

EFFECTS OF FORAGE AVAILABILITY ON HOME RANGE AND POPULATION DENSITY OF *MICROTUS PENNSYLVANICUS*

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ABSTRACT.—The hypothesis that territoriality of female meadow voles (*Microtus pennsylvanicus*) regulates population size was tested during four breeding seasons by using radiotelemetry to determine home range, dispersion, and use of vegetative cover in crownvetch (*Coronilla varia*) fields. The percentage of transient voles in the population was related directly to density. The percentage of transient females increased as nearest-neighbor distances between females decreased. Territory size for females was related inversely to available forage, supporting the hypothesis that territory size is a function of availability of food. I conclude that the quantity of forage is a factor in controlling population density.

Most research on small mammals has been conducted in habitats in which food or shelter is not likely to be limiting and the species under study is abundant. To investigate the role of forage availability in population regulation, I worked in suboptimal habitat. A crownvetch (*Coronilla varia*) field is considered suboptimal habitat for meadow voles (*Microtus pennsylvanicus*), in that feeding trials (Jones, 1978; Shenk et al., 1974) and laboratory analyses (Barnes et al., 1974) have shown that crownvetch is not only avoided by voles as forage, but is toxic as well (Barnes et al., 1974; Gustine et al., 1974; Shenk et al., 1974). I found that adult voles reject crownvetch when it is provided with other foods. When voles from crownvetch fields were fed solely crownvetch and water, they died within 3 days (Jones, 1978).

A decline in the density of a population may occur when all nontoxic forage is consumed and individuals are forced to eat toxic species (Freeland, 1974). An inadequate supply of protein, caused by insufficient nitrogenous foods (Mattson, 1980), could result in death of juveniles (White, 1978). These two hypotheses are complementary, for one of the modes of action of plant toxins is to bind proteins in the contents of the digestive tract; hence, a switch to a toxic forage could reduce adsorption of protein already ingested (Reese, 1979). In response to herbivory, plants may increase defensive secondary compounds. Hence, the effect on available protein potentially would vary with the degree of herbivory to which the plant was subjected (Chew and Rodman, 1979; McKey, 1979). If either of these two hypotheses is correct, voles from areas in which forage is scarce would most likely show signs of physiological stress. However, Cummins (1981) found no evidence of such stress in voles from crownvetch fields. Furthermore, Krebs and Myers (1974) suggested that the fraction of plant material eaten by voles is too small for food to be a limiting factor.

Territoriality can provide a mechanism by which density of a population can be held below the limits of available forage. Existence of territoriality in females was suggested by Bujalska (1970, 1973) for *Clethrionomys glareolus* and seen in *M. pennsylvanicus* by Madison (1979, 1980a, 1980b). The female-territory hypothesis is that females unable to secure a territory will be unable to breed and will disperse. Therefore, density is determined by the number of females holding territories, and is held below that at which forage would be directly limiting.

METHODS

This study was conducted in late spring and summer, 1979–1982. Five study sites were established in commercial crownvetch fields within a 15-km radius of State College, Centre Co., Pennsylvania. The areas and number of traps on each of the five study sites are as follows: 2.5 ha, 100 traps; 5.7 ha, 256 traps; 3.6 ha, 183 traps; 1.9 ha, 84 traps; and 1.1 ha, 49 traps. A yearly shift in study sites was necessitated by agricultural practices because crownvetch is grown in rotation with corn. The 1.1-ha site was grass covered and located within the drainage basin of a large crownvetch field.

As a result of preliminary studies conducted in 1976, all traps were spaced at 15-m intervals. Sherman live traps (5.0 by 6.5 by 17.4 cm) baited with Purina rat chow and rolled oats were placed under the vegetation at each grid intersection and examined twice daily (Jones, 1984). These grid points provided known locations for the radiotelemetry bearings and vegetation measurements.

