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MOVEMENTS OF MEADOW VOLES IN WINTER: IMPLICATIONS FOR VOLE MANAGEMENT IN ORCHARD HABITAT

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Abstract: The movements of meadow voles in a field population were studied using radiotelemetry during fall and winter. The voles changed from a dispersed, solitary dispersion pattern during early autumn to social clusters with communal nesting during winter. This shift occurred as the daily median temperature approached freezing. Movement was inhibited and localized during winter, except under snow when the voles exhibited a freedom of movement not experienced during other times of the year. Overwinter management of meadow voles in orchard habitats is discussed in view of these findings.

INTRODUCTION

Numerous papers have reported details on space use, movements, and survivorship of meadow voles in natural and orchard habitats during spring, summer and autumn (e.g. Madison 1978a,b, 1979, 1980a,b, 1981a,b; Madison et al. 1981; Madison et al. 1982; Pagano & Madison 1981, 1982; Webster & Brooks 1981a,b), but only a few studies report data of this kind during winter (Madison 1983; Pagano & Madison, 1981; Webster & Brooks 1981b). Since meadow voles are active throughout winter, and since severe gnaw damage to apple trees can occur during winter, an understanding of the movements and general winter biology of meadow voles would seem to be essential for a total cultural management program in orchard habitat. This paper reports the results of a detailed radiotelemetry study of meadow voles through autumn and winter, and attempts to apply the findings toward improving vole management procedures in commercial apple orchards.

METHODS

Meadow voles (*Microtus pennsylvanicus*) were live-trapped from Green Brothers Apple Orchard near Binghamton, New York. Between 29 July and 4 August 1981, 11 voles (5 females, 6 males) over 20 g were obtained from different traps and transported to a trapped-out field enclosure at a nearby study site in Apalachin, New York.

The enclosure consisted of corrugated fiberglass paneling surrounding a 28 x 30 m section of old field habitat (Fig. 1). The walls extended 50 cm above and 20 cm below ground level. The base of the wall below ground level was bordered with large sized gravel to prevent burrowing under the panels. The interior of the enclosure contained a 6 x 5 grid of Longworth live traps, two per station, with 5.5 m between stations. With the appearance of litters in October,

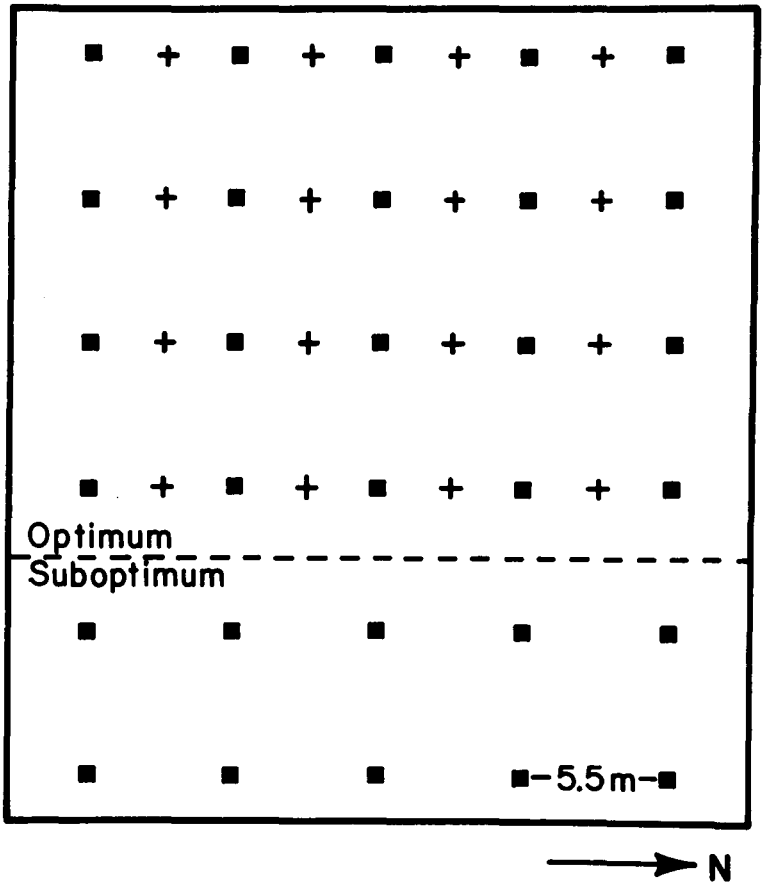

Fig. 1. Enclosure used for overwinter studies of meadow voles in Apalachin, New York. The locations of the permanent live-trapping stations (■) and the supplemental live traps (+) are indicated. Two live traps were at each permanent station; one trap was set at each supplemental station. The dashed line separates the mown (suboptimum) and unmown (optimum) areas within the enclosure.

