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Proceedings of the Fifth Eastern Pine and Meadow Vole Symposium, Gettysburg, PA, March 4-5, 1981

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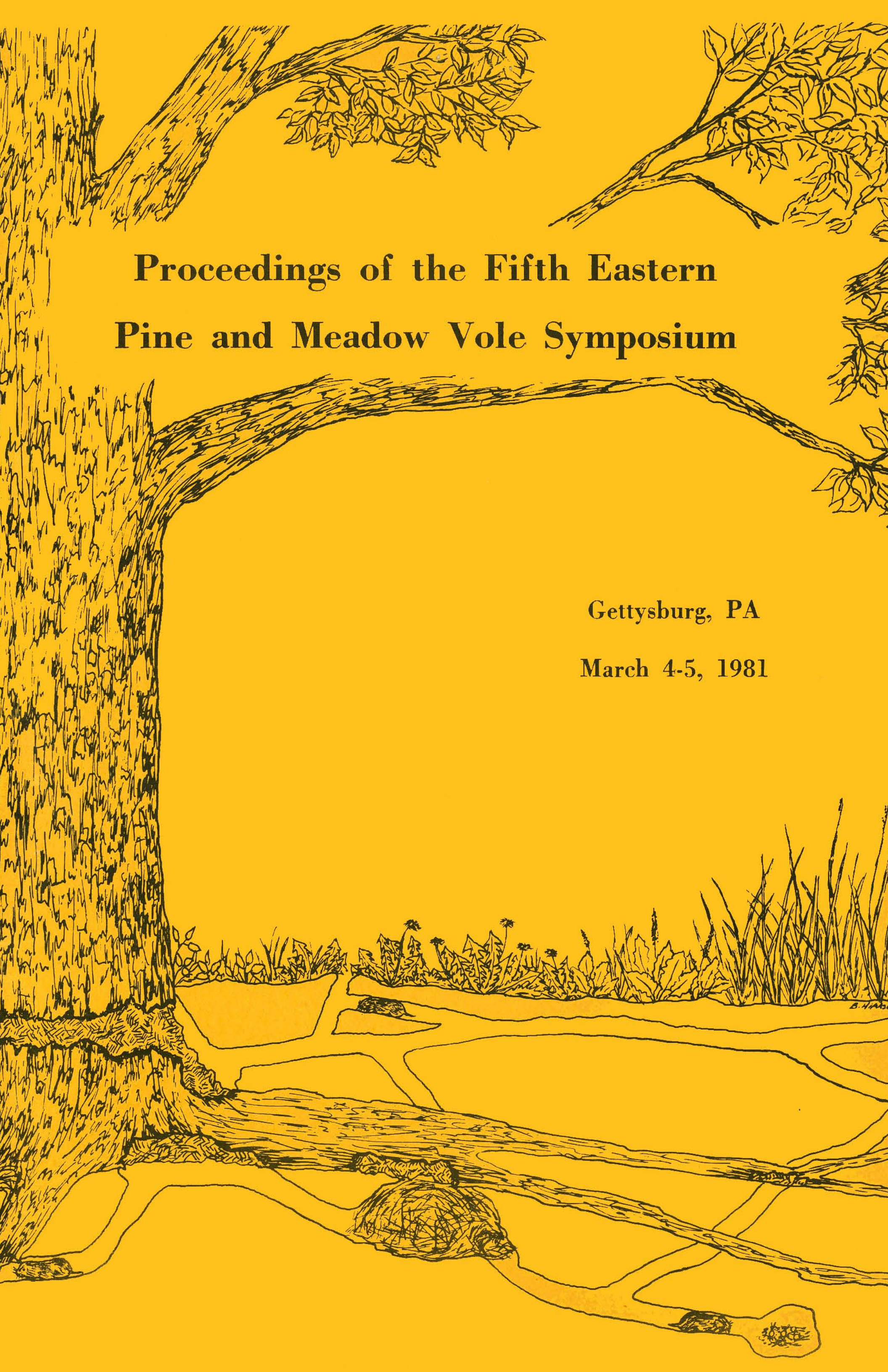

Proceedings of the Fifth Eastern Pine and Meadow Vole Symposium

Gettysburg, PA

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PROCEEDINGS OF THE FIFTH EASTERN PINE AND MEADOW VOLE SYMPOSIUM

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EDITOR

ROSS E. BYERS

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Editor's note: The papers in the Proceedings appear as originally written.

HIGHLIGHTS OF THE FIFTH EASTERN PINE AND MEADOW VOLE SYMPOSIUM

The Fifth Eastern Pine and Meadow Vole Symposium was held at the Sheraton Inn-Gettysburg, Gettysburg, Pennsylvania March 4 and 5, 1981, for the purpose of assessing the current status of research, extension, and industry programs relating to the problem of vole damage to fruit trees. The meeting was intended to create a problem solving atmosphere in which growers; various governmental agencies such as EPA, USDA, USDI; the chemical industry; and university personnel could observe the current thrusts of research and extension programs and their potential impact on future control strategies.

By the 1981 meeting the influence of the USDI contract monies for pine and meadow vole research had begun to show. Both the quality and quantity of research papers was increased. Information relating to the ecology, behavior, physiology, movements, population monitoring, reproduction, and control methodology of these animals had been generated by the various research groups. The meeting provided an excellent opportunity for various research groups to interact and to assimilate the meaning of various research programs with regard to vole damage control.

A tour of the Pennsylvania State University Fruit Research Laboratory at Biglerville and fruit grower operations was arranged by Dr. George M. Greene (Pomologist) and Mr. Tom Piper (Adams County Extension Agent). The excellent local arrangements and registration were handled by Drs. George Kelley and Wally Tzilkowski. Although the pine vole appeared to be a problem in some Pennsylvania orchards, the meadow vole was the predominating species. Emphasis on cultural control appeared to be evident in the local orchards visited. This may be in part due to the species most prevalent and the extension service approach to the control problem.

In all, the Fifth Eastern Pine and Meadow Vole Symposium was probably one of the most important symposia to date. The quality of the presentations was impressive and data represented useful and much needed information. What was more gratifying was the productive exchange of information and ideas which went on "after hours" between the researchers, extension personnel, growers, and chemical representatives throughout the symposium. The cooperative spirit of those involved in vole biology research, damage control and the support offered by USDI funding were certainly responsible for increased understanding of the vole control problem.

THE STATUS OF ENDRIN - 1981

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As reported in 1980, at the Fourth Annual Pine and Meadow Vole Symposium, the use of endrin would be subject to the EPA Administrator's decision as delineated in the EPA Position Document 4. The details of his decision and the resulting prohibitions and restrictions were given at last year's Symposium and are contained in the official publication of the 1980 Symposium in the article by Lawrence S. Ebner and Harvey S. Gold.

The EPA RPAR decision permitted the continued use of endrin for a number of important uses. Among these was the use of endrin for pine and meadow vole control. The restrictions imposed by the RPAR were to be effected by means of label changes that would be officially requested by EPA by notices to registrants of endrin labels. Compliance with these label changes would continue the label registration. Failure to comply would result in cancellation of the label registration.

At the time of last year's Symposium the official EPA notification to endrin label registrants had not yet been made. In September 1980, EPA notified registrants by registered mail of the required label changes and timetable for compliance. Since that time, Velsicol has complied and revised its endrin labels (including the Endrin 1.6 EC label containing the orchard mouse control use) in accordance with the EPA requirements. Velsicol's Endrin 1.6 EC label is valid and Velsicol will continue to produce and sell endrin for those uses currently permitted by law. Therefore, endrin is available for use in controlling pine and meadow voles in those states where the use is permitted.

VOLE DAMAGE AND CONTROL METHODS IN ONTARIO ORCHARDS

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In Ontario, herbivorous mammals inflict extensive damage upon fruit tree orchards and hardwood plantations (Radvanyi 1974 a, b; C. Dufault pers. commun., Hikichi pers. commun.). Nevertheless, surprisingly little research has been directed toward reduction or control of this damage and, therefore, growers continue to suffer substantial annual economic losses. Ontario appears to offer no specific guidelines to assist growers in developing effective long-term control programs for mammalian pests in their orchards. Recommended methods of control are limited to brief, general pamphlets most of which have shown little substantive change over the past few decades. There have been virtually no experimental studies of the recommended control methods, and there are almost no data on the identity of the species causing damage nor on the extent and cost of the damage. Finally, there has been no investigation of safer, more economical or more effective alternatives to the traditional means of control (Miller 1976; Hikichi pers. commun.).

In 1977, some Ontario growers expressed concern at the amount of damage caused by mammalian pests and compiled a rough estimate of the extent of this problem in several areas of the province (Table 1). At that time, the Ontario Ministry of the Environment (OME) solicited proposals for research on control of voles in Ontario orchards, but no funds were actually allocated. In 1980, the Ontario Apple Marketing Commission officially recognized a need for vole research in the province and requested that we submit a proposal for research to investigate the source and extent of the damage and a means of reducing destruction of fruit trees by voles. At present, the Ontario Ministry of Agriculture and Food (OMAF) and the Ontario Pesticides Advisory Committee (OPAC) have agreed to assist the Apple Marketing Commission in funding two studies of vole damage in orchards.

In this paper, we present a summary of present knowledge of the extent of vole damage to Ontario orchards and we summarize the methods of control presently recommended and describe some of the problems in vole control specific to Ontario.

Table 1. Wildlife damage survey in Ontario orchards (1977)

		Estimate of trees damaged			With treatment	
Area	Acres	Mice	Rabbit	Deer	# trees damaged	# trees killed
A	1,900	350	30	30		75
B	2,500	2,199	359	235	2,995	356
C	6,000	3,000	1,500	---	6,060	400
D	19,700	1,458	40	20	600	400
E	1,258	653	395	687	199	107
F	2,761	700	10	---	300	80
G	3,250	800	---	---	800	50
H	633	4,061	500	21	3,220	575
Total	38,003	13,221	6,034	983	14,174	2,042

Species Causing Damage to Fruit Trees

While it is evident that deer and "rabbits" often damage Ontario fruit trees, most growers seem to feel that "mice" are the major mammalian source of tree deaths and injury. However, there are few quantitative data that can be used to assess how much damage can be attributed to different pest species. It is probable that meadow voles (Microtus pennsylvanicus) cause most damage. Pine voles (M. pinetorum) have a very limited distribution in Ontario, being confined to a narrow strip of land along the shore of Lake Erie (Petersen, 1966), and so their importance, if any, is limited to these areas.

Extent of Damage

Apples, pears, peaches and grapes as well as hardwood plantations are injured by rodents. Usually, the main stem and lower branches of young trees are attacked. Root damage is less extensive. Vole damage begins in August and continues through fall and winter, presumably when alternate food sources are scarce or less nutritious. Many areas of Ontario experience deep winter snow cover that offers ideal habitat for the voles. Girdling then occurs below the snow crust, making detection of damage and application of effective control more difficult (OMAF Publ. #64 1981). Occasionally, voles breed under the winter snow (Brooks et al. 1976). In such instances, limiting control to the fall season would be ineffective unless the population was eliminated totally at that time. Therefore, the extended winter season and the possibility of winter breeding produce a major problem in vole control in Ontario.

Another problem in developing a single control program for the province is that orchards occur over a wide area of considerably varied terrain, climate and habitat. This means that it is difficult both to coordinate and plan control measures because of the distance involved and because the populations that are causing problems may differ in species, numbers and other qualities. For example, attempts to provide province-wide monitoring of levels of vole populations to predict potential damage or to assess levels of control to be applied are impractical because of the diversity of the areas where orchards occur.

Methods and Recommendations for Control

At present, there is very limited and mostly outdated information to direct growers in controlling voles. A recent OMAF factsheet (Ells and Hikichi 1979) provides one page of information for control of voles in orchards. Methods suggested there are traditional and have remained virtually constant over the past 40 years.

Suggestions for control fall into 3 broad categories, mechanical and chemical control and habitat manipulation. It appears that Ontario growers primarily rely on the first two methods, but there has been no systematic evaluation of their relative effectiveness.

Mechanical protection is labor intensive and usually recommended for use in combination with other methods. Most publications indicate that mechanical protection has several limitations (e.g. labor costs, growth of mould, bark damage, failure to protect roots or to protect stem in deep snow, replacement cost etc.) (Agric. Can. Publ. #1153, 1975; OAC Report 1938; Thompson 1943; Ells and Hikichi 1979) and, therefore, are of little value by themselves.

Pitfall traps and snap traps are sometimes recommended for control (MacNay 1965) but it is difficult to imagine anyone using these traps to control voles in large operations because of the labor involved and because of their limited effectiveness. A comprehensive control program in Alberta using tree guards, pitfalls and snap traps was unsuccessful (Radvanyi 1974b).

Habitat manipulation has been less popular as a means of control for voles. Many growers resist clean cultivation or planting of other crops in their orchards (F. Harris pers. commun.) and wish to retain their orchards in sod. Typical recommendations include removal of prunings, rubbish and weeds that provide cover. Brooks et al. (1976) and Radvanyi (1974) reported that mowing did not kill voles or even drive them from an area. However, populations in mowed habitats suffered higher winter mortality than in old fields and leaving straw on harvested fields in fall led to massive increases in vole densities within a few weeks (Brooks et al. 1976).

Removal of sod is often not effective if there is good snow cover. With deep snow, packing is recommended (Thompson 1943). Removal of fallen fruit is recommended to reduce orchard attractiveness to voles and to increase bait acceptance. Ideally, habitat manipulation gives long term and more complete protection, and has no detrimental side effects. However, it is costly and meets with grower skepticism and resistance.

Rodenticides are usually recommended as solutions to vole problems after mechanical and habitat controls have been applied. Zinc phosphide, diphacinone, chlorophacinone, warfarin and pindone are some of the recommended rodenticides (Ells and Hikichi 1979). Many compounds are now banned or severely restricted for use (e.g. endrin, red squill, hydrogen cyanide, methyl bromide, thallium sulphate, toxaphene). The acceptable chemicals have various degrees of restriction depending upon toxicity and concentration. Many chemicals are effective if eaten but have low acceptance by rodents (e.g. zinc phosphide; Buckholtz pers. commun.). There has been little experimentation with this problem. Resistance to specific chemicals is either not reported or occurs sporadically in independent populations of voles. Most recommend applying the pesticides in fall (Sept. - Nov.) (Thompson 1943, Ells and Hikichi 1979). Radvanyi (1974 a, b) reported good and mixed success at reducing populations with anticoagulants (Rozol) in hardwood plantations. However, he also found reinvasion was rapid and felt that winter control was limited. Radvanyi (1974b) has recommended bait stations of his own design, but limited field trials by others suggest that growers find them too time consuming (Hikichi, pers. commun.).

In summary: Ontario has conducted very little research into control of voles in fruit tree orchards. Recommendations for control have changed little in the past 40 years and there appears to have been no proper assessment of the effectiveness of these recommended methods. Recent high levels of damage have led to requests from growers for an assessment of the problem and for development of more effective control measures.