Voles captured four or more times were classed as residents, and those captured fewer times as transients (Blair, 1951; Flowerdew, 1978). The center of activity was calculated for all residents. The distance to the nearest neighbor of the same sex, to the nearest neighbor of any sex, and the mean distance of the five nearest neighbors of the same or any sex were calculated. These measures provide a measure of density around each individual.

Several times each month the number of residents on each grid was estimated by use of the best-model-selection procedure in the CAPTURE program (Otis et al., 1978). To reduce behavioral heterogeneity in capture probability, data were grouped by sex and age (White et al., 1982); juvenile animals <10 g were omitted until their sex could be determined (Nichols et al., 1981). The exclusion of juveniles also helps to meet the closure assumptions of the computer model. Capture probability was increased and time variation reduced by pooling the morning and evening samples (White et al., 1982). Accordingly, when the same animal was captured in the morning and evening samples, it was counted as one capture for the population estimate but both captures were used in the movement analysis.

Two receivers (164–165 MHz, AVM LA-12, AVM Instrument Co., Livermore, CA) and three-element Yagi antennas were used throughout the study. The radiocollar consisted of an AVM SM1 mouse-style transmitter powered by an RM312t2 battery soldered to a section of insulated-solid-copper wire. Battery-transmitter units were coated in beeswax and encased in Plas-T-Pair (Rawn Company Inc., Spooner, WI). The transmitters were attached in the field to voles anesthetized with ketamine hydrochloride (100 mg/ml at 44 ml/kg—Weisbroth and Fudens, 1972).

Captures and telemetry locations were plotted on vegetation-cover maps. Telemetry locations were divided into periods for analysis. A period included about 30 consecutive locations (approximately 3–4 days), and was separated from each sequential period by at least 8 h. The following home-range measures were calculated for each period: mean activity radius, center of activity (Dice and Clark, 1953), observed-range length (Stickel, 1954), convex-area polygon (Southwood, 1966), and minimum-area-versus-probability estimate (Anderson, 1982). A square-root transformation was used on the activity radii. Multiple comparisons (Dunn, 1964) were used following Kruskal-Wallis tests of home-range measures. This multiple-comparison procedure controls for experimentwise error rate (Daniel, 1978).

Plant-species coverage was determined for all species intersected by each of four 1.78-m lines extending NE, SE, SW, and NW from each trap point by recording the coverage classes proposed by Daubenmire (1959) as modified by Bailey and Poulton (1968). Coverage along the four lines was averaged to determine the coverage value for each species at that trap point. The species were grouped into the classes: crownvetch, grasses, and total potential forage, which included all species but crownvetch.

In areas of activity of radiocollared voles, vegetation also was sampled at 7.5-m intervals on the 2.5-ha site, and at 5-m intervals on all other sites. In 1980, an unexpected early harvest of vetch on the 5.7-ha site prevented completion of such supplemental samples.

To characterize the vegetation available to a specific telemetered vole, I calculated its 95% mean recapture radius (Calhoun and Casby, 1958) based on radiotelemetry locations, then averaged the vegetation values within the area described by this radius. To determine the vegetation visited, I averaged the vegetation values only for locations visited by each vole. Hence, a location visited 10 times contributed 10 times to the vegetation-visited value and only once to the vegetation-available value.

Data management, calculation of vegetation available, most home-range measures, and regression and correlation was conducted by use of SAS procedures (SAS Institute Inc., 1982); nonparametric tests were performed by use of SPSS (SPSS, 1983) on The Pennsylvania State University's IBM 370/3033 and 4031 computers. Minimum-area-versus-probability estimates were calculated by use of the program HOME-RANGE (Anderson, 1982).

RESULTS

During four seasons, 79 different adult voles were fitted with radio transmitters. Voies for which >11 telemetry locations were recorded were used in analyses. Because of predation, transmitter failure, and the lack of complete vegetation data for some females in 1980 (because of the early harvest), only 39 of the 79 voles collared were used in the analysis.