16 supplemental traps were placed within the optimum habitat (see below), one trap between each trap station within each row, thus creating 2.75 m trap spacing within rows. All traps were placed under trap shelters designed after Iverson & Turner (1969). A 28 x 10 m section of the enclosure had been mown weekly with a power hand mower, and the clippings removed, during the summer to establish a suboptimum habitat or "dispersal sink" (Lidicker 1975). The remaining 28 x 20 m section was not mown and served as the optimum habitat. The 11 meadow voles added to the enclosure created a beginning density of 131 voles/ha. These voles and their descendents constituted the study population.

The voles within the enclosures were censused monthly: 4 Aug, 27 Sept, 17 Oct, 13 Nov, 5 Dec, 20 Jan. Each census followed 3 to 5 days of prebaiting with a small amount of sunflower seeds and an apple slice per trap. This procedure resulted in the capture of most voles known by telemetry and previous capture to be within the enclosure. During each census, the voles were marked or identified by toe-clipping, sexed, checked for reproductive condition (testes scrotal or non-scrotal, vagina perforate or not, nipple condition), and weighed.

Radiotelemetry was used to monitor the movements and spacing of voles at regular intervals. This monitoring also provided additional information on vole presence and absence between the trap censuses. Usually all the voles over 20 g were given radiotransmitter implants. Voles to be given radiotransmitters were retained during a census, taken to a laboratory facility at the field site, anesthetized with ether, given (I.P.) a miniature SM-1 radiotransmitter/Hg-13 battery unit encapsulated with Elvax paraffin (Mini-Mitter Co., Indianapolis, IN), and then released within 8 h of capture. Formal radiotracking occurred at least 5 days after surgery. The radiotelemetry equipment (AVM Instrument Co., Dublin, CA) and methodology were similar to those reported earlier (Madison 1978a, 1980a). Using a LA-12 radioreceiver and hand-held Yagi antenna, we obtained positions each hour for each vole from 0700 to 1800 h, a time period giving a reasonable estimate of movement and home range size for comparative purposes (Madison 1984). Regular paths were used in the enclosure for obtaining positions. These paths did not create barriers to movement, since voles were frequently observed running across these paths. After snow cover, tunnel openings on adjacent sides of these paths and fecal pellets on the snow joining these openings were commonly observed.

The home range of each vole was considered to consist of a convex polygon formed by a line connecting the peripheral positions of the 10 recorded during each tracking session (Madison 1984). The distance of movement of the geometric centers of each home range (Hayne 1949) between successive radiotracking sessions was also calculated. Voles were considered to be nesting together when their radiotelemetry signals emanated from the same location during the same hourly check. The nesting "cluster" consists of the voles actually cohabiting a nest during an hourly check. The nesting "constellation" consists of all those voles that were found in the same general area and used the same nest(s).

The occurrence and identity of predators was determined by the presence of fox, weasel or cat tracks in the snow next to discarded transmitters, by the location of transmitter packages (top of snow or ground, in weasel nests), by blood stains on the snow surface, and by tooth marks in the paraffin of the discarded transmitters.

Temperature and snow depths were measured at the study site on numerous occasions. Since these values were very similar to those recorded at the Broome County airport 21 km away, the values recorded at the airport were used in the analysis of daily temperatures.

RESULTS

General. A total of 32 voles were radiotracked during 6 tracking sessions from 4 October 1981 to 2 February 1982, with an average of 17.3 voles tracked per session (Fig. 2). Forty-two voles were known to have occupied the enclosure at some point during this period. The 10 voles not radiotracked were offspring who did not survive to a large enough size (20 g) for radiotracking (8) or were adults who did not survive to the onset of the tracking sessions (2). The study was terminated on 12 Feb following the abrupt loss to predators of 16 of the 17 voles present at that time. The initial density of 11 voles in the enclosure increased to 38 by late October (452/h), but declined to 17 by early February (202/h) (Fig. 3a). The proportion of the trappable offspring that survived to early February was greater for males (50%) than for females (25%). There was a significant imbalance in the number of male to female offspring (22:9) that reached the trappable population ($\chi^2 = 5.45$, $p < 0.05$).

Growth and Reproduction. For the 7 adults present at each census through 20 Jan, the mean weight began at 32 g on 4 Aug, increased to 39 g on 27 Sept, then decreased to 34 g by 20 Jan (Fig. 3b). Among the juveniles, both the September and October cohorts grew to a mean of 31 g by 20 Jan (Fig. 3b).

Reproductive condition gradually regressed between 27 Sept and 13 Nov. On 27 Sept, the 4 males that survived to 13 Nov were scrotal. Three were scrotal in mid-October, while only one was scrotal in mid-November (male 4, Fig. 4). Among the 5 females, two had litters in September and 4 had litters in late October (Fig. 2). No evidence of pregnancy was observed after October. Since nesting clusters became apparent in October, social nesting and breeding activity overlapped in time.

