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ABSTRACT: Free-ranging, sexually mature meadow voles (Microtus pennsylvanicus) were tracked using radiotelemetry from June through August 1974, 1975 and 1978. Up to 20 voles were monitored concurrently to derive estimates of intraspecific spacing and natural predation in an effort to clarify processes involved in the limitation of population growth.

The daily ranges of the males, as compared to those of the females, were larger, more variable in size, and changed location more from one day to the next. Adult females usually maintained territories free of other females; males overlapped considerably among themselves. Males temporarily moved into the areas occupied by estrous females, indicating intrasexual competition among males for access to receptive females.

Predation, primarily by three snake species, the domestic cat, and weasels, accounted for the deaths of 30 of 93 voles monitored with radiotelemetry during the three summers. The intensity of predation varied with the reproductive state of the meadow vole, occurred in bursts through the summer, and was selective for voles living nearer suboptimal habitats.

M. pennsylvanicus are socially organized into territorial, maternal-young units during the breeding season. By being territorial, breeding females set in motion a sequence of behavioral events that results in population limitation and potentiates population cycling.

INTRODUCTION: Effective methods for the biological control of meadow voles (Microtus pennsylvanicus), or for the use of meadow voles as an agent in the control of pine voles (Bart & Richmond, 1978), depends on a clear understanding of the movements, space requirements, and vulnerabilities of meadow voles to the abiotic and biotic environment. This paper reports recent research findings on space use and natural predation among free-living meadow voles, and briefly discusses a model sequence of regulatory events for the species.

Previous information on space use, home range size and territoriality in meadow voles is rather indirect and, in some cases, contradictory, primarily because of the difficulty of observing voles in grass runways or in underground tunnels (Ambrose, 1973; Getz, 1961, 1972, 1978). Information on the impact of predators on meadow voles is also limited, although certain studies are noteworthy (Pearson, 1964, 1971). Limitations imposed by trapping techniques or by the secretive habits of meadow voles were largely overcome in the present study by the use of miniaturized, radiotelemetry equipment (AVM Instruments, Champaign, Illinois).

METHODS: Three different populations of meadow voles have been studied using radiotelemetry: Quebec, Canada (1974), Front Royal, Virginia (1975), Binghamton, N.Y. (1978). Rich, old field habitat was chosen in each case. Longworth live traps in grid systems were used to capture the voles, and routine information was collected on weight, sex, reproductive condition and wounding. For radio-tracking, all the voles (0.7 oz or more) captured in each study area were fitted with radiotransmitter collars, each transmitter being pre-tuned to a separate frequency (see Madison, 1977, 1978a, b, for further details on technique). After the voles were given transmitters and returned to the field, the locations of all the voles were measured each hour for 24 hours, once or twice weekly. On all other days at least two positions were recorded for each vole.

The 24-h monitoring sessions gave a set of 24 positions for each vole. The outer positions of each set were joined by a perimeter line to form a convex polygon. The resulting 2-dimensional shape, termed the daily range, was considered to be an approximation of the area within which the particular vole spent the major portion of its time during one biological time unit (the 24-h day). Grouping data over longer periods (e.g., over two weeks or one month) gives unreliable information on space utilization and overlap between voles. The daily ranges shift between sessions, and long term data frequently indicate overlap between voles that never existed in the daily records. In addition to daily range information, data were collected on movement, the incidences of predation, and a variety of other variables (see Madison, 1978, a, b).

RESULTS AND DISCUSSION: During 1975 and 1978 when 24-h monitoring procedures were used (just 2 to 8 positions were recorded per 24-h period in 1974), a total of 331 twenty-four hour records were obtained from a total of 34 male and 35 female voles. In all, 8,352 positions were recorded during the 24-h monitoring sessions for these two years; over 13,000 were recorded overall for the three years.

Range size. The average daily range size was 0.06 acres for males and 0.02 acres for females (Table 1). The difference in daily range size was significant (comparison for 1975 data: $t_s = 3.17$, $t_{.05} = 2.23$, $p < 0.05$). When the daily ranges were combined and the cumulative size quantified, there was a linear increase in range size with the number of positions for both males ($b_{y \cdot x} = 12.5$ ft^2/position) and females ($b_{y \cdot x} = 3.6$ ft^2/position). However, there was no change in daily range size through the summer. Thus, the cumulative range size reflects regular changes in the location of the daily range, as indicated in Fig. 1.