No significant correlation (Spearman rank) was found between number of telemetry locations and size of the home range as determined by any of the measures used. Most home-range

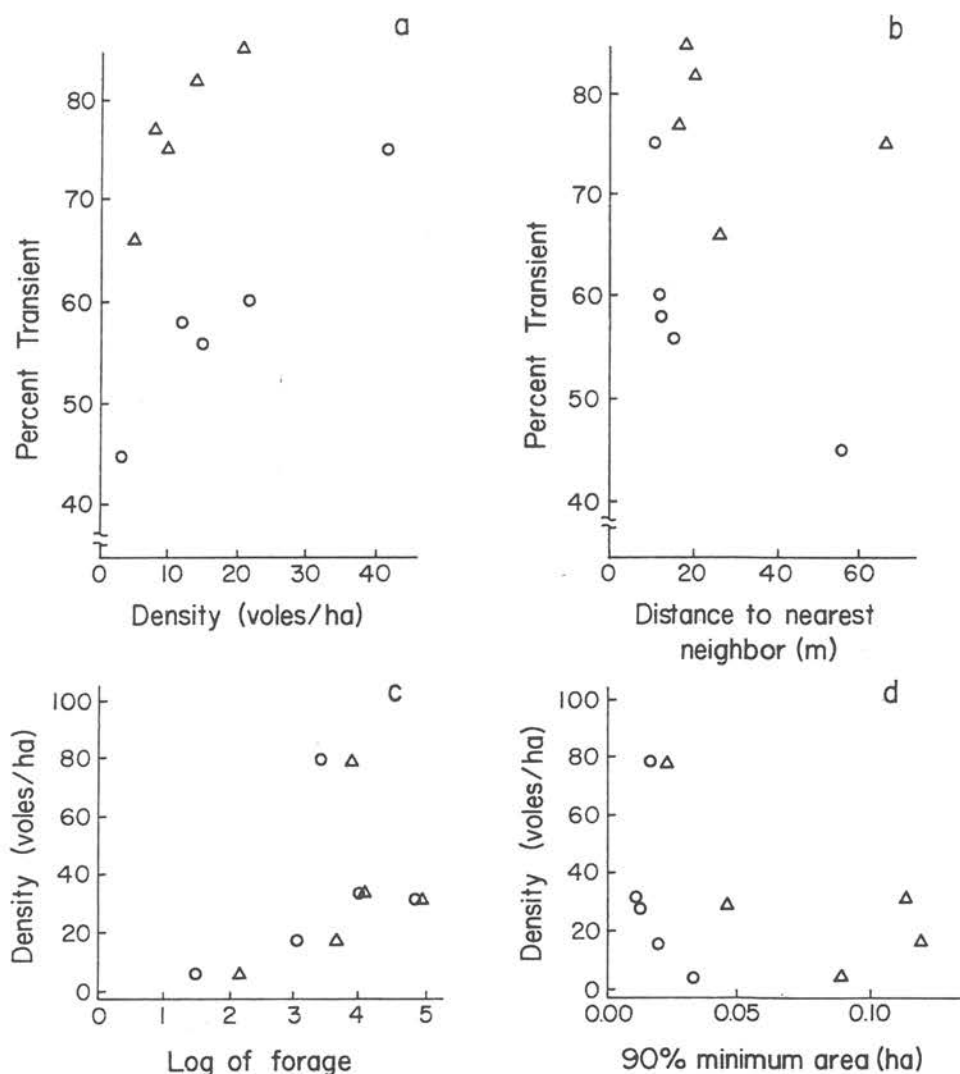


FIG. 1.—Characteristics of meadow vole populations at five sites in Centre Co., Pennsylvania, 1979–1982 (males represented by triangles, females by circles): a, the percentage of the population considered transient in relation to the median estimate of density; b, the percentage of the population considered transient in relation to the mean distance to a nearest neighbor of the same sex; c, the mean estimate of density in relation to the logarithm of available forage within home ranges; d, the mean estimate of density in relation to the 90% probability estimate of the minimum-area home range.

measures derived from radiotelemetry data were similar; males had larger home ranges than females whether linear or area measures were used.