Space Use and Movement. Home range size decreased between 4 and 25 Oct, with the 8 voles present both days showing a significant decrease ($\chi^2 = 4.5$, $p < 0.05$) (Fig. 3c). The decrease for the adults was from 52.1 m^2 to 21.9 m^2. The values after 25 Oct increased to values in late January and early February similar to those in early October.

Home range overlap differed only slightly between the adult males and females (Fig. 4). The 100% polygons of the adult females

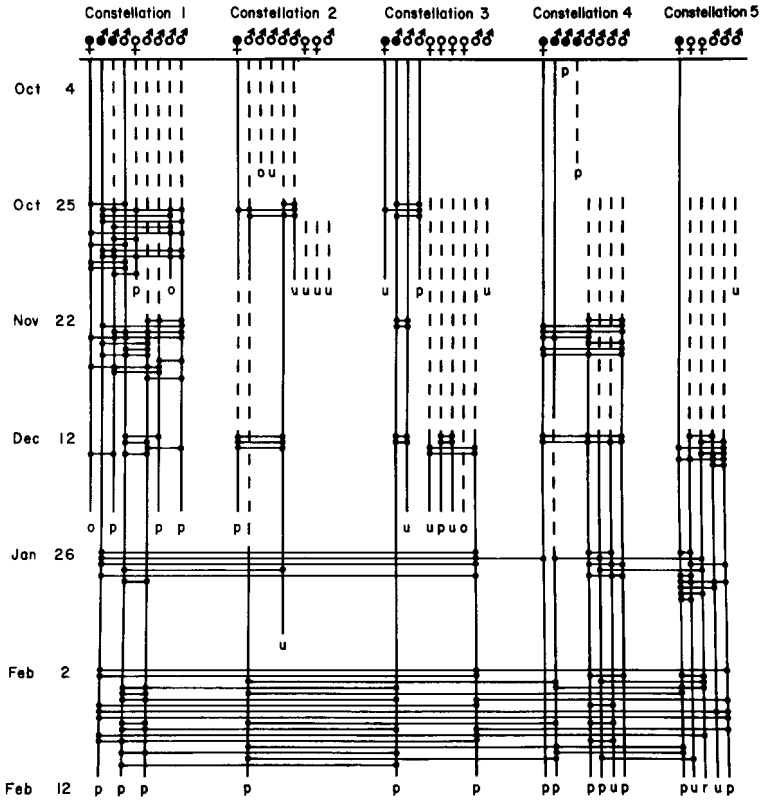

Fig. 2. Time record of births, deaths, radiomonitoring, and cluster and constellation associations of all meadow voles in the enclosure on the dates indicated. The original voles introduced are indicated by darkened sex symbols. All other voles are descendants. Each horizontal line shows one case of clustering by 2 or more voles; the dots show the participants. Dashed vertical lines show voles present but not radiotracked; solid vertical lines show radiotracked voles. The fate of each vole is indicated; o, over-etherized during surgery; p, predation; u, unknown fate due to vole disappearing from the enclosure, probably the result of predation; r, recovered at the end of the study.

