research on diet quality and nutritional physiology of *Microtus*.

California voles (*Microtus californicus*) undergo 2- to 4-year cycles of abundance as do many other microtine rodents. There is no general agreement on the causes of population declines or the causes of the delay in recovery of the populations after a decline. Christian and Davis (1964) attributed the decline of high populations to endocrine exhaustion owing to increased behavioral interactions. Chitty (1955, 1967) and Krebs (1964) also thought that mutual interference is important, but they postulated selection for aggressive animals with low viability at high populations as the cause of declines. Predation was supported by Pearson (1966) as a major influence causing the delay in population recovery but he thought it insufficient to cause the decline. Lack (1954) suggested that microtine populations crash when food supplies deteriorate and that recovery of the population is delayed until there are sufficient nutrients. Supporting evidence for this nutrient-recovery hypothesis was reported by Pitelka (1957*a*, 1957*b*) and Schultz (1964).

Which factors are important for production of microtine cycles will remain in doubt until suitable field experiments are completed, but a start in that direction has been made. Krebs and DeLong (1965) reported on a population of *Microtus californicus* for which they supplied grain and fertilized vegetation. The population responded by showing high body growth rates and good reproductive rates, but it still started to decline during the breeding season. However, neither the adequacy of the natural diet and of supplements in relation to nutrient requirements of *Microtus* nor the effects of feeding stations on social structure were known.

Little information about the composition of diet and nutritional requirements of nondomesticated herbivorous mammals exists. Probably the best information to date about the composition of microtine diets is based on stomach content analyses of 47 *Microtus ochrogaster* and 43 *M. pennsylvanicus* taken from many different locations at many different times of year (Zimmerman, 1965). Little has been done on the nutrient contents of diets or on the nutritional requirements of microtines. Schultz (1964) reported that levels of phosphorus, calcium, and nitrogen declined in forage samples after a lemming high, and Negus and Pinter (1966) reported that fat extracts of wheat sprouts added to laboratory diets increased the reproductive performance of *M. montanus.*

Apparently there are no detailed studies in which dietary composition is compared with the condition of populations of herbivorous rodents. This study was designed to get such information for *Microtus californicus,* a microtine that has received considerable attention recently (Batzli, 1968; Brant, 1962; Church, 1966; Greenwald, 1957; Hoffmann, 1958; Houlihan, 1963; Krebs, 1966; Lidicker and Anderson, 1962; Marsh, 1962; Pearson, 1960, 1966). The vegetation available for food and the influence of the voles on their own food supply were studied concurrently (Batzli and Pitelka, 1970).

STUDY AREAS

Although the Richmond Field Station (University of California) is surrounded by light industry in the city of Richmond, it is protected from public access by fences and has about 12 acres (5 hectares) of open fields, which have been fallow since 1950. A 2-acre (.809-hectare) plot surrounded by dirt roads was live-trapped periodically from July 1965 through November 1968, at approximately monthly intervals during the second half of the study.

Vegetation at Richmond was the Coastal Prairie type described by Munz and Keck (1950). Introduced annual grasses (*Avena fatua, Lolium multiflorum, Bromus rigidus, B. mollis*) and native perennial grasses (*Danthonia californica, Hordeum brachyantherum*) were dominant, but forbs formed up to 30 per cent of the standing crop during the summer. This study area included grids 6 and 7 designated by Krebs (1966) and DeLong (1967) during their studies of *M. californicus* and *Mus musculus* demography. The barrier between the grids was removed.

A second study area, on the Russell Reservation of the University of California, was located in the Briones Hills, 10 mi. E Richmond. A site was established there to get comparative data from a different type of grassland. Voles on the 1-acre (.405-hectare) plot were live-trapped from January through November 1968 at 2 to 3-month intervals. The site was at 1000 feet elevation and had been protected from grazing for 3 years.

Vegetation at Russell was the Valley Grassland type described by Munz and Keck (1949). Annual grasses, the same species as at Richmond, dominated the vegetation, but *B. rigidus* was by far the most important (45 to 65 per cent of the standing crop throughout the year). A different perennial grass, *Elymus cinereus,* also was present and formed nearly pure stands on 10 per cent of the plot.

Both study areas have a Mediterranean climate, that is, warm, dry summers and cool, wet winters, but there were differences in weather. More summer fog and winter rain occurred at the coastal site. Maximal summer temperatures were higher, and minimal winter temperatures were lower at the inland site. Annual grasses germinated after the autumn rains, usually late October to early November. The peak standing crop occurred early in the dry season, usually late May to early June, and maximal seed fall occurred in June and July. Details of both the weather patterns and the vegetational structure and composition were given in Batzli and Pitelka (1970).

The vertebrate fauna included a variety of possible competitors and predators of *Microtus* at each site. House mice (*Mus musculus*) were common at Richmond (one to 30 per acre), but only one was caught at Russell. Harvest mice (*Reithrodontomys megalotis*) were common at Russell (15 to 50 per acre), but none was caught at Richmond. Two jackrabbits (*Lepus californicus*) occasionally visited the Richmond field and one ground squirrel (*Spermophilis beecheyi*) resided in the field from August through November of 1966. Mule deer (*Odocoileus hemionus*) regularly visited the Russell field. Pocket gophers (*Thomomys bottae*) were common in both fields (five to 10 active burrows per acre).

The same avian predators occurred at both sites, sparrow hawks (*Falco sparverius*), red-tailed hawks (*Buteo jamaicensis*), and horned owls (*Bubo virginianus*). Scats of mammalian predators were rare at Richmond, and no carnivores were seen there. Carnivore scats were found regularly at Russell and feral cats were seen there. Foxes (*Urocyon cinereoargenteus*) have been seen and trapped at Russell (A. Sikora, personal communication). Gopher snakes (*Pituophis catenifer*) and racers (*Coluber constrictor*) were seen regularly during the summers at Richmond, but no snakes were seen at Russell. Two predators were observed taking voles at Richmond, a sparrow hawk and a gopher snake.

METHODS

Longworth live traps were used for the mark and recapture studies at both sites. Since Krebs (1966) had shown that *M. californicus* might not be captured randomly, procedures were designed to maximize the catch so that enumerations of the populations would be relatively complete. Grids with 7.5-meter intervals were staked, and two traps were set within 3 meters of each stake and next to any runways or holes that were present. Each sampling period consisted of a 3-day prebaiting period, during which traps containing hen scratch (corn, wheat, and sorghum) were locked open, and of enough trapping days (usually 3) to get a recapture percentage of greater than 75 per cent. Traps were relocated after each capture, and traps were removed after each trapping period.

During the winter, traps were checked only in the morning, but during summer, traps were checked also in the afternoon. Boards were placed over the traps to minimize trap deaths. Few voles were lost except on an unexpectedly sunny day, 2 Novmber 1967, when 15 voles (15 per cent of the population) succumbed to heat exhaustion. Ten of these were males, and the population continued to increase (Fig. 1).

Fingerling fish tags were attached to the right ear. Inasmuch as left ears were seldom torn, a torn right ear was taken to mean that a tag had been lost. The greatest loss of tags occurred between 6 August 1968 and 11 September 1968 when 11 tags (7 per cent of the surviving marked voles) were lost. All other monthly losses were less than 5 per cent. Survival data were corrected for the loss of ear tags.

Sex, location of capture, weight in grams, external signs of reproductive activity, ectoparasites seen when blowing on the hair, and fresh tail and body wounds were recorded for each vole when caught. All voles were released at the point of capture. Population characteristics were compiled from histories of individual animals. Estimates of the size of trapped areas included a boundary strip whose width was about half the distance between trapping stations (4 meters).

In order to get stomach samples for food habit determinations, snap traps were set in runways after live traps had been removed (usually 3 to 10 days after) during each of four seasons: after germination of the annual grasses (December and January), at the height of the growing season (March and April), after drying of annual grasses (June and July) and before the autumnal rains (September and October). Twenty-five traps were set in groups of five in representative parts of the fields so that stomachs would be representative of the diets for the whole population. No more than 10 per cent of the population was taken at any time. At low population levels, feces were collected from live-trap boards left at the stakes between trapping periods and used for supplementary information on food habits.