For all sites combined, convex-area polygons averaged larger for males than females (Wilcoxon two-sample test, $P < 0.001$; Table 1). The convex-area polygons were larger for males than females on each site, significantly so on three of the five grids. The same pattern was seen in the observed-range length, the mean-activity radius, and the minimum-area-for-75% probability estimates (Table 1). Multiple comparisons of home-range measures for females showed the convex polygon and mean-activity radius to be significantly larger on the 3.6-ha site than on any other

TABLE 1.—Mean home-range measures for male and female meadow voles, Centre Co., Pennsylvania, 1979–1982. Wilcoxon two-sample tests were used for male to female comparisons. Kruskal-Wallis tests were used for between-year comparisons (females only), with multiple comparison experimentwise error rate of 0.05.

Area of site (ha)	Convex polygon				Observed-range lengths (m)		Mean activity radii (m)		Minimum area for 75% probability (ha)	
	δ		φ							
	Area (ha)	n	Area (ha)	n	δ	φ	δ	φ	δ	φ
2.5	0.05	2	0.32 ^a	6	33	31 ^{ab}	9.6	5.8 ^a	0.15	0.01 ^{ab}
5.7	0.15 ^{**}	3	0.04 ^a	15	70 ^{**}	31 ^{ab}	16.0 ^{**}	6.9 ^a	0.08 ^{**}	0.01 ^{ab}
3.6	0.37 ^{**}	16	0.08 ^b	18	122 ^{**}	49 ^a	32.0 ^{**}	13.4 ^b	0.05 [*]	0.02 ^a
1.9	0.13	1	0.02 ^a	17	117	26 ^{ab}	40.7	5.9 ^a	0.08 [*]	0.01 ^b
1.1	0.07 [*]	2	0.01 ^a	8	38 [*]	17 ^b	11.4 [*]	4.1 ^a	0.03	0.01 ^b
\bar{X}	0.28 ^{**}	24	0.04	64	101 ^{**}	33	26.8 ^{**}	8.0	0.56 ^{**}	0.01

* $P < 0.05$.

** $P < 0.01$.

^{ab} Means in the same column with the same letter are not significantly different.

site. Multiple comparisons for males were not possible because of the small samples in some years.

For both males and females, the percentage of the population defined as transient showed a direct relationship to the density estimate ($r = 0.9$, $P < 0.05$, Spearman rank correlation coefficient; Fig. 1a). For females, a perfect inverse relationship was seen between the percent transients and the mean distance to the nearest female neighbor (Fig. 1b).

For females, a significant negative Spearman rank correlation existed between the distance from females to nearest males, in addition to females, were included, the correlations remained the potential forage ($r = -0.85$, $P < 0.001$) at locations visited by the females. There was a significant positive Spearman rank correlation ($r = 0.38$, $P < 0.001$) between the log of coverage by crownvetch and the distance from a female to her nearest female neighbor. When the distances from females to nearest males, in addition to females, were included the correlations remained significant but their strength decreased. No significant correlations were found between male-male distance and vegetation.

For males, log of forage visited and the observed-range length were correlated negatively, indicating that as density of forage decreased voles moved longer distances (Table 2). The same relationship was seen for both the convex-area polygon and the mean square root of the activity

TABLE 2.—Correlations between selected home-range measures of meadow voles and either distance to the nearest neighbor or measures of vegetative cover, Centre Co., Pennsylvania, 1979–1982. A square-root transformation was used on the mean activity radius.