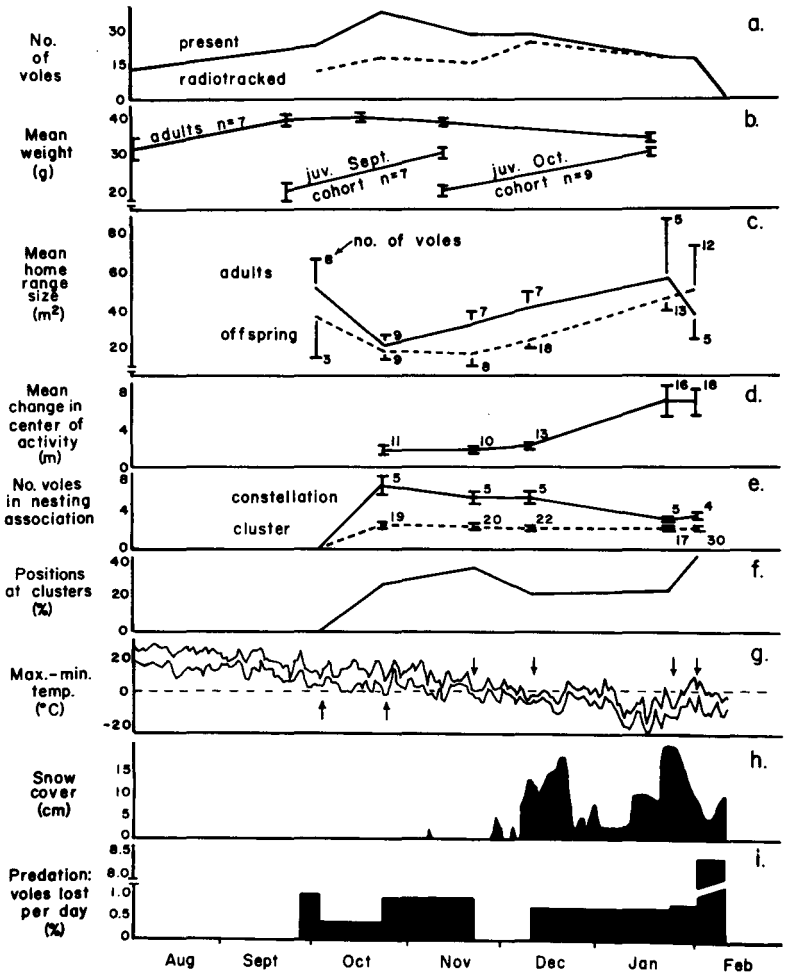

Fig. 3. Record of vole density, weight change, home range size, space use, weather conditions and predation in the enclosure during the fall and winter of 1981/1982 in Apalachin, New York. The arrows in the temperature graph (g) show the dates of radiotracking. The vertical brackets show ± one standard error of the mean.

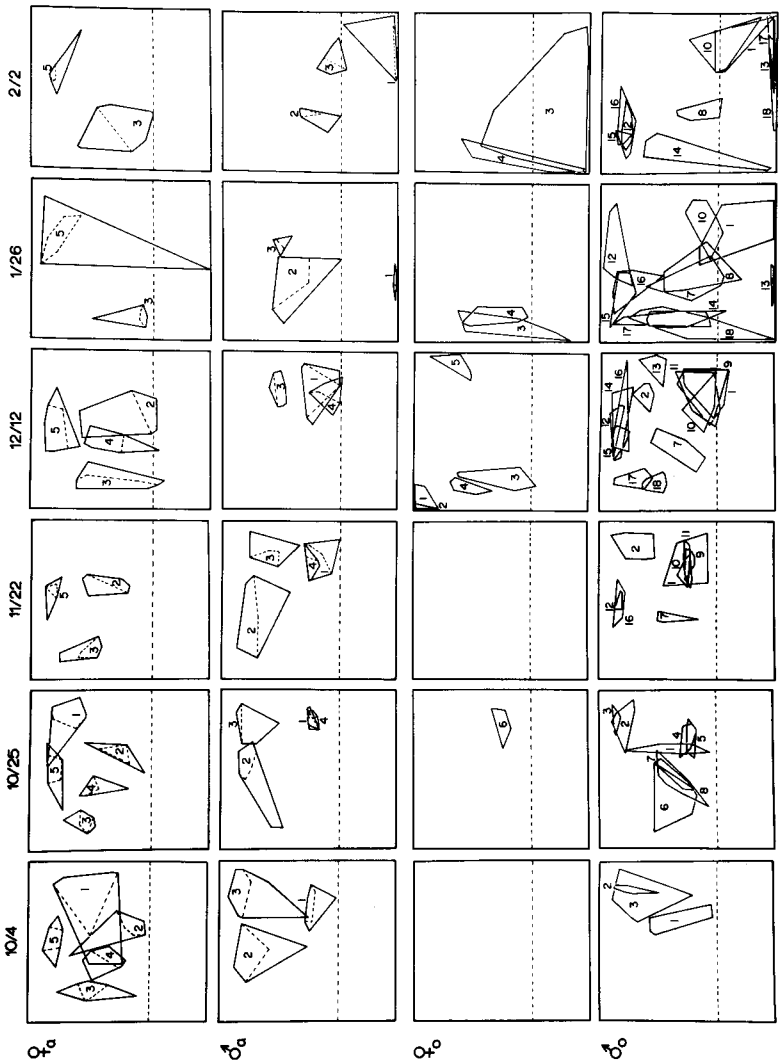

Fig. 4. Ten-hour home ranges (solid line polygons) of adult female (♀a) and male (♂a) meadow voles and their female (♀o) and male (♂o) offspring during six radiotelemetry sessions in the enclosure in Apalachin, New York. The home ranges belonging to the different sex-age classes are plotted separately for easier interpretation. The different voles within each sex/age class are indicated by different numbers. The dashed lines within each adult home range indicate 80% polygons (the two most extreme positions from the center of activity are omitted, and a new 8-hour home range drawn, in order to show areas of more intense utilization).

showed occasional overlap, but the 80% polygons showed no overlap. Among the adult males, two home ranges overlapped and two did not. When all the adults and offspring are considered, the overlap between the males becomes much more extensive than that between females (Fig. 4).

