

IMPORTANCE OF VEGETATIVE COVER TO CYCLES OF *MICROTUS* POPULATIONS¹

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Abstract. A hypothesis is presented that a site-dependent threshold level of vegetative cover is necessary for a population of *Microtus* to increase in numbers sufficiently to undergo a multi-year cycle. The hypothesis is supported by results of studies in grassland habitats in the tallgrass prairie of Oklahoma and Minnesota, the mixed grass prairie of South Dakota, and the shortgrass prairie of Colorado. Levels of cover below the threshold sometimes support resident, breeding populations of voles. Levels above the threshold may influence amplitude, duration, and synchrony of *Microtus* cycles.

Key words: Colorado; grasslands; habitat selection; *Microtus*; Minnesota; Oklahoma; population cycles; population regulation; South Dakota; vegetative cover.

INTRODUCTION

This contribution originated with a statement by one of us that, "Given control of the gate to the herefords, I can regulate any phase of a *Microtus* cycle except the decline." This prompted us to search our own data and those in the literature on the quantitative relationship between vegetative cover and fluctuations in numbers of small mammals. We now are better able to advance a testable hypothesis on the subject. That is, some threshold level of cover is necessary for a population of *Microtus* to increase in numbers sufficiently to undergo a multi-year cycle. The threshold probably will prove to be a sharp gradient wherein a small increase in cover has a large influence on population fluctuations, and undoubtedly is site specific. Once cover reaches this threshold level, a population usually, but not necessarily, undergoes cyclic fluctuations. Above the threshold, quantity of cover probably influences the amplitude and perhaps the duration between peaks of a cycle. Local populations that appear to be cycling out-of-phase with adjacent populations may result from local variation in level of cover.

We use "cycle" as we interpret its use by Krebs and Myers (1974:278); "fluctuation" is no more precise, and we have used the two terms synonymously. Both refer to an increase, peak, decline, and low in population number that cannot be explained on the basis of single-year changes in density resulting from seasonal patterns of breeding and mortality. They do not imply regularity, although regularity usually is observed.

Several authors have studied the importance of cover in habitat selection by *Microtus* (Eadie 1953, Mossman 1955, LoBue and Darnell 1959, Ogilvie

and Furman 1959, Wirtz and Pearson 1960, Tester and Marshall 1961, Zimmerman 1965, Getz 1970a, 1971, Hansson 1971). In fact, even the most naive student of mammals traps for *Microtus* in dense grassy vegetation. Despite this obvious relationship, the importance of cover has been associated only peripherally with microtine population fluctuations, and then with the decline phase, either of natural populations (Thompson 1955, Pitelka 1958) or those in enclosures (Krebs et al. 1969). Depletion of food or essential nutrients, rather than of cover per se, usually has been associated with the decline (Schultz 1964, Batzli and Pitelka 1970). We are the first to propose a specific quantitative relationship between *Microtus* population fluctuations and vegetative cover. We reiterate that our hypothesis focuses on the importance of cover to allow the increase phase to proceed to a peak, and we do not suggest it is cause for decline. We continue to view the decline as the most enigmatic phase of most cycles.

In the context of the hypothesis proposed by Chitty (1960:107) and subsequently expanded (Chitty 1967, Krebs et al. 1973) we would predict that low cover levels never provide an environment in which any "specific condition" can alter significantly the susceptibility of voles to various forms of mortality, because all voles living in a low cover habitat are highly vulnerable. Thus, the peak phase is never achieved. Attributes of cover that allow cycling will be essential to a complete understanding of microtine cycles, but their complete elucidation is not essential to the validity of the hypothesis.

STUDY SITES

Our studies were conducted at five localities. Three of these, designated Oklahoma (OK), South Dakota (SD), and Colorado (CO), are sites of the U.S. International Biological Program (IBP) Grassland

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Biome. The other two, designated Minnesota Upland (MN-Upland) and Minnesota-Wetland (MN-Wetland), are among the research sites available at the University of Minnesota. Each site is described briefly below.

The OK site is located 19.3 km north and 8.0 km east of Shidler, Osage County, Oklahoma, within the tallgrass prairie. The area is characterized by uncultivated upland pastures. Dominant grasses in the study pastures were little bluestem (*Andropogon scoparius*) big bluestem (*A. gerardi*), and switch grass (*Panicum virgatum*). The average January temperature at OK is 2.7°C and the average July temperature there is 27.7°C. The average annual precipitation is 93.0 cm, with 63.5 cm being received from April to September. Risser (1970) provided a detailed description of this site.

One grid was established in a pasture that had not been grazed or burned for several years. Another was in a moderately grazed pasture across a narrow road and \approx 200 m from the ungrazed grid. When established in May 1972, it had been grazed uniformly. One third was fenced with barbed wire at that time to prevent trespass by cattle, so that it became an ungrazed vegetational island within a larger, grazed pasture.

