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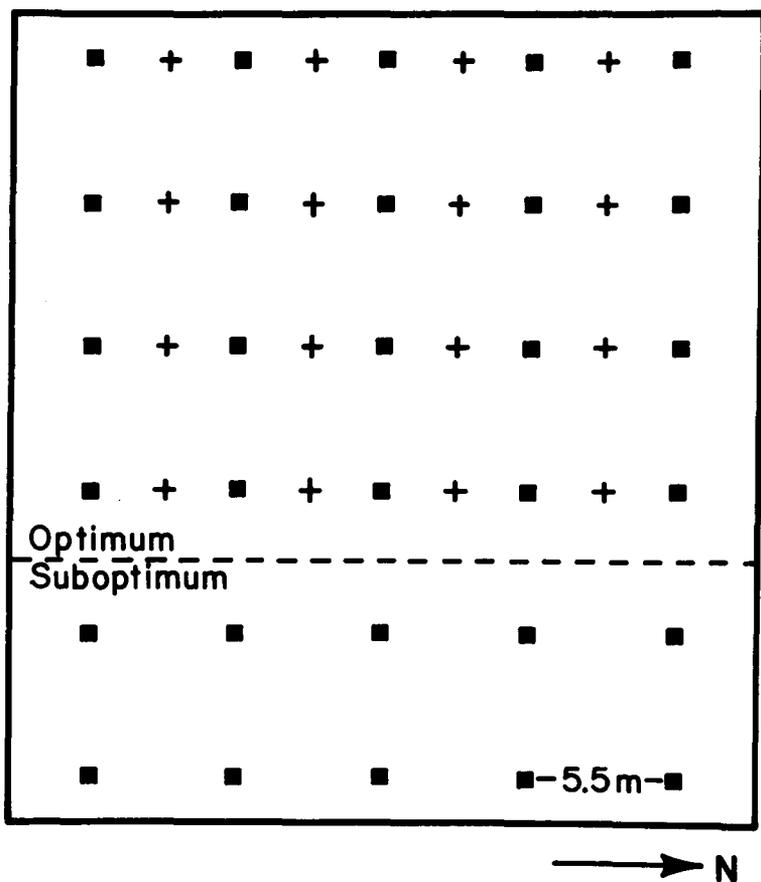
Fig. 1. Enclosure used for overwinter studies of meadow voles in
    Apalachin, New York. The locations of the permanent live-
    trapping stations (■) and the supplemental live traps (+) are
    indicated. Two live traps were at each permanent station; one
    trap was set at each supplemental station.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

