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MOVEMENT TYPES AND WEATHER CORRELATES IN FREE-RANGING MEADOW VOLES

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ABSTRACT: Meadow voles (Microtus pennsylvanicus) were radiotracked in their natural environment from June through August 1974, 1975 and 1978. Four different types of movement were observed: residency, shifting, wandering and dispersal. Next to the residency pattern, wandering was the most common form of movement and probably was important during breeding activities. Dispersal was a rare event and is probably confused with wandering in the existing literature.

A total of 17 weather variables were analyzed for correlations with vole movement. Male voles showed a distinct tendency to move more widely during periods of dry weather. The latter was attributed to the negative effects of dry weather on the ability of male voles to detect the odors of male competitors. Thus male voles were less inhibited in their search for receptive females during dry weather. Female voles showed no major change in movement with different weather conditions.

INTRODUCTION

Considerable insight about population control and regulation in rodents can be obtained by close examination of the movements and behavior of individual rodents in the field, especially the movements that occur in response to changes in the environment. The usefulness of this direct information satisfies both applied and basic research needs. An ongoing series of studies on meadow voles has attempted to quantify and account for different patterns of movement (Madison, 1978a, b, 1979, 1980a,b); but to date, the types of movement and the effect of weather variables on movement have not been described. These topics are the subject of this paper.

METHODS

Details of the study populations and radiotelemetry methods can be obtained elsewhere (Madison, 1979). Briefly, miniature radio-transmitter collars with separate frequencies were attached to free-ranging meadow voles weighing 20 g or more. Three different populations were studied from June through August in 1974, 1975 and 1978. Positions were obtained on the location of each vole at regular intervals, usually once/hour for 24 hours, once or twice/week. Up to 20 voles were monitored concurrently, and several were tracked regularly for 3 months.

The daily range of each vole was compiled from the 24 positions obtained for each vole over a 24-hour period. Each range was represented by the area enclosed by a line connecting the outermost positions for the 24-hour period. Changes in the location or size, or both, of the daily range from one week to the next were used to describe the

types of movements observed and to measure correlations between movement and weather conditions.

The analysis of weather variables was performed using the field data from 1978. The field site this year was within 5 miles of the Broome Co. Airport, which recorded a wide variety of weather information. A high degree of correspondence between the airport data and the limited information collected at the field site (e.g., total precipitation, continuous temperature, relative humidity and barometric pressure data) allowed the exclusive use of the airport data for the analyses.

Seventeen weather variables were quantified along with movement for each vole on each day of radiotracking. The area of the daily range was used as an indicator of movement. Spearman rank correlation coefficients (Siegel, 1956) were calculated between movement and each weather variable. The 17 weather variables were as follows:

T_1 Mean temperature on tracking day

T_2 Mean temperature change from previous day

T_3 Mean temperature change from mean of previous three days

P_1 No. of days since accumulation of any rain

P_2 No. of days since accumulation of 0.2 inches of rain

P_3 No. of days since accumulation of 0.5 inches of rain

RH_1 Mean relative humidity on tracking day

RH_2 Mean relative humidity change from previous day

RH_3 Mean relative humidity change from mean of previous three days

W_1 Mean wind speed on tracking day

W_2 Mean wind speed change from previous day

W_3 Mean wind speed change from mean of previous three days

S_1 Percent available sunshine on tracking day

S_2 Change in percent available sunshine from previous day

S_3 Change in percent available sunshine from mean of previous three days

BP Mean barometric pressure on tracking day

DL Daylength on tracking day

RESULTS

Types of Movement. Four basic types of movement were observed. These vary along a continuum from strong philopatry and exclusively localized movements within the daily range to sudden and permanent