Sex and measure	Observed range length	Minimum area for probability of		Convex polygon	Mean activity radius
		75%	90%		
Males					
Nearest male	-0.33	-0.21	-0.21	-0.40*	-0.51**
Nearest vole	-0.00	-0.14	-0.14	0.02	-0.04
Grass	-0.03	-0.08	-0.09	-0.08	-0.13
Potential forage	-0.45*	-0.05	-0.07	-0.47*	-0.42*
Crownvetch	0.39*	0.09	0.10	0.33	0.31
Females					
Nearest female	0.57***	0.63***	0.62***	0.69***	0.75***
Nearest vole	0.49***	0.49***	0.48***	0.56***	0.64***
Grass	-0.63***	-0.50***	-0.51***	-0.63***	-0.77***
Potential forage	-0.62***	-0.62***	-0.63***	-0.69***	-0.80***
Crownvetch	0.48***	0.31**	0.32**	0.44***	0.59***

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

radius. The lack of association of the vegetation with the minimum-area-probability estimate is because it measured intensity of space use, not the extent of it. The distance to the nearest male was associated negatively with both the convex-area polygon and the activity radius (Table 2). This indicates that larger home ranges of males tended to overlap those of other males more than smaller home ranges of males did. For females, a common pattern was seen between home-range measures and the measures of density and vegetation (Table 2). As any of the home-range measures increased, the distance to the nearest neighbors also increased.

The distance to the nearest neighbor of the same sex (D) can be predicted ($r^2 = 0.66$, $F = 26.02$, $P < 0.0001$) for females based on the mean square root of the activity radius (AR) and the log of the total potential forage available within the home range (PF):

$$D = 10.15 \text{ AR} - 8.52 \text{ PF} + 20.85 \quad (1)$$

The corresponding equation for males was not significant.

When the average densities of voles per site were plotted against the mean cover by forage available within the home ranges, a positive slope resulted for both males and females (Fig. 1c). Population density and minimum area for 90%-probability home-range estimates were related inversely (Fig. 1d).

DISCUSSION

Territoriality often has been invoked as a mechanism that limits density in the best habitats or controls the total size of the breeding population (Brown, 1969a, 1969b). This study provided an opportunity to determine if forage availability influences the size of individual territories, hence, ultimately affects density.

The stabilizing effect of territoriality on numbers of adult female voles was first suggested by Bujalska (1970, 1973) for *Clethrionomys glareolus*. Madison (1980b) introduced the female-territory hypothesis in which female meadow voles establish and defend territories, and those females unable to establish a territory are unable to breed. Therefore, the population is limited by the number of breeding females. Boonstra and Rodd (1983) tested this hypothesis for meadow voles by manipulating sex ratios. Removal of males seemed to have little effect on females, whereas removal of females caused a population decline in the males. Their results support the hypothesis that females are spatially oriented (territorial) whereas the males are not. In the present study, I found a stronger correlation between territory size for females and the distance to the nearest female neighbor, as opposed to the nearest neighbor of any sex. The inclusion of males in the data set reduced the strength of the association, because males are not excluded from a female vole's territory. These findings support the female-territory hypothesis.

Territoriality also regulates population density by inducing dispersal of individuals that do not hold territories. Movement of transient animals away from their natal area prevents resource exhaustion (Gaines and McClenaghan, 1980; Lidicker, 1975). I found a direct relationship between population density and the percentage of transient individuals in the population. The inverse relationship between the mean distance between female nearest neighbors and the percent of transient individuals in the population underscores the relation of territory size of females to population regulation. Because transient individuals are surplus breeders in vole populations (Blair, 1951; Flowerdew, 1978), the number of breeders appears to have been limited in proportion to the density.

Cummins (1981) reported that densities of meadow voles are lower on crownvetch fields than on nearby old fields. If this difference were related directly to resource exhaustion, I would expect to find indications of food stress in the population with the lower density. However, voles taken from crownvetch fields in June and August were larger, heavier, and had greater organ masses than voles collected in old fields (Cummins, 1981). Additionally, no significant differences were found between the two groups in counts of corpora lutea, living embryos, or resorbing embryos. These results indicate that female voles on crownvetch sites were able to establish territories that provided sufficient forage for successful reproduction.