Stomachs and large intestines were preserved in 5 per cent formalin until the contents could be examined. Contents were identified by comparing epidermal structures with those in a reference collection of plants from the field. This method was described in detail by Williams (1962) and used by Zimmerman (1965). Two wet-mounted slides of unstained material were examined for each stomach.

Whether a plant was a monocot or dicot and the part of the plant (root, stem, leaf, or head) usually could be determined, but many fragments were too small for identification to species. In order to compare the composition of diets with the composition of available vegetation some refinements in technique were required. A point sampling procedure analogous to that used on dietary samples of domestic herbivores (Van Dyne and Heady, 1965) was designed. Using a microscope with a mechanical stage, 25 random field positions were examined for each slide (50 positions per stomach), and the fragment nearest the center of the field which contained at least a few epidermal cells was identified as precisely as possible. About half (40 to 60 per cent) of plant stem and leaf fragments could be identified to species in this manner, but neither the roots nor the heads of grasses could be identified.

Snap-trapped voles and those found dead in live traps were autopsied in order to get information on reproductive condition. For males, the length of testes, the visibility of epididymal tubules, and the length of the seminal vesicles were measured. For females, the number and length of embryos, the number of placental scars, and the number of corpora lutea and albicantia were recorded.

After the removal of the digestive tract, but not the mesentaries, the fat content of the carcass was determined. Carcasses were dried for 7 days in a forced air oven at 60°C, ground with a mortar and pestle and run through a Kimax fat-extracting apparatus for 12 hours using petroleum ether as a solvent. The fat content was determined by difference in dry weight before and after the extraction.

RESULTS

Population Characteristics

Results of mark and recapture indicated that neither males nor females were recaptured randomly. Tests for the comparison of recaptures of marked and unmarked voles when new individuals are not being recruited, and for the comparison of members of the marked segment of the population (Table 1), gave results similar to those reported by Krebs (1966). The hypothesis

TABLE 1.—*Summary of tests for randomness of recaptures at Richmond. Tests were based on those described in Leslie* et al. *(1953).*

Time Sex	No. captures	Chi-square	d.f.	Probability of results if random
	MARKED VERSUS UNMARKED SEGMENTS			
July–September 1967				
Male	140	13.2	2	$< .005$
Female	139	15.2	2	$< .005$
July–September 1968				
Male	282	10.3	2	$.01 > P > .005$
Female	281	9.8	2	$.01 > P > .005$

Time Sex	Estimate of no. marked	Observed no. marked	Percentage difference 100(O-E)/E
	WITHIN MARKED SEGMENT		
February–October 1968			
Male	255.5	291	13.9
Female	237.3	274	15.5

of random recapture should be rejected, thus invalidating the estimation of population characteristics by techniques such as the Lincoln Index and those of Jolly (1965). Therefore, high frequencies of marked voles were required to indicate the state of the populations.

Eleven snap trappings, scattered through all seasons, came within a week of the last live trapping, so an independent estimate can be made of the per cent of voles marked during a live-trapping period. The percentage of snap-trapped voles that were marked varied between 77.8 and 100 per cent based on sample sizes of four to 15. Summing these samples, 97 of 108 voles were marked. Because *M. californicus* is sedentary (Brant, 1962; Krebs, 1966), these results suggest that about 90 per cent of the weaned voles were being caught by the live traps. Owing to the high percentage of marked voles, Lincoln Index estimates of the populations closely approximated the minimum numbers (Fig. 1).

The population of *M. californicus* at the Richmond site crashed in 1964 (Krebs, 1966). Data in Fig. 1 indicate that recovery to high levels took 4 years, although habitat observations 50 meters away and across a road indicated a peak population 1 year earlier. A lack of synchrony in the fluctuations of local populations in the San Francisco Bay region has been noted previously (Marsh, 1962; Krebs, 1966). However, the Russell population appeared to be in phase with the Richmond population; both peaked at 150 to 160 per acre in the spring of 1968. Neither population reached 1968 levels during the spring of 1969, although habitat observations indicated moderate numbers present. The declines thus seemed to be the *H* type of

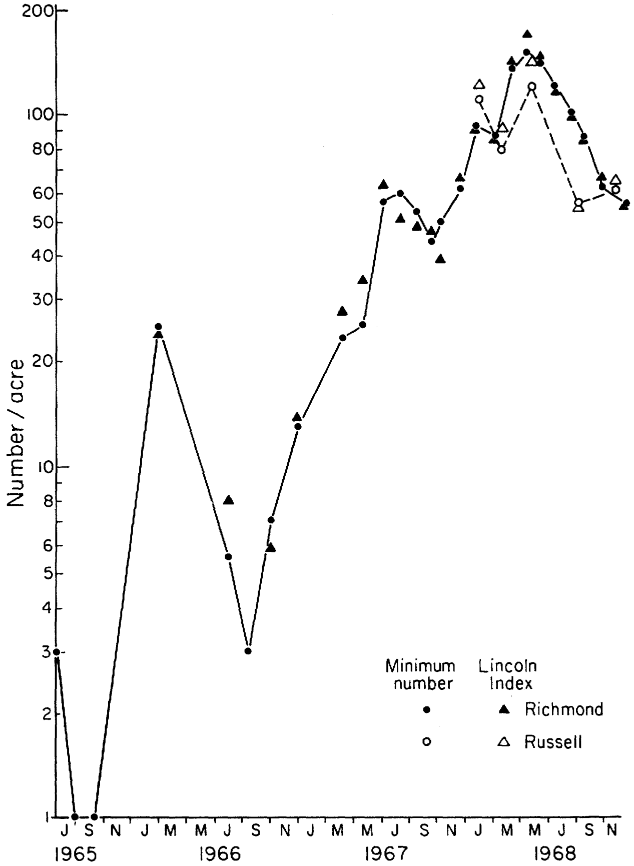

FIG. 1.—Density estimates at the Richmond and Russell sites based on the minimum number present and on Lincoln Index estimates.

Chitty (1955) where moderate numbers are present the year following high numbers as opposed to the G type where the decline is rapid and individuals are scarce the following year.

Seasonal patterns of population growth occurred at both sites. Populations generally increased during the winter and spring, though growth slowed or was set back in mid-winter, and declined during the summer and autumn. Although there are differences, similar seasonal patterns and peak densities have been reported for other mark-recapture studies of *M. californicus* in grassland. Previous estimates of peak densities included 180 to 250 per acre (Marsh, 1962), 100 to 465 per acre (Krebs, 1966), 125 to 200 per acre (Pearson, 1966), and 250 per acre (Batzli, 1968).

Age classes for the population were determined on the basis of weight. Greenwald (1957) found that most females became reproductively active as they reached weights of 30 to 35 grams (including embryo weight) although a few matured more quickly. Males generally did not mature until they reached weights of 40 grams. Males surviving several months usually weighed more than 40 grams, but some young females were more than 40 grams when pregnant and less than 40 grams when not pregnant. Hatfield (1935) described the development of three pelages for *M. californicus.* Replacement of the juvenile pelage began after weaning at about 21 days (20 to 25 grams), and the molt into adult pelage began at about 55 days (35 to 40 grams). Three age classes were used for analysis of structure of the population in this study: juveniles (25 grams or less for males and females), subadults (26 to 40 grams for males and 26 to 35 grams for females) and adults (more than 40 grams for males and more than 35 grams for females).

Adults were usually the most abundant segment of the trappable population at both sites and were particularly important in late summer through autumn of each year (74 to 98 per cent of the population) and in the winter of 1968 (76 to 92 per cent). Juveniles were most abundant after autumnal rains (December and January) and in spring (April and May) when they formed 17 to 25 per cent. Subadults were most important after autumnal rains (23 to 41 per cent), in spring (25 to 42 per cent), and in summer of the dry years 1966 and 1968 (48 to 54 per cent). During the wet year of 1967, adults formed most of the population in summer (87 to 98 per cent). The lack of juveniles during each of the summers indicated a pause in breeding, but other structural changes could have resulted from seasonal changes in breeding, body growth, or survival (or all three).