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MEADOW AND PINE VOLE CONTROL IN 1980 FIELD PLOTS

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Abstract. Broadcast treatments of Volak (Brodifacoum), Rozol (Chlorophacinone), ZP Rodent Bait AG, and Ramik-Brown (Diphacinone) gave excellent to good control of voles in decreasing order of effectiveness. A saccharin formulation of Ramik-Brown or doubling the concentration of diphacinone to 0.01% did not result in any additional control over the current formulation. Hand placement of ZP Rodent Bait AG at 1 to 3 lbs/A gave excellent control of voles. Place packs of ZP Rodent Bait AG were not opened at all sites, however, residual activity from apple activity data indicated that this product gave excellent control. Additional field and laboratory evaluations are suggested.

Low broadcast rates of Rozol at 9 lbs/A did not give adequate control of pine and meadow voles. The FMC Zinc Phosphide corn and oat formulation did not perform well even when compared to even lower rates of ZP Rodent Bait AG in broadcast trials.

The caching response of pine and meadow voles were found to differ markedly in one field experiment. Over 60% of the sites visited by pine voles had over 25 grams of blank pellets removed in a 24 hour period. Less than 2% of the meadow vole sites had 25 g removed in the same period of time.

Methods and Materials:

1) Field trials --- Evaluation of pine and meadow vole control plots was determined using methods previously described (1,2). In these experiments, plots were blocked according to pre-treatment activity readings by first ranking plots from high to low and assigning treatments randomly into activity categories high, medium, and low. Data summarized in Tables 1 and 2 were taken from orchards having approximately 35 trees per acre (35' X 35').

2) Since plastic packaged bait has the advantage of continuous availability to voles as well as non targets, site covers (split tires or cinder blocks, 2 X 8 X 16 inches) were evaluated as a station for placing plastic packaged Volak or ZP packets. Volak or ZP packets were placed in 47 sites in each of 3 replicate plots of tires or cinder blocks in an attempt to give immediate control. This treatment was then followed within 45 days with another treatment so that packets would then be available for the next 6 month period.

A control plot was not maintained in close proximity to this orchard since continued invasion might have taken place.

3) To determine if pine and meadow voles had a different caching behavior in the field, two orchards were selected with similar tree ages and spacings. Sixty sites were determined to be active using the

apple indexing technique. Animals were live trapped, toe clipped and released. Data indicated 50 meadow voles and 60 pine voles visited the 60 active sites in the two blocks. Some trees were eliminated from the experiment in both blocks if voles were not trapped at these trees. One pine vole was trapped in the meadow vole block but no meadow voles were found in the pine vole block. Three different pellet sizes were placed in the sites by blocking the 60 sites into 3 blocks according to the degree of feeding on an apple and the number of voles visiting the sites. This assured a more equal distribution of pellet sizes among animals visiting various sites in the field. Fifty grams of pelleted bait were allowed to remain in the sites for a 24 hour period. Pellets were of 3 sizes: 0.22, 0.32, 0.48 mm in diameter and having 1,315 pellets/50 g, 714 pellets/50 g and 294 pellets/50 g respectively. The bait was oven dried in paper bags for 24 hours at 100°C.

Results and Discussion: Broadcast data (Table 1) show that Rozol (CPN) applied at 9 lbs/A is inadequate and that rates should be nearer 20 lbs/A. The ZP Rodent Bait AG gave respectable control at 11 lbs/A but the 14 lbs/A rate appeared to give better control even though not statistically different. The FMC ZP grain treatment at 16 lbs was totally inadequate for control of pine and meadow voles. Hand placement of the ZP Rodent Bait AG at 1-3 lbs gave good control. The results between ZP Rodent Bait AG and the FMC grain bait indicate that inadequate control with grain baits has been the formulation rather than the method of application (hand or broadcast baiting).

The CPN-grain pellet from Lipha (Table 2) appeared to be equal or superior to the CPN-wax pellet used in the USA (Tables 1 and 2). The whole grain-CPN wheat has performed the poorest over the last 2 years field work. The Velsicol DPN formulations gave about the same control level with little if any additional benefit from the .01% DPN level of toxicant or the addition of saccharin. The BFC and the ZP Rodent Bait AG broadcast baiting gave excellent control at rates near 20 lbs/A. Good control of voles was achieved with two applications of packaged Volak bait applied either in the spring of 1979 or the fall of 1980. Populations however did not go to zero as expected and apparently an adequate number of voles existed in the area so that by the fall of 1979 or fall of 1980, the number of packets opened over the period show that voles had existed under 70% or more of the trees in both years in both the tire and cinder block treatments. Cinder blocks or tires as site covers gave similar results. Although the population as indexed on apples remained low from one season to the next, two applications of packets per year were required to maintain an unopened packet at the site. The ZP packet placed in December 1980 gave a good reduction in the population. However, activity on apples placed at the sites remained at 8-10% activity. These results are similar to the results of hand placed and broadcast ZP Rodent Bait in Tables 1 and 2.

Even though Lanier, Estep and Dewsbury (3) found that the meadow and prairie voles were strong hoarding animals under laboratory conditions, under field conditions during the period when orchard baiting is being conducted (December) the meadow vole was not a strong caching vole. The pine vole however has a much stronger hoarding response (Table 1). No differences were found between the amounts of 3 pellet sizes cached by pine voles. Theoretically, broadcast baits made in the smaller pellet sizes would be more likely to intercept normal vole ranging. With acute toxicants like ZP Rodent Bait the interception of only one pellet would be a lethal dose. We believe more studies should be conducted on the optimum pellet size.

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Table 1. Effect of broadcast and hand placed rodenticide baits on pine and meadow vole activity and populations treated November 5, 1980.

Treatment	Rate kg/ha	Rate lb/acre	% Highly active sites[z] Nov 4	% Highly active sites[z] Nov 21	% Active sites[z] Nov 4	% Active sites[z] Nov 21	Voles/plot Nov 25-Dec 1	Voles/site[y] Nov 25-Dec 1	% Control
Control			59 a[x]	51 a	80 a	67 a	29 a	.95 a	0
0.005% CPN - broadcast	10	9	58 a	33 ab	81 a	50 ab	10 bc	.32 bc	66
0.005% CPN - broadcast	19	17	39 b	9 cd	79 a	19 bcd	3 c	.12 bc	87
0.010% DPN - broadcast	21	19	56 a	5 cd	81 a	15 cd	4 bc	.14 bc	85
2% ZP - Pellet - broadcast	12	11	58 a	4 d	83 a	15 cd	4 bc	.14 bc	85
2% ZP - Pellet - broadcast	16	14	54 ab	3 d	82 a	6 d	2 c	.07 c	93
2% ZP - Grain - broadcast	18	16	52 ab	20 bc	84 a	40 abc	13 b	.42 bc	56
2% ZP - Pellet - hand placed	1	1	61 a	9 cd	84 a	19 bcd	3 c	.10 bc	89
2% ZP - Pellet - hand placed	3	3	51 ab	3 d	83 a	3 d	3 c	.11 bc	88

[z] Apples placed in 2 holes or runs 5-15 cm below the soil surface on opposite sides of the tree trunk were examined 24 hours after placement. Percent highly active sites refer to sites having a portion of apple of 2.5 cm removed by vole feeding. Percent activity refers to all sites having vole tooth marks on the apple.

[y] The population consisted of a mixture of 47% pine voles and 53% meadow voles.

[x] Mean separation, within columns by Duncan's Multiple Range Test, 5% (3 replicates per treatment).

Table 2. Effect of broadcast rodenticide baits on pine and meadow vole activity and populations treated October 30, 1980.

Treatment	Rate kg/ha	Rate lbs/A	% Highly active sites[z] Oct 22	% Highly active sites[z] Nov 14	% Active sites[z] Oct 22	% Active sites[z] Nov 14	Voles/plot Nov 17-21	Voles/site[y] Nov 17-21	% Control
Control			62 a[x]	71 a	87 a	88 a	30.7 a	1.28 a	0
0.005% CPN-Wheat	27	22	59 a	10 de	87 a	20 cd	3.0 bc	0.13 bc	90
0.005% CPN (USA)	22	18	50 a	4 ef	83 a	21 cd	.7 c	0.13 c	98
0.005% CPN (French)	22	18	47 a	0 f	85 a	0 e	0 c	0.00 c	100
0.005% DPN-pellet	24	19	48 a	24 bc	81 a	38 bc	3.7 bc	0.15 bc	89
0.005% DPN + Saccharin pellet	27	22	64 a	30 b	87 a	58 b	7.7 b	0.32 b	75
0.010% DPN + Saccharin pellet	24	19	55 a	15 cd	87 a	24 cd	4.3 bc	0.18 bc	86
0.005% BFC-pellet	21	17	44 a	0 f	81 a	3 e	0.0 c	0.00 c	100
2% ZP-pellet	26	21	55 a	0 f	87 a	10 de	1.0 c	0.04 c	97

[z] Apples placed in 2 holes or runs 5-15 cm below the soil surface on opposite sides of the tree trunk were examined 24 hours after placement. Percent highly active sites refer to the sites having a portion of apple of 2.5 cm removed by vole feeding. Percent activity refers to all sites having vole tooth marks on the apple.

[y] The population consisted of a mixture of 52% pine voles and 48% meadow voles.

[x] Mean separation, within columns by Duncan's Multiple Range Test, 5% (3 replicates per treatment).

Table 3. Caching response of pine and meadow voles given 50 grams of bait/active site under field conditions (December 18, 1980).

Treatment	Pellet diameter (cm)	Pellet number per 50 g	Wt/pellet (g)	% of sites with more than 25 grams removed after 24 hours	
				Meadow	Pine
Small pellets	0.24	1,316	0.04	0.8 a	70 a
Medium pellets	0.32	714	0.07	0.0 a	57 a
Large pellets	0.48	294	0.17	1.7 a	60 a

Three pellet sizes were placed in 20 active sites each in two orchards previously determined by 5 days of live trapping to contain either pine voles or meadow voles. Fifty meadow voles and 60 pine voles were live trapped - toe clipped - released at 60 sites in each of two separate orchard blocks over a 5 day period. Using the Schnabel estimator (3) the meadow vole population was estimated at $47 \pm^{15}_{11}$ voles/60 sites and the pine vole population at $91 \pm^{45}_{31}$ voles/60 sites.

NON-TARGET SPECIES HAZARD OF BRODIFACOUM USE IN ORCHARDS FOR MEADOW VOLE CONTROL

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This year we entered into our second year of non-target species hazard assessment of Brodifacoum used (BFC; ICI Americas, Inc.) as an orchard rodenticide. The primary emphasis of this work has been to investigate the effects of BFC on birds of prey through secondary poisoning. The hazard level of BFC to raptors should be dependent on the levels found in post-treatment collections of meadow voles (Microtus pennsylvanicus). Post-treatment collections of meadow voles were made during both the 1979 and 1980 field trials. The residue analysis from the 1979 collections are now available (through the courtesy of ICI Americas, Inc.) and will be discussed.

The 1979 field trial was conducted at an orchard near Front Royal in Warren County, VA. The orchard had a heavy infestation of meadow voles. Broadcast applications of VOLAK (trade name of ICI Americas, Inc.) containing 0.005% (50 ppm) BFC were made to sections of the orchard. An area of 7.4 ha was treated at a rate of 45.9 Kg/ha (approximately 40 lbs/A) and a second section was treated at 10.5 Kg/ha (approximately 10 lbs/A). It was not originally planned to treat at 2 different rates but there were difficulties with the spreader calibration. In hindsight, these rate differences led to some interesting comparisons of post-treatment body burdens found in the voles.

Meadow voles were collected by kill-trapping from the orchard treated at 10.5 Kg/ha on days 1, 2, and 5-9 post-treatment. Collection of voles from the 45.9 Kg/ha area were similarly made on days 3-7, 18, and 19 post-treatment. In general, mean residue levels from voles trapped on the 10.5 Kg/ha area were less than those from the 45.9 Kg/ha area. Daily means in voles from the 10.5 Kg/ha area ranged from 0.36-2.59 ppm. Greater than 90% of the voles sampled on day 1 post-treatment from the 10.5 Kg/ha area carried detectable burdens of BFC indicating rapid and widespread distribution of the BFC throughout the meadow vole population.

Mean daily residue levels in voles from the 45.9 Kg/ha ranged from 3.53-5.64 ppm. Residue levels from this area showed no sign of declining even 19 days post-treatment. The incidence of voles from this area with detectable BFC residues was greater than 95% of the voles sampled. This observation with a similar observation in the area treated at 10.5 Kg/ha indicated a high probability that any vole caught by a raptor in the treated area would be carrying a BFC burden.

Four cottontail rabbits (Sylvilagus floridanus) and 3 gray-eyed juncos (Junco hyemalis) were found dead in the orchard during ground searches in 1979. The mean residue level of these specimens was <1 ppm and BFC intoxication was suspected. Two opossums (Didelphis marsupialis) and 4 starlings (Sturnus vulgaris) were collected in the treated areas by shooting. These specimens contained no detectable BFC residue.

In the fall of 1980 we conducted a radiotelemetry study in the same location as the 1979 field trial. The orchard was broadcast with VOLAK (0.001% BFC) at 9.1-11.4 Kg/ha (20-25 lbs/A). Three screech owls (*Otus asio*), 1 barn owl (*Tyto alba*), and 1 American kestrel (*Falco sparverius*) were captured within the borders of the orchard and fitted with radio transmitters. The owls were located daily during the post-treatment period. The screech owls were collected for BFC residue analysis during the fourth week after the final section of orchard was treated.

Mortality of 1 screech owl occurred during the post-treatment period but the cause of death cannot be definitely attributed to BFC poisoning until residue analyses of the carcass are completed. The barn owl disappeared from the study area during the post-treatment period immediately after a heavy windstorm and is presumed to have left the area. The kestrel was last observed in the orchard 70 days after the last VOLAK application and apparently suffered no ill effects from the rodenticide use.

Four cottontail rabbits were found dead in the orchard during the 1980 trial as were 2 gray-eyed juncos. Residue analyses have not been completed on these specimens at this time.

PINE VOLE ACTIVITY RESULTS FOR 1979-1980 TOXICANT APPLICATIONS

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The toxicants were placed in an apple orchard consisting of 'Rome' and 'Golden Delicious' trees planted in 1954 at a distance of 20 by 20 feet and thinned to 20 by 40 feet in 1972. Pine voles have been for several years the dominant vole infesting the orchard and have caused an 8% tree loss. Vole activity sites were selected at 30 trees per treatment. Bait applications of brodifacoum (Volak) and chlorophacinone (Rozol) were made by hand placement under roofing pads at one activity site per tree. A treatment was included using the "Mouse-ateria", as the bait station for comparison with the roofing pad bait station. An attempt was made to place the open end of the "Mouse-ateria" at one active vole site per tree. One packet of the Volak bait was placed in each "Mouse-ateria". Pre-baiting vole activity ratings were made December 5-6, 1979. Amount of apple eaten was used as the criterion indicator for activity. Activity rating was based upon the scale of 0 to 10, where 0 = no portion of apple eaten, 3 = less than 50% of flesh eaten, 5 = 50 to 80% of flesh eaten, 8 = 100% of flesh eaten, and 10 = flesh and skin completely consumed. Post-baiting observations of bait consumption was made December 17, 1979. Post-bait activity rating, using apple as the indicator, was made June 3, 1980.