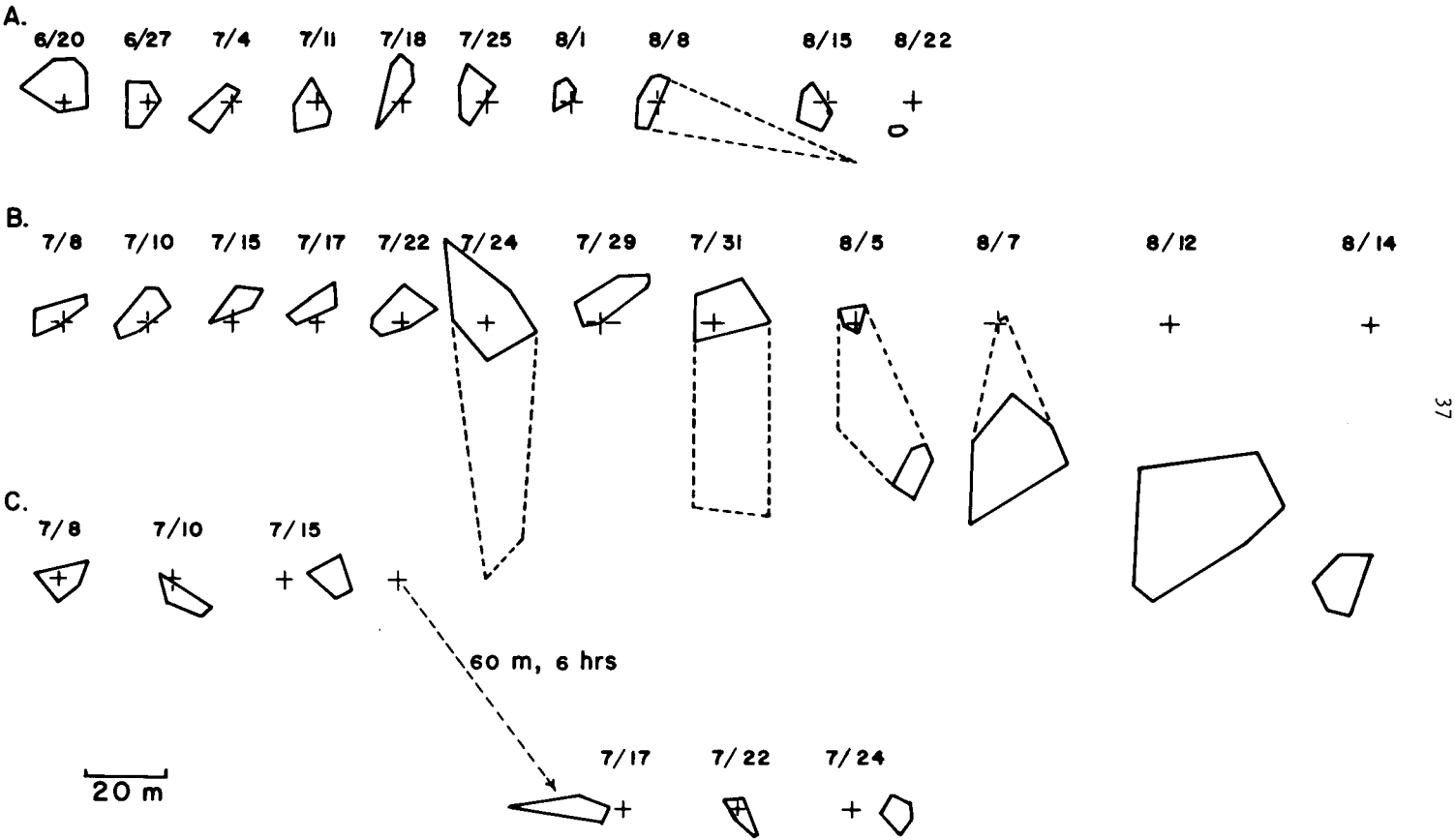
changes in the daily range. Several different types of movement can be observed in each vole, thus the categories are not mutually exclusive.

Residency. This pattern of movement is one where the vole remains in the same area (has the same general center of activity) from one week to the next. The successive daily ranges usually overlap, and the center of activity shows little net change in location throughout the tracking period. Movements within the daily range are typically small foraging (territory maintenance?) loops of about 2-4 hours followed by short bouts of sleep. Whereas sleeping during the summer day occurs almost anywhere within the daily range (e.g., in a side tunnel of grass runway), sleeping at night is usually within simple grass nests. Only lactating females sleep at elaborate nests, and these nests are utilized both day and night. This pattern of movement in voles tracked for 3 weeks or more was shown by 69% of the males (20 of 29 voles) and 89% of the females (24 of 27 voles) (Table 1). Fig. 1A shows one female exhibiting residency and one case of wandering.

TABLE 1. Frequency of movement types observed among moderately dense populations (varied from 45 to 110 voles per acre) of subadult and adult meadow voles from June through August. The residency and shifting categories only include voles tracked for three or more weeks.