Shifts in the centers of activity between tracking sessions were larger when accompanied by both snow cover and predation (26 Jan, 2 Feb) than when accompanied by only snow cover (12 Dec) or predation (25 Oct, 22 Nov) (Figs. 3d,h,i; 5). The shifts measured on 26 Jan and 2 Feb were significantly larger than those on 25 Oct, 22 Nov and 12 Dec ($t_s = 13.2$, $p < 0.001$) (Figs. 4, 5). Supporting this shift in movement is a significant increase in the number of home ranges that entered the suboptimum area after December ($\chi^2 = 4.4$, $p < 0.05$). In addition, 12 home areas in January and February appeared to be disfigured by the enclosure wall, whereas before January only the home areas of two female offspring (Nos. 1, 2; Fig. 4), who had left their maternal constellation (Constellation 3, Figs. 2, 6), showed this distortion.

Nesting Associations. Nest use during the hourly telemetry checks was solitary on 4 Oct, but shifted by 25 Oct to nesting clusters, which averaged 2.4 voles per cluster ($\chi^2 = 2.42 \pm 0.73$, N = 108) (Figs. 2, 3e). No significant difference in cluster size occurred between any of the tracking sessions. Sixty-nine percent of all clusters involved just two voles. Three voles slept together in 22% of the nesting clusters. The largest cluster of 5 voles was recorded on just 3 of the 108 occasions of clustering. The analysis of gender preference in clusters showed fewer female-female and more male-male associations than would be expected by random pairing within the constellations ($\chi^2 = 8.5$, $p < 0.02$).

Nesting constellations averaged 7.0 voles on 25 Oct, but this decreased significantly to 3.2 voles by 26 Jan ($U = 0.5$, $p < 0.01$, Mann-Whitney U-test) (Fig. 3e). Each of the 5 nesting constellations that persisted through 12 Dec was made up of one adult female, her offspring, and, in 3 of 5 cases, one or more adult males (Figs. 2, 6). The constellations changed to mixed lineage membership between 12 Dec and 26 Jan, during which time predators had reduced the population by 30%. The number of constellations was reduced from 5 to 4 by early February.

Weather Factors. Since cluster nesting would be predicted to be more frequent with colder environmental temperatures, the occurrence and frequency of clustering was compared to environmental temperature and snow cover, the latter having a moderating effect on temperature at ground level (Pruitt 1957; Fuller et al. 1969). Clustering first occurred between 4 Oct and 25 Oct, a 21-day period during which the daily minimum temperature fell below 0°C for the first time (Fig. 3f, g). During radiotracking on 25 Oct, the minimum was the lowest for the period (-3°C; -10°C with wind chill adjustment). By 22 Nov, the minimum had dropped below 0°C on several occasions; and during radiotracking on 22 Nov, the mean was -4°C (-14°C with wind chill adjustment). Since there was no snow cover and an average wind of 4.5 m/sec

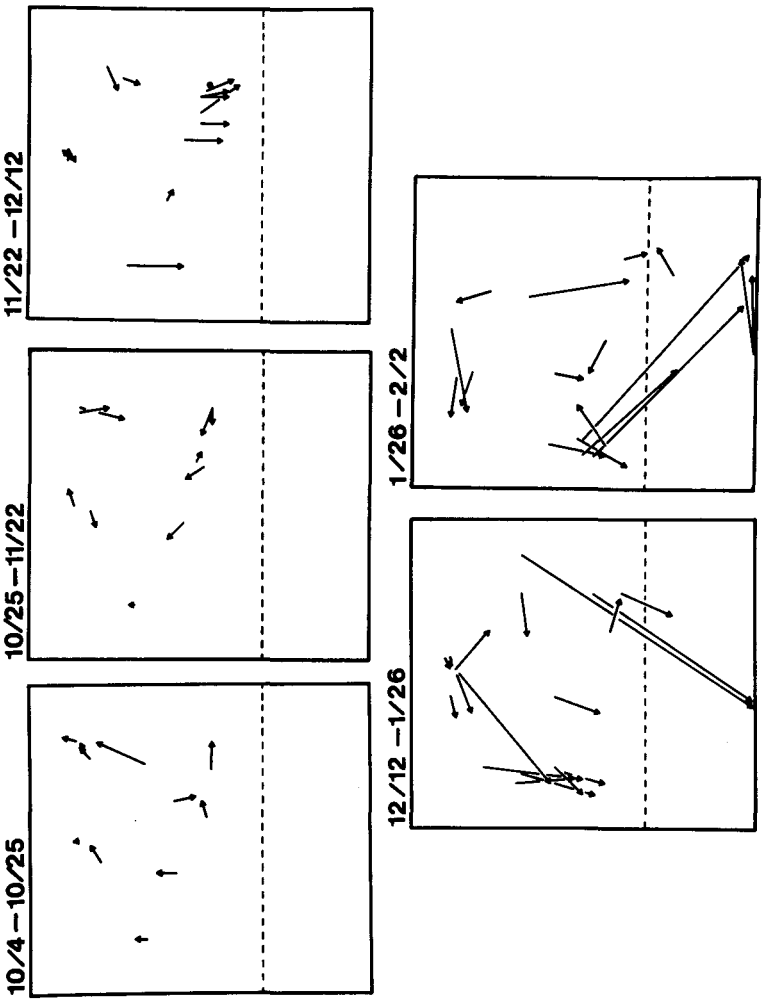

Fig. 5. The changes in center of activity (geometric centers of mass) for all voles radiotracked between the dates indicated for the five time intervals during the fall and winter in Apalachin, New York. The arrows show the distance and direction of movement.