16 supplemental traps were placed within the optimum habitat (see be-
low), one trap between each trap station within each row, thus creat-
ing 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 re-
maining 28 x 20 m section was not mown and served as the optimum
habitat. The 11 meadow voles added to the enclosure created a be-
ginning 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 posi-
tions. 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 (χ^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 (χ^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
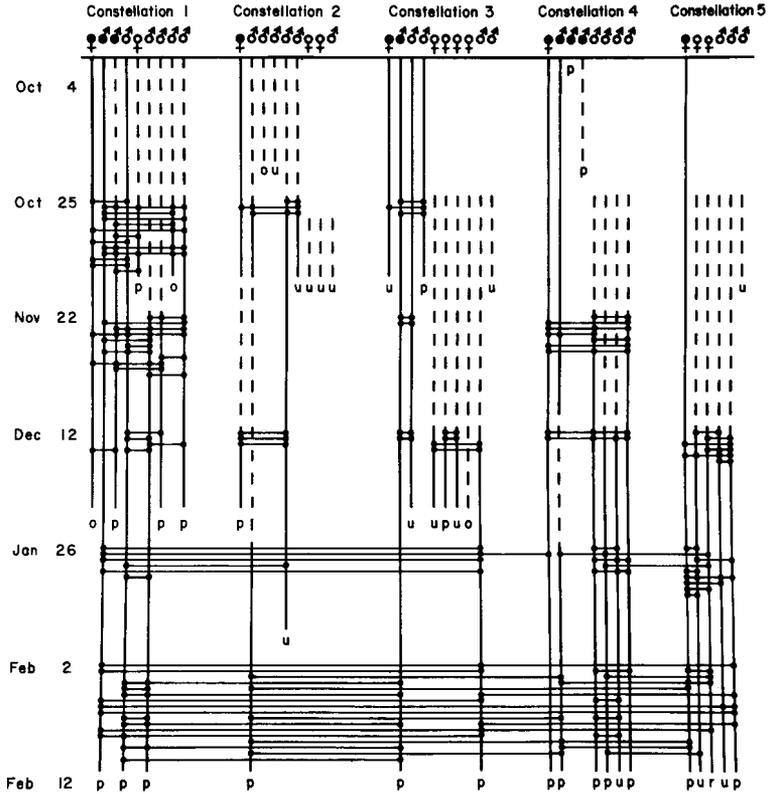
Fig. 2. Time record of births, deaths, radiomonitoring, and cluster and constellation associations of all meadow voles in the en- closure on the dates indicated. The original voles introduced are indicated by darkened sex symbols. All other voles are descendants. Each horizontal line shows one case of 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.
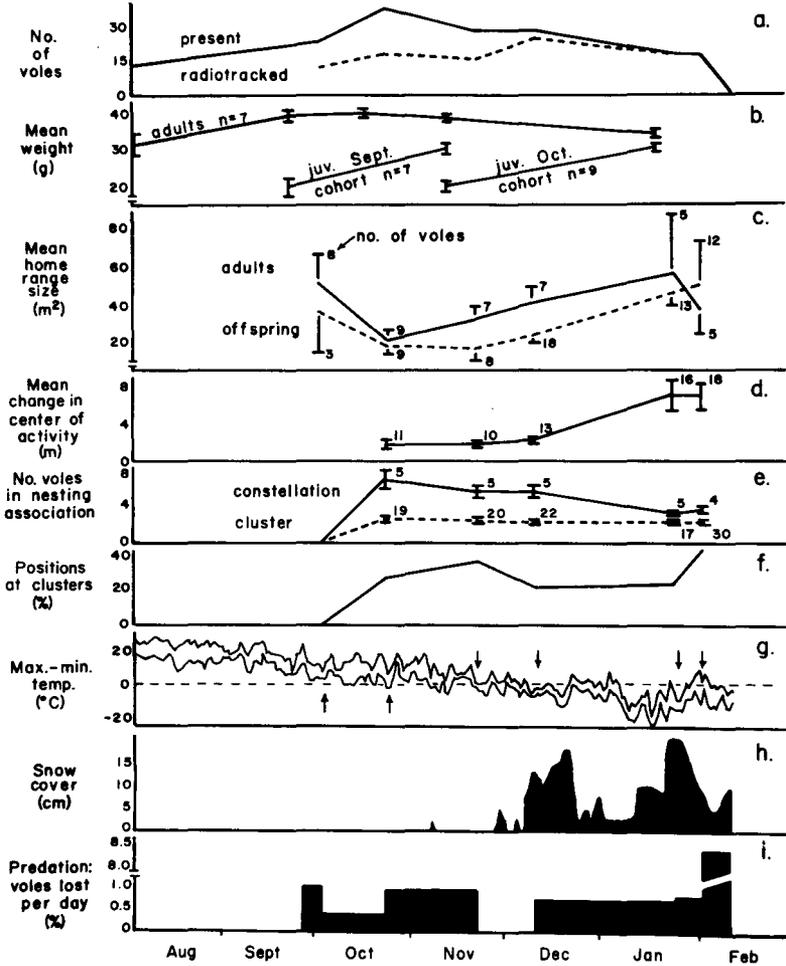
Fig. 3. Record of vole density, weight change, home range size, space
use, weather conditions and predation in the enclosure during the
fall and winter of 1981/1982 in Apalachin, New York. The arrows
in the temperature graph (g) show the dates of radiotracking.
The vertical brackets show ± one standard error of the mean.
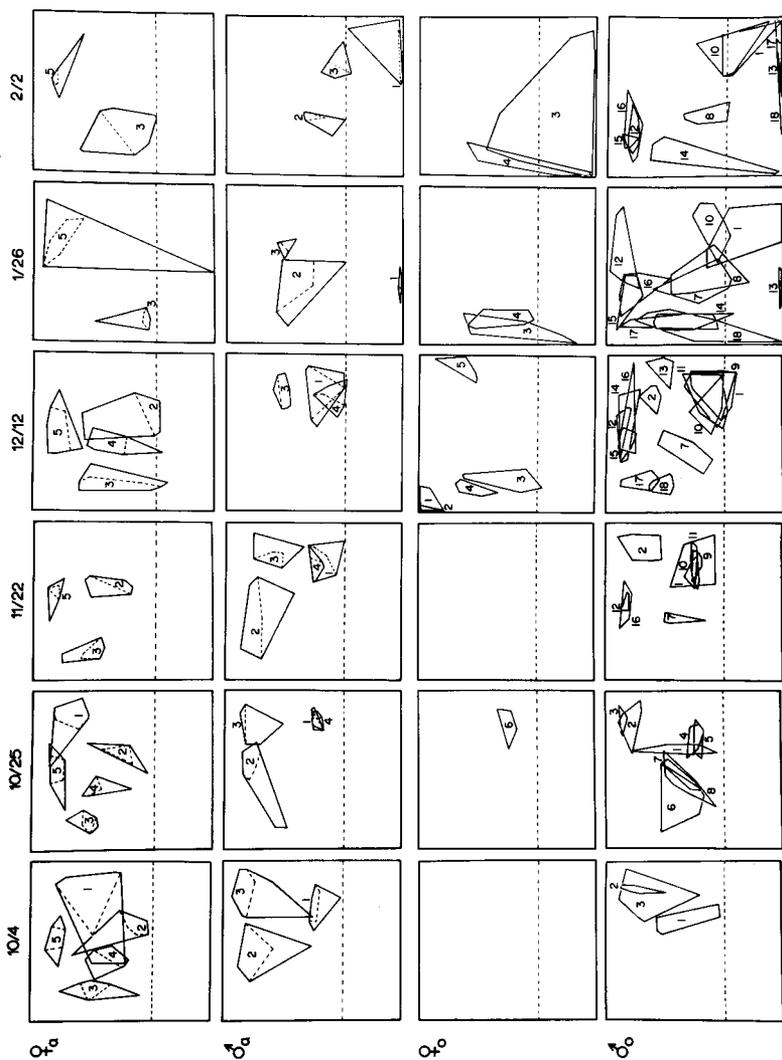
Fig. 4. Ten-hour home ranges (solid line polygons) of adult female
(♀ₐ) and male (♂ₐ) meadow voles and their female (♀ₒ) and male
(♂ₒ) offspring during six radiotelemetry sessions in the enclo-
sure in Apalachin, New York. The home ranges belonging to the
different sex-age classes are plotted separately for easier in-
terpretation. 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 posi-
tions from the center of activity are omitted, and a new 8-hour
home range drawn, in order to show areas of more intense utiliza-
tion).