The following bait treatments were applied December 11, 1979:

1. Chlorophacinone 11.2 kg/ha (10 lb/A) or 75 gms/tree.
2. Brodifacoum 50 gram packet per tree (7.4 kg/ha or 6.6 lb/A).
3. Brodifacoum loose bait 50 gms/tree.
4. Brodifacoum 50 gm packet placed in mouse-ateria bait station, 1 per tree.
5. Control - no toxicant.

Table 1. Percent of sites having bait completely removed from placement site one week following bait placement.

Material	Percent of sites having bait completely removed
Chlorophacinone (Rozol)	40
Brodifacoum (Volak) packets	27
Brodifacoum (Volak) loose	70
Brodifacoum (Volak) packets in mouse-ateria	0

The Volak packeted bait at 15% of the pad site locations had been covered with dirt and a new vole trail established around the packet. Only 10% of the packets placed in the "Mouse-ateria" had been opened.

Table 2. Effectiveness of vole toxicants six months following treatment application.

Treatment	Pre-treatment 12-6-79	Post-treatment 6-3-80	Percent Reduction
Chlorophacinone (Rozol)	7.34	4.99	23.5
Brodifacoum (Volak) packet	7.81	5.38	24.3
Brodifacoum (Volak) loose	8.06	4.57	34.9
Brodifacoum (Volak) packet in mouse-ateria	7.94	6.76	11.8
Control - no Toxicant	7.44	7.37	0.7

The packeted Volak placed in the "Mouse-ateria" was still untouched at 89% of the sites when vole activity ratings were made six months following treatment application. Even though activity was present under the roofing pad, some of the Volak packeted bait under the site pad remained unopened through the six month period between the time of application and the June 3, 1980 post-treatment vole activity ratings.

EXPERIMENTAL RESULTS OF CHLOROPHACINONE GROUND SPRAYS IN NORTH CAROLINA

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ABSTRACT: Field experiments with chlorophacinone (CPN) ground sprays seem to be more effective in control of pine voles in North Carolina orchards when the percentage grass cover under tree drip lines is high. Preliminary laboratory results seem to confirm this observation.

Our group has carried out a number of field trials of the efficacy of ground sprays for controlling pine voles in orchards. In reviewing these tests with special reference to inconsistency of results with chlorophacinone (Hayne 1977) an apparent relationship to the amount of grass cover was noted, and laboratory trials were started to test this question.

METHODS: The field experiments were carried out in privately-owned orchards in Henderson County, N.C. Each experimental plot of about 2.0 acres contained a central data area and a buffer zone; the basic design was described by Sullivan and Hayne (1978).

Vole activity was monitored before and after treatment by live trapping and the apple sign test. Blood coagulation times were also recorded but are not reported here. Toxic ground spray was applied by using an angular boom that distributed the material evenly from the tree trunk out to the drip line. An operating pressure of 125 to 135 psi was used; this is lower than recommended but we feel that using this lower pressure reduces drift and keeps most of the toxicant under the tree. The application rate was varied in a study of this factor.

Laboratory tests were carried out in metal boxes using methods described by Davis et al. (1980) with the difference that in some boxes sod with a vigorous growth of grass was used instead of bare soil. In one set of boxes containing sod we added a measured amount of water to simulate rainfall (325 ml/day with 12 animals, 700 ml/day with 10).

RESULTS: Table 1 shows the results of the field tests. The higher the percentage ground cover, the more effective the apparent control. The laboratory results (Table 2) are consistent in that at the same application level, mortality seemed to be higher with sod. Use of simulated rainfall seemed to have little effect on the outcome.

DISCUSSION: These results indicate that chlorophacinone ground spray is most effective in the presence of vegetational ground cover, in this case, grass. Horsfall et al. (1974) observed that the ingestion of this lethal agent by mice may be enhanced by the presence of forbs in the treated greenery. Both observations are consistent with the label advice not to spray bare ground. At present we conclude that where there is little or no vegetation under the trees, chlorophacinone ground spray may not be expected to provide good control of voles.

There may be need to look at other ground sprays under these same conditions.

Table 1. Field trials of chlorophacinone ground spray listed in order of amount of grass cover.

Application per sprayed acre		Grass		Percent activity apple sign test		Number of voles live-trapped		
gal	lb ai	percent cover	mean height in	pre	post	pre-treatment marked	post-treatment marked	post-treatment unmarked
682	0.34	98	9	62	0	39	13*	14*
652	0.33	98	6	70	0	23	0	0
681	0.34	95	7	30	0	17	0	2
555	0.28	90	8	8	0	5	0	1
500	0.25	75	6	79	29	4	1	16
577	0.29	70	6½	38	29	9	1	7
624	0.20	35	6	54	42	97	53	15
693	0.35	10	5	33	33	6	0	3

To qualify for inclusion in this table the test must have had either 4 animals marked and released before treatment or 10 percent active stations with the apple sign test.

*Caught in first 48 hours after spraying; no capture after 72 hours.

Table 2. Laboratory tests of toxicity to pine voles of chlorophacinone applied to bare soil and to sod.

Treatment		Number of voles (died/total)	
cover	lb ai per acre	treated	control
Bare soil	0.2	2/16	0/6
	0.4	4/4	0/2
Sod, no water	0.2	12/12	0/2
Sod, with water	1.2	19/22	0/4

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AN APPROACH TO DETERMINE THE ECONOMIC THRESHOLD LEVEL FOR PINE VOLES

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The effectiveness of orchard management, as in any agricultural system, is judged on the total quantity and quality of the produce and on the financial return per unit of investment. Decisions affecting orchard management are based ultimately on economic factors.

This economic criterion should, therefore, be applied to all orchard pest management decisions--including control of the pine vole (*Pitymys pinetorum*). The purpose of this paper is to describe an approach we are taking to identify factors useful in estimating the economic threshold which can form the basis for cost-effective management of the pine vole and the meadow vole (*Microtus pennsylvanicus*) in apple orchards.

Dyer and Ward (1977) and Dolbeer (1981) state that the decisions in management of pest species should be based on economics. Key factors in economics-based pest control include: estimation of losses caused by short- and long-term damage as a function of pest populations; cost of measures to control the pest within defined population levels; and the opportunity costs of the control measures. When these factors are known the pest control specialist, the orchard manager, and the researcher can make wise judgements on actions to take against the depredating species.

Rodent damage control in apple orchards has evolved largely through use of standard orchard practices. Studies are not available to quantify the levels of damage necessary to determine what control measures are economically justified, or even to identify the range of damage that would establish cost-effectiveness.

There are several reasons for this lack of knowledge. The damage done to apple trees is not easily observed, described, or measured. There is probably not a simple linear relationship between bark removal and economic damage. In addition to these difficulties and because the tree is a perennial, there is cummulative damage as well as recuperative and compensatory processes. In numerous situations, compensatory growth has been suggested and actually demonstrated (Dyer 1973, 1975, 1976, Dyer and Bokhari 1976, Harris 1974, Hutchinson 1971, Pearson 1965, Vickery 1972, Westlake 1963, and Woronecki *et al.* 1976).

To date, only a few attempts have been made to address the economics of pine vole or meadow vole damage in orchards. Pearson (1976, 1977) and Pearson and Forshey (1978) examined the relationship between the presence of voles and tree damage expressed as a reduction in crop value. A few authors have made some theoretical and speculative estimates of damage (Kennicott 1957, Hamilton 1938, Garlough and Spencer 1944, Biser 1967, and Byers 1974). Recently Sullivan *et al.* (1980) have reported some standard survey work examining the magnitude and causes of tree mortality. This gives some concept of economic damage, but cannot be used to isolate even the benefits of current rodent control techniques. Ferguson (1980) and Luttner (1978) have also produced some very broad economic generalizations by extrapolating form rodenticide use figures. These, however, are only measures of standard acceptable orchard practice, and cannot form the basis for vole management in orchards.

A simple description of damage to an apple tree root system is not available. The depth to which damage extends is available only as antedotal information (Benton 1952). Even the simplest understanding of rodent damage, and the response of the tree to such damage, is not currently available. No studies are available which relate the death of trees to the removal of root tissue. There is no information to suggest at what level tissue removal may begin to impair growth, or at what level growth impairment may begin to reduce crop yields and the productive life-span of the tree.

Such information is essential to wise management, and might suggest that 100% control, an industry standard, may be neither necessary nor desirable. We have proposed three studies that should help define the economic threshold level of pine voles and improve our understanding of and recommendations for the moderately damaged tree. These types of studies should also aid in identifying methods useful for making careful damage assessments that are now lacking in pine vole control literature.

METHODS

The first study will address the unsubstantiated hypothesis that vole density is a most important factor in root damage. This study will involve enclosing known vole populations within 0.008 ha fenced plots which contain eight apple trees. The trees are McIntosh on M-26 rootstock and are in their ninth leaf. Vole populations equivalent to 247, 494, and 740+ (family group) voles per ha will be placed within enclosures. Harvest records, shoot growth and leaf analyses, which have been collected during previous research projects, will continue to be done for all trees in each enclosure. When shoot growth, leaf nutrient analysis, and tree specific crop loads are correlated with vole densities, this study should yield information directly related to the economic threshold. If root systems within the enclosed plots are excavated, an even fuller understanding of vole damage on trees should be gained.

To study the long-term, cummulative effects of pine vole damage, a second study will examine the root systems of damaged mature trees. By selecting trees of poor, moderate, and high vigor, a correlation between levels of root damage and the various degrees of tree vigor may be established. A few trees will be removed by excavating all root material greater than 1 cm in diameter. Root material will be sectioned into approximately straight cylindrical segments. The distance between the root crown and each segment will be recorded, and the surface area will be estimated (Π·diameter·height). The portion of the surface area which has been damaged will be estimated using a helical line-transect to sample damaged and undamaged bark on each root segment. The amount of damaged tissue, recorded within 0.5-m zones of the root crown, will be correlated against shoot growth, leaf nutrient analysis, and tree specific harvest records. It is expected that most root systems would not be totally excavated but will be sampled by cutting a 2-m deep trench across the diameter of the dripline (through or immediately adjacent to the tree base). A 15-cm segment of each root exposed will be removed and handled as detailed above. The location (vertical and horizontal) of each exposed segment will also be noted.

The third and later study would examine the possibilities that a damage level accumulated over years of exposure would cause a significantly different reduction in yield than does a one-time exposure to the same damage level. This question can be approached by excavating the root crown and proximal portion of all roots attached to the crown. The desired percentage of damage will be obtained by measuring the total circumference of the exposed roots and the girdling of that portion of the total circumference which is prescribed by the damage category. The levels of damage chosen for each category will correspond to the levels of root girdling observed in the second study.

CONCLUSIONS

The three studies will improve our knowledge of the dynamic relationship between voles, damage, and actual economic loss. The expected insights are numerous and may form the basis for new control techniques. It is disconcerting not to have a good, even simple, understanding of the actual damage (root tissue removal) done by pine voles. A systematic examination of this first order damage is important because it has never been done, and in its absence we may be missing important understandings relating to the functional mechanisms and more importantly the control of pine vole damage.

Through a simple comparison of results from our three studies, several additional observations should be possible. By comparing results from the second and third studies, the importance of damage location (e.g., root hair versus root girdling) and secondary damage (e.g., fungus) should be understood. Comparisons from these studies should also identify damage levels of no or only temporary significance. The results from the first study will be the most direct attempt to determine an actual economic threshold population available to date. This should also provide additional understanding of the relative importance of root hair feeding versus root girdling.

Dolbeer (1981) urged animal damage control researchers to spend half their effort in the study of the economic implications of damage and damage control. Although studies proposed here do not reach this goal, they will begin to improve our understanding of the economics of pine vole damage particularly for the soil types, and age classes of trees in these studies. Only through a fuller understanding of the relationship between voles, trees, crop loss and control efficacy, can we refine our ability to consistently make the most appropriate and economically-sound management recommendations for the control of pine vole damage in commerical apple orchards.

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COMPARISON OF SAMPLING DESIGNS FOR VOLE POPULATION STUDIES

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Introduction

In the summer of 1980 we initiated a large-scale vole population study in the lower Hudson Valley of New York and had questions regarding trapping designs and sampling procedures. Would samples reflect populations as they occurred in the orchard or would results merely be artifacts of the trapping design?

Renzulli et al. (1980) examined how time interval between trapping periods, trap spacing, and grid size affected demographic estimates in meadow voles, Microtus pennsylvanicus, in non-orchard habitats. In other small mammal studies conducted in non-orchard habitats, 2 traps per station are often utilized to avoid the exclusion of animals or compare different types of traps (Krebs 1966, Beacham and Krebs 1980, Glass and Slade 1980, Rose and Gaines 1978, Stickel 1954, Rose et al. 1977). Few, however, actually evaluate the relative efficiency of 1 versus 2 traps per station. Stickel (1954) found a slight increase in number of captures per individual when 2 traps were used instead of 1, but no conclusions were reached.

The relative efficiency of different trapping designs in sampling vole populations in orchards has received little attention. McAninch (1979) found that Sherman live traps were more efficient than snap traps when one of each was placed under the dripline, but other information is limited. Likewise, questions concerning effects of trap movement, day versus night trapping, and trappability need to be addressed in the orchard where densities are often higher than in other habitats and where vole movements are highly influenced by tree and row spacing (Gettle 1975). Thus, a pilot study with the following objectives was initiated:

1) To study the effects of 1 and 2 traps per tree (trap station) and movement of traps during a trapping session on the size and composition of vole sample obtained.
2) To determine the minimum number of trapping sessions needed to mark at least 80% of the trappable population under the different trapping

designs.
3) To determine if any segments of the population are being excluded from capture by trapping only during daylight hours.
4) To determine if trappability of sex and age groups differs within each trapping design or between designs.

Methods

The study area, located in the Minard apple orchard near New Paltz, New York, was a 0.4 ha orchard block bordered on 1 side by a paved road, another by a gravel road and hedgerow, and on the other 2 sides by orchard driveways. Apple trees were spaced at 9 m intervals in rows which were likewise 9 m apart. The block was 6 rows wide and 10 trees long. Each trap station consisted of a circle defined by the dripline of the tree and was divided into 4 equal quadrants.