The per cent of females in the population varied from 20 to 100, but these extremes occurred during low densities in the summer of 1965 when only two to five voles were caught during a trapping period. Chi-square was used to test the hypothesis of equal sex ratios in the populations throughout the study. The hypothesis could be rejected ($P < .05$) from February through May of 1968 at Richmond (53 to 59 per cent females) and during May of 1968 at Russell (64 per cent females)—when population densities were high.

The use of scrotal testes as an external sign of reproductive activity was not reliable in this study. Of 51 autopsied males with visible tubules in the caudal epididymides, a character indicating the presence of spermatozoa (Greenwald, 1957), only 33 (64.7 per cent) had been classified as scrotal. Forty-six of the autopsied females were in reproductive condition, having either embryos or recent (heavily pigmented) placental scars. External signs varied in their reliability when compared to this standard. Sixty-four females had perforate vaginas, and this sign would have over-estimated the number of reproductive females by 39.1 per cent in spite of two pregnant females that were nonperforate. Open pubic symphyses (pubic bones separated by more than 1 millimeter) occurred in 42 females as did enlarged teats (more than 1 millimeter in diameter). Two out of the three external signs were positive in 43 (93.5 per cent) of the reproductive females. Although

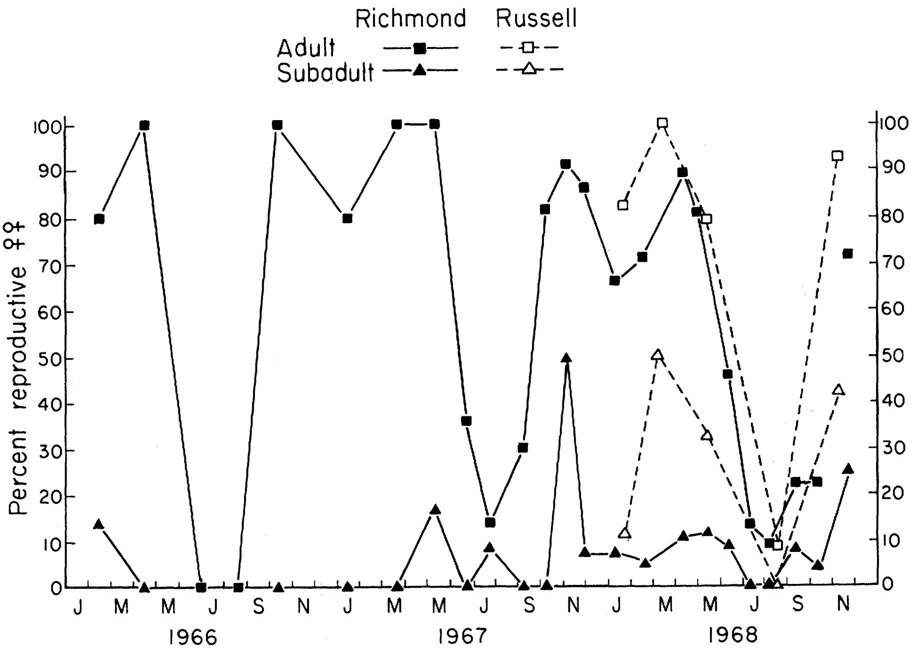

FIG. 2.—Per cent of reproductive females at the Richmond and Russell sites.

this criterion missed some early pregnancies in primiparous females, it provided the most accurate indication of female reproductive condition. Therefore, the per cent of females with two or more positive external signs was used as a measure of breeding intensity.

Seasonality of breeding was clear in both populations (Fig. 2), and changes in breeding intensity occurred rapidly. If the breeding season is defined as that period when more than 50 per cent of the adult females are in reproductive condition, the breeding season ended in late May or early June in all years and began in the middle of September in 1966 and 1967. The breeding season began in late October or early November at Richmond in 1968. Thus breeding declined with the drying of vegetation each spring,

TABLE 2.—*Comparison of mean litter sizes (± 95 per cent confidence limits) during different seasons. Analysis of variance indicated no differences between sites, but there were significant seasonal differences* (P < .0005).

	Early growing season (November–January)		Height of growing season (March–April)		Dry season (May–October)	
	N	Mean	*N*	Mean	*N*	Mean
Richmond	9	3.4 ± 0.9	13	5.2 ± 0.8	5	3.6 ± 0.7
Russell	11	3.0 ± 0.8	4	6.0 ± 1.3	6	3.3 ± 1.1

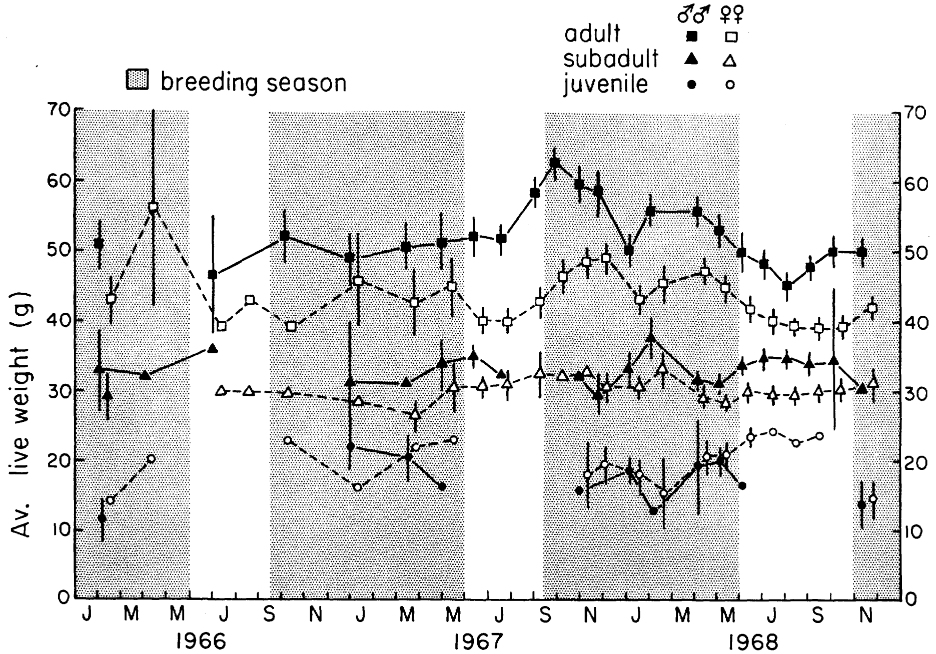

FIG. 3.—Live body weights at Richmond. Vertical lines give 95 per cent confidence limits for means based on five or more observations.

but it increased before the autumn rains in 1966 and 1967. The occurrence of breeding before the rains was confirmed by the presence of juveniles in October and early November.

A delay in the return of the breeding season after high densities was found also by Krebs (1966) and possibly by Marsh (1962). The decline in breeding during winter (late December to early February) noted in these populations also was reported by Greenwald (1957). Krebs (1966) did not observe a winter pause, but his criterion for breeding intensity (perforate vagina) may have overestimated the number of reproductive females.

Two other aspects of the female reproductive effort deserve comment. First, more reproduction by subadult females occurred during the year with high densities (1968) than in 1966 and 1967. This trend was similar to that reported by Krebs (1966) except that subadult breeding continued after high densities during the autumn of 1968 at both Richmond and Russell. Second, litter sizes as determined by counts of embryos and fresh uterine scars (Table 2) showed seasonal differences similar to those reported by Hoffmann (1958) and Greenwald (1957). Smaller litters were produced in the dry season and autumn than in early spring.