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 (χ^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 (χ^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 (χ^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
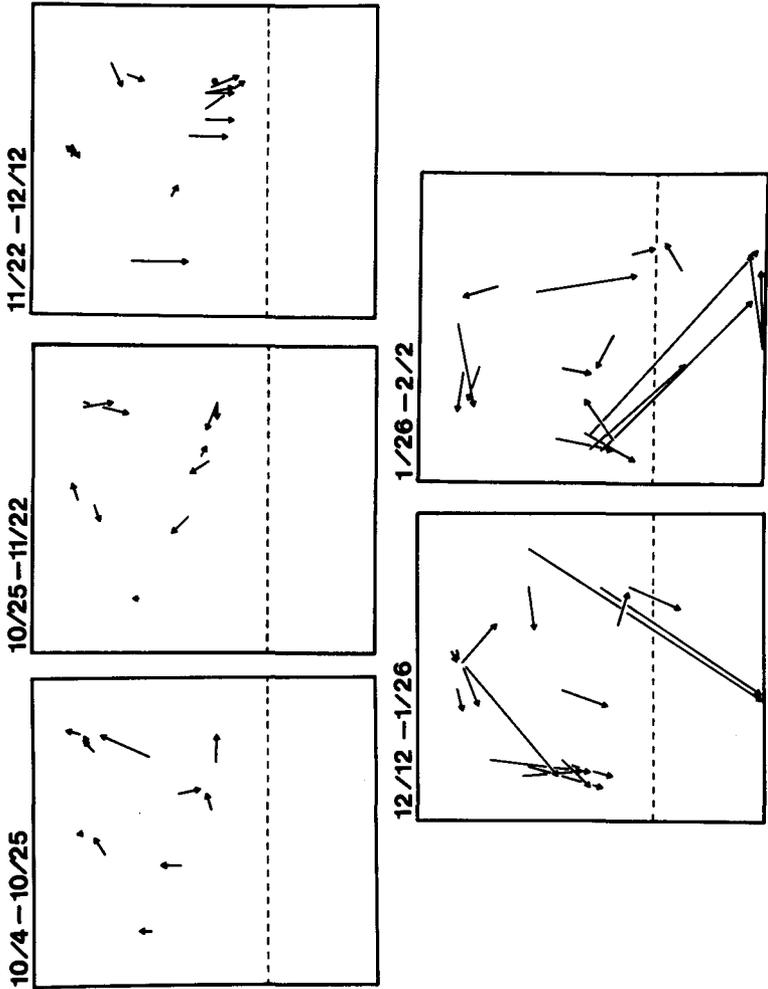
Fig. 5. The changes in center of activity (geometric centers of mass) for all voles radiotracked between the dates indicated for the five time intervals during the fall and winter in Apalachin, New York. The arrows show the distance and direction of movement.
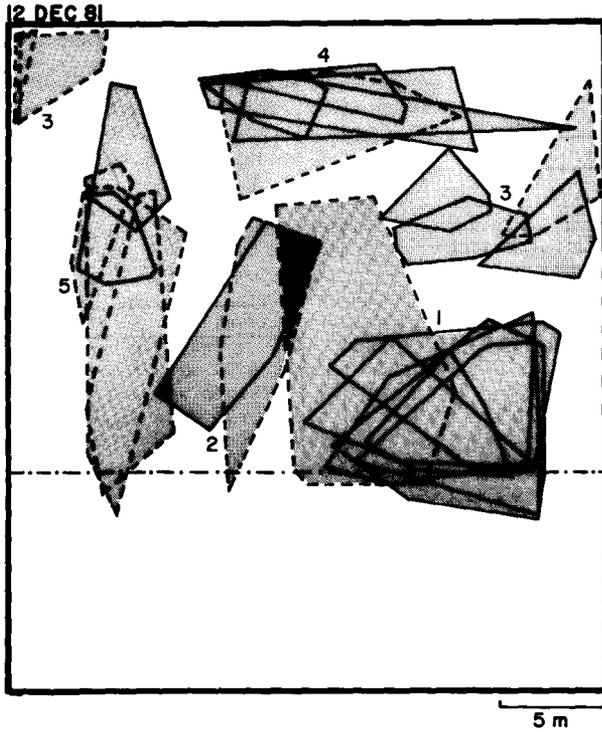
Fig. 6. The 5 constellations of meadow voles on 12 December 1981 in
Apalachin, New York. The male (——) and female (---) home range
perimeters are shown, and each constellation is shaded and
numbered. The dark shading shows areas of constellation overlap.