The experiment was divided into 3 phases:
Phase 1: From June 28 to July 2, 1980, 2 Sherman live traps (5x5x18cm) were randomly placed in 2 of the 4 quadrants under the dripline of each tree within the vole runway system. Traps were checked every 3-4 hours during the day hours and closed at night. Two trapping sessions, i.e., a 3-4 hr interval culminating with a trap check, were conducted each day. After 6 trapping sessions, when few new voles were being captured, traps were moved to the 2 remaining quadrants around the same tree, so that eventually all 4 quadrants under the tree had been trapped. Three more trapping sessions were conducted, after which traps were set overnight for a final session. Voles were sexed and classified as adults or immatures (juveniles and subadults) based on body weight and the condition of mammae and genitalia.
Phase 2: This phase of the experiment, conducted July 3 to 5, began the day after Phase 1 ended in order to minimize the impact of vole movements into and out of the study area. Two traps were placed in the runways of each of 2 randomly chosen quadrants under the dripline. Two trapping sessions were conducted per day for a total of 6 sessions; traps were not moved.
Phase 3: This phase was conducted on July 6-7 and immediately followed Phase 2. One trap was placed in a randomly chosen quadrant at each tree. Five trapping sessions were conducted, 2 on the first day and 3 on the second. Traps were not moved.
Statistical tests were from Sokal and Rohlf (1969).

Results and Discussion

The number of new voles captured after the first 3 trapping sessions was low under all 3 trapping designs for all sex and age groups (Figs. 1,2,3). The trappable population under each phase of the experiment was defined as the total number of individual voles captured, i.e., 64, 49, and 33 for Phases 1,2, and 3, respectively.

Eighty to 90% of the trappable population were captured by the third trapping session in all phases of the experiment (Table 1). The number of new voles captured declined linearly with successive trap sessions for the first 2 phases (Fig. 1,2,3, Table 2). These regressions were significant ($P<0.05$) for most sex and age groups in Phase 1 and 2 but not Phase 3. By comparing the slopes of the regression lines

Table 1. Cumulative percent and number of original pine vole captures for the first 3 trapping sessions for the comparison of the 3 phases of an experiment conducted June 28 to July 7, 1980 near New Paltz, New York.

Trapping Session	Phase I (N=64) percent	Phase I (N=64) number	Phase 2 (N=49) percent	Phase 2 (N=49) number	Phase 3 (N=33) percent	Phase 3 (N=33) number
1	50.0[a]	32	55.1	27	60.6	20
2	76.6	49	83.7	41	75.8	25
3	79.7	51	89.8	44	78.8	26

[a] Chi-square test revealed no significant differences (P<0.05) between the 3 phases during trapping session 1, 2, or 3.

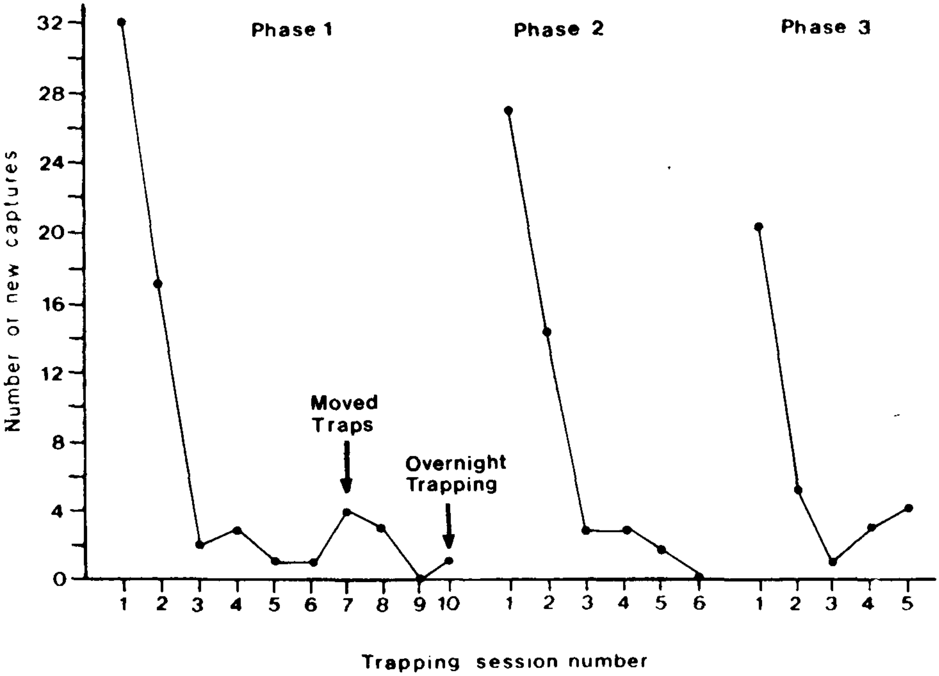

Fig. 1. Number of pine voles captured in each trapping session during the comparison of 3 phases of an experiment conducted June 28 to July 7, 1980 near New Paltz, New York.

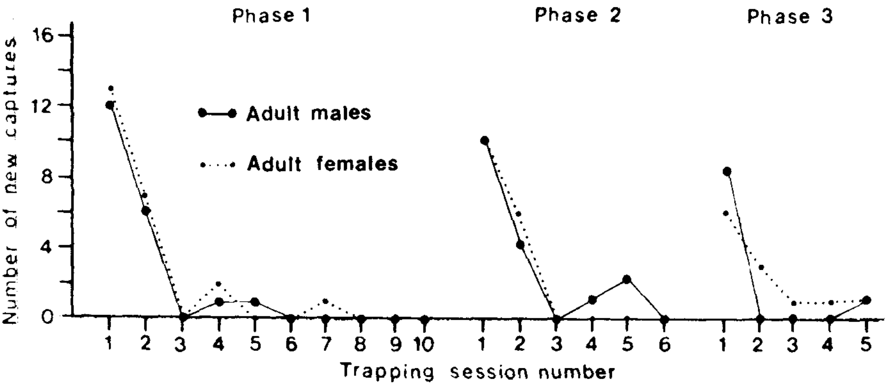

Fig. 2. Number of adult male and female pine voles captured in each trapping session during a comparison of 3 phases of an experiment conducted June 28 to July 7, 1980 near New Paltz, New York.

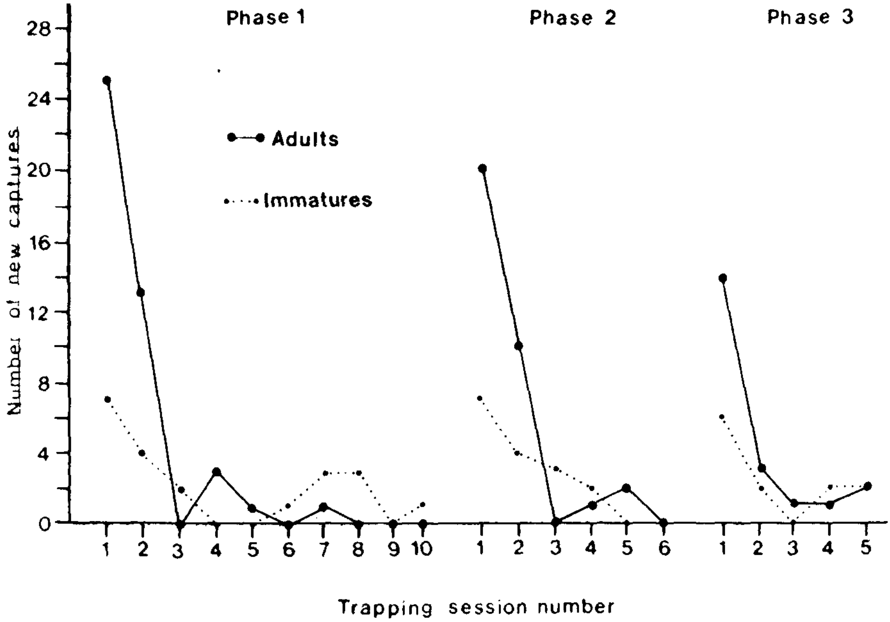

Fig. 3. Number of adults and immatures captured in each trapping session during the comparison of 3 phases of an experiment conducted June 28 to July 7, 1980 near New Paltz, New York.

Table 2. Regression statistics of original vole captures on trap session number for the comparison of 3 phases of an experiment conducted June 28 to July 7, 1980 near New Paltz, New York.

Total Voles		Phase 1	Phase 2	Phase 3
Slope	=	-2.3636	-4.8857	-3.4000
Intercept	=	19.4000	25.2667	16.8000
R^2	=	0.4880	0.7639	0.4957
P	=	0.0246	0.0228	0.1844
Adult Males				
Slope	=	-0.9333	-1.5714	-1.4000
Intercept	=	7.1333	8.3333	6.0000
R^2	=	0.5061	0.5933	0.4016
P	=	0.0210	0.0731	0.2509
Adult Females				
Slope	=	-1.0242	-1.9429	-1.2000
Intercept	=	7.9333	9.4667	6.000
R^2	=	0.5088	0.7078	0.7500
P	=	0.0206	0.0358	0.0577
Immature Voles				
Slope	=	-0.4061	-1.3714	-0.8000
Intercept	=	4.3333	7.4667	4.8000
R^2	=	0.3029	0.9315	0.3333
P	=	0.0992	0.0018	0.3081

of any one sex or age group between Phases 1, 2, and 3, we could determine if the rate of capturing the trappable population varied with the trapping design. Likewise, by comparing the slopes of lines within any one phase, differences in rates of capture for the different sex and age groups for any one trapping design could be determined. Because most of the trappable population had been captured by the third trapping session and the number of new captures after this point were negligible and appeared to fluctuate randomly (Figs. 1, 2, 3), regressions of new vole captures on trap session number were also calculated for the first 3 sessions.

Comparison of the slopes of these regression lines indicated no significant differences existed within the total vole group, adult male group, or immature group.in Phases 1, 2, or 3. However, slopes of lines for adult females were significantly different (P=0.0103) between Phases 1 and 3, a result that might have been due to the small sample size of Phase 3. A comparison of slopes within any one phase of the experiment indicated no significant difference in rates of capture between adult females and adult males for any given phase. However, rates of capture of adults versus immatures differed significantly within Phase 1 (P=0.0017) and within Phase 2 (P=0.0052). Adult sex ratios did not differ significantly between Phases 1, 2, or 3, nor did adult to immature ratios, further evidence that the 3 different trapping designs sampled the same population (Table 3).

Table 3. Comparison of sex and age ratios of pine voles for the three phases of an experiment conducted June 28 to July 7, 1980, near New Paltz, New York.

	Phase 1	Phase 2	Phase 3
Adult males[a] / Adult females	0.87:1 (n=43)	1.06:1 (n=33)	0.75:1 (n=21)
Adults[b] / Immatures	2.05:1 (n=64)	2.06:1 (n=49)	1.75:1 (n=33)

[a] X^2 test revealed no significant difference ($P<0.05$) from a 1:1 ratio in any phase of the experiment

[b] X^2 test revealed no significant difference ($P<0.05$) from a 2:1 ratio in any phase of the experiment

Estimates of relative abundance or population density from Phases 1, 2, and 3 provided an additional basis for comparing the 3 trapping designs. Mean catch per unit effort did not differ significantly between the 3 phases ($P<0.05$)(Table 4). A Lincoln Index (Lincoln 1930)

Table 4. Comparison of number of captures of pine voles per 100 trap sessions for the 3 phases of an experiment conducted June 28 to July 2, 1980, near New Paltz, New York.

Trapping Session Number	Pine Voles Captured/100 Trap Sessions[a]		
	Phase 1	Phase 2	Phase 3
1	30.33	23.18	34.19
2	20.56	19.57	23.93
3	9.30	17.72	13.33
4	17.06	24.03	16.81
5	16.81	20.51	25.64
6	14.72	13.56	-
7	10.05	-	-
8	22.22	-	-
9	9.28	-	-
10	13.56	-	-
MEAN±S.D.	16.39±6.65	19.76±3.82	22.78±8.13

[a] Captures per 100 trap sessions were corrected for sprung traps (Nelson and Clark 1973).

was used to compute population estimates. Confidence limits ($P=0.95$) were calculated according to Bailey (1951). An estimate of 75.7±8.7 was computed for Phase 2 and 71.4±9.0 for Phase 3 using the 64 voles trapped in Phase 1 as the number marked and released. A second estimate of 78.1±8.6 was calculated for Phase 3 utilizing the 64 originally marked voles plus 7 new voles marked in Phase 2 for a total of 71 marked and released voles. Differences in the population estimates were not significant ($P<0.05$).

Moving traps to different quadrants around a tree did not markedly change the sex or age composition of the catch. A total of 7 new voles, 1 adult female and 6 immatures, was captured in Phase 1 subsequent to moving traps (Fig. 3). Four of these 6 immatures were recaptured in subsequent trapping sessions indicating that they were not being excluded from capture by other, possibly more dominant, voles. Although 7 new voles were captured upon moving traps, the age ratios indicate that the same population was sampled with trap movement (Phase 1) and without trap movement (Phases 2 and 3)(Table 3). One possible explanation for the capture of 6 new immature voles upon trap movement is that these voles might have just entered the trappable population about the time that traps were moved. In any event, it seems probable that these immatures would have been captured without trap movement in Phase 1 because a substantial proportion of immatures were captured after the first 3 trapping sessions in Phases 2 and 3 (Fig. 3).

The 1 overnight trapping session produced only 1 new immature vole captured on the periphery of the study area. Thus, it appears that no segment of the population was excluded from capture by trapping only during the daytime.

Phases 2 and 3 involved less effort than Phase 1. Traps were not moved, and fewer trapping sessions were involved. As expected, fewer voles were captured in Phases 2 and 3. However, trapping success did not change markedly (Table 4), and new segments of the population were not encountered. Only 14.3% of the voles captured in Phase 2 and 9.1% of those captured in Phase 3 were captures of new, unmarked individuals.

Often, more than 1 trap per station is recommended to reduce the probability that the capture of an individual will prevent the capture of another at the same location. A trap station is said to be saturated with traps if at least 1 of 2 or more traps at a station remains unoccupied. Trap station saturation is particularly important to mark-recapture estimators that assume equal trap exposure or probability of capture for all individuals in a population.

In spite of high trapping success for each trapping session (9% to 30%) and vole densities of approximately 175/ha, trap station saturation was achieved with 2 traps per station. During any given trapping session, 2 occupied traps were found at only 3% of the stations in Phase 1 and at 5.8% of the stations in Phase 2. These percentages increased to 3.5 and 6.5, respectively, when the data were adjusted for sprung traps (Nelson and Clark 1973).