Mean body weight, another aspect of the populations related to age structure, showed seasonal and annual changes (Fig. 3). Samples of juveniles were too small to show significant trends. Subadult weights increased after breeding declined in the winters and again in the late spring of 1968 probably as a result of decreased recruitment of young subadults. Adult size roughly paralleled breeding condition, though small samples of low populations produced wide confidence limits. Weights of females were correlated with pregnancy rates, but male weights showed no recurring fluctuation. Weights of adult males increased during late summer periods and were highest in the expanding population during the autumn of 1967 and the winter of 1968. Krebs (1966) also noted high weights for males in expanding populations. These changes in weight could be due to changes in growth rates, changes in recruitment, or differential survival rates of different sized voles (or all three).

Instantaneous growth rates were calculated when there were sufficient recaptures (January 1967 through November 1968) for each sex and age class using the formula of Brody (1945). Growth rates were greater for juveniles (0.4 to 3 per cent per day) than for subadults (0 to 1 per cent per day) and greater for subadults than for adult males (0 to 0.4 per cent per day). Adult females were not considered owing to the influence of pregnancy on weight changes. Juvenile growth was greatest during the breeding season and declined through the late breeding season and summer. Subadults grew at a rate of 0.5 per cent per day during the summer of 1967, but the rate dropped to zero during the summer of 1968. The continuing maturation of subadults probably produced the unusually large per cent of adults in the summer of 1967. Adult males grew little during the breeding season, but they showed growth spurts during both summers that accounted for the increasing mean body weights seen during that season. Growth rates for all age classes dipped during the breeding pause in the winter of 1968, but growth rates increased thereafter as did weights.

Minimal survival rates, corrected for losses of ear tags, are given in Fig. 4. In spite of some small samples, there were clear population trends. Survival was generally high at the start of the breeding season and low, particularly for juveniles and subadults, at the end of it. When breeding decreased, survival increased markedly and declined only slightly during the summer. Adult males survived particularly well during the summer of 1967, which together with summer growth could account for high weights (more old males) seen early in the 1968 breeding season. The unusually good survival of subadult females during late summer and autumn accounted for the preponderance of females during the 1968 breeding season. Overall survival seemed higher during the 1968 breeding season than in 1967, thus confirming Krebs' (1966) report of better survival in expanding populations.

The Russell population was not trapped as often during 1968 as was the one at Richmond, but similar changes in weight were seen. Adult males declined in weight during the last half of the breeding season and into summer but recovered by the next breeding season. Growth and survival rates at Russell were also similar to those at Richmond. Juvenile and subadult growth rates declined through the last half of the breeding season, but subadults

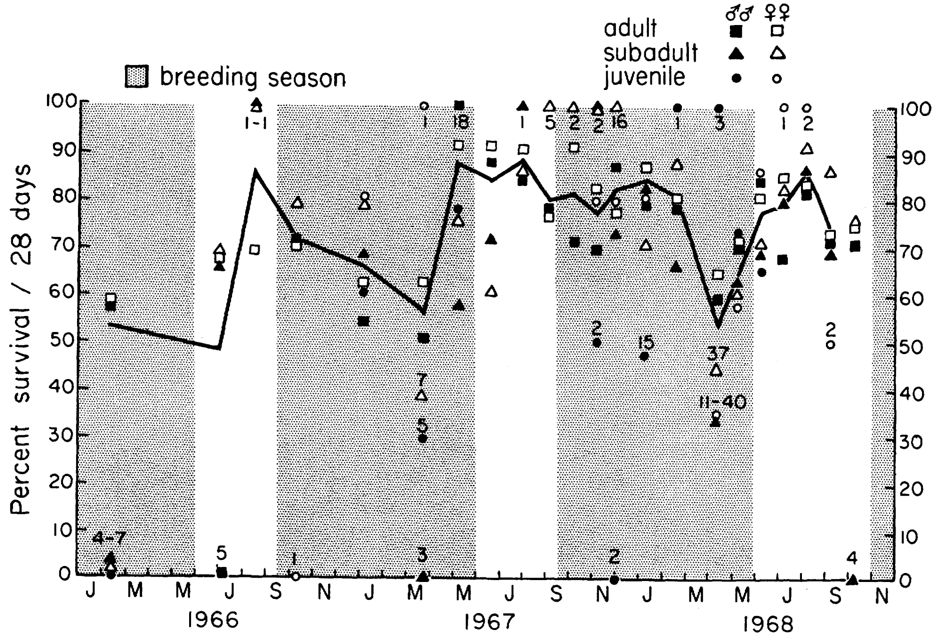

FIG. 4.—Minimal survival rates at Richmond. Rates for a given date were based on the survival of individuals from that date to the next trapping period. Numbers near extreme observations give the number of individuals in the cohort that produced that value. The heavy line represents survival for the population as a whole.

and adult males showed some growth in late summer. Survival was relatively low in the last half of the breeding season and increased when breeding stopped.

Two aspects of behavior were looked at during this study, movement and fighting. Average distance moved between first and second captures during a trapping period and average distance moved between trapping periods were calculated as indices of short-term and long-term movements, respectively. Inasmuch as trapping periods were not uniformly spaced, the long-term index was calculated as movement per 28 days. Frequencies of fresh wounding on the tail or body were calculated as an index of aggressive behavior.

Short-term movement data for Richmond are summarized in Fig. 5. Short-term movements were similar for males and females during the summer (average about 8 meters). Movement of adult females was no different during the breeding seasons, but the movements of males and immature females were more variable and usually were greater. No differences appeared to be associated with changes in density. Seasonal patterns and the magnitude of long-term movements were similar to short-term movements. The only seasonal difference in movement at Russell was that long-term movements

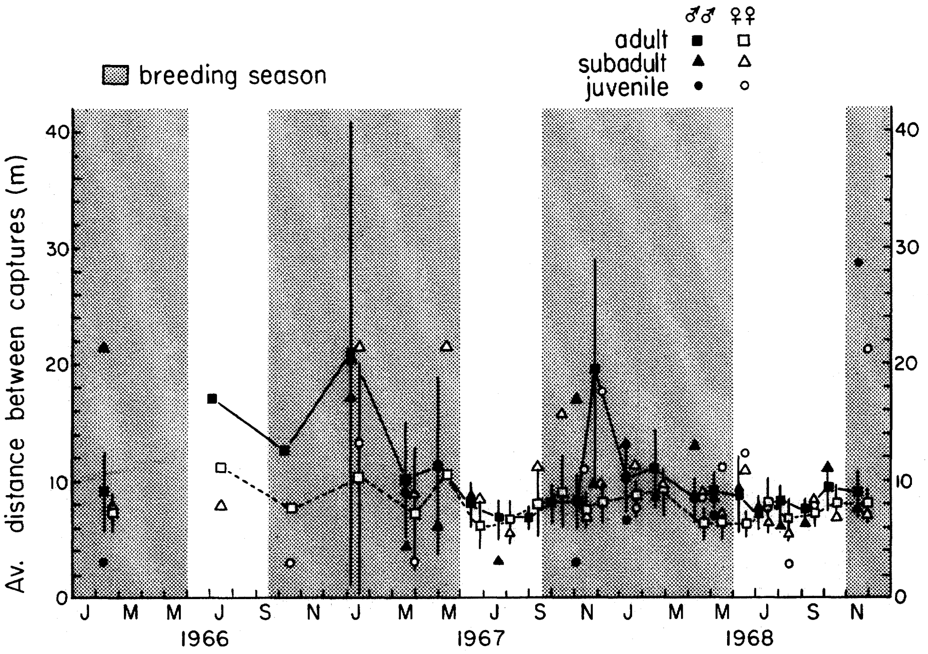

FIG. 5.—Short-term movements by voles at Richmond. Vertical lines represent 95 per cent confidence limits for means based on observations of five or more adults.

usually were greater during the breeding season. Short-term movements were of the same magnitude at both sites, but long-term movements seemed to be less at Russell. The smaller movements per 28 days might have occurred because the distance moved was not proportional to the time between trapping periods, and the trapping periods were farther apart at Russell than at Richmond, particularly during the nonbreeding season.