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 micro-
tines. 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 off-
spring 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 (Constella-
tion 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 be-
gins to wane during the fall, and as group nesting becomes progres-
sively 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 cap-
tures 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 indi-
cates an optimum group size of 2 to 3 voles per nesting bout and a
"cost" associated with nesting singly or in larger clusters. The dis-
advantage 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 clus-
ters 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 starva-
tion. 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 occa-
sional 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 group-
ings, then something about constellation size and proximity must in-
crease 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 to-
gether 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 con-
stellations 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.

REFERENCES CITED

Allee, W.C., A.E. Emerson, O. Park, T. Park, and K.P. Schmidt. 1949. Principles of Animal Ecology. W.B. Saunders Co., Philadelphia, Pennsylvania, 837 pp.

Chelkowska, H. 1978. Variations in numbers and social factors in a population of field voles. Acta Theriol., 23: 213-238.

Christian, J.J. 1980. Endocrine factors in population regulation. Pp. 55-115, In: M. Cohen, R. Malpass, H. Klein (eds.) Biosocial Mechanisms of Population Regulation. Yale University Press, New Haven, Connecticut, 406 pp.

Frank, F. 1957. The causality of microtine cycles in Germany. J. Wildl. Mgt., 21: 113-121.

Fuller, W., L. Stebbins and G. Dyke. 1969. Overwintering of small mammals near Great Slave Lake, northern Canada. Arctic, 22: 34-55.

Gebczynski, M. 1969. Social regulation of body temperature in the bank vole. Acta Theriol., 14: 427-440.

_____. 1975. Heat economy and energy cost of growth in the bank vole during the first month of postnatal life. Acta Theriol., 29: 379-434.

Gebczynski, Z., and M. Gebczynski. 1971. Insulating properties of the nest and social temperature regulation in Clethrionomys glareolus (Schreber). Ann. Zool. Fennici, 8: 104-108.

Getz, L.L. 1972. Social structure and aggressive behavior in a population of Microtus pennsylvanicus. J. Mammal., 53: 310-317.

Gorecki, A. 1968. Metabolic rate and energy budget in the bank vole. Acta Theriol., 13: 341-365.

Hansson, L.H., and W. Grodzinski. 1970. Bioenergetic parameters of the field vole, Microtus agrestis L. Oikos, 21: 76-82.

Hayne, D. 1949. Calculation of size of home range. J. Mammal., 30: 1-18.

Hill, R. 1976. The ontogeny of homeothermy in neonatal Peromyscus leucopus. Physiol. Zool., 49: 292-306.