Trappability, calculated according to a modification of Beacham (1979), was highest for adult females and lowest for immatures in all 3 phases, but the difference was significant only in Phase 1 ($P=\leq0.05$)

(Table 5). Immatures differed significantly between Phases 1 and 2

Table 5. Trappability indices of sex and age groups of pine voles trapped during 3 phases of an experiment conducted June 20 to July 7, 1980 near New Paltz, New York.[a]

	Phase 1	Phase 2	Phase 3
Adult Males	.321 (n = 19)	.456 (n = 15)	.420 (n = 7)
Adult Females	.357 (n = 23)	.531 (n = 16)	.446 (n = 13)
Immatures	.188 (n = 24)	.398 (n = 18)	.320 (n = 15)

[a] Trappability = $$\frac{\sum^{N} \frac{\text{No. of captures for an animal}}{\text{No. of possible captures for that animal}}}{N}$$

where N is the number of animals captured at least once

(P<0.05). Trappability decreased slightly for all groups in Phase 3, possibly because fewer traps were set. The lower trappability indices of immatures for all phases agree with the lower rates of capture revealed in the regression analysis. These combined data suggest that perhaps immatures are subject to underestimation in any trapping design.

Summary and Conclusions

Different sex and age groups of a pine vole population were sampled in equal proportions in Phases 1, 2, and 3. We conclude that one trap per tree will adequately sample a pine vole population in most orchard studies unless a very high number of captures is required as with Jolly-Seber survival estimates (Arnason and Baniuk 1980). In our study, voles were captured in both traps only 3 to 6% of the time when 2 traps were placed at each station. Thus the use of 1 trap per tree is justified to reduce effort and increase replication.

Approximately 80 to 90% of the trappable population under each trapping design were captured by the third of 6, 3-4 hr trapping sessions. Regardless of trapping design, the first 3 trapping sessions were the most important for the capture of new voles. For most studies we feel it is not necessary to move traps or extend trapping far beyond 3 trapping sessions unless it is necessary to capture nearly all voles present or a large number of recaptures.

In studies involving pine voles, traps are often checked only once or twice daily (McAninch 1979, Hayne 1977, Paul 1970). However, by using a 3-4 hr trapping interval, up to 3 trapping sessions can be completed per day. This interval seemed to allow voles adequate time to encounter traps, and trap mortality was practically eliminated. Likewise, trapping only during the day reduced the possibility of trap mortality on cold nights and did not appear to exclude any segment of the population from capture.

Trappability was somewhat lower for immatures than for adults regardless of trapping design. Adult females appeared to be slightly more trappable than either adult males or immatures. Hayne (1978), however, reported no difference in trappability of these groups when he trapped for 2 trapping sessions, each 24 hr long. Possibly relative trappability differs with length of trapping session, season, or reproductive condition. This study supports Hayne's (1977) conclusion that some voles are trapped more often than others, an important bias if trapping is continued over a long period of time.

Acknowledgments

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Seasonal Variations in Movements and Habitat Use by Pine and Meadow Voles

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Abstract: Free-ranging pine voles (*Microtus pinetorum*) and meadow voles (*M. pennsylvanicus*) were radiotracked in a maintained apple orchard environment in August and December 1980. Meadow voles maintained larger home ranges than pine voles in the summer, but had similar-sized ranges in December. The home ranges for both species decreased with the onset of winter. Pine and meadow voles showed a strong tendency to remain within rows and to restrict most of their movement to areas beneath the canopy. Despite some overlap in space use between the species, the movements of both vole species suggested mutual avoidance. Differences in habitat utilization between pine and meadow voles was also suggested.

INTRODUCTION

This study focuses on the interactions of the two vole species generally co-inhabiting the orchards of the Hudson Valley, New York, namely the pine vole (*Microtus pinetorum*) and the meadow vole (*M. pennsylvanicus*). Movement and habitat use data are being collected on a seasonal basis using radiotelemetry techniques as a primary research tool. The main purpose of the research is to gather information that will aid in the development of a vole management program.

METHODS

Site Selection

Choice of a specific research site was based on heterogeneity. The 0.7 habitat site chosen consists of eight rows with sixteen trees in each row. Row spacing is 11 meters and tree spacing is 5 meters. Trees range from five years to greater than thirty years in age. Odd numbered rows have trees greater than thirty years old alternating with interplants five to ten years old. Even numbered rows include trees twenty years old or younger. The vegetation and soil variables measured on the site show considerable variability as well.

Under the above circumstances, it was hypothesized that the two vole species would be more likely to make choices and show habitat preferences, and any tendency for pine and meadow voles to separate would be more evident.

Trapping and Telemetry

Trapping was conducted monthly to collect population data and once a season to collect animals for radiotelemetry. Two traps were placed at every other tree for four checks over a two day period. The traps were then shifted to the alternate trees for checks over another two day period.

Animals selected for the telemetry work were taken to a field station where radiotransmitters were surgically implanted in the intraperitoneal cavity (see Madison et al. in this issue for details regarding equipment and methodology). The animals were then released at the position of capture within twenty-four hours of surgery. After a several day recovery peiod, radiotracking was begun.

Seasonal radiotelemetry sessions were comprised of three twenty-four hour periods. Each twenty-four hour period consisted of three different eight hour segments, each segment being monitored once during a 48 hour period. Thus, a twenty-four hour cycle was completed in two days. All animals were located every half-hour. It was felt that this sampling regime should give an adequate sample of data points to obtain representative movement and habitat use patters for each animal.

Only adult females were used during the telemetry sessions. The decision to use only females was based on the observations that female meadow voles have more stable home ranges than males (Madison, 1980), and thus would have more definitive habitat use patterns. Pine voles appear to have no great sexual differences in movement patterns (FitzGerald and Madison, these proceedings), but only female pine voles were used in order to keep methods standardized for the two species.

Habitat

Figure 1 is a schematic representation of the collection of habitat data. Measurements for each soil and vegetation variable were taken one meter from the base of the tree. Four sampling points were located around each tree on the study site as shown in the diagram. The triangles represent the areas of effect for each habitat sampling point. Telemetry positions falling in any one of the triangles take on the particular habitat values obtained at that sampling point.

The habitat variables included in this study are as follows (see McAninch, 1979, for details):

- Tree
  - Age
  - Canopy Coverage
  - Density (Light Reception)

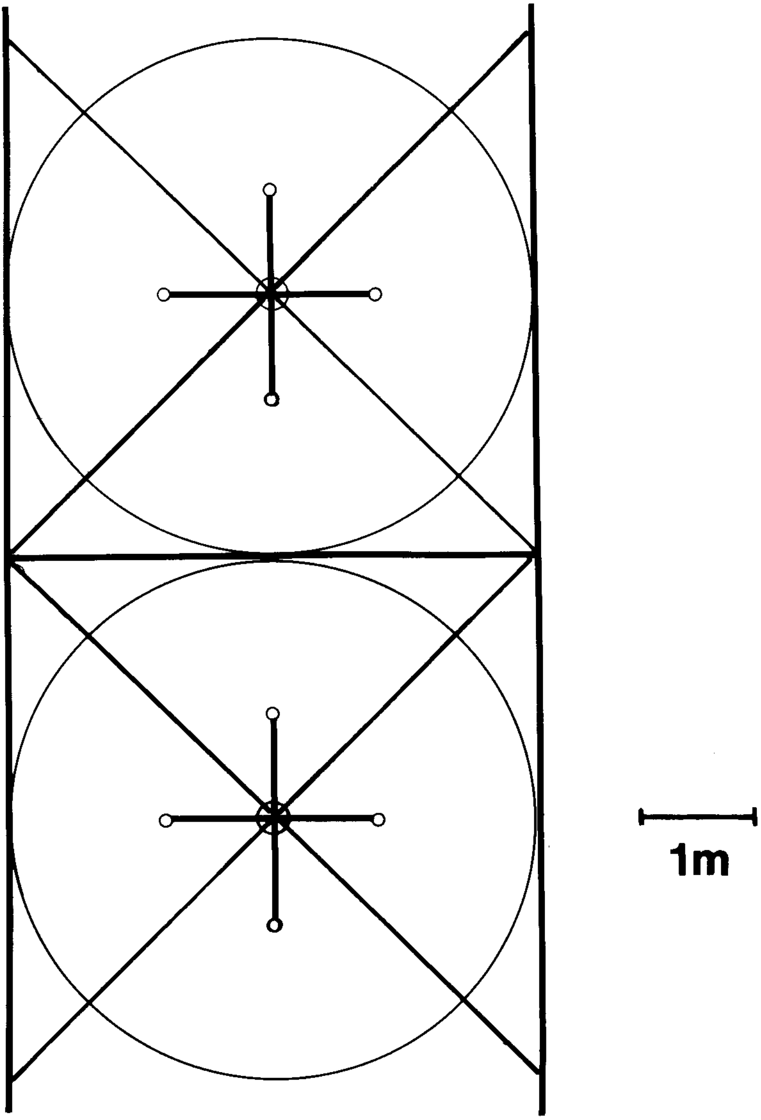

Figure 1: Schematic diagram representing the methods of habitat data collection. Sampling points are indicated by the small circles; the tree trunk, by the medium sized circles; and the canopy, by the largest circles. See text for further explanation.

- Soil
  - Organic Matter
  - Moisture
  - pH
  - Compaction
  - Litter Depth
  - Litter Composition
- Vegetation
  - Ground Cover
    - Composition
    - Coverage
    - Horizontal Density
    - Debris

Statistical Analysis

Regression analysis was performed on the habitat and telemetry data. Correlations were obtained by regressing the telemetry positions for each species on the values for each habitat variable. The correlation coefficients were then tested for statistical significance and assigned "+" values (for positive correlation), "-" values (for negative correlations), or "0" values (for no correlation). The meadow and pine voles were then compared on a relative basis for any differences in habitat preferences.

RESULTS AND DISCUSSION

Movements

Two telemetry sessions have been completed thus far. The first was conducted in late August, 1980 and the second in early December, 1980. Comparisons of movement patterns of the two vole species and the seasonal changes that occur are shown in Table 1. Home range areas were calculated using the 100% minimum polygon method as described by Michener (1979).

Table 1: Movements and average home range size for female meadow and pine voles during August and December telemetry sessions.

Season	Vole Species	No. Voles Analyzed	Telemetry Positions[1]	Row Crossings	Home Range (m^2)
Aug.	Meadow	3	120	12	66.7 ± 3.0
	Pine	3	144	2	40.3 ± 2.0
Dec.	Meadow	5	577	2	17.0 ± 0.8
	Pine	6	700	0	18.6 ± 0.9

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[1] The Discrepancy between August and December in the total number of telemetry positons obtained for each vole species was casued by battery failure, a problem which has since been corrected.

Table 1 shows row crossings to be a rare event. During August one individual accounted for all twelve of the meadow vole crossings. Pine voles rarely crossed rows. In December there was virtually no crossing of rows for either species as compared to the total number of positions obtained per species. The low frequency of movement across rows for both seasons indicates a stong within row orientation for female pine and meadow voles.

Table 1 also shows that female meadow voles maintain larger home ranges than female pine voles in the late summer, but in December the ranges of the two are practically the same. In addition, home range size decreased considerably for females of both species with the onset of winter. This information is visually represented in Figures 2 and 3. The decrease in home range area could be due to a change in food supply, a decrease in reproductive activity, climatic changes, or a combination of these factors.

During August considerable overlap occurred among three female voles in the area of one tree (Fig. 2). Two pine voles, while not overlapping to any great extent themselves, enveloped nearly all of a single meadow vole home range. Although they utilized many of the same areas, the three individuals were never located in the same 2 m^2 area at the same time.

Two cases of overlap occurred between female pine and meadow voles during the December telemetry (Fig. 3). These voles overlapped (within the same 2 m^2 area at the same time) during only 5% of the telemetry positions recorded for these individuals. However, in one case the pine vole and meadow vole were not separable by time or horizontal distance.

The data suggests a possible mutual avoidance between pine and meadow voles. Although overlap of home ranges does exist, females of the two species appear to avoid contact. Further study is needed on the possible separation of female pine and meadow voles in time or space. Space in this sense includes both horizontal and vertical components.

Habitat Use

Possible explanations for seasonal changes and interspecific differences in movement patterns could lie in habitat factors. One such factor is the area covered by the tree canopy. A striking characteristic of a mature apple tree is the extent of influence of its canopy.

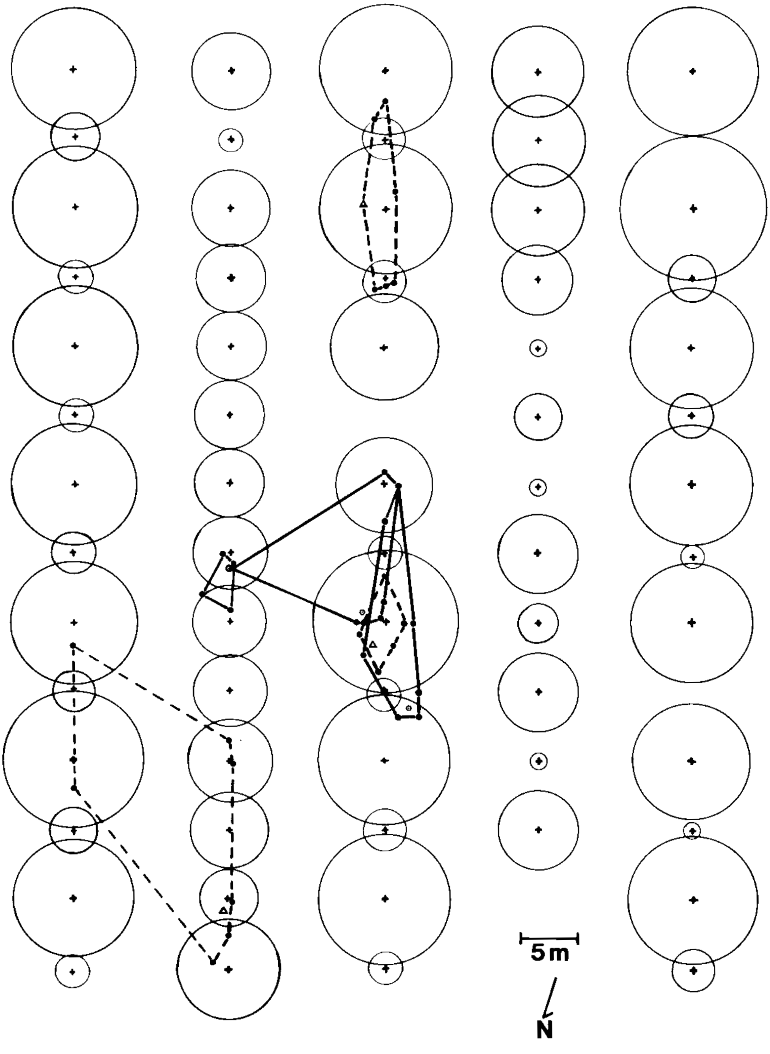

Figure 2: August telemetry data. Pine vole home ranges are indicated by solid lines; nests, by circles with dot. Meadow vole home ranges are indicated by broken lines; nests, by open triangles. Crosses represent tree locations and large circles are measured tree canopies.