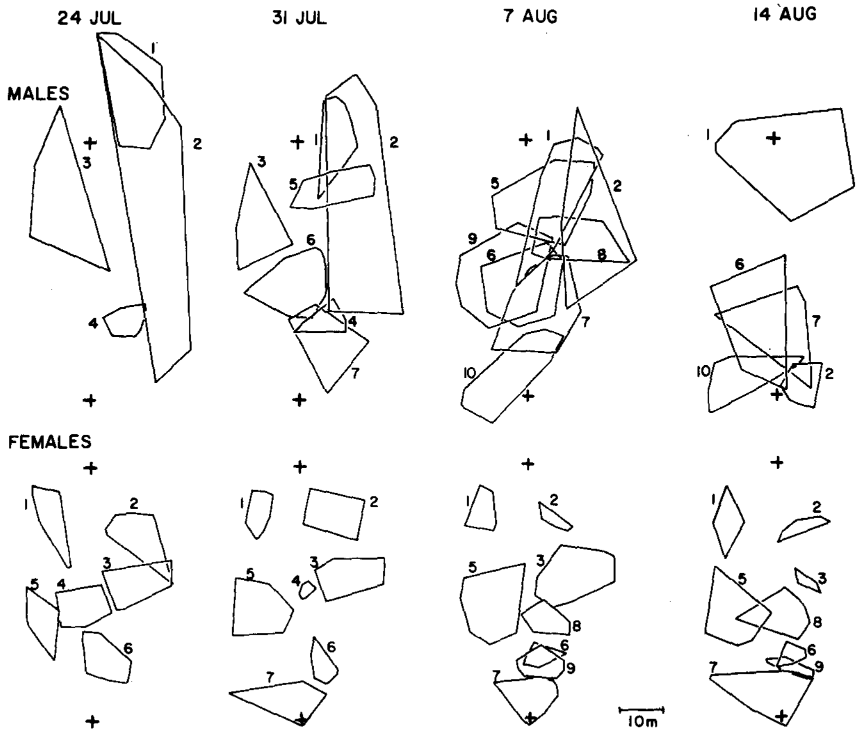

Fig. 1. 24-Hour daily ranges of all the adult meadow voles present in the study area at weekly intervals on the indicated dates in 1975. The ranges of the males and females are plotted separately for clarity. The original spacing can be restored for any day by superimposing the two pairs of reference markers (+). The different individuals have been identified by numbers to allow a comparison of range size and location from one week to the next.

Table 1. Daily range sizes determined by radiotelemetry for meadow voles (0.07 oz. and heavier) for June through August, 1975 and 1978.

[1]Year	Sex	No. voles studied	No. 24-h periods	Ave. area ft^2 (acre)	Standard error of mean (ft^2)	[2]Largest area measured (acre)
1975						
	Male	16	77	2319 (0.05)	67	0.23
	Female	15	72	849 (0.02)	19	0.05
1978						
	Male	18	95	2935 (0.07)	91	0.49
	Female	20	87	739 (0.02)	31	0.15

[1]Density in 1975 was 45 voles/acre (June) and 80 voles/acre (August); in 1978, 54 voles/acre (June) and 110 voles/acre (August).

[2]The minimum daily range in all cases was less than 0.01 acre.

Range exclusiveness. Females showed a high degree of exclusiveness in their daily ranges, with only 6% of the female positions falling within the range perimeters of other females. In contrast, males overlapped considerably, with 57% of the male positions falling within the range perimeters of other males. The overlap between males and females was extensive, just as was the overlap between males (Fig. 1).

Reproductive correlates of space use. The size and location of the daily range varied according to two reproductive events. First, the size of the daily range decreased markedly in the female in association with parturition, followed by re-expansion of the range in association with weaning of the young (Madison, 1978b). The decrease in size is conspicuous for female 4 (31 July), 2 (7 Aug), and 3 (14 Aug) (Fig. 1). The second finding is that males overlapped significantly more among themselves and with females when the latter were in estrus, than with each other or with the same females when the latter were 6 to 12 days before or after the onset of estrus (Fig. 2). In Fig. 2, the extension of the male ranges to include part or all of the range of the female in estrus (female 7, 14 Aug; female 3, 7 Aug) is evident. These latter data suggest intrasexual competition among the males for access to receptive females, which is consistent with the finding that wounding is essentially restricted to the males during the breeding season (pers. obs., Christian, 1971a; Rose, 1979).