	No. voles	No. 24-h periods	Residency	Shifting	Wandering	Dispersal
1974						
Males	8	37	1	2	3	1
Females	8	39	3	0	2	0
1975						
Males	16	77	8	3	6	1
Females	15	72	10	2	4	0
1978						
Males	18	95	11	4	8	0
Females	20	87	11	1	4	1
Total						
Males	42	209	20	9	17	2
Females	43	198	24	3	10	1

Fig. 1. Types of movement by meadow voles during radiotracking. (A) adult female in 1978 at Binghamton, N.Y. (23 g on 6/20, 45 g on 8/22) showing the residency pattern, except on 8/8 when the female wandered. On 8/8 the female was 7 days into lactation and 7 days into a postpartum pregnancy. She gave birth to litters on 8/1 and 8/21. (B) adult male in 1975 at Front Royal, Virginia (32 g on 7/8, 48 g on 8/14), showing the shifting pattern (7/31-8/14) and wandering (7/24). (C) adult male in 1975 at Front Royal, Va. (33 g on 7/8, 37 g on 7/24) showing dispersal that occurred between 0400 h and 1000 h on 7/16. "+" signs indicate reference points. (Figure on next page.)


A.
6/20
6/27
7/4
7/11
7/18
7/25
8/1
8/8
8/15
8/22
B.
7/8
7/10
7/15
7/17
7/22
7/24
7/29
7/31
8/5
8/7
8/12
8/14
C.
7/8
7/10
7/15
60 m, 6 hrs
7/17
7/22
7/24
20 m

Shifting. This pattern consists of the normal daily movements described above, except that the center of activity gradually shifts in one general direction to a new location. Movements into new regions alternate with movements back into recently occupied areas, but after about 3 weeks the new daily range is entirely non-overlapping with the former daily range. The shifting can result in oscillatory movements between widely separate areas, or be the result of movements into the most adjacent, previously unoccupied area. Shifting movement in voles tracked for 3 weeks or more was shown by 31% of the males (9 of 29 voles) and 11% of the females (3 of 27 voles) (Table 1). Fig. 1B shows a male exhibiting shifting movement and one case of wandering.

Wandering. Wandering is a sudden, temporary movement by a vole noticeably outside of the normal daily range. It is defined as any movement separated from the periphery of the daily range by at least one daily range diameter and lasting for no more than 12 hours. Typical trips are about 2 hours duration, but some lasted up to 9 hours. While the same general region may be visited again after a few weeks, the time, distance and duration of wandering are unpredictable. The departure and return of the vole is very rapid, and usually escapes radiomonitoring. Among all years, 23% of 43 female voles wandered during 198 vole-days, while 40% of 42 males wandered during 209 vole-days (Table 1). Fig. 1A,B show two cases of wandering, one by a female on 8/8 and one by a male on 7/24.

Dispersal. Dispersal is very similar to wandering, except that the vole does not return to the daily range. Usually a residency pattern appears at the new location. One of the 43 female voles tracked was observed to disperse, while two of the 42 male voles dispersed (Table 1). Fig. 1C shows one of the two cases of male dispersal where the male moved to a new daily range 60 m away in less than 6 hours. The male not represented moved 80 m away in less than 3 hours; the one female moved 61 m away in less than 3 hours.

Weather Correlates of Movement. A total of 182 vole-days and the associated weather conditions were used in the analysis of weather factors in 1978. For males, a lack of precipitation emerged as an important weather variable correlated with increased movement (Table 2). The positive correlations with temperature and barometric pressure were associated with dry weather, as was the negative correlation with day-length. When daylength was decreasing during July and August, conditions were generally dryer. The nearly significant correlations with relative humidity, wind and % available sunshine also fit the dry day pattern of increased movement for males. For females, a positive correlation occurred between temperature and movement, but no other correlations were statistically significant.

DISCUSSION

Essentially no previous study of Microtus has attempted to define the types of movement observed in free-ranging individuals. The residency pattern in M. pennsylvanicus is stereotyped and consistent with the short term activity patterns observed for the species (Graham, 1968; Madison, 1980b; Webster, 1979).

The shifting pattern where a vole gradually changes its daily range reflects the movement of some voles into low-lying, moist areas during

Table 2. Spearman rank correlation coefficients (r_s) between movement, as measured by area, and selected weather variables (see text for definitions).