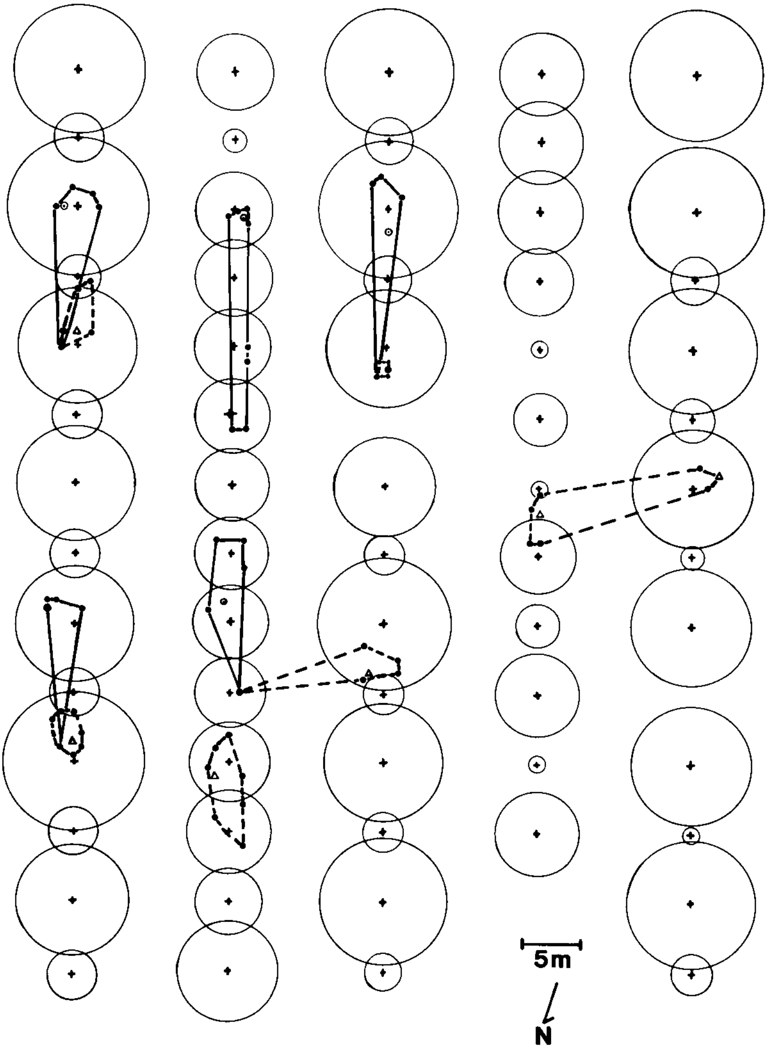

Figure 3: December telemetry data. Pine vole home ranges are indicated by solid lines; nests, by circles with dot. Meadow vole home ranges are indicated by broken lines; nests, by open triangles. Crosses represent tree locations and large circles are measured tree canopies.

Two of the three pine voles, for a combined total of 21 positions, moved outside the canopy corridor in August. This represents about 15% of the total pine vole positons obtained for the first telemetry session. Meadow voles remained entirely within the canopy area. During December one meadow vole accounted for all 57 telemetry positions falling outside of the canopy covered areas, which is about 10% of the total positions obtained for meadow voles. No positions were obtained for pine voles outside of the canopy covered areas at this time. Although during both telemetry sessions animals did cross rows, no positions were actually located in the aisles between rows.

Again the data suggest a strong within row orientation for females of both species. It appears as though canopy coverage is of more importance to the pine and meadow voles than actual age of the tree under which they are found. Although an individual might be found under a young interplant, the vole could still be within the influence of an older tree due to the extent of the tree's canopy.

Female pine and meadow voles appear to use certain habitat characteristics differently (Tables 2 and 3). During August, pine and meadow voles showed a negative correlation with grass cover, but differed in their use of forb cover. These results could be due to a seasonal change in food and/or cover availability, with grasses maturing in early summer and giving way to forbs in August.

Table 2: Correlation coefficients between vole distribution and habitat characteristics for August. Positive correlation +; Negative correlation -; and No correlation 0. All values were tested at the .05 level of significance. Df for meadow voles = 118 and pine voles = 142.

Habitat Variable	Meadow Vole Correlation	Pine Vole Correlation
Ground Cover: Grass	- (-0.41)	- (-0.15)
Ground Cover: Forbs	+ (0.42)	0 (0.04)
Ground Cover: Bare Ground	+ (0.48)	+ (0.59)
Soil Compaction	- (-0.34)	- (-0.42)
Horizontal Veg. Dens., 0-25 cm	+ (0.70)	- (-0.18)
Horizontal Veg. Dens., 0-1 m	+ (0.22)	+ (0.26)
Ground Litter Depth	0 (0.05)	+ (0.85)

Also from Table 2, meadow voles show a positive correlation with horizontal vegetation density from 0-25 cm, but have no correlation with ground litter depth. Pine voles, on the other hand, had only a slight preference for areas of less horizontal vegetation density (0-25 cm) but were strongly attracted to areas of greater ground litter depth. This could be related to the surface orientation of the meadow vole and the requirement of a dense vegetative cover through which it can move and feed. The more fossorial pine vole may not require the heavy vegetative cover for protection or food, yet desire ground litter as a cover under which they can burrow.

As indicated by the correlations with soil compaction, both species also prefer looser soils in which they can burrow and form runways. Telemetry work suggests that both species utilize underground runways. Direct observations indicate that meadow voles as well as pine voles construct underground tunnel systems, although the extent of burrowing for each species may differ.

Several habitat variables studied in August were not applicable in December due to the change in seasons. From Table 3, however, it is evident that a seasonal shift in preference occurred in at least one habitat variable. Meadow voles, in December, shifted to a slightly negative correlation with horizontal vegetation density (0-25 cm), while pine voles at the same time showed no preference for high or low values. This could be related to the fact that most of the above ground vegetation had died by December.

The two species showed no change in preference for ground litter depth between seasons, except that pine voles did not show quite as strong a positive correlation as in August. Although having a positive correlation with ground litter depth, the movements of pine voles tended to be away from areas with a higher percentage of leaf cover. Meadow voles showed a slight positive correlation with leaf litter.

Apple drops during the late summer and autumn supply a good source of moisture and food. Pine voles appeared to prefer areas with greater numbers of apples; meadow voles showed only a weak positive correlation. The number of apples found on the ground in any location can be directly related to the age and productivity of the trees in the immediate vicinity. However, such correlations as found between the voles and apple drops could very well be related to other preferred habitat characteristics chosen prior to fruit maturation.

Table 3: Correlation coefficients between vole distribution and habitat characteristics for December. Positive correlation +; negative correlation -; and No correlation 0. All values were tested at the .05 level of significance. Df for meadow voles = 575 and for pine voles = 698.

Habitat Variable	Meadow Vole Correlation	Pine Vole Correlation
Ground Cover: Leaf Litter	+ (0.23)	- (-0.52)
Horizontal Veg. Dens., 0-25 cm	- (-0.16)	0 (0.02)
Ground Litter Depth	0 (0.01)	+ (0.21)
Apple Count	+ (0.15)	+ (0.46)

The results presented here are only preliminary findings, and further analysis will be conducted on the data in the future. What has been learned to this point will aid in the collection of data during the second field season. One area of importance that needs further study is the possibility that females of the two species are mutually avoiding each other in time and/or space. The results shown here also suggest possible differences between pine and meadow voles in habitat use patterns. A closer look at such habitat variables as ground cover composition, horizontal vegetation density, and ground litter depth is needed.

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Radiotelemetric Evaluation of the Effect of Horticultural Practices On Pine and Meadow Voles in Apple Orchards: I. Rotary Mowing

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Abstract: Pine voles (Microtus pinetorum) and meadow voles (Microtus pennsylvanicus) were studied in three apple orchard plots in the Hudson Valley of New York during June and July 1980. Selected voles from each plot were given miniature radiotransmitters and then tracked before, during, and after rotary mowing.

A total of 11 pine voles and 6 meadow voles were tracked. Home range size was much larger for meadow voles than pine voles. During mowing, meadow voles were noticeably affected by the mower; pine voles were not. No change occurred in the area utilized before and after mowing for either species, nor did any significant mortality result from the treatment. Voles of both species showed a slight but significant tendency to remain closer to the tree rows after mowing. We conclude that rotary mowing has a negligible effect on vole movement and survival under the conditions of this study.

INTRODUCTION

Pine and meadow voles are among the most poorly understood pest species in apple orchards, yet they regularly cost east coast apple growers millions of dollars in production each year. Considerable effort has been spent in trying to develop effective controls, but the secretive habits of voles are not easily studied. In addition, these rodents have a phenomenal ability to recover from temporary population declines. The problem of effective control is further confounded by the presence of two vole species that have different habitat preferences, diets, and behavior patterns (FitzGerald & Madison, 1981; Madison, 1980, 1981; McAninch, 1979; Pagano & Madison, 1981) and hence would likely require different methods for the most effective biological control.

The present study is the first of an ongoing series of studies devoted to measuring in what way different horticultural practices actually affect the movements and survival of both pine and meadow voles. Radiotelemetry is used to overcome many of the methodological shortcomings of previous studies. In this study, we report the effect of rotary mowing on vole movement and survival.

METHODS

The study was conducted on three separate apple orchard plots within Stanley Orchards (owned by Stanley Cohn), Modena, Ulster County, New York from 23 June to 7 July 1980. In the "pine vole plot," the habitat consisted of old trees with wide spacing between the rows and trees. Forbs were common under the trees. Pine voles predominated about 4:1 over meadow voles in this habitat, and only pine voles were studied here. In the "meadow vole plot," the habitat consisted of trees less than 10 years old, and the spacing between rows and trees was much smaller. Meadow voles were essentially the exclusive residents in this area. Rich grass growth and more furrowed ground characterized this habitat. Only meadow voles were studied here. In the third "mixed species plot," old trees and young tree interplants were common. This habitat was more heterogeneous in tree age and ground cover than the other two. Both species of vole were equally abundant, and both were studied.

After an initial census period during May and June, we attempted to select three adults of each sex of each species for radiotracking from the 3 study plots, making 6 pine voles from the pine vole plot, 6 meadow voles from the meadow vole plot, and 6 of each species from the mixed species plot. These animals would then be studied intensively using radiotelemetry before, during and after the mowing operation.

The radiotelemetry methods used have been reported previously (Madison, 1977; Mineau & Madison, 1977). The one exception to the cited methodology is that, instead of being attached to collars, the radiotransmitters were encapsulated in parafin (Elvax, Minimeter) and implanted within the intraperitoneal cavity (see Smith, 1979, for similar techniques). A one cm incision was made in the ventro-lateral abdominal wall for this implant, and the incision was closed with 4-0 sutures (muscular layer) and a wound clip (skin). The voles were anesthetized with ether during the operation, and all voles were released within 24 hours of the operation. Subsequent trapping revealed that all wounds healed quickly and that no losses occurred because of the surgery. The radiotransmitter-battery packages weighed from 2 to 3 grams each (depending on the battery used), which is about 10% of total body weight.

From the time of surgery on 23 to 25 June, the voles were given an additional 5 days to recover from the surgery. Then, 20 "before" positions were obtained on each of the voles over a 40 h period from 1600 on 30 June to 0800 on 2 July. Mowing occurred between 0800 and 1600 on 2 July, during which time the movements of 9 voles were observed in response to the passing of the mower. The "after" period of 20 positions was from 1600 on 2 July to 0800 on 4 July. The voles were collected from 5 to 7 July to recover the transmitters.

The mower used was a tractor-hauled rotary mower. The rotary unit was offset 4 feet behind the tractor, and therefore allowed some mowing under the canopy of the apple trees. Blade height was variable at about 4 to 5 inches above the surface in order to keep the blades from hitting rocks or other objects extending above the ground. Because younger trees had a smaller canopy, mowing was closer to the tree base in the meadow vole plot, but here the furrowed soil gave compensating protection from exposure.

The data were analyzed two ways. First, to derive an estimate of area, the outer points of each series of 20 positions were connected to form a convex polygon. The area inside the perimeter line for each vole was measured before and after mowing. A second analysis was conducted to determine whether voles stayed closer to the tree rows after mowing. For this analysis, the distance from each position to the nearest tree row was measured. For both types of analyses, the number of voles with larger or smaller areas, or with positions farther away from or closer to the tree row, were compared before and after mowing using Chi square analyses.

RESULTS

General. Of the original 24 voles that were expected to be monitored with radiotelemetry, only 23 individuals were given transmitters: 6 voles in each of the pine and meadow vole plots, and 11 in the mixed species plot. Of these 23 voles, only 17 were monitored throughout the study period: 6 in the pine vole plot, 4 in the meadow vole plot, and 7 in the mixed species plot. The positions on these 17 voles constitute the data set used in the analysis. Of the 6 voles omitted from the analysis, one (a meadow vole) was killed by the rotary mower, 4 could not be tracked because of premature battery failure (a problem since resolved), and one disappeared (either taken away by a wide-ranging predator or just never recaptured after battery failure).

Home range size was conspicuously different between pine and meadow voles (Table 1). Five of the 6 home ranges for meadow voles were larger than the 11 ranges recorded for pine voles (Figs. 1,2,3). For meadow voles, males tended to have larger home ranges than females, but the small sample size precludes any conclusive statement. No such trend existed for pine voles. Finally, meadow voles routinely moved between rows, whereas pine voles rarely did so. Five of the 6 meadow voles had ranges spanning 3 to 5 rows, and the one female that remained within a row moved along 7 trees in the row. For pine voles, only two of the 11 voles moved into an adjacent row, and one of these two did so only once. One female pine vole was unusual in that movements occurred along 13 trees in one row (Fig. 3).

Effects During Mowing. While the rotary mower was moving along the rows, the movements of the 9 voles (4 pine, 5 meadow) with radio-transmitters were observed closely. A distinct difference emerged in the response of the two species. The pine voles showed little or no movement (1-2 m maximum) during the 8 passes made by the mower over pine vole burrow systems. For meadow voles, all 5 showed movement during the 10 passes made by the mower into their living areas. Of the 5, 2 moved from 1 to 4 trees away in the same row, and 3 moved into the adjacent rows. "Fleeing" or "rapid" movements were observed up to 20 m ahead of the approaching mower. Only during the second pass of the mower for one meadow vole did the vole appear to enter a burrow system. Otherwise, all meadow vole movement seemd to be on the surface. All pine vole movement appeared to be underground.

Table 1. Home range size and distance to tree row before and after rotary mowing for pine and meadow voles during early July 1980.

Variable	Sex	N	Sample Means[1] Before	Sample Means[1] After	No. voles with larger means Before	No. voles with larger means After
Area (m^2)						
M. pennsylvanicus						
	M	3	1034±928	1337±837	0	3
	F	3	440±648	287±381	2	1
M. pinetorum						
	M	6	15±18	24±33	2	4
	F	5	25±28	13±8	3	2
					7	10
Distance (m)						
M. pennsylvanicus						
	M	3	0.7±0.4	0.4±0.1	2	1
	F	3	0.3±0.1	0.2±0.2	2	1
M. pinetorum						
	M	6	1.1±0.5	0.8±0.6	5	1
	F	5	0.6±0.4	0.4±0.3	4	1
					13	4

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[1] Sample means are averages ± 1 standard deviation of the mean values for each vole

Effects Before and After Mowing. The sizes of the home ranges were measured before and after mowing for both species. No significant changes occurred in home range size (Table 1), and no shifts in home range location were evident (Figs. 1,2,3).

