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SOCIAL BEHAVIOR AND ACTIVITY PATTERNS OF MEADOW VOLES IN RELATION TO SEASONAL CHANGE AND SNOW COVER

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Abstract. Activity and social behavior of free-ranging meadow voles (*Microtus pennsylvanicus*) were examined in summer, fall and winter using capture-recapture and radiotelemetry. The composition of our study population changed from predominantly reproductively-active (RA) voles in summer and fall to entirely nonreproductively-active (NR) voles in winter. RA males had larger activity areas than RA females. Activity areas of RA females did not overlap with those of other RA females, but activity areas of RA males overlapped extensively with those of both RA males and RA females. However, any contact among RA voles was rare, unless females were estrous. NR voles showed greater overlap of activity areas and lower levels of activity than did RA voles. Space use and activity were similar for NR males and females and their activity underwent little seasonal change. In winter, voles shared nests. There were few differences in activity between day and night or between crepuscular periods and the rest of the day. There was some synchrony of activity patterns among voles, especially within groups sharing nests in winter. Activity patterns of RA males and RA females were out of phase with each other. The general shift from primarily solitary behavior in summer to increased social tolerance and nest sharing in winter is at least partially explained by the corresponding seasonal change in sexual status of the population.

Introduction

Although microtine rodents have been studied extensively in the past few decades, it is only recently that we have begun to examine their social behavior. This interest has developed with the suggestion by Chitty (1967) and many others that social behavior may play a significant role in fluctuations in population numbers. In addition, innovation in radiotelemetric technology has made field studies of the behavior of these cryptic mammals more fruitful than it was in the past (e.g. Brooks and Banks 1971, Madison 1980).

It is well known that microtines undergo pronounced morphological, physiological and demographic changes concomitant with seasonal change (e.g. Sealander 1972; Whitney 1976; Mallory et al. 1981). However, there is a lack of information on how vole activity and social behavior is modified when the animals are confined under winter snow cover. Here, we describe how social behavior and activity patterns changed from summer to winter in a population of the meadow vole (*Microtus pennsylvanicus*). In particular, we relate these changes to changes in

reproductive status of members of the population and to the presence or absence of snow cover.

Methods

The study was conducted in old field habitat near Cambridge, Ontario (42°25'N, 80°20'W). Detailed descriptions of the study area and statistical methods may be found in Webster and Brooks (1980, 1981, in press). The main points are sketched briefly here. Trapping was conducted one or two days per week from June 1977 to April 1978. Sherman live traps were placed one per station at 5-m intervals on a 0.2-ha grid. Captured voles were classified as reproductively-active (RA) or nonreproductively-active (NR) and were ear-tagged with numbered metal tags, then released. All radiotagged voles weighed more than 25g. Movements of radiotagged voles were monitored every 20 min for one 24-h period each week from August 1977 to April 1978.

For analysis, the trap grid was divided into a 1-m^2 grid and the 1-m^2 occupied by a radiotagged vole was recorded each time the animal was located (fix). A vole's activity area was defined as the space it occupied in a 24-h period, and the area included all 1-m^2 occupied by the vole or intersected by a straight line connecting successive fixes. The data were divided into a summer (no-snow) period (August-December 1977) and a winter (snow) period (January-April 1978). To assess how neighboring voles shared space, we measured size of overlap area of neighbors, time spent in overlap area, time shared in overlap area and time spent in contact. Observed values were compared with expected values (Webster and Brooks in press).

To determine activity, we measured the number of 20-min intervals in which a vole changed location (frequency of movement), distance moved, and average step length (i.e. distance moved/frequency of movement). In addition, we measured the time voles spent at or away from their nest (winter only); timing of the onset of activity relative to day, night and crepuscular periods and relative to activity of other voles.

Results

In summer most voles were reproductively active, whereas, in winter most were not. RA males had larger activity areas than all other groups. None of these other groups differed significantly from each other (Table 1). When sexes were combined, RA voles had larger activity areas than NR voles. Size of activity areas of NR voles did not differ between summer and winter.

Table 1. Size of activity area occupied by radiotagged voles during a 24-h period. Number of observations in parentheses.

Season	Reproductive condition	Size of activity area ($m^2 \pm SD$)	
		Male	Female
Summer	RA**	102 ± 49* (17)	57 ± 22 (15)
	NR	36 ± 12 (6)	32 ± 20 (3)
Winter	NR	17 ± 12 (10)	28 ± 12 (13)

* Significantly larger than all other groups ($p < 0.05$).
** Significantly larger (sexes combined) than either NR group ($p < 0.05$).