Microtus ochrogaster was the only microtine rodent at OK. Other species of mammals captured on the grids were *Blarina carolinensis*, *Cryptotis parva*, *Spermophilus tridecemlineatus*, *Perognathus hispidus*, *Reithrodontomys montanus*, *R. fulvescens*, *Peromyscus maniculatus*, *P. leucopus*, *Sigmodon hispidus*, and *Mus musculus* (Birney 1974).

The grid at the SD site was located on the Cottonwood Range Field Station, which is 4 km east of Cottonwood, Jackson County, South Dakota. The grid was placed in a summer-grazed pasture, which had been lightly grazed each year since 1942. Under good range conditions, the vegetation of the field station is dominated by midgrasses, especially western wheatgrass (*Agropyron smithii*) and green needlegrass (*Stipa viridula*), with an understory of shortgrasses, consisting mainly of blue grama (*Bouteloua gracilis*) and buffalo grass (*Buchloe dactyloides*). The average annual temperature on the field station is 8.2°C, with the average daily temperature in January being -7.2°C and in July 23.7°C. The average annual rainfall at the station is 38.7 cm, with May (7.1 cm) and June (7.6 cm) being the wettest months. See Lewis (1970) for additional information on the SD site.

Both *M. ochrogaster* and *M. pennsylvanicus* occur at the SD site, but of the two only *M. ochrogaster* was taken on the grid. Other mammals trapped on the grid were *S. tridecemlineatus*, *Thomomys talpoides*, *P. hispidus*, *R. montanus*, *P. maniculatus*, and *P. leucopus*.

The CO site is located on the USDA Agricultural Research Service Central Plains Experimental Range, \approx 20 km northeast of Nunn, Colorado, and 40 km south of Cheyenne, Wyoming. Jameson (1969) described the native shortgrass range vegetation as consisting basically of blue grama and buffalo grass, supplemented in many areas by other shortgrasses and some midgrasses. Average daily high and low temperatures in January are 4.4°C and -12.2°C; those for July are 26.7°C and 10.0°C.

Data on small mammals were collected on eight adjacent 1-ha study plots (S $\frac{1}{2}$ sec. 21, T. 10 N, R. 66 W, Weld County, Colorado). Pretreatment vegetation consisted predominantly of blue grama and buffalo grass. Two plots were treated with sufficient water beginning the spring of 1971 to maintain soil H₂O potential > -0.8 bars throughout each growing season. Two plots were treated with sufficient nitrogen (applied as ammonium nitrate) beginning in the spring of 1970 to maintain soil nitrogen levels 50 kg/ha higher than control plots not treated with nitrogen. Two plots were treated with both water and nitrogen as above, and two plots were untreated (Lauenroth and Sims 1973). Small mammals were trapped from July 1971 to October 1974. *Microtus ochrogaster* is the only microtine rodent occurring at CO. Other species of mammals captured on the grids were *S. tridecemlineatus*, *T. talpoides*, *Dipodomys ordii*, *P. maniculatus*, and *Onychomys leucogaster*.

The grid at the MN-Upland site is located in the NW $\frac{1}{4}$ sec. 21, T. 34 N, R. 23 W, Isanti County, Minnesota, which is a part of the Cedar Creek Natural History Area owned and managed by the University of Minnesota. The site is \approx 45 km north of Minneapolis. The field where the grid was established was farmed from about 1900 until 1966, then allowed to begin secondary succession. During the 4 yr of study, grasses predominated, with Kentucky blue grass (*Poa pratensis*), timothy (*Phleum pratense*), quack grass (*Agropyron repens*), and panic grass (*Panicum* sp.) being especially common in the lower, more densely covered areas. Triple-awned grass (*Aristida* sp.), little bluestem, and in some places foxtail (*Setaria* sp.) were common on the drier sections of the heterogeneous grid (see Moore 1973). *Microtus pennsylvanicus* was the most abundant small mammal captured on the MN-Upland grid. Other species captured there were *Sorex cinereus*, *Blarina brevicauda*, *Tamias striatus*, *S. tridecemlineatus*, *Geomys bursarius*, *P. maniculatus*, *P. leucopus*, *Clethrionomys gapperi*, *M. musculus*, *Zapus hudsonius*, and *Mustela erminea*.

The MN-Wetland site is located within the Carlos Avery Game Management Area, an area of \approx 9,500 ha owned and managed by the Minnesota Department of Natural Resources. It lies roughly 30 km

northeast of Minneapolis and 20 km southeast of the MN-Upland site, in Anoka County, Minnesota. The area, generally flat and poorly drained, is \approx 60% wetland and 40% upland. A detailed description of the area was given by Rand (1953). Mean annual precipitation at the two Minnesota sites is 63.0 cm. Average temperature in January is -10.9°C and in July, 22.4°C . Both areas usually are snow-covered from December until March.