When the distances of the positions of each vole to the nearest tree row were measured, both pine and meadow voles stayed closer to the tree rows after mowing. This observation was statistically significant for pine voles ($\chi^2 = 4.45$, $p < 0.05$), and for both species combined ($\chi^2 = 4.8$, $p < 0.05$), but not for meadow voles separately. It should be mentioned, however, that the actual distances were small, usually less than one meter.

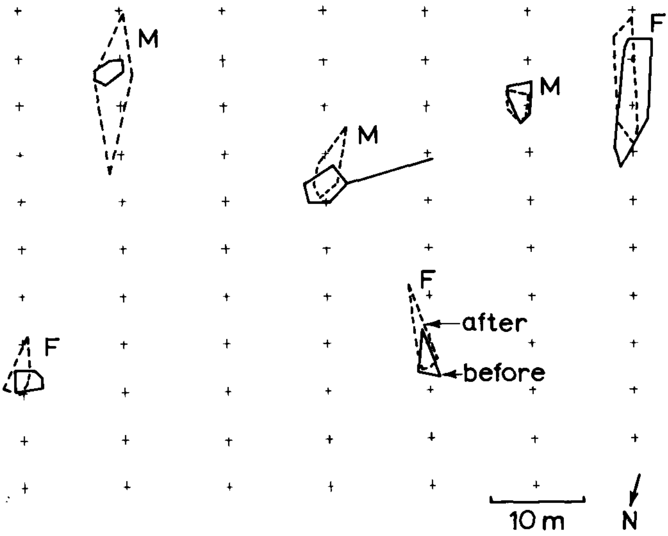

Fig. 1. Home ranges of male (M) and female (F) pine voles before (solid line) and after (dashed line) mowing in the pine vole plot. Tree positions are shown by "+" symbols. Rows extend roughly along a north-south axis.

DISCUSSION AND CONCLUSIONS

The data clearly show that under the conditions of this study, rotary mowing has only a marginal effect on vole movements and survival. The small but significant adjustments in pine vole movement in response to mowing are somewhat surprising because of the expectation that pine voles would not be bothered by mowing of grass above the peripheral margins of their burrow systems. What is being measured here could be a reduction in occasional surface activity by pine voles in these areas. Meadow voles, in being much more wide-ranging and apparently used to traversing open areas between rows, showed no statistically significant changes in movement before or after mowing. However, their "frenzied" response to the mower, in contrast to pine voles, implies that their momentary activities are substantially upset during rotary mowing. In what way this response might be used for control purposes can only be speculated upon at this stage in our studies.

What clearly has to be done is to mow all the vegetative cover beneath the apple trees. Both vole species depend at least to some degree on this cover, and rotary mowing between rows only trims the edges of these linear vegetative refuges. It is speculated that if

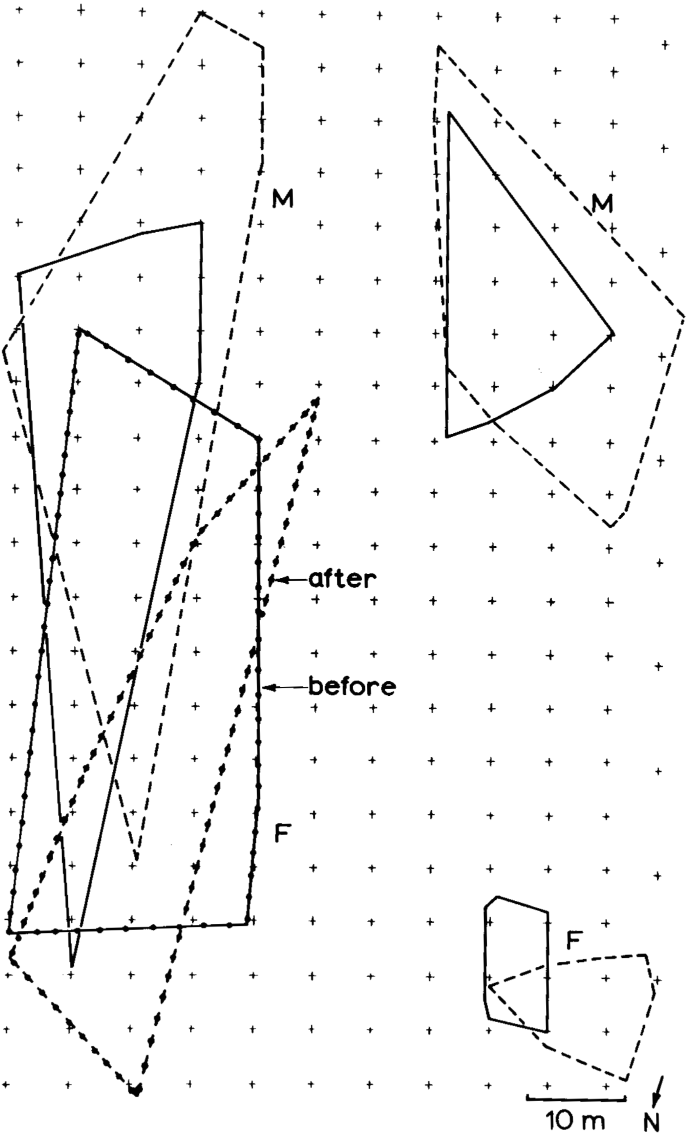

Fig. 2. Home ranges of male (M) and female (F) meadow voles before (solid line) and after (dashed line) mowing in the meadow vole plot. Dots are drawn along the perimeter lines of one vole's home range to aid reading of the figure. See Fig. 1 for further details.

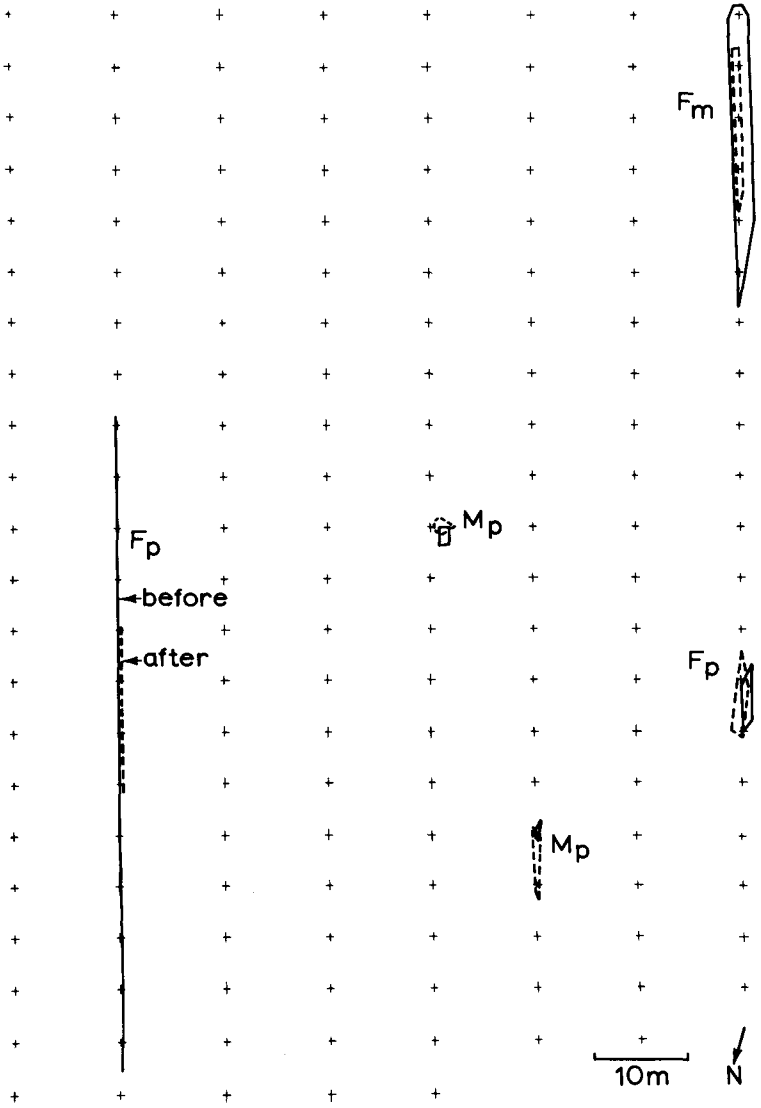

Fig. 3. Home ranges of male (M) and female (F) pine (p) and meadow (m) voles before (solid line) and after (dashed line) mowing in the mixed species plot. See Fig. 1 for further details.

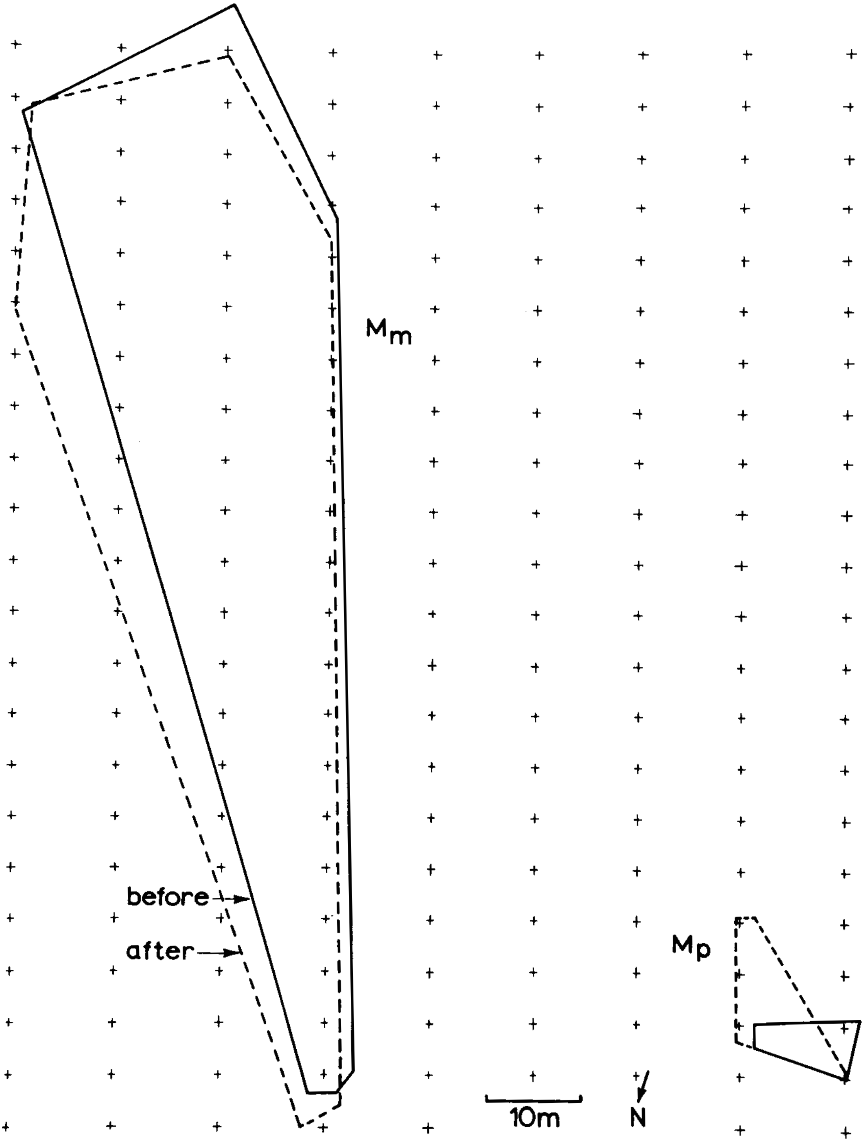

Fig. 3 (continued). This section of the study plot is south of the previous section.

all the vegetation were mown, and the clippings either collected or pulverized, the meadow vole population would be extremely vulnerable to all kinds of loss (exposure to predators and weather extremes) and be forced to enter the burrow systems along the tree rows. Just what effect this forced habitation would have on the movements and survival of pine and meadow voles is not known, but this is one problem that will be explored during 1981. The fact that meadow voles do not commonly enter burrows under the stress of rotary mowing suggests that there may be some dangers in doing so. We hypothesize that pine vole families are hostile toward meadow voles in pine vole burrow systems.

ACKNOWLEDGEMENTS

This investigation was made possible by a research grant from the U.S. Fish and Wildlife Service (Contract 14-16-0009-79-066). We thank Jay McAninch, Donna Stockrahm, and Steve White for assistance at different times during the study. We also extend our thanks to the Hudson Valley fruit growers, especially Stanley Cohn and Steve Clarke, who provided facilities and financial and advisory support many times during this and related research projects.

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Spacing, Movements, and Social Organization of a Free-Ranging Population of Pine Voles Microtus pinetorum

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Abstract: Free-ranging pine voles (Microtus pinetorum) were radiotracked in a maintained orchard environment from August to November 1980. Pine voles existed in discrete non-overlapping family units with an average of 6.5 individuals per family unit. Home ranges of family members overlapped extensively, and all the members of a single family unit utilized one or two communal nest sites within the family's territory. Males ranged slightly farther than females, and females spent more time in the nest than did males. The mating system appeared to be promiscuous with a high degree of social tolerance among pregnant and lactating females and scrotal males of the same family group.

INTRODUCTION

The development of an effective integrated pest control program depends on a complete understanding of the biology and ecology of the pest species. This includes a thorough understanding of how the pest is socially organized in time and space. Social behavior influences the immediate effectiveness of a control measure, and is probably involved in the compensatory breeding that follows the sudden population declines resulting from the control.

Besides the anecdotal evidence that pine voles are 'loosely colonial' (Paul, 1970; Boyette, 1966) or occur in locally abundant aggregations (Benton 1955; Hamilton, 1938), little is known about the social structure of this major pest species in an orchard habitat. The present study was designed to provide a detailed description of the pine vole social system. Such information could lead to the development of new control techniques, or permit the application of present controls with better timing and greater effectiveness.

METHODS

A 0.7 hectare (1.75 acre) study grid was established within a large apple orchard block in Modena (Ulster County), New York. The study grid consisted of eight rows (10 meters apart) of sixteen trees each (5 meters apart). The grid was live trapped every two months using two Sherman live traps at each tree (128 trees; 256 traps). First, the traps at odd (or even) numbered trees were opened, baited and checked at three hour intervals for a total of four checks. Then, the traps at even (or odd) numbered trees were opened, baited and treated in the same manner. Each census period took four days to complete.