Resident females show a strong positive association with grasses, both in their dietary selections and sites of capture. These females also show a significant inverse association between the forage visited and the distance to the nearest female neighbor, indicating that as available forage increases, the distance between individual females decreases. This result in higher densities in those portions of the habitat richer in forage. A significant inverse association also was seen between available forage and space used, indicating that as forage increases, territories of females become smaller. The differences in the direction of the correlation coefficients between nearest-neighbor distances and home-range size for males and females results from the nonterritoriality of males and the territoriality of females. These results parallel Batzli's (1974) findings of higher densities of *M. californicus* associated with patches of perennial grass (their primary food) rather than the dominant annual grasses. As expected, Batzli (1974) failed to show a significant association between male-male distances and forage quality.

Clumping in the best sections of the habitat also was reported by Grant and Morris (1971). I showed that breeding females get the best clumps in terms of forage availability. Capture locations of different segments of the population support Bergeron and Juillet's (1979) findings of differences in the diets of males and females. Home ranges of adult resident females lie within areas of significantly higher grass content, whereas transients, many of which were prereproductive, were captured in areas with greater amounts of toxic vegetation. Bergeron's (1980) findings of greater use of toxic plants by preadults in peak years is consistent with my finding transients being captured in areas with less available forage. These preadults appear to be forced into unfamiliar habitat with a lower forage quality, hence may encounter and ingest larger amounts of toxic species.

As the density of food items decreases, foraging costs increase because of greater search times (Mac Arthur and Pianka, 1966). During pregnancy and lactation, microtines show a 100% increase in energy requirements (Kaczmarek, 1966; Migula, 1969), which raises the minimum density of forage required by reproductive females above that of males and nonreproductive females. Heasley (1983) modeled energy allocation in pregnant and lactating laboratory mice; he emphasized that with a reduced intake of food by maternal females, juvenile survival decreases. Therefore, reproductive females that occupy the best food patches (e.g., grasses) forage at lower costs and should be more successful than those in suboptimal areas. Sherman (1984) showed that following parturition, females shifted their activity to areas within their home ranges that contained greater concentrations of forage. A reduction in movement of these female meadow voles at parturition and during early lactation was found by Sherman (1984) and Madison (1978, 1981), who suggested that this may reflect an altered foraging strategy with the necessity of having to concentrate activity around a fixed nest site.

The magnitudes of various measures used to predict density should vary for males and females, based on their respective patterns of space use. Females hold stable territories that vary in size with available forage, and both forage quantity and territory size were significant in predicting space use by females. Males are not territorial, wander in search of receptive females, and have lower nutrient requirements. Neither home-range size nor quantity of forage were significant in predicting spacing behavior of males. The relationships between distance to the nearest neighbor of the same sex and both the potential forage in the home range and the mean square root of the activity radius were significant for females but not for males. For females, the negative forage term in equation 1 indicates that as forage availability decreases, the distance between females increases. The positive home-range term is an indication of the direct relationship between home-range size and distance between females. Both of these are significant in predicting distance to the nearest female. If the distance to the nearest vole of either sex is predicted, the home-range term ceases to be significant. This supports the hypothesis that female territoriality only results in the exclusion of females. Males appear to be insensitive to territorial boundaries.

In their study of population cycles in meadow voles, Birney et al. (1976) suggested that a minimum density of cover is necessary for voles to increase. I believe that for reproductive females, the forage value of the cover is the critical factor, as I did not find reproductive voles

in areas of pure crownvetch. In their cover-level hypothesis, Birney et al. (1976) predicted that transients will be found in areas of lower cover, whereas I found them in areas in which food availability was lower. They predicted breeding populations where cover density was high; I found them in areas in which food availability was higher.

Populations of *Microtus pennsylvanicus* are limited by the number of breeding females, which in turn are limited by available space in which to establish a territory. The size of these territories varies with the quantity of forage available within them, and they appear to function as a means of insuring an adequate supply of food. Therefore, at the low end of the food-availability spectrum, social behavior limits the population density below that at which food stress occurs. Food availability influences the size of the territory, hence the population density, but the limitation is not direct. Nonterritorial males appear to respond to locations of females and, therefore, indirectly, to herbage. These data support the hypothesis that home-range size is a function of availability of forage. Coupled with the female-territory hypothesis, I suggest that forage is a controlling factor in population density.

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