Activity areas of RA females had almost no overlap with those of neighboring RA females, but all other neighboring pairs had much larger areas of overlap (Table 2). Sizes of the areas of overlap in these other groups were quite similar. However, a comparison between Tables 1 and 2 shows these overlap areas represent very different proportions of the total activity areas of the different groups of voles. For example, for NR voles the area of overlap represented over 50% of their total activity area, whereas this proportion was much less for RA voles. Overlap areas between RA females represented only 2% of their total areas.

Table 2. Size of the area of overlap between pairs of neighboring voles. Number of neighbor pairs in parentheses.

Season	Area of overlap ($m^2 \pm SD$)		
	RA ♂↔[a] RA ♀	RA ♀↔RA ♀	RA ♂↔RA ♂
Summer	13.9 ± 11.6 (12)	1.2 ± 1.9 (4)	13.0 ± 14.0 (5)
	NR ♂↔NR ♀	NR ♀↔NR ♀	NR ♂↔NR ♂
Winter	14.7 ± 6.5 (6)	14.2 ± 5.4 (4)	Insuff. Data

[a] Refers to the overlap between the types of voles indicated.

The proportion of time that RA voles spent in overlap areas did not differ significantly ($p > 0.05$) from expected, where the expected values were based on the ratio of overlap area to total activity area. However, NR voles spent over 80% of their time in overlap areas and this was significantly ($p < 0.02$) greater than the expected value. The amount of time pairs of neighboring voles simultaneously used the overlap area did not differ from expected ($p > 0.05$), but in winter neighbors shared overlap areas 10 times as much as in summer.

During summer, RA voles were in contact with another vole less than 1% of times they were located and there was no significant difference between observed and expected values. In winter, however, voles were in contact about 40% of the time and these observed values were significantly greater than expected ($p < 0.01$). This high amount of contact occurred because voles shared nests in winter.

We used the number of double captures as an independent measure of the amount of contact among voles, because the two animals must be close together to be captured together in a Sherman trap. A significantly greater proportion of the population ($\chi 2 = 45.16$; $p < 0.001$) was involved in double captures in winter than in summer. Almost all animals involved in double captures were NR voles.

Comparisons of level of activity between day and night showed that most groups moved more during the day, but usually these differences were not significant. Voles showed no significant difference between day and night in distance moved nor in average step length. There were also no significant differences between crepuscular activity and activity during the rest of the day in frequency of movement, distance moved, or average step length. Similarly, neither sex showed any significant difference between night and day for any of these measures of activity.

Synchrony of activity among voles occurred both in summer and winter, but was better defined in winter. This synchrony was most obvious when the percent of voles away from the nest is compared for different times of day. Individuals sharing a particular nest synchronized its use so that all tended to be in or out of the nest together. RA females appeared to time their activity out of phase with that of RA males. NR voles in summer were intermediate to RA males and females and similar to NR voles in winter.

Voles showed a strong tendency to leave the nest and become active in the 80 min prior to the onset of daylight ($\chi 2 = 5.4$, $p < 0.025$) and then to become inactive again within 80 min after daylight commenced ($\chi 2 = 8.4$, $p < 0.005$). They generally ceased activity in the 100 min centered around the onset of darkness ($\chi 2 = 6.09$, $p < 0.05$), but showed no apparent tendency to time the start of activity bouts using the onset of darkness as a cue.

When data for both sexes within seasonal groups were pooled, RA voles had a higher frequency of movement, moved a greater distance and had a greater average step length than NR voles. Winter and summer NR voles did not differ from each other in any of these measures.

During winter, the two sexes did not differ significantly in lengths of their short activity periods (Table 3). Almost equal time was spent at and away from the nest. The sexes did not differ in the amount of time they spent active during a 24-h period nor did their indices of exploration differ significantly (Table 3).

Table 3. Measures of activity taken during 24-h observation periods in winter. Number of observations in parentheses.