Krebs (1966) found increased long-term (14-day) movements of males during the breeding season, but he also found greater movement at lower densities when comparing different populations. Marsh (1962) reported a similar relationship between density and home range diameter, but his results might not have been statistically significant.

Wounding increased during breeding seasons for the Richmond population as a whole and for adult males in particular (Fig. 6). The amount of wounding was not greater at higher populations as expected; if anything, it was lower ($P < .10$ based on $\chi^2 = 3.04$, d.f. $= 1$). More wounding of adult males and less wounding for the population as a whole occurred at Russell during the 1968 breeding season, but the peak for wounded males (15 per cent) was still below those for 1966 and 1967 at Richmond.

Increased wounding has been reported for lemmings during years of high density (Krebs, 1964), but wounding of *M. californicus* during the course of a cycle has not been investigated. Houlihan (1963) reported that an

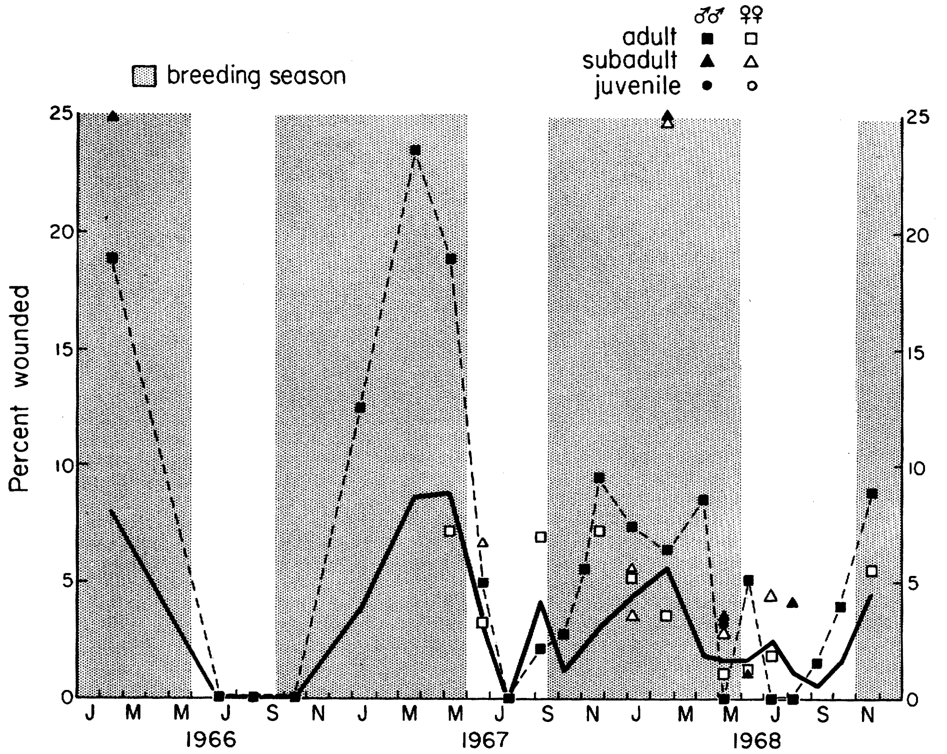

FIG. 6.—Frequency of new wounds on the body and tail of voles at Richmond. Heavy line represents the frequency for the population as a whole.

inclosed population of *M. californicus* with *ad libitum* food and water showed aggressive behavior and a high wounding frequency (26 per cent) during a decline, but the peak density of 4770 per acre was far above the 100 to 500 per acre reached by natural populations.

Another possible indication of stress on the populations was the frequency of ectoparasitism. Parasites were recorded as present or absent and included fleas (75 to 80 per cent of the total number of ectoparasites), lice, and mites. Although examination of the voles was not thorough, and some samples were small, there seemed to be a seasonal trend of increased parasitism in late summer and autumn (Fig. 7). Linsdale and Davis (1956) reported on the frequency of flea infestations on *M. californicus* collected for many years in the Coast Range about 110 miles south of Richmond. Their data indicated that the highest incidence of parasitism (40 to 50 per cent infested) occurred from September through November.

Annual differences in the frequency of parasitism also occurred at Richmond. Highest levels (50 per cent of mice infested) were reached after the 1968 population peak. Apparently an increase in voles resulted in an increase

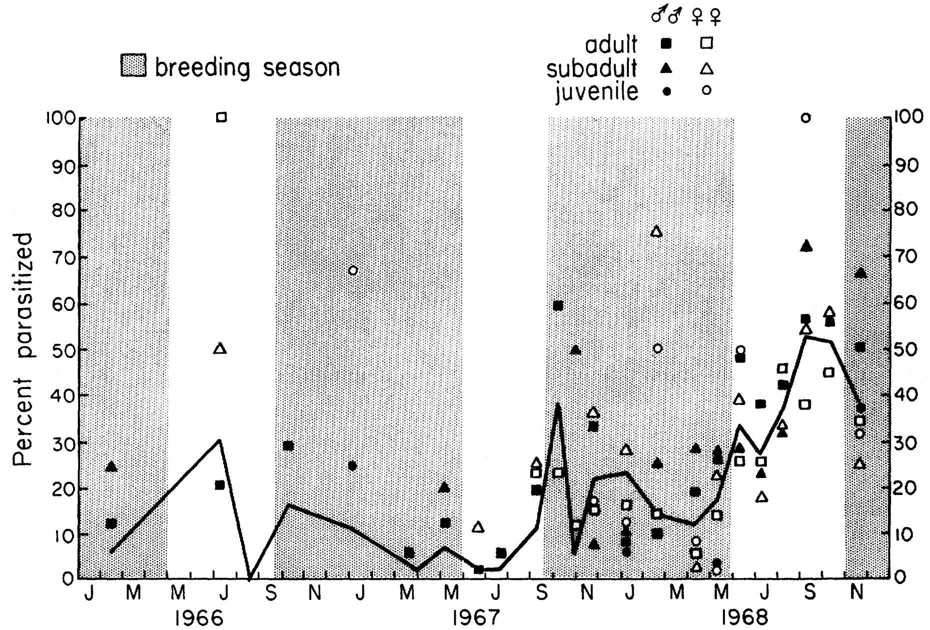

Fig. 7.—Frequency of ectoparasites on voles at Richmond. Heavy line represents frequency for the population as a whole.

of their ectoparasites, and it is possible that the increased parasitism indicated poorer body condition.

Seasonal trends also occurred in the index of body fat (grams fat per gram dry lean weight) at both sites (Fig. 8). Analysis of variance showed that females had more fat reserves than males ($P < .05$), but both sexes showed seasonal changes ($P < .05$). Fat reserves declined through the breeding season, but when breeding stopped, reserves accumulated rapidly. During the summer, fat reserves declined again. Low values for 1967 may have reflected only the small sample sizes for females; males showed no significant differences between years. The low fat reserves at the start of the breeding season following the peak density were not an artifact of the sex ratio within the sample and suggested relatively poor body condition for that season.

In summary, a series of seasonal (within years) and annual (between years) changes in the condition of *M. californicus* occurred during this study, and several have also been found in other studies. Seasonal changes included: 1) greatly reduced proportions of reproductive females during summers and slightly reduced proportions during midwinter; 2) larger litter sizes during the height of the growing season (March and April) than at other times; 3) decreased juvenile, subadult, and adult growth during midwinter with recovery thereafter, and declining juvenile growth rates late in the breeding

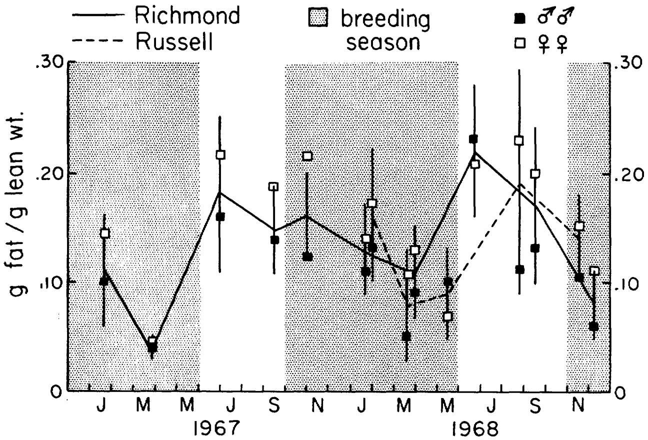

FIG. 8.—Fat indices for *M. californicus* at Richmond and Russell. Horizontal lines connect means of samples with males and females lumped. Vertical lines represent 95 per cent confidence limits for the means.

season and into the summer; 4) a late summer increase in growth rate and live body weight of adult males; 5) relatively high survival rates at the beginning of the breeding season, low survival (particularly of juveniles and subadults) near the end of the breeding season, and increased survival when breeding ceased; 6) increased movement of males and juveniles during the breeding season; 7) greater incidence of ectoparasitism during late summer and autumn than at other seasons; 8) declining fat reserves throughout the breeding season, rapid recovery when breeding stopped and a slow decline through the summer.