Weather	Male		Female	
factor	r_s	p	r_s	p
T_1	0.22	0.033*	0.26	0.015*
T_2	0.16	0.117	0.11	0.301
T_3	0.17	0.098	0.12	0.283
P_1	0.28	0.007**	0.02	0.848
P_2	0.33	0.001***	0.02	0.820
P_3	0.27	0.007**	0.08	0.480
RH_1	-0.18	0.078	-0.07	0.521
RH_2	0.01	0.922	-0.19	0.070
RH_3	-0.11	0.285	-0.18	0.091
W_1	-0.17	0.090	0.03	0.812
W_2	-0.03	0.782	0.18	0.091
W_3	-0.08	0.422	0.12	0.252
S_1	0.19	0.064	-0.09	0.410
S_2	-0.01	0.937	0.17	0.117
S_3	0.19	0.069	0.08	0.472
BP	0.27	0.009**	0.13	0.232
DL	-0.28	0.007**	-0.08	0.442

* = significant at 0.05 probability level; ** = 0.01 significance level; *** = 0.001 significance level

dry periods in the summer. Other voles have been observed to shift their ranges away from regions of socially contested space. Implied in these movements is that there exists unoccupied space in or near the border of the shifting vole into which the vole can move.

Wandering movements of a few hours and extending up to four daily range diameters away appear to be significant among adults during the breeding season, and are likely associated with reproductive events. For example, males often temporarily move out of their daily ranges and enter the ranges of neighboring, estrous females (Madison, 1980). Wandering could reflect the male's effort to mate with receptive female neighbors especially if the latter are prone to move widely when they near parturition and estrus (females have a postpartum estrus and may actually mate during parturition). Such wide scale movement (wandering) by the females around parturition and estrus has been reported, and may be necessary to promote outbreeding or reduce the chance of male cannibalism of the newborn young (Madison, 1978a).

Dispersal under the conditions of this study was surprisingly rare. The contemporary acceptance of the importance of dispersal in rodent population biology (e.g., Lidicker 1975; Tamarin, 1977) may be overemphasized, and estimates of dispersal may be inflated artificially by the inclusion of many cases of wandering into the dispersal estimate. The sudden, permanent departure of a vole from its daily range is a bold action, one where the likelihood of reproductive success at home must be very low, or one where the rare incident of reproductive success at large must result in considerable reproductive gain (such as founding a new population), or both. The increased predation on dispersing voles is commonly recognized, and predation on voles intensifies in suboptimum areas (Madison, 1979). It is of course possible that dispersal is more common in voles less than 20 g, or more frequent among voles from September through May, but these possibilities do not alter the unexpected finding of so few dispersing voles among all the subadult and adult members of the study populations during the main breeding period from June through August. The reason for so little dispersal, if it is to be expected under the moderate density conditions in this study, is not known.

Little information exists on how weather factors affect movement in Microtus, especially concerning the day-to-day variations in movement. The available data indicate that activity tends to increase during wet weather (Bider, 1968) or that voles prefer more moist habitat (Getz, 1961). However, Pearson (1960) found that activity was highest at times of lowest vapor pressure, hence during dry periods. The latter observation is consistent with the findings in the present study, at least for males. Some of the activity observed previously during wet weather could be associated with nest abandonment when the nest becomes wet (Stark, 1963). It probably is safe to say that Microtus requires high degrees of moisture in its diet (Pearson, 1960), and therefore thrives in moist habitats, assuming other factors as food and cover are adequate. However, dry conditions appear to be a definite stimulus for movement among males, and this weather variable should be studied further.

An explanation for increased movement during dry weather must consider the sex-dependent nature of the effect. Thus, shifting or wandering into moist areas during dry weather is not a very satisfactory explanation. One possible explanation for the high correlation between

male movement and dry weather is suggested by Madison (1980). Movements of voles are heavily influenced by odors produced by conspecifics. The detection of these odors in the environment is directly proportional to the ambient relative humidity (Regnier & Goodwin 1977). If males are normally inhibited from wide-ranging movement in optimum habitat by the presence of odors of other males, then a reduction in the apparent chemical presence of males during dry weather would release males from their social inhibition and allow them to search more widely for receptive females. Not only might the apparent presence of competing males be decreased, but the likelihood of a trespassing male being detected by a resident male would be reduced. The reduced chance of detection during dry weather would make non-rain periods the optimum time for wide range reconnaissance runs by sexually active males. That normal inhibition of movement probably occurs, and that detection by other males is potentially injurious, is supported by the high frequency of wounding among sexually mature male voles (Christian, 1971; Rose, 1979). There is no obvious advantage for females to invade other female territories, so increased movement during dry weather is not expected for females (Madison, 1980a).

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