	NR ♂	NR ♀
Average length of short activity period (h ± SD)	3.5 ± 0.6 (7)	3.0 ± 0.5 (13)
Average length of component of short activity period away from nest (h ± SD)	1.8 ± 0.5 (7)	1.5 ± 0.4 (13)
Average length of component of short activity period at nest (h ± SD)	1.8 ± 0.5 (7)	1.5 ± 0.3 (13)
Time spent active (away from nest) (percent of day ± SD)	48 ± 12 (7)	50 ± 8 (13)
Index of exploration (m/h ± SD)	5.0 ± 2.8 (7)	7.1 ± 2.4 (13)

Discussion

These results indicate that RA male M. pennsylvanicus rarely contact other voles and are neither attracted to nor repelled by areas used by other individuals except when females are in estrus. RA males were observed to congregate around estrous females. Aggression among RA males seemed only to occur when estrous females were present, and there was no evidence that males defended territories. Similar observations have been made by Madison (1980). Christian (1971) found that wounding of RA males increased with density. This makes sense because whereas RA males are always ready to mate, at any given time there are probably few receptive females. At high densities, there are more males competing for females and therefore more aggression and wounding occurs.

In contrast to RA males, RA females occupied mutually exclusive activity areas. However, we observed no territorial defense nor any contact among these females. Our data indicated that a female's use of overlap areas was random with respect to presence or absence of neighboring females, but this may have occurred simply because the overlap area was so small that they had little chance of encountering

each other. Females used overlap areas randomly with respect to presence or absence of RA males and again contact was infrequent unless the female was in estrus.

It is uncertain why RA females occupy mutually exclusive activity areas. They may require sole access to a particular resource, such as cover, food or nest sites. However, this seems unlikely because the thick vegetation in the study area indicates that these resources were abundant, and because the females' activity areas were overlapped extensively by males that would compete for the same resources. Alternatively, space itself may be the required resource. In some microtines, RA females may kill young of other females (Mallory and Brooks 1980). Therefore, RA females may maintain exclusive space to reduce the risk to their young from such attacks.

In the present study, NR voles had a high degree of social tolerance. This result is consistent with reports that NR voles show less wounding than do RA voles (Christian 1971, Rose 1979). In the subnivean environment, NR voles were highly social. They shared nests, had large overlap areas and spent a great proportion of their time in the overlap area and in contact with neighbors. There is no evidence that voles sharing a nest derived from an extended maternal family, and interchange of individuals between nests was observed. Communal nesting in winter occurs in several species of voles, but the present study provides the first evidence for winter communal nesting in M. pennsylvanicus.

Voles huddling together have lower oxygen consumption per gram body weight and have lower food consumption than voles that are not huddling (Gebczyńska and Gebczyński 1971). Shared nest use, therefore, may conserve energy by providing voles with a more favorable thermal environment than they could maintain alone. This effect would be enhanced by the synchrony of nest use we observed in winter voles.

Structuring of the social system in winter to optimize energy conservation is probably particularly important in vole species such as M. pennsylvanicus, which tend to nest on the ground surface. The winter nests had poor insulative properties, and lack of a well-insulated winter refuge would increase the value of social behavior that enhanced energy conservation.

In our study, the voles were active at all times of day in both summer and winter and did not appear to select any portion of the day for activity. Field studies in the literature are contradictory, some suggesting that meadow voles are most active in the day; others suggesting they are most active at night. It is likely voles alter their activity pattern according to their surroundings. When there is heavy vegetative or snow cover they are equally active at all times of day.

Nonreproductive voles had a similar pattern of activity in summer and winter, and there were no apparent differences between the sexes. However, patterns of activity of RA males and RA females appeared to be out of phase. This may allow females to be at their nests to defend their young when males are most active (Mallory and Brooks 1978).

Summary: This study indicates that social structure and activity patterns of individual meadow voles are labile and are altered by changes in reproductive status. These changes are influenced by seasonal, and other environmental changes. Presumably, such behavioral variations are adaptive responses of individuals to ambient conditions and do not usually occur as a result of selection for different genotypes as suggested by many authors recently. Hence, the characteristic features of the vole population change with regular environmental shifts because of the flexibility of the individual members of the population. In summer, if RA voles predominate, their behavior patterns predominate. At high densities, however, mating competition (for example) may inhibit sexual maturation of young males and social behavior of NR voles may become common in the population. Spacing behavior in RA females may inhibit sexual maturation in females. Hopefully, further investigation of social systems will help us derive better hypotheses regarding the interaction between behavior and population dynamics. This information will be useful as well to those who wish to apply various control regimes to vole populations.

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