Trapping grids in the wetland (SW $\frac{1}{4}$ sec. 18, T. 32 N, R. 22 W, Anoka County) were located in a large grass-sedge meadow where the water table is at or near surface level most of the year. Spring growth of new vegetation often emerges through standing water, but dead vegetation from previous seasons extended above water level during all 3 yr (1973–75) of the study. The gridded area is dominated by reed canary grass (*Phalaris arundinacea*), but reed grass (*Calamagrostis canadensis*) and sedge (*Carex* sp.) grow with or replace the dominant in some areas. These species form a mosaic of continuous cover reaching 1–2 m in height by mid-summer. Litter or mulch varies from 10 to 25 cm deep and provides dense cover throughout the year.

Microtus pennsylvanicus was the only species of the genus trapped on the wetland grids. Other species taken there were *Sorex arcticus*, *S. cinereus*, *B. brevicauda*, *Condylura cristata*, *P. leucopus*, *C. gapperi*, *Z. hudsonius*, and *M. erminea*.

METHODS

Density estimates of *Microtus*

All estimates of numbers of *Microtus* are derived from live-trapping on permanently staked grids. All trapping was done with Sherman live-traps baited with rolled or crimped oats, either plain (CO) or mixed with peanut butter (SD, OK, and MN-Upland) or either peanut butter or anise oil (MN-Wetland). Distance between trapping stations was 15 m at MN-Upland, SD, and OK, 9 m between columns and 15 m between rows at CO, and either 7.5 m or 15 m between columns and 15 m between rows at MN-Wetland. One trap (CO, MN-Wetland in 1974–75, and MN-Upland in 1974) or two traps (SD, OK, MN-Wetland in 1973, and MN-Upland in 1971–73) were set per station. Grid size was 3.24 ha at SD and OK (ungrazed); 7.29 ha at MN-Upland; 1.10 ha on the cattle enclosure within the grazed pasture at OK, and 2.08 ha in the unfenced, grazed portion of that pasture; 0.57 ha at CO; and 1.08, 1.44, and 1.63 ha at MN-Wetland. Data from the MN-Wetland grids were pooled to yield a single monthly estimate of density when more than one grid was trapped.

Trapping frequency varied from as few as two sampling periods per year to as often as every 2 wk

during the growing season. Sampling periods varied from 3 to 10 days, but usually were 5 or 7 days. Three-day trapping was associated with the 2-wk trapping schedule at MN-Upland in 1971 and 1972; census data obtained within a given month were pooled and treated as though from a single trapping period. Ten-day censuses were conducted at OK and SD in 1970.

Density of *Microtus* on each plot for each sampling period was estimated by dividing the total number of different individuals captured by the effective area of trap-grid influence. The latter was calculated as the area within the staked grid plus that area within a boundary strip having a width of half the distance between two trapping stations. To make comparable density estimates from the dissimilar techniques, the following assumptions were necessary: (1) enough traps were available and duration of trapping was adequate at all times to census the trappable population; and (2) differences in grid size and bait did not alter probability of capture of trappable voles.

Analysis of cover

We use cover to mean above ground vegetation. At some sites (IBP) this represents the sum of above-ground biomass (live and standing dead vegetation) plus litter or mulch. At the two Minnesota sites, these were collected together and not separated prior to being weighed.

Aboveground biomass of plants at IBP sites was clipped from 0.5-m² plots, oven-dried, and weighed. Litter was vacuumed from the same plots after removal of standing vegetation, oven-dried, and weighed. The amount of soil and mineral material included in litter samples was determined by ashing each sample and subtracting weight of the residue. At the Minnesota sites, vegetation was clipped from 0.25-m² plots, dried at room temperature (Upland) or in an oven (Wetland), screened to remove soil, and weighed.

Sampling of vegetation at IBP sites was biweekly during the growing season, and monthly during the nongrowing season (sample sizes were 6–10 at CO and OK, and \approx 20 at SD). Samples ($n = 289$) were taken at MN-Upland in September and October in 1971 and 1972, with a sample originating from near the center of the area between each set of four stations on the grid. Our cover estimate for each station is a mean derived from the adjacent clipping sites. Five 0.25-m² plots were sampled at MN-Wetland in early May 1975. When quantitative data were not available at two MN sites and from the unenclosed portions of the grazed grid at OK, we have used the estimates from other sampling periods. Although not precise, we believe they are realistic based on visual inspection of the grids.