Annual changes that seemed to be related to changes in population density included: 1) increased breeding by subadult females at high population levels; 2) delayed start of the breeding season after a population high; 3) large body size of adult males owing in part to increased survival in an expanding population; 4) higher proportions of females during the breeding season of the year with peak density owing to a high rate of female survival; 5) higher survival for the population during the breeding season of the peak year than in the year preceding the peak in density; 6) higher rates of ectoparasitism in the autumn following the peak in density than in preceding years; 7) low fat reserves at the beginning of the breeding season following the peak in density.

Food Habits

The diet of *Microtus* was determined mostly from the analysis of stomach contents, but also by analyses of fecal contents at low population densities during the dry season. Because food items could vary in digestibility, the results from stomach contents and fecal pellets of the same voles were compared for five individuals from each of five trapping periods during 1968

TABLE 3.—*Per cent composition of diet at Richmond based on point samples of stomach contents and feces of the same voles. Chi-square tests of homogeneity were used to compare the distribution of the following dietary components in gastric and fecal samples—grass heads, leaves, stems, and roots of grasses, and leaves, stems, and roots of forbs.*

	Stomach contents			Fecal contents	
	No. points	Per cent		No. points	Per cent
Wet Season (November–March)—15 Mice					
Grass					
heads	10	1.3		13	1.7
leaves	592	78.9		619	82.5
stems	69	9.2		55	7.3
roots	2	0.3		2	0.3
Forb					
heads	0	0.0		0	0.0
leaves	70	9.3		58	7.7
stems	3	0.4		1	0.1
roots	1	0.1		0	0.0
Vole hair	3	0.4		2	0.3
Totals	750	99.9		750	99.9
	Chi-square = 2.2		d.f. = 2	$.40 > P > .30$	
Dry Season (June–September)—10 Mice					
Grass					
heads	363	72.6		442	88.4
leaves	21	4.2		7	1.4
stems	10	2.0		10	2.0
roots	2	0.4		3	0.6
Forb					
heads	0	0.0		0	0.0
leaves	77	15.4		28	5.6
stems	13	2.6		5	1.0
roots	10	2.0		2	0.4
Vole hair	4	0.8		3	0.6
Totals	500	100.0		500	100.0
	Chi-square = 42.2		d.f. = 2	$P < .0005$	

(Table 3). Because fecal analysis underestimated the forb content by two-thirds in summer, but not in winter, data from fecal pellets were corrected for this effect.

Several techniques have been used to determine the food habits of *Microtus*, the most common being the examination of cut stems and food caches (Hatt, 1930; Jameson, 1947; Martin, 1956; Marsh, 1962; Thompson, 1965). When taking regular vegetative samples at Richmond (Batzli and Pitelka, 1970), the

TABLE 4.—*Ranges for per cent of diet contributed by vegetative parts of plants at different seasons and locations. Numbers in parentheses indicate the rank of the plant based on frequency of cuttings during all seasons at Richmond.*

	December–January		March–April		June–July		September–October	
	Richmond	Russell	Richmond	Russell	Richmond	Russell	Richmond	Russell
MONOCOTS								
Avena fatua (2)	9.2–48.9	3.0–3.8	19.2–20.3	10.9	0–1.2	4.4	0–1.8	0
Bromus mollis (6)	0.4–1.0	0–1.4	5.7–7.4	0	0–1.2	0	0–1.8	0
Bromus rigidus (4)	1.0–4.2	36.5–58.6	1.8–15.6	45.8	0–1.9	16.2	0	3.6
Danthonia californica (3)	3.0–21.0	0	12.2–15.6	0	0–3.6	0	0–3.4	0
Elymus cinereus	0	0–2.1	0	14.5	0	0.5	0	0.4
Hordeum sp. (5)	0–0.4	0–0.4	0–2.8	0	0–1.9	0.5	0–0.3	0
Juncus sp. (9)	0	0	0	0	0	0	0	0
Lolium multiflorum (1)	26.6–39.2	7.7–8.6	33.6–44.8	22.5	0.8–6.5	8.5	0–0.3	0
Sisyrinchium bellum (14)	0–0.5	0	0–0.7	0	0	0	0	0
Sitanion jubatum (15)	0	0	0	0	0	0	0	0
DICOTS								
Anagallis arvensis (18)	0	0	0	0	0	0	0	0
Aster exilis (16)	0–0.4	0	0	0	0	0	0	0
Calendula arvensis	0	0	0	0	0	0	0–0.2	0
Dipsacus fullonum (11)	0	0	0	0	0–14.4	0	0–7.8	0
Erodium sp.	0–1.8	0	0–0.5	0	0	0	0	0
Geranium dissectum (12)	0.3–2.0	0	0–0.5	0	0–0.4	0	0	0
Hemizonia luzulaefolia	0	0	0.2–1.8	0	0–0.4	0	0	0
Medicago hispida	0	0–0.8	0–0.5	0	0–1.6	0	0	0
Oenothera ovata (10)	0–4.2	0	0–0.4	0	0	0	0–0.5	0
Picris echioides (7)	0–3.5	0	0–0.5	0	0–3.6	0	0–15.6	0
Plantago lanceolata (8)	1.6–4.2	0	0	0	0–5.4	0	0–14.0	0
Ranunculus californicus (17)	0–0.3	0	0	0	0–5.4	0	0	0
Rumex sp. (13)	0–2.5	0–0.9	0.4–0.5	0	0–7.2	0.6	0–0.7	0
Sida hederacea	0	0	0	0	0–2.4	0	0–2.5	0
Vicia sativa	0–6.4	0–6.4	0–1.4	0	0–0.8	0	0	0
Wyethia angustifolia	0–0.5	0	0–0.5	0	0	0	0	0

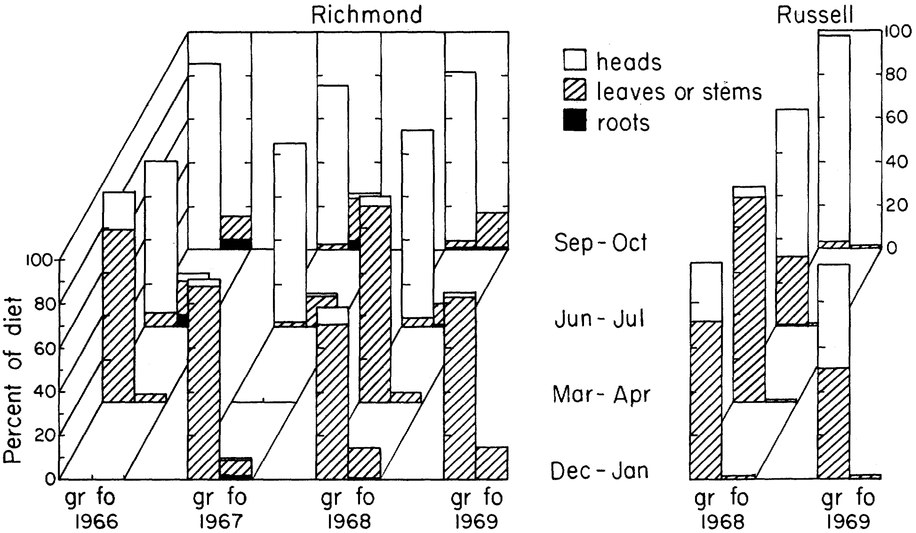

FIG. 9.—General composition of the diet of *M. californicus* at Richmond and Russell in terms of the kind of plant and part of plant (*gr*, grass; *fo*, forb).

frequencies of cuttings of various plants within 2 meters of 25 sampling stations were recorded. The rather variable results were compared for all seasons, and the plants were ranked in order of importance in the cuttings.