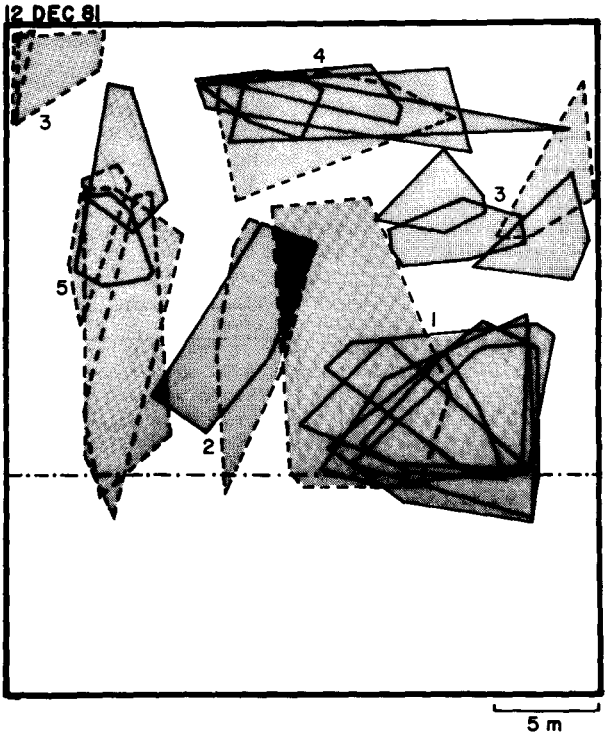

Fig. 6. The 5 constellations of meadow voles on 12 December 1981 in Apalachin, New York. The male (——) and female (---) home range perimeters are shown, and each constellation is shaded and numbered. The dark shading shows areas of constellation overlap.

on 25 Oct and 22 Nov, the perceived ground temperature was at least as cold as that measured. For both of these days, the percent of the vole positions involved in clusters was higher than the values during tracking on 12 Dec and 26 Jan, when the snow cover was 12 cm and 20 cm, and the minimums were -7°C and -15°C, respectively (Fig. 3f,g). The subnivean temperatures for 12 Dec and 26 Jan varied from 0°C to -2°C. The greatest percent clustering was on 2 Feb, when the minimum temperature was -12°C (-21°C with wind chill adjustment). The snow cover on this day varied from 0 to 10 cm, 40% of the suboptimum area being blown free of snow. Eight of the 17 voles had home ranges in areas with 0 to 5 cm snow, and another 6 voles had ranges bordering this area of scant snow cover. Thus, the data show that occurrence of social nesting is inversely related with ground level temperature.

Predation. Predation was probably responsible for the death of 35 of the 42 voles living in the enclosure between 4 Aug and 12 Feb, but only 22 deaths could be directly attributed to predators. The period of snow cover gave a much better record of predator activity in the enclosure than did the snow-free period. The most common predator was an ermine (*Mustela erminea*), who was directly responsible for at least 8 of the 13 deaths between 2 and 12 Feb. During this period, the ermine utilized an existing vole nest, lining it with the fur of its prey. Six transmitters were retrieved from this nest, and two others were retrieved from dead but intact voles, one in a snow tunnel and one in a nest. The latter two voles died from skull fractures (revealed by autopsy) inflicted by ermine. The next most active predator was a small canid, probably a fox. Six vole deaths were directly attributed to fox because of vole disappearance and the occurrence in the same area of blood and urine stains on top of the snow next to muzzle depressions and canid tracks. Based on the 35 probable cases of predation, the most intense period of predation occurred between 2 and 12 Feb (Fig. 3i).

DISCUSSION

General Findings. The breeding activity observed through October agrees with other findings for meadow voles (Christian 1980). Thus, the population high during late October and the decline after October following the curtailment of breeding was expected. The reduced home range size late in October was likely the result of the nursing activity of four females (Madison 1978a), as well as the high density at that time. The increased home range size after October probably reflects the cessation of lactation by the females, declining density, and the shelter for less inhibited movement provided by the more or less continuous snow cover beginning in late November (see later discussion).