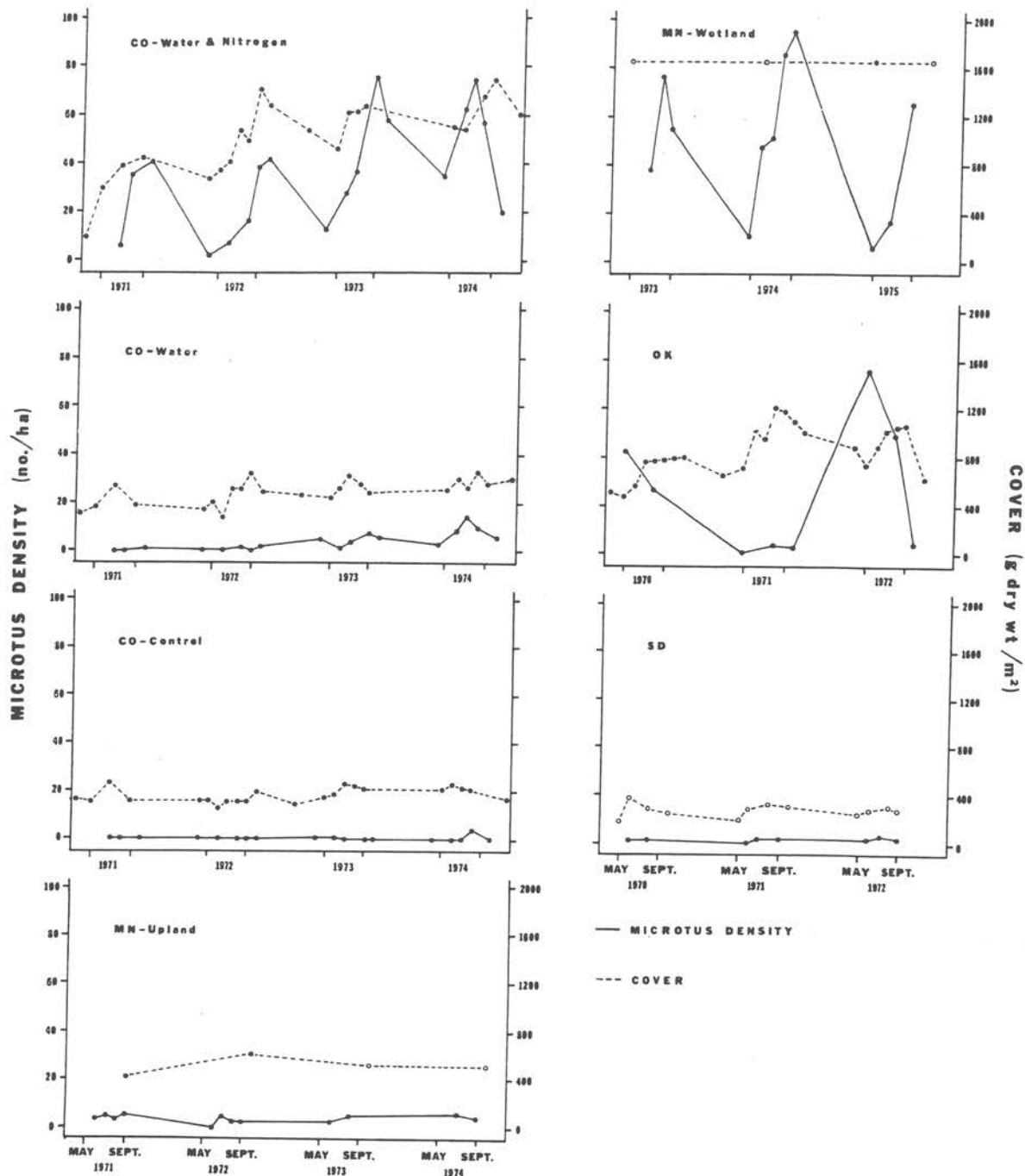


FIG. 1. Change in vegetative cover and density of *Microtus* in seven grassland habitats. Data points for cover are represented by open circles in all cases where data were extended beyond periods of data collection (represented by closed circles), and at the SD sites where cover was estimated as a proportion of that measured on an adjacent, ungrazed plot.

RESULTS

Only two of the populations of voles studied were interpreted as undergoing cycles of the type normally associated with microtine rodents (Fig. 1). On the nitrogen/water treatment plots at CO, cover ac-

cumulated rapidly during the first summer, increased during the second summer, then remained high in subsequent years. The vole population responded by undergoing a decline in summer and fall of 1974 after having peaked in July. The decline occurred despite the high level of cover and continued applica-

tion of nitrogen and water. We interpret the declines there in 1971 and 1972 as having resulted from winter mortality in the absence of population recruitment. Lower cover during the first winter relative to subsequent winters may have been an important contributory factor in the population decline to a density of 1.8 voles/ha in the spring of 1972, which was no higher than that of the previous spring. Cover on this grid appeared to reach a level roughly three times greater than that on the control. The population in each of the two subsequent years (1973 and 1974) was successively higher (12.4 and 34.4 individuals/ha in April). The population peaked in September of 1973 rather than October, as it had the previous 2 yr when the spring population had been relatively lower. The early fall decline in 1973 may have been the first hint of unseasonal or cyclic decline, which was much more pronounced the following year. The rapidity with which the *Microtus* responded during the first year to a sharp increase in available cover is noteworthy.