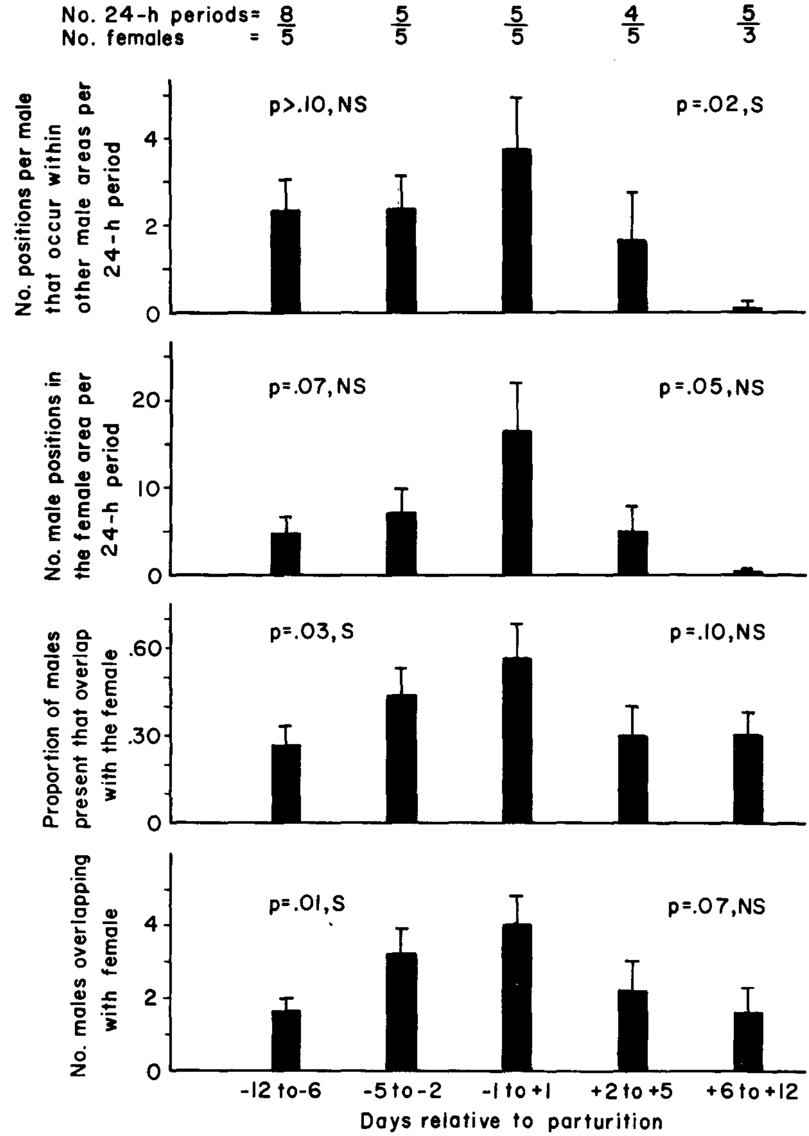

Fig. 2. Extent of position and area overlap between males and between males and females relative to females before, during and after parturition (= postpartum estrus), in 1975. Standard errors are plotted above each vertical bar. Statistical comparisons were made only between the samples 6 to 12 days to either side of parturition and the time of parturition (-1 to +1 days).

Predation. During the three summers during which voles were studied with radiotelemetry, 30 of the 93 voles with transmitters were known to have been killed by predators (domestic cats, snakes and weasels being the more dominant predators, respectively) (Table 2). Another 11 voles disappeared, and these could have been the victims of wide-ranging avian or mammalian predators. These predators could have easily transported their vole prey beyond the 30 to 100 yard range of the radio-tracking equipment, making documentation of predation essentially impossible.

Table 2. Predation on meadow voles (0.07 oz. and heavier) wearing transmitter collars during the months June, July, and August for three different years.