Extended Maternal Families and Male Recruitment. The observed occurrence of social nesting during fall and winter corroborates, and is validated by, similar findings in unenclosed populations of meadow voles (Webster and Brooks 1981b), *M. xanthognathus* (Wolff and Lidicker 1981), *M. montanus* (Jannett 1978), and *M. arvalis* (Chelkowska 1978; Frank 1957). The existence of these units as minimally overlapping, extended maternal families during late fall has not been reported

previously for meadow voles, although Frank (1957) and Jannett (1978) report the occurrence of extended maternal families in other microtines. While Jannett (1978) hypothesizes that these family groupings represent a reproductive strategy on the part of the breeding female during times of high population density, the social groupings observed could just as easily represent a density independent, adaptive response to colder environmental temperatures during the fall. Why Webster and Brooks (1981b) did not observe extended families in meadow voles is probably the result of insufficient sample size during the fall, which resulted, in part, from social grooming damage to transmitter collars with the advent of social nesting. Adjustments in collar design allowed ample data by January, when mixed lineage groups were observed.

The normal pattern of extended family formation during the fall is by the retention of offspring within the breeding territory of the female (Frank 1957; Jannett 1978). Two noticeable departures from this pattern occurred in the present study. One was that the nesting groups formed by the incorporation of one or more adult males into the female territory, as well as by the recruitment of offspring. Another was that male offspring were selectively recruited into the female's territory.

Several findings support the pattern of differential tolerance and recruitment of males. First, the imbalanced sex ratio of offspring indicates that many female young do not survive to the trappable population during the fall. Second, the survival of censused daughters to 26 Jan (25%) was less than that for sons (50%). Third, the one case of a breakup of a family constellation before 26 Jan (Constellation 3, Fig. 6) involved two daughters who moved across the enclosure to the opposite wall, where they lived until their disappearance a week later. Fourth, only one of the 3 adult females who had daughters actually nested with them, whereas all 5 females nested with their sons (Fig. 2). Finally, the only female offspring (Nos. 1, 2; Fig. 4) surviving to February were those of the only adult female observed to nest with her daughters.

The finding of lower survivorship and recruitment among female offspring during fall and winter occurs occasionally (Frank 1957; Jannett 1978), but explanations are few. We hypothesize that in meadow voles female intolerance of daughters during the fall is not too surprising, since females normally exclude other females, but not males, from the breeding territory. All five females in this study were reproductively active during the fall. As breeding activity begins to wane during the fall, and as group nesting becomes progressively more important for survival, increased female tolerance would be expected to occur first toward those voles in the population against whom social intolerance was least apparent at the peak of the breeding season. Familiar males, and especially sons, would fall into this category. The finding of more frequent multiple trap captures involving adult females with male offspring versus adult females with female offspring in a fall population of meadow voles supports this prediction (Getz 1972). Why tolerance to the point of nest sharing occurs before reproduction is completely terminated, at least for some females (Constellations 2 & 3, Fig. 2), is probably an out-

come of the benefits of huddling for the development and survival of late season young (see Madison 1983; Hill 1976).

Mixed Lineage Groups. The loose, mixed lineage constellations formed after 12 Dec are similar to those reported by Webster and Brooks (1981b) for unenclosed populations of meadow voles and by Wolff and Lidicker (1981) for free-ranging *M. xanthognathus*. Wolff and Lidicker hypothesized several advantages for living in mixed lineage groups, as opposed to family or kin groups, including the reduction of inbreeding and a reduced chance that entire family lines may be lost to predation. An alternative hypothesis is that mixed lineage groups have no independent significance, and that they form as a byproduct of the adaptive response of each individual to maintain a certain number of dependable nesting partners for the benefits of huddling during winter. Thus an important question becomes not why the groups are of mixed family lines, but what factors regulate group size and which of these factors changed after December in the present study to cause the observed adjustments in space use and social nesting.

Regulation of Group Size and Dispersion. The common occurrence of nesting groups beginning in the fall, but absent during the summer (Madison 1980a, 1981b), implicates strong selective advantages for social nesting over winter. The stability of cluster size despite large changes in both constellation size and population density indicates an optimum group size of 2 to 3 voles per nesting bout and a "cost" associated with nesting singly or in larger clusters. The disadvantage in nesting alone during cold weather is well documented, at least with respect to energy and possibly moisture conservation (Gebczynski, 1969, 1975; Gebczynski and Gebczynski 1971; Gorecki 1969; Hansson and Grodzinski 1970; Madison 1983; Trojan and Wojciechowska 1968; Wiegert 1961). However, the costs or risks of nesting in clusters with more than 3 voles, or in constellations with a few more than that, has not been examined. Two primary risks are over-utilization of local resources (food, shelter) and increased susceptibility to predation. That declining food resources may have stimulated movement and the breakdown of family constellations is rejected because voles showed no weight reduction or declining physical condition during January and February, nor were there any deaths attributable to starvation. Also, starving voles would not likely move into and remain within the suboptimum area, which had very little food and cover, when much better areas were available in adjacent parts of the optimum habitat.