It appears that we were monitoring a 2-yr cycle on the ungrazed grid at OK. The population was high at the initiation of trapping in early 1970 (42.7 individuals/ha in May), reached a low in early 1971 (estimate of zero in May), peaked in early 1972 (75.9 individuals/ha in May) and was declining at the end of the study (3.9 individuals/ha in October). Cover was high throughout the study; to the human eye, the habitat looked ideal for voles all 3 yr.

A comparison of change in cover and vole density resulting from cessation of grazing in a tallgrass pasture at OK is provided in Fig. 2. When the cattle enclosure was established in May 1972, cover and voles were comparably low in the enclosure and in the control. By August, cover within the enclosure had increased sharply, and the population of *Microtus* was responding with marked increases in density. By autumn, the density of voles was 23.6 individuals/ha in the ungrazed plot and only 1.0 individuals/ha in the grazed control. The population in the enclosure was clearly responding rapidly to the sharp increase in cover.

Cover at MN-Wetland was highest of all sites and supported the highest density of voles observed (76.3 individuals/ha in August 1973, 94.4 individuals/ha in September 1974, and 64.0 individuals/ha in September 1975), but we saw no unequivocal evidence of cycling because the population was low by the subsequent spring of each year (Fig. 1). Data from a longer time span are clearly needed. We predict that cycles should occur there, but perhaps some other factor such as the remarkably high density of short-tailed weasels (*Mustela erminea*) on the grid (D. D. Baird, *personal observation*) or mortality resulting from spring flooding reduced winter densities

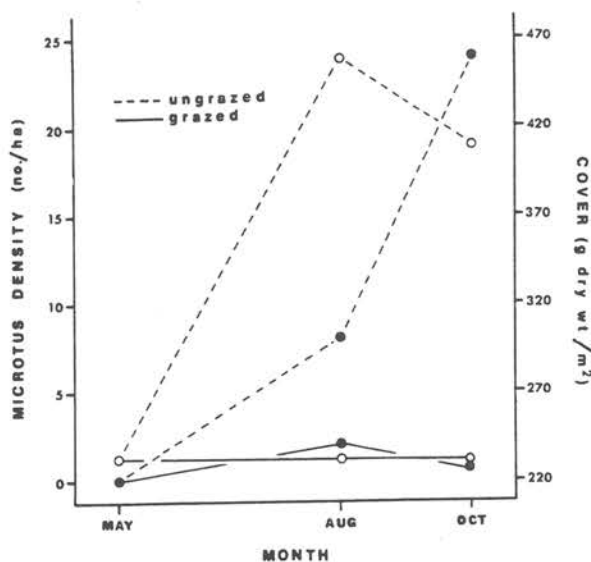


FIG. 2. Change in vegetative cover (open symbols) and density of *Microtus ochrogaster* (solid symbols) in a grazing enclosure and in the surrounding grazed pasture within the tallgrass prairie of Oklahoma.

sufficiently to prevent adequate spring populations for the completion of the increase phase of a cycle. Thus, although cover appears to be a necessary condition for cycling, it alone may not be a sufficient condition for a population to cycle.

On the irrigated but unfertilized grid at CO, we observed a population living in cover that increased gradually to near the hypothesized threshold level during the 4 yr of treatment. Densities of *M. ochrogaster* reached highs of 7.0 individuals/ha in September of the 3rd year of treatment, and 14.1 individuals/ha in July of the 4th year. We interpret this slow increase as a response to increase in cover. The fact that some voles were reproductively active and were recaptured at later trapping periods clearly indicates that they were residents of a breeding population and not merely transients. This important point is supported also by the existence of burrow systems and deep, well-used runways. Transients would have had neither. It is likely that cover (450–600 g/m²) was approaching the threshold level.

Cover on the ungrazed control at Pawnee (CO) showed little change over 4 yr, and the population of *M. ochrogaster* there reached a high of only 3.5 individuals/ha in August 1974. Because no runways or burrows were observed on these grids, voles captured there may have been transients rather than members of a resident population. No *Microtus* were trapped on either of two grids on ungrazed plots that received only nitrogen and failed to show increase in cover.