Iverson, S., and B. Turner. 1969. Under-snow shelter for small mammal trapping. J. Wildl. Mgmt., 33: 722-723.

Jannett, F.J., Jr. 1978. The density-dependent formation of extended maternal families of the montane vole, Microtus montanus nanus. Behav. Ecol. Sociobiol., 3: 245-263.

Lidicker, W.Z., Jr. 1975. The role of dispersal in the demography of small mammals. Pp. 103-128, In: F.B. Golley, K. Petrusewicz, and L. Ryszkowski (eds.) Small Mammals: Their Productivity and Population Dynamics. Cambridge University Press, England, 451 pp.

MacLean, S.F., B.M. Fitzgerald, and F.A. Pitelka. 1974. Population cycles in Arctic lemmings: Winter reproduction and predation by weasels. Arctic Alpine Res., 6: 1-112.

Madison, D. 1978a. Movement indicators of reproductive events among female meadow voles. J. Mammal., 59: 835-843.

_____. 1978b. Behavioral and sociochemical susceptibility of meadow voles (Microtus pennsylvanicus) to snake predators. Am. Midl. Nat., 100: 23-28.

_____. 1979. Impact of spacing behavior and predation on population growth in meadow voles. Pp. 20-29, In: R.E. Byers (ed.) Proc. Third Eastern Pine and Meadow Vole Symposium. New Paltz, New York.

_____. 1980a. Space use and social structure in meadow voles, Microtus pennsylvanicus. Behav. Ecol. Sociobiol., 7: 65-71.

_____. 1980b. Movement types and weather correlates in free-ranging voles. Pp. 34-42, In: R.E. Byers (ed.) Proc. Fourth Eastern Pine and Meadow Vole Symposium. Hendersonville, North Carolina.

_____. 1981a. Time patterning of nest visitation by lactating meadow voles. J. Mammal., 62: 389-391.

_____. 1981b. An integrated view of the social behavior of Microtus pennsylvanicus. The Biologist, 62: 20-33.

_____. 1983. Group nesting and its ecological and evolutionary significance in overwintering microtine rodents. Bull. Carnegie Museum of Nat. His. (In Press) 21 pp.

_____. 1984. Activity rhythms and spacing. In: R. Tamarin (ed.) Biology of New World Microtus. Amer. Soc. Mammal. Spec. Publ. (In press) 55 pp.

Madison, D., R. FitzGerald, R. Pagano, and J. Hill. 1981. Radio-telemetric evaluation of the effect of horticultural practices on pine and meadow voles in apple orchards: I. Rotary Mowing. Pp. 45-53, In: R.E. Byers (ed.) Proc. Fifth Eastern Pine and Meadow Vole Symposium. Gettysburg, Pennsylvania.

Madison, D., R. Pagano, and R. FitzGerald. 1982. Radiotelemetric evaluation of the effect of horticultural practices on pine and meadow voles in apple orchards: II. Herbicide Application. Pp. 74-79, In: R.E. Byers (ed.) Proc. Sixth Eastern Pine and Meadow Vole Symposium. Harpers Ferry, West Virginia.

Pagano, R. 1982. Coexistence of two vole species, Microtus, in an orchard. M.A. Thesis, State University of New York at Binghamton, Binghamton, New York. 52 pp.

Pagano, R., and D. Madison. 1982. Radiotelemetric evaluation of the effect of horticultural practices on pine and meadow voles in apple orchards: III. Use of Orchard Border Habitats by Meadow Voles. In: R.E. Byers (ed.) Proc. Sixth Eastern Pine and Meadow Vole Symposium. Harpers Ferry, West Virginia.

Pruitt, W.O., Jr. 1957. Observations on the bioclimate of some taiga mammals. Arctic, 10: 131-138.

Trojan, P., and B. Wojciechowska. 1968. The effect of huddling on the resting metabolism of the European common vole, Microtus arvalis (Pall.). Bull. Acad. Pol. Sci., Cl. II, 16: 107-109.

Webster, A.B., and R.J. Brooks. 1981a. Daily movements and short activity periods of free-ranging meadow voles, Microtus pennsylvanicus. Oikos, 37: 80-87.

_____. 1981b. Social behavior of Microtus pennsylvanicus in relation to seasonal changes in demography. J. Mammal., 62: 738-751.

Wiegert, R.G. 1961. Respiratory energy loss and activity patterns in the meadow vole, Microtus pennsylvanicus pennsylvanicus. Ecology, 42: 245-253.

Wolff, J.O., and W.Z. Lidicker, Jr. 1981. Communal winter nesting and food sharing in taiga voles. Behav. Ecol. Sociobiol., 9: 237-240.