Table 4 gives the percentage of stomach contents contributed by vegetative parts at different seasons and the overall rank of food plants on the basis of cutting frequencies. Ranking of cuttings succeeded in identifying the most important food items, and the four most important (*Lolium multiflorum*, *Avena fatua*, *Danthonia californica*, and *Bromus rigidus*) were even ranked correctly. But there was no way to get percentage composition of the diet from data on frequency of cuttings.

From shortly after germination until drying of the annual grasses in late spring, most of the diet was composed of grass stems and leaves (Fig. 9). Throughout summer and autumn until the rainy season arrived, grass seeds predominated in the diet. The diet at Richmond contained more forbs (more were available), and the samples taken after germination of grass seeds contained more grass seeds at Russell than equivalent samples from Richmond. Both the seasonal and site differences in diet were significant (analysis of variance, $P < .0005$).

Some of the extra seeds in the diets at Russell following germination of grass seeds were taken from the live traps as indicated by the presence of seed coats of corn. Data on utilization of seed crops (Batzli and Pitelka, 1970) and observations on penned voles (W. Z. Lidicker, Jr., personal communication) suggested that *M. californicus* may store seeds during the dry season. Any seeds eaten by voles when held in live traps would have cleared the stomach by the time of snap trapping (3 days later), and voles may have been eating seeds taken from the traps and stored during the prebaiting period.

The diet at Russell that followed germination of grass seeds in 1969 might have contained large amount of seeds because it was taken only 2 weeks after the first autumnal rains when the diet was in transition from seeds to stems and leaves. The relatively large proportion of stems and leaves eaten in late May at Russell also might have been a result of sampling during a transitional period.

Although insects and fungi have been found in the stomachs of other species of *Microtus* (Zimmerman, 1965), neither was found in stomachs of *M. californicus*. Hair was found regularly in small amounts throughout the year and probably was ingested during grooming activities. One stomach from Richmond in January 1968, contained mostly hair and striated muscle.

Results of vegetational sampling documenting food availability at Richmond and Russell (given by Batzli and Pitelka, 1970) were used to determine food preferences for major items of the diet. Inasmuch as grass seeds could not be identified to species, preference indices (percentage composition of diet to percentage composition of vegetation) could be calculated only for periods when vegetative parts of plants were the major part of the diet (Fig. 10). Not only were the annual grasses *Avena fatua*, *Lolium multiflorum*, and *Bromus rigidus* among the most important species in the diet (Table 4), but they also had the highest preference indices. Grazing trials run by Marsh (1962) also suggested that these grasses were particularly palatable to *M. californicus*, and they have been designated as preferred grasses in this study. These preferred grasses are introduced species. Thompson (1965) ran grazing trials which suggested that *M. pennsylvanicus* also prefers introduced grasses and legumes.

Other annual grasses, perennial grasses (*Danthonia*, *Elymus*, *Hordeum*) and forbs were less palatable at both sites, and *Avena* was less palatable at Russell than at Richmond. The drop in preference for *Avena* at Russell might have been due to the greatly increased availability of another palatable grass, *B. rigidus*, at that site. Forbs rose in preference in late summer when their importance in the vegetation was also greater. Occasional meals of stems and leaves of *Picris*, *Plantago*, and *Sida* or the tap roots of *Dipsacus* and *Oenothera* accounted for the increased forb consumption in late summer at Richmond (Table 4).

When data were pooled in categories of preferred grasses, nonpreferred grasses, and forbs, the summary showed that *M. californicus* continued eating mostly preferred grasses during the breeding season at all population levels. Analysis of variance again showed significant difference in the composition of diet at the two sites ($P < .0005$) owing largely to the greater consumption of forbs and nonpreferred grasses at Richmond. In general, preferred food plants received the greatest grazing pressure at high population densities, and both the standing crop and seed production of preferred grasses were markedly

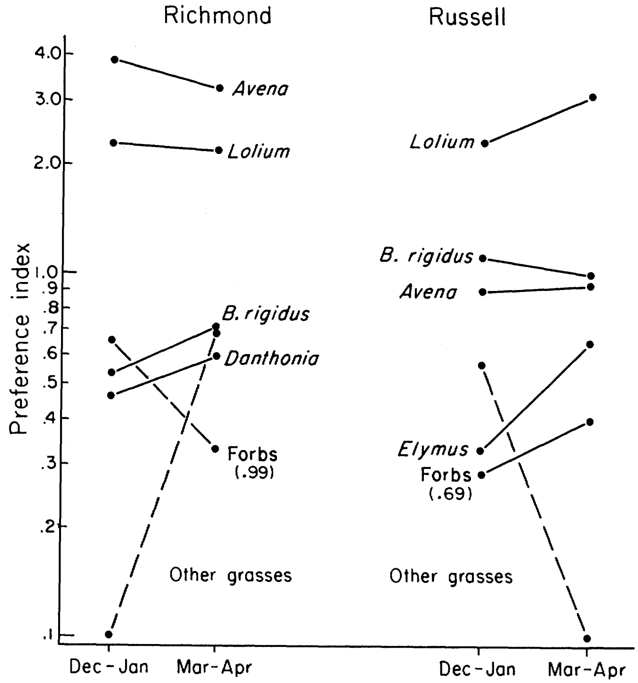

FIG. 10.—Mean preference indices for dietary items for *M. californicus* at Richmond and Russell during seasons when vegetative parts of plants predominated in the diet. A value greater than one suggests preference, and a value less than one suggests avoidance. Numbers in parentheses are preference indices for forbs in late summer-early autumn.

reduced in 1968 (Batzli and Pitelka, 1970). Thus at high populations, preferred foods might have been more difficult for the voles to get.

In summary, *M. californicus* was found to eat mostly grass stems and leaves during the wet winters and mostly grass seeds during the dry summers. Increased consumption of the vegetative portions of forbs occurred in late summer and early autumn. The continued preference for certain grasses, *Avena fatua*, *Lolium multiflorum*, and *Bromus rigidus*, at high population levels led to a marked decline in their abundance in the vegetation and, therefore, in their availability to the voles.

DISCUSSION

Several of the changes in the breeding of the two populations studied could have been influenced by the quality of the diet. Cessation of breeding coincidental with low body growth rates, survival rates and fat reserves could be symptomatic of a nutritional deficiency. Furthermore, it is at this time (late spring) that the diet changed from one dominated by green forage to one dominated by seeds. The rapid recovery of survival rates and fat reserves upon cessation of breeding and change of diet might indicate that more than a simple caloric deficiency was involved. Although fat reserves were replenished, breeding was not resumed.

Breeding resumed in some years before autumn rains, but there was also a slight dietary change at this time. An increase in the consumption of green forbs and occasional meals of *Danthonia californica*, a perennial grass that starts new growth before autumn rains, could influence breeding. In addition, litter sizes were smaller in the autumn breeding season than in spring, another possible nutritional effect. The midwinter declines in breeding activity and body growth occurred at a time when the grasses grew slowly and were subject to frost damage, so food quality could have been involved here also.

Of course, there were other environmental factors that correlated with seasonal changes in breeding. For instance, *M. californicus* is known to require fairly large amounts of water (10 per cent of body weight per day), and marked weight losses occur when only two-thirds of the normal water intake is supplied (Church, 1966). Cessation of breeding during summer could be due to water shortage. Nothing is known about the utilization of water from summer dew or fog, but if water were chronically in short supply during the nonbreeding season, significant weight losses would be expected. On the contrary, weights remained stable or increased during late summer.