The population of *M. ochrogaster* at SD was low throughout the study, reaching a high of only 2.8

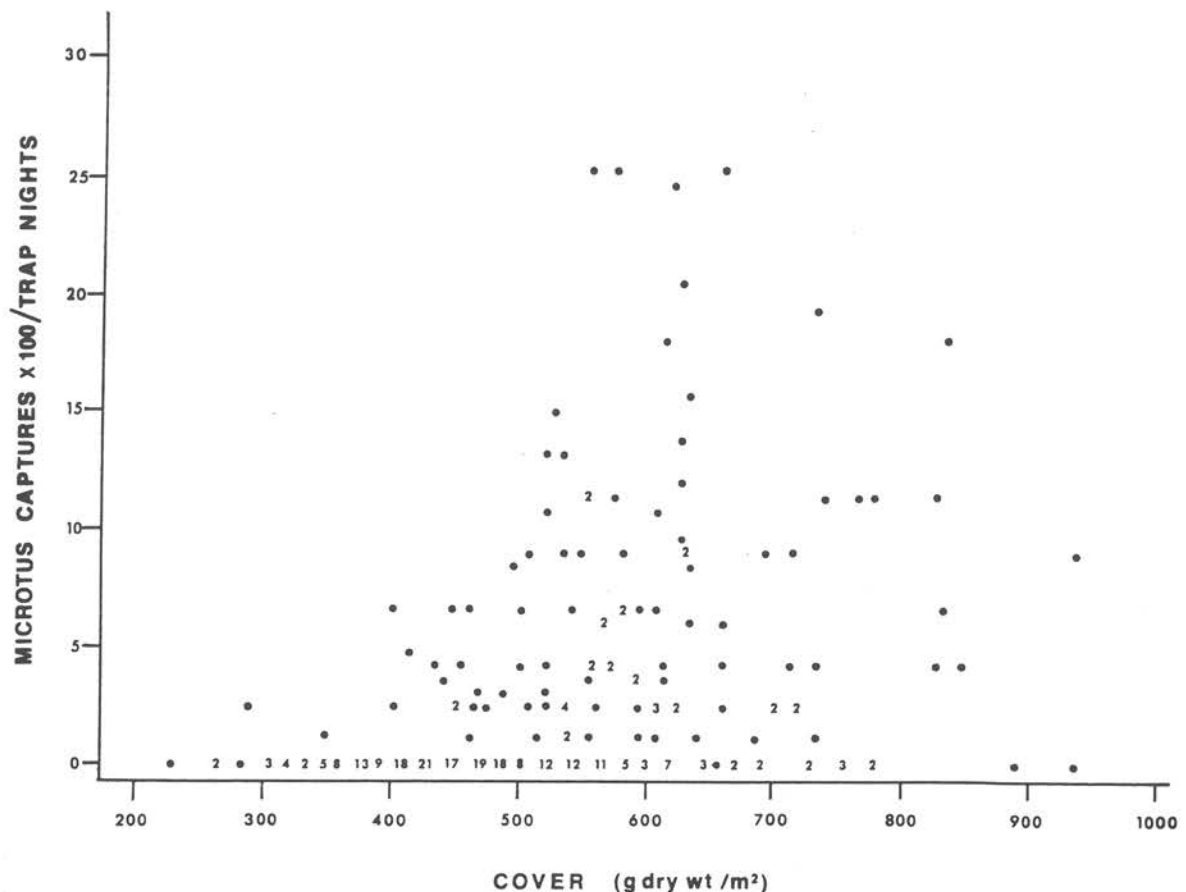


FIG. 3. Relationship between amount of vegetative cover at individual trapping stations (two traps per station) and number of captures of *Microtus pennsylvanicus* standardized by trapping effort on a heterogeneous grid in Minnesota during 1971 and 1972. Numerals are used to represent two or more trapping stations.

voles/ha in July 1972 (Fig. 1). The grazed pasture there is maintained in a constant range condition year after year through regular adjustment of grazing intensity; cover, especially litter, is always low. Cover on the SD grid apparently was not sufficient for the population to exceed the low or earliest increase phase of a cycle. Most voles captured were residents rather than transients based on the criteria described above.

The population of *Microtus pennsylvanicus* at MN-Upland (Fig. 1) underwent some seasonal variation, but no variation in density that we consider cyclic. Most of the breeding, resident voles were trapped in a few areas of dense cover. Measures of average cover or average density of voles do not provide a complete picture of population changes or of use of available cover. The vegetative heterogeneity on the MN-Upland grid provides an opportunity to consider habitat selection of voles given a natural choice of cover levels. When number of captures per trapping effort of *M. pennsylvanicus* at the 324 trapping stations on the grid in 1970 and 1971 is plotted against mean cover at each trapping station

for the 2 yr (Fig. 3), it can be seen that voles tended to avoid habitat having less cover than ≈ 400 g/m² (voles were captured at only 4 of 59 stations having less cover). Traps at only 12% of the 169 stations having < 500 g/m² cover captured one or more *Microtus* during the 2 yr. Those at 56% of the remaining 155 stations captured voles. Variation in cover > 600 g/m² seemed not to be especially important as regards habitat selection.