Year	Sex	No. voles tracked	[1]No. known vole prey	Known predation (%)	[2]No. voles lost	Voles lost (%)	[3]Maximum predation possible (%)
1974							
	Male	11	4	36	3	27	63
	Female	11	6	54	0	0	54
1975							
	Male	16	6	38	1	6	44
	Female	15	4	27	0	0	27
1978							
	Male	20	3	15	4	20	35
	Female	20	7	35	3	15	50
Total							
	Male	47	13	28	8	17	45
	Female	46	17	37	3	6	43
	Combined	93	30	32	11	12	44

[1]Transmitter collar was recovered with vole remains; most abundant predators included two snake species (see Madison, 1978) and, probably, domestic cats and weasels.

[2]The disappearance of voles could have been the result of long distance dispersal or, more likely, of the removal of the vole from the study area by a wide-ranging predator (fox, raptor).

[3]This value is the addition of the percent of voles lost to predators and the percent lost due to unknown factors.

Three findings relative to the above data are important. First, in 1975 it was found that snakes (Coluber constrictor, the black racer, and Elaphe obsoleta, the black rat snake) preyed selectively on female voles and their newborn litters and on the most sexually active males (Madison, 1978a). Second, in both 1974 and 1978 predation was found to occur explosively at different times during the summer, instead of occurring uniformly throughout the summer. For example, 13 of the 17 instances of predation or vole disappearance during the summer of 1978 occurred during three, one day periods (20 June, 21 July, 15 Aug). Third, analysis of the locations of the voles that were taken as prey revealed that vulnerability to predation was associated with proximity to suboptimum habitats. For example, 14 of the 25 voles (56%) living within 70 ft of suboptimum habitat in 1978 were taken as prey. This compares with the loss of 3 of 15 voles (20%) living greater than 70 ft from suboptimum habitat. The difference was most pronounced among females where 9 of 10 individuals were taken within 70 feet of the suboptimum area, but only 4 of 10 females were taken beyond this distance.

A model of population regulation. The above data for Microtus pennsylvanicus indicates breeding-rearing territories among females during the breeding season. The potential then exists for population limitation by females, who by maintaining exclusive areas restrict the number of females attempting to breed in a given area. By limiting their own numbers, breeding females limit recruitment and the number of females available to males. The latter limitation would intensify intrasexual competition among mature males, which in turn would lead to increased wounding and emigration among males, to the appearance of greater numbers of transient males from adjacent areas (thus potentiating infanticide; Mallory & Brooks, 1978; Brooks, pers. comm.; Webster, pers. comm.), and to an increase in the rate of pregnancy failure (Mallory & Clulow, 1977) and infant mortality (Calhoun, 1963). The latter events would result from the increased interference of courting males in the activities of the pregnant or lactating females. The females failing to produce offspring defend larger areas than lactating females (Madison, 1978b), which leaves less area for, and reduces postpartum pregnancies among, the successful female breeders. In addition, the females experiencing pregnancy failure would tend to cycle continuously and mate more frequently and therefore increase the number of females available for mating (hence, reducing a disparate "operational" sex ratio; Emlen, 1976). The resulting increase in the relative number of receptive females at any point in time would tend to support or satisfy a larger population of sexually active males, whose competitive courtship activities would further disrupt the normal rearing activities of the few females producing litters. Stress related phenomena (Christian, 1971a, b, 1978) would considerably intensify with advanced stages of the above events. Lowered recruitment into a population coupled with high ambient predation rates would create a population decline whose magnitude and duration would be in proportion to the predation pressure (Pearson, 1971) and the degree to which the production of new young, who could serve as the next generation of breeders, was forestalled.

The above events have been described for M. pennsylvanicus (Brooks & Webster, pers. comm.; Christian, 1971; Getz, 1961, 1972, 1978; Gray & Dewsbury, 1975; Madison, 1978a, b, this study) or were derived logically from what is known for M. pennsylvanicus. The events are at the least consistent with the theory that territoriality may limit population density (Brown & Orians, 1970; Stokes, 1974; Verner, 1977; Watson & Moss, 1970). The best supporting evidence for related events among microtines other than M. pennsylvanicus comes from studies by Bujalska (1973), Frank (1957), Jannett (1978), Myllymaki (1975), Redfield et al. (1978) and Viitala (1977).

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