Several findings suggest that both cluster and constellation size, as well as the distance between constellations, are governed to a major extent by predation. For predation to be an important factor, it must have the potential of causing substantial losses. That ermine alone impose such a threat is demonstrated in this study and others (MacLean et al. 1974). In our study, a single ermine killed one constellation of voles and portions of two others in adjacent areas within a 10-day period. Judging from these data, we speculate that a vole's chance of survival may be better in a semi-isolated constellation of 3 voles than in a larger one that is either more or less isolated. The rationale is that a smaller constellation would provide fewer cues for predators. The semi-isolated, but not overly isolated, distribution

would make the voles more difficult to find but still allow the occasional survivor of a mass kill to find a new constellation to re-establish the huddling benefits. Constellations that are too large or too close will provide incentives for a predator to return to an area that has produced prey, or even to settle in an area and gradually move from one constellation to the next. The accumulation of prey fur for use in nest construction is an added benefit for ermine.

If predators are selecting against voles who live in larger groupings, then something about constellation size and proximity must increase the susceptibility of a given vole to predation. We noticed considerable concentrations of breathing holes, exposed tunnels, feces, and tracks in areas of major constellations, especially when partial snow melt-offs occurred. These likely provide clear visual signals to wide-ranging predators.

Predators should also have an effect on cluster size, if predators such as ermine are able to move within the subnivean tunnels of voles, enter nests, and swiftly kill the occupants. The normal cluster size of 2 to 3 voles and the mean constellation size of 3.2 to 7 voles show that all the voles closely cohabiting a small area rarely sleep together at any one time. Instead, it is not uncommon to find 2 to 3 voles in each of two nests in the cohabited area. Thus, factors other than resource competition must influence cluster size. We hypothesize that nesting in small clusters reduces susceptibility to predation.

Finally, predation should affect the movement pattern of voles, assuming that voles can detect the presence of predators either directly (odors, visual contact) or indirectly (sudden disappearance of one or more group members). Under these circumstances, the voles should have evolved the ability to weigh the costs of immigration or dispersal (e.g., chance of not finding other voles, exposure to severe weather, exposure to predators, temporary loss of dependable shelter) against the chance of future predation in the same area. As far as predator detection is concerned, it is likely that voles can smell weasels in an area, since weasel scat and scent is quite obvious to man. Vole immigration or dispersal in the present study was clearly correlated with the combined occurrence of predation and snow cover. It is inferred that the risk of moving into new areas during the winter when there is no protective snow cover is too great to permit such movement. Such movement is even uncommon at other times of the year when temperatures are no threat to survival (Madison, 1984). Thus, it is not so much the moderation in temperature caused by the snow that permits greater freedom in movement, but the added shelter, presumably from predators.

Consequences of Optimum Group Size for Cycling. We hypothesize that an optimum group size in overwintering meadow voles makes this species particularly susceptible to multi-annual cycles of abundance. The logic is as follows. If the size and proximity of the nesting constellations decrease substantially during fall and winter because of predation or other factors (e.g., disease, food shortage, parasites), then a point could be reached where many voles could no longer find, and benefit from, nesting partners. At this point, the population could experience a precipitous rate of decline due to the loss of

benefits from huddling. This accelerated loss at low densities during winter would explain the extreme declines and multi-annual lows observed in natural, particularly northern, populations (Finerty 1980). The assumption is made that densities fall so low that breeding success in the spring is rare or widely scattered. Populations cannot increase to the optimum winter level until the second or third year, or until a mild winter (e.g., one with a long, continuous snow cover and higher temperatures) coupled with low predation enables wide-scale survival of solitary individuals. Since northern or alpine regions generally have colder winters, overwinter crashes would be more common in these areas. However, because of the moderating influence of snow cover on ground temperatures (Pruitt 1957), crashes would be most common in those northerly latitudes with less or intermittent snow covers, where exposure to low temperatures and predators would increase. Since survivorship at some moderate winter density would be higher than at low or very high densities, the result would be akin to an "Allee Effect" (see Allee et al. 1949). Experiments are needed to test this hypothesis by manipulating dispersion and group size and by controlling predation in free-ranging populations.

Implications for Vole Management in Orchards. Winter is a particularly important time to control meadow vole activity in orchards. This is so because meadow voles cause severe girdling damage during winter and have the potential of moving widely under snow. Existing cultural practices attempt to reduce meadow vole damage during winter by reducing populations during spring, summer and fall through habitat manipulation and rodenticide use. We propose that meadow voles can be controlled most effectively during the winter because this is the time when they are the most clumped in distribution, the most vulnerable to weather, and the most in need of food and shelter. In areas of snow cover, the occurrence of "breathing" holes in the snow along tree rows could be used as local cues for highly targeted rodenticide application. Where snows do not occur, the introduction of communicable disease or parasite organisms, or rodenticides that are spread by social grooming, would be particularly effective because of the clustering behavior of overwintering meadow voles. Such treatments would be most effective during the coldest time of the winter when clustering is most common.

ACKNOWLEDGEMENTS

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