DISCUSSION

To begin to understand why a threshold level of cover should exist, it is necessary to consider what cover provides that allows a cycle to be initiated. Elton (1939), Frank (1956, 1957), Getz (1971), and others have considered the importance of cover to animal populations. Attributes of cover can be organized into biotic and abiotic components.

Of the biotic components, protection from predators, especially diurnal predators that rely primarily on sight, is a major consideration. Predators may be most influential during the low phase of a cycle. If able to exist on another source of food, predators

may intensify and prolong the low phase, thereby delaying initiation of the increase phase (Pearson 1971). They apparently never or only seldom cause the decrease and certainly do not act alone to cause cycles (Krebs and Myers 1974). However, Getz (1970a) concluded that heavy predation on voles by crows was responsible for rapid decline of a population where cover had been removed.

As defined here, cover is essentially synonymous with vegetation, which means that *Microtus* utilize it as food. Kalela (1962) interpreted cycles of small mammal populations as a phenomenon related to overall community production, especially as regards variation in nutritive value of food plants. French et al. (1976) have shown the relatively low digestive efficiency of small grazing herbivores. Batzli and Pitelka (1970, 1971), after study of *M. californicus* in the field, and Krebs and Myers (1974), after review of literature on the subject, concluded that grazing by *Microtus* can have a marked effect on vegetative cover. Appreciable depletion of cover resulting from grazing by *Microtus* would be expected only during late increase and peak phases. We did not detect any destruction of the habitat by voles at our sites, but that is not to say that the habitat as used by a vole did not deteriorate as a result of their grazing activities.

A third important biotic influence of cover involves behavioral interactions with conspecifics. Individuals would be more likely to make contact when cover is low than when it is dense (Krebs et al. 1971). Additionally, dense cover may allow activity during daylight, whereas low cover may restrict foraging time or intensify intraspecific encounters if young and subordinate individuals are forced to feed during a reduced crepuscular or nocturnal activity period. Warnock (1965) demonstrated that cover reduced fighting and mortality of crowded captive *M. pennsylvanicus*. Krebs (1970), Krebs et al. (1973), and Myers and Krebs (1974) provide good discussions of the importance of behavioral interaction and dispersal in regulation of microtine populations. Based on observation of *M. ochrogaster* in captivity and on the studies by Warnock (1965) on *M. pennsylvanicus*, we think that cover also provides some form of psychological security, but we are ill-prepared to defend that notion on a firm scientific basis.

Influence on the microhabitat (Hopkins 1954) probably is the single most important abiotic effect of cover. This may be moderation of humidity or moisture per se (see Getz 1965, 1971), penetration of light (Mossman 1955, Getz 1970b), or an indirect effect on temperature, plant growth, and soil moisture or texture (Murie 1969). Additionally, heavy cover would prevent dense packing of snow, making the subnivean space more hospitable. This should be especially important at the Minnesota sites where

continuous snow cover for several months is an annual event. In areas such as MN-Wetland where the water table is high, or elsewhere where flooding occurs, cover may provide refuge when soil burrows are inaccessible.

We reiterate that cover is only one index of the environment wherein voles live, and thus it is what cover provides, and not cover alone, that is important to cycling of *Microtus* populations. The relative importance of factors associated with cover are not constant, and we conclude that the threshold we hypothesize is actually a sharp, site-specific gradient in effect of cover levels.

Data presented in Fig. 3 on utilization of habitat on the MN-Upland grid suggest that a cover level between 400 g/m² and 550 g/m² might reasonably be considered as the threshold level. It appears that ≈ 600 g/m² is critical at CO, whereas 450–500 g/m² may be important at OK. Perhaps drier sites or sites having large populations of predators (or other stress factors) might have higher thresholds than less adverse sites. Even at a single site, the threshold would not be an exact amount of cover, but rather it is a critical range where a small increase has a large influence on "success" of voles during the increase phase.

One might hypothesize that another, lower threshold level of cover exists that allows for the establishment of resident breeding populations. Perhaps the level of cover on the nitrogen-only plots and that on the control plots at CO were below this level. During 2 yr of intensive trapping at the CO site in grazed pastures away from the experimental study plots, only one *M. ochrogaster* was captured. After being marked and released, this animal was never encountered again. Obviously, then, voles move across such low cover areas, but they do not establish residency.