The midwinter breeding pauses came at the coldest part of the year and might reflect a direct effect of low temperature on the voles. Little is known about the actual temperature conditions for the voles or about the influence of temperature on their breeding. Temperatures rarely reached freezing at Richmond, however, and other species of *Microtus* in more extreme climates sometimes breed under the snow (Hamilton, 1937; Martin, 1956; Frank, 1957).

Decreased availability of preferred foods during high population densities might have made it increasingly difficult for the voles to get a suitable diet, and changes in quality of the preferred foods might also have occurred. Such changes could have accounted for the delay in the start of the breeding season following peak densities, for the relatively low fat reserves in the autumn following peak densities and the continued decline of the population during the 1969 breeding season. While the nutrient-recovery hypothesis remains unproved as a causal factor in microtine cycles, changes in the condition of the Richmond population and dramatic changes in the availability of preferred foods fulfilled some of the preconditions for operation of the postulated mechanisms. The decomposition of most of each year's crop within 1½ years might indicate too rapid a rate of nutrient cycling, however.

Application of the results of this study to experiments in the field will require additional work on diet quality and nutritional physiology for species of *Microtus*. Determinations of the chemical composition of natural diets, digestibility of the nutrients and influence of natural diets on growth and reproduction should have priority.

ACKNOWLEDGMENTS

During much of this work the senior author was supported by a National Institutes of Health Predoctoral Fellowship. Statistical calculations were done with the aid of facilities provided by the University of California Computer Center at Berkeley. We also thank Dr. William Z. Lidicker, Jr., and Dr. Harold F. Heady for their consultations and critical readings of the manuscript. Andrea Hammond, Robert Jones, and David Hawes provided competent assistance in the laboratory and the field.

LITERATURE CITED

BATZLI, G. O. 1968. Dispersion patterns of mice in California annual grassland. J. Mamm., 49: 239–250.

BATZLI, G. O., AND F. A. PITELKA. 1970. Influence of meadow mouse populations on California grassland. Ecology, 51: 1027–1039.

BRANT, D. H. 1962. Measures of the movements and population densities of small rodents. Univ. California Publ. Zool., 62: 105–184.

BRODY, S. 1945. Bioenergetics and growth. Reinhold, New York, 1023 pp.

CHITTY, D. 1955. Adverse effects of population density upon the viability of later generations. Pp. 57–67, *in* The numbers of man and animals (J. B. Cragg and N. W. Pirie, eds.), Oliver and Boyd, Edinburgh.

———. 1967. The natural selection of self-regulatory behaviour in animal populations. Proc. Ecol. Soc. Australia, 2: 51–78.

CHRISTIAN, J. J., AND D. E. DAVIS. 1964. Endocrines, behavior and population. Science, 146: 1550–1560.

CHURCH, R. L. 1966. Water exchanges of the California vole, *Microtus californicus*. Physiol. Zool., 39: 326–340.

DELONG, K. T. 1967. Population ecology of feral house mice. Ecology, 48: 611–634.

FRANK, F. 1957. The causality of microtine cycles in Germany. J. Wildlife Mgt., 21: 113–121.

GREENWALD, G. S. 1957. Reproduction in a coastal California population of the field mouse *Microtus californicus*. Univ. California Publ. Zool., 54: 421–446.

HAMILTON, W. J., JR. 1937. The biology of microtine cycles. J. Agric. Res., 54: 779–790.

HATFIELD, D. M. 1935. A natural history study of *Microtus californicus*. J. Mamm., 16: 261–271.

HATT, R. T. 1930. The biology of the voles of New York. Roosevelt Wildlife Bull., 5: 513–623.

HOFFMANN, R. S. 1958. The role of reproduction and mortality in population fluctuations of voles (*Microtus*). Ecol. Monogr., 28: 79–109.

HOULIHAN, R. T. 1963. The relationship of population density to endocrine and metabolic changes in the California vole, *Microtus californicus*. Univ. California Publ. Zool., 65: 327–362.

JAMESON, E. W., JR. 1947. Natural history of the prairie vole (mammalian genus Microtus). Univ. Kansas Publ., Mus. Nat. Hist., 1: 125–151.

JOLLY, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration—stochastic model. Biometrika, 52: 225–247.

KREBS, C. J. 1964. The lemming cycle at Baker Lake, Northwest Territories, during 1959–62. Arctic Inst., Tech. Paper, 15: 1–104.

———. 1966. Demographic changes in fluctuating populations of *Microtus californicus*. Ecol. Monogr., 36: 239–273.

KREBS, C. J., AND K. T. DELONG. 1965. A *Microtus* population with supplemental food. J. Mamm., 46: 566–573.

LACK, D. 1954. Cyclic mortality. J Wildlife Mgt., 18: 25–37.

LESLIE, P. H., D. CHITTY, AND H. CHITTY. 1953. The estimation of population parameters from data obtained by means of the capture-recapture method. III. An example of the practical application of the method. Biometrika, 40: 137–169.

LIDICKER, W. Z., JR., AND P. K. ANDERSON. 1962. Colonization of an island by *Microtus californicus*, analysed on the basis of runway transects. J. Anim. Ecol., 31: 503–517.

LINSDALE, J. M., AND B. S. DAVIS. 1956. Taxonomic appraisal and occurrence of fleas at the Hastings Reservation in central California. Univ. California Publ. Zool., 54: 293–370.

MARSH, M. P. 1962. Food as a factor regulating the numbers of the California vole (*Microtus californicus*). Unpublished Ph.D. dissertation, Univ. California, Berkeley, 201 pp.

MARTIN, E. P. 1956. A population study of the prairie vole (*Microtus ochrogaster*) in northwestern Kansas. Univ. Kansas Publ., Mus. Nat. Hist., 8: 361–416.

MUNZ, P. A., AND D. D. KECK. 1949. California plant communities. Aliso, 2: 87–105.

———. 1950. California plant communities—supplement. Aliso, 2: 199–202.

NEGUS, N. C., AND A. J. PINTER. 1966. Reproductive responses of *Microtus montanus* to plants and plant extracts in the diet. J. Mamm., 47: 596–601.

PEARSON, O. P. 1960. Habits of *Microtus californicus* revealed by automatic photographic records. Ecol. Monogr., 30: 231–249.

———. 1966. The prey of carnivores during one cycle of mouse abundance. J. Anim. Ecol., 35: 217–233.

PITELKA, F. A. 1957*a*. Some characteristics of microtines cycles in the Arctic. Pp. 73–88, *in* Arctic biology (H. P. Hansen, ed.), 18th Annual Biol. Colloq., Oregon State College.

———. 1957*b*. Some aspects of population structures in the short-term cycle of the brown lemming in northern Alaska. Cold Spring Harbor Symp. Quant. Biol., 22: 237–251.

SCHULTZ, A. M. 1964. The nutrient-recovery hypothesis for Arctic microtine cycles. II. Ecosystem variables in relation to Arctic microtine cycles. Pp. 57–58, *in* Grazing in terrestrial and marine environments (D. Crisp, ed.), Blackwell's, Oxford.

THOMPSON, D. Q. 1965. Food preferences of the meadow vole (*Microtus pennsylvanicus*) in relation to habitat affinities. Amer. Midland Nat., 74: 76–86.

VAN DYNE, G. M., AND H. F. HEADY. 1965. Botanical composition of sheep and cattle diets on a mature annual range. Hilgardia, 36: 465–492.

WILLIAMS, O. 1962. A technique for studying microtine food habits. J. Mamm., 43: 365–368.

ZIMMERMAN, E. G. 1965. A comparison of habitat and food of two species of *Microtus*. J. Mamm., 46: 605–612.

Museum of Vertebrate Zoology and Department of Zoology, University of California, Berkeley, California 94720 (present address of Batzli: Department of Animal Science, University of California, Davis, California 95616). *Accepted 9 November 1970.*