Our hypothesis of the relationship between cover and population cycles of *Microtus* is illustrated in Fig. 4. An example of the lowest level of cover, at the left of the schema, would be the CO experimental plots treated only with nitrogen, where no voles were taken in 4 yr. The control plots at CO would be examples of habitats having low levels of voles, perhaps nonbreeding transients dispersing from other populations. Noncycling populations below the threshold but consisting of breeding residents would be typified by SD, probably by the grazed control at OK, and perhaps by MN-Upland. Sites just under the threshold and on the verge of cycling would be the irrigated plots at CO and perhaps MN-Upland. Sites to the right of the threshold level, i.e., those characterized by cycling, would be the ungrazed grid at OK and the water and nitrogen experimental plots at CO. MN-Wetland and the ungrazed exclosure at

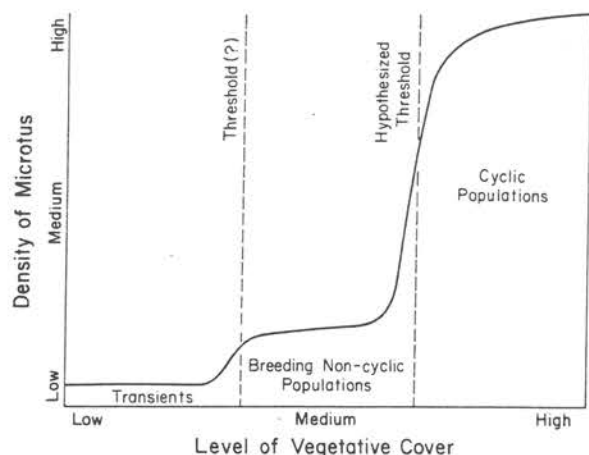


FIG. 4. Schematic representation of cover level hypothesis. Population densities of *Microtus* may be at any level within the area under the curve. The threshold (?) at the left is not a part of our basic hypothesis, but it may exist.

OK probably are of this category, but our limited data do not permit placement of them in the schema.

Our hypothesis is based on our belief that populations may live in habitats characterized by cover levels insufficient to permit cycling. However, Krebs and Myers (1974:386–388) concluded that, "Some populations may not fluctuate, but none of this type has been studied carefully." Populations at SD, the CO control plot, and probably MN-Upland show no evidence of cycling. It is conceivable, however, that our noncyclic populations were actually cycling, but were doing so in habitats lacking sufficient cover for the population peak to be distinguished from the low. Such an interpretation emphasizes the problem of what level of change in density constitutes a cycle.

Cover may be an important influence on the amplitude of *Microtus* population cycles. Krebs and Myers (1974:387) stated that, "The amplitude of the fluctuations is not necessarily larger in more northern populations." If variation in amplitude is not strictly a function of latitude, then some other factor or factors must be important to such variation. Lidicker (1973) has shown for *M. californicus* that population "lows" may be relatively high in some habitats (insular in this instance). Relatively high densities, including those during a low phase, may be possible only at high cover levels.

Cover levels also may be important to the periodicity and apparent synchrony of cycles. Krebs and Myers (1974:387) have noted that, "The periodicity of cycles is variable, three to four years is typical, some cycles may be two or five years in length." Populations living in cover sufficient for rapid increase (such as our OK site) or for high numbers of individuals during lows (such as the insular population studied by Lidicker 1973) may cycle in 2 or

3 yr, whereas those living in cover levels only slightly above the threshold could be characterized by longer cycles, with predation or other factors prolonging the low phase and delaying the increase. Krebs and Myers (1974), however, view the increase as one of the least variable parts of the cycle.

Regarding synchrony, Krebs and Myers (1974) stated: "Fluctuations sometimes occur in synchrony over large geographical areas (thousands of square miles). Synchrony is seldom absolute, however, and local out-of-phase populations occur. Synchrony is not continental or world-wide." We suggest that local out-of-phase populations may result from local out-of-phase manipulations of cover, such as was seen on the cattle enclosure at OK in 1972 when one population was increasing rapidly while one only 200 m away was declining. The tendency toward synchrony over large areas may result from large areas having similar cover (usually as a result of similar weather patterns; see Krebs and Myers 1974) and the fact that dispersal and movements of individuals would tend to equilibrate density of nearby populations, as discussed by Krebs et al. (1973). The minimum size of a local patch of cover necessary to support an out-of-phase population is unknown, as is the importance of proximity and type of intervening habitat to the equilibration of population numbers.

This presentation of our hypothesis places great emphasis on one factor, cover, but we hope we have made it clear that we view the total of the interrelationships between both the internal (such as genetic, physiological, and behavioral) and external (such as cover, predators, and intra- and interspecific interactions) environment of voles as being important to the biology of microtine fluctuations (see also Frank 1957 and Lidicker 1973). At present, the crucial tests of our hypothesis have not been conducted. It is our hope that this report will stimulate research on the importance of cover to the population biology of microtine rodents.

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C. J. Krebs, W. Z. Lidicker, L. Oftedahl, and H. B. Tordoff.

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