Captured animals were marked (toe clip), sexed, weighted, checked for reproductive condition (males: scrotal or non-scrotal; females: pregnant, lactating, perforate and/or imperforate), examined for pelage status (adult or juvenile) and aged. Animals under 16 grams were considered to be juveniles; animals 16 to 20 grams, subadults (unless they were reproductively active in which case they were considered to be adults); and animals greater than 20 grams, adults.

Radiotelemetry was employed in order to record the exact position of individual voles in time and space. Conventional radiotelemetry equipment was used (AVM Instrument Co., Champaign Illinois), including SM-1 transmitters, multiple LA-12 radioreceivers, and handheld Yagi and mini-loop antennae. Voles to be given radiotransmitters were transported to the lab in individual cages. After ether anesthesia, each vole was given a radiotransmitter package, which was encapsulated in wax and surgically implanted into the abdominal cavity (I.P.) through an incision in the ventrolateral abdominal wall. Each radiotransmitter-battery unit was pretuned to a different frequency, and each weighed approximately 10% of the vole's total weight. Voles with implants were returned to their original capture sites within six hours of their capture, and data collection was delayed several days to allow the animals to adjust to the package.

Since we were looking for a maximum amount of vole interaction, and since preliminary recapture data suggested very little cross-row movement, voles within a single central tree row were chosen to be radiotagged. Every pine vole greater than 20 grams, and selected pine voles greater than 16 grams, were implanted with transmitters on two separate occasions. The first telemetry session covered a period from August 25 to September 10, 1980, and involved 18 animals (10 males, 8 females). The second session ran from October 21 through November 15, 1980, and involved 22 animals (12 males, 10 females). Each telemetry session consisted of recording hourly positions on each individual for a total of five 24 hour periods.

RESULTS AND DISCUSSION

Trapping data suggested that certain individuals could be grouped together, since they were consistently caught in the same traps within the same row (Fig. 1). Only six out of 256 recaptures exhibited cross row movement.

Telemetry data confirmed the group associations found in the trapping data and clearly demonstrated cohesiveness within groups and segregation between groups. Cohesiveness within groups was shown by the extensive overlap between members of each social group (Fig. 2). Telemetry and trapping data indicated that group members were individuals belonging to the same family, since young grew to adult size voles within their parental groups. The average family unit of the five monitored contained 6.5 individuals, with an average composition of 1.7 adult scrotal males, 0.8 adult non-scrotal males,

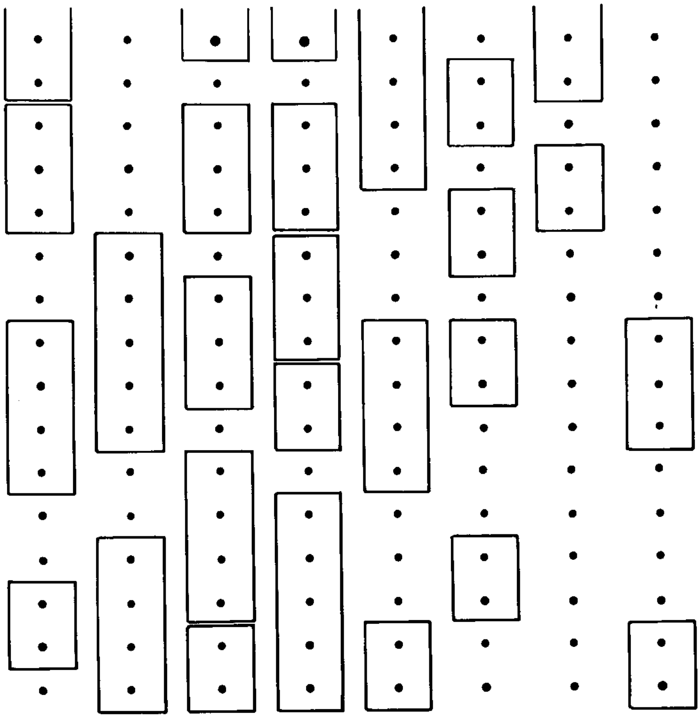
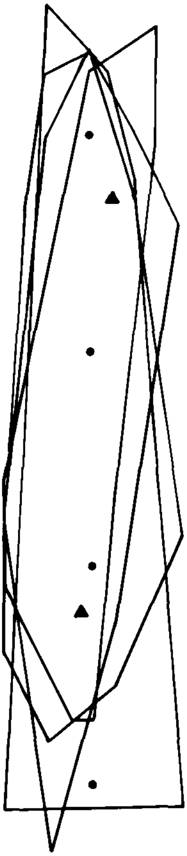


Fig. 1. Individual groupings of pine voles revealed by trapping data. Dots = trees, boxes = groups of associated individuals.

1.7 reproductively active females (i.e. pregnant, lactating and/or perforate), 0.7 subadults, and 1.6 juveniles. All family members utilized one or two communal nest sites within the family territory, and it was not uncommon to find all the members of a single family unit in the same nest at the same time. Nest sites were assigned to those locations which constituted a minimum of 20% of the total positions for all family members. Our criterion for nest sites was confirmed in preliminary studies and when predators (skunks?) excavated some nest locations in the present study. Fifty-three percent of all positions for all males were recorded at next sites, while this figure was 57% for females.

Fig. 2. Telemetry derived home ranges of four family unit members. Each range is represented by the area enclosed by a line connecting the outermost positions recorded during one telemetry session. Dots = trees, triangles = nest sites. Distance between adjacent trees = 5 meters.

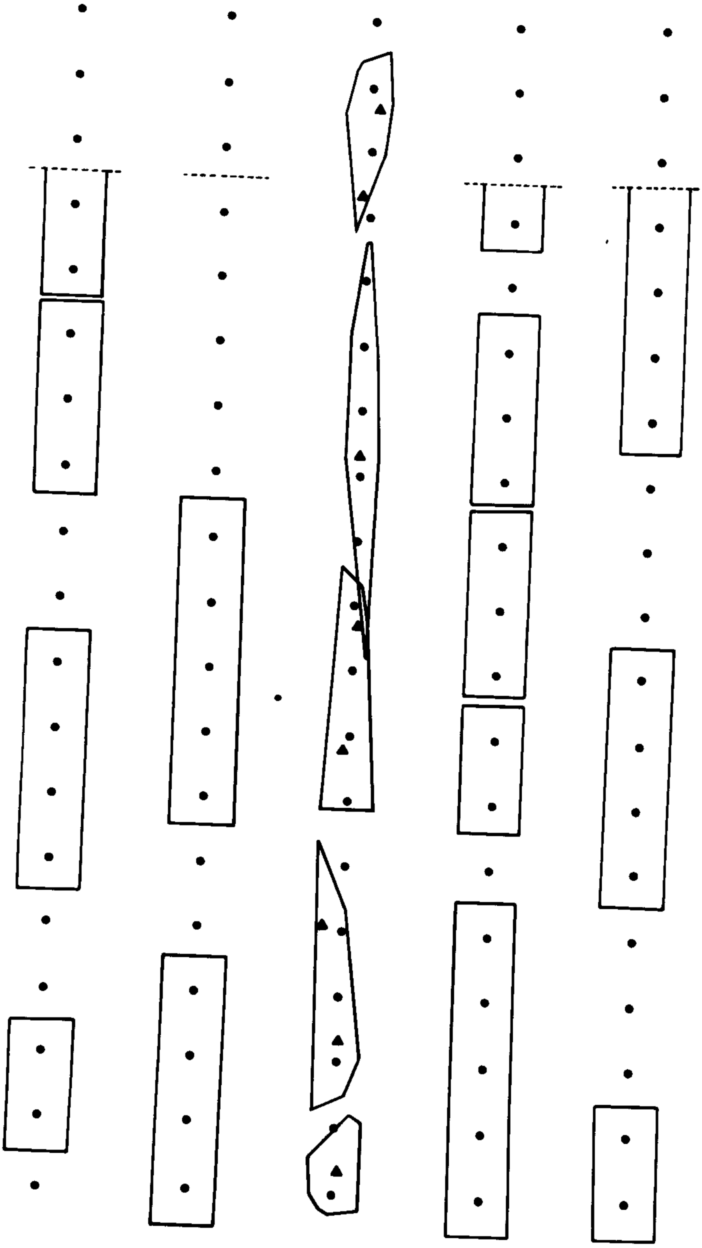


The mating system appears to be promiscuous within family groups; and a high degree of social tolerance exists between all family members, regardless of age or reproductive condition. Pregnant and lactating females were often found together at the same nest site, as were scrotal males.

A second significant finding reinforced by telemetry was that each family unit was a discrete, non-overlapping entity, primarily restricted to several trees within a single tree row (Fig. 3). Family units demonstrated a high degree of impermeability and permanence, thus existing as closed social units.

Home range estimates derived from the telemetry data indicate linear ranges with an average width for both males and females of three meters (conforming to the approximate dripline of the trees within the row). Males had slightly longer home ranges ($\bar{X}$ = 18.6 meters, N = 22) than those estimated for females ($\bar{X}$ = 14.1 meters, N = 18). The average family unit occupied a territory 16.6 meters long and 3.0 meters wide (N = 5).

Fig. 3. (on next page) Home ranges of the widest ranging individual from each family unit (polygons). Segregation between family units is nearly complete. Boxes illustrate the degree of segregation apparent from trapping data. Dots = trees, triangles = nest sites.



Future research will include a continuation of the censusing procedure for the collection of base line data on reproduction, mortality and dispersal. In addition, three more telemetry sessions are scheduled (March-April, May-June and July-August). These sessions, along with trapping data, should provide the information needed to answer the following questions:

1) How permanent are these family units? Are they stable throughout the year?

2) To what extent are the family units impermeable to outsiders? Do scrotal males or receptive females cross social boundries during the peak breeding season?

3) What is the mode of dispersal? How are the new family units formed?

4) How much time is spent in and out of the nest, by which family members, on what timetable?

Hopefully, these and other questions will be answered in the upcoming months.

ACKNOWLEDGEMENT

This investigation was made possible by a research grant from the U.S. Fish and Wildlife Service (Contract 14-16-0009-79-066). We thank Jay McAninch, Ralph Pagano, Donna Stockrahm and Jeff Hill for their assistance. We would also like to thank all the Hudson Valley fruit growers that have cooperated with us on this study, especially Stanley Cohn and Steve Clarke.

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COLONIZATION OF AN ABANDONED ORCHARD BY PINE VOLES (MICROTUS PINETORUM)

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Habitat selection by pine voles (*Microtus pinetorum*) has been attributed to cover density (Goertz, 1971; Paul, 1970) soil condition (Benton, 1955; Fisher and Anthony, 1980), and food resources (Noffsinger, 1976; Paul, 1970). Goertz (1971) reported that pine voles were distributed in diverse habitats, but there was a close correlation with height and diversity of grass. Miller and Getz (1969) found populations in sloping upland woods, Benton (1955) in dry woods, and Paul (1970) in hardwood slopes with a close correlation between distribution and amount of ground cover. Soil type has been examined by Benton (1955) and Fisher and Anthony (1980) and they have shown that pine voles are associated with light soils containing moderate layers of humus. These factors are important to reduce predation, moderate the effect of rain and temperatures, and permit the excavation of fossorial nests and tunnels.

Noffsinger (1976) has demonstrated that the amount of digestible energy and availability of food sources were important factors affecting birth and death rates of pine voles when abandoned and maintained orchards were compared. Behavioral characteristics of pine voles have been associated with decreased meadow vole density as pine voles appear to be a more aggressive species (Smith, 1975). Paul (1970) has shown that pine voles appear to replace meadow voles when they are sympatric in favorable habitats. Trapping and telemetry methods indicate that pine voles have low dispersal capacity and home ranges 100 m^2 or less in size (Gettle, 1975).

All these reports are from established pine vole populations and not from the initial colonizing event and subsequent development of a local population. Therefore, this research project is directed at understanding what site qualities permit pine vole colonization in areas where they have been historically absent, but where its competitor, the meadow vole (*Microtus pennsylvanicus*), is common.

METHODS AND MATERIALS

In an isolated abandoned orchard in Montgomery County Virginia, which contained an established meadow vole population, two grids (0.25 hectare in size) were established in June 1980. Each grid consisted of four tree rows (10 trees per row) and 5 aisle rows with 94 and 102 trapsites per grid. The grids were separated by 35 meters of continuous habitat and were trapped monthly (7000 trap nights to date). Aisle rows had large Sherman traps 5 meters apart and tree rows had 2 small Sherman traps at each tree site. Traps were baited with crimped oats and apples and were placed in vole runs. All tree traps were dug into runs and covered with tar paper.

Meadow vole and white footed mice (Peromyscus leucopus) populations were monitored throughout the study while pine vole populations were monitored after the release of 94 pine voles (47 male, 47 female) in September. Two pairs were released at each tree on the central portion of the control grid. All trapped animals were ear tagged, toe clipped, sexed, measured (total length and body length), and reproductive condition recorded (teats, vagina, and testes). All trap and recapture data was recorded on grid maps to note the areas of overlap and movement patterns within the population. Population densities for all species were calculated by a modified Lincoln index and MNKA both before and after pine vole introduction. Pine voles were originally released on one grid (control) but subsequent movement patterns lead to their establishment on the other grid (experimental).

RESULTS AND DISCUSSION

Meadow vole population estimates were 71 per 0.25 hectares on the control grid and 30 per 0.25 hectare prior to the introduction of pine voles. White footed mouse population densities varied between 10 and 25 per 0.25 hectare throughout the sample period. After the introduction of 97 pine voles to the control grid, a marked decline of meadow voles occurred reducing the density to 41 per 0.25 hectare. The experimental grid showed no decline in density and as these are paired grids the density changes on the control grid are attributable to the presense of the pine voles. By the November trapping period meadow vole density on the control grid recovered to 75 per 0.25 hectare. Between the introduction (September 20) and the November assay, pine vole density declined from 94 to 14 per 0.25 hectares on the control grid. The experimental grid density of meadow voles increased from 30 in October to 51 in November. Pine voles initially colonized the experimental grid (from the control grid) in October and continued to colonize through December reaching a stable density of 30 per 0.25 hectare. From November to December the densities of meadow voles on both grids exhibited a normal winter decline to a stable over-winter density between 30 and 40 per 0.25 hectare. Of the original pine vole introduction, 34% are known to be alive with 5 new unmarked animals caught since the October introduction. By backdating, based on size and weight, these were born on the grids in late October, early November and early January.

Pine voles were primarily located on the experimental grid with 58% of captures on tree rows, which is not satistically different (X^2=0.72) from random. The general movement of pine voles from the site of release was from the control to the lower half of the experimental grid. Trap recapture data indicates that pine voles showed a strong preference for that habitat section. Meadow voles shifted in distribution both on the control and experimental grids. The center of meadow vole distribution prior to pine vole introduction on the control grid was located between trapsites 7 and 12 on all rows but following the introduction meadow vole's shifted to occupy the range between trap site one and seven.

Both microtine species co-occurred at less than 3% of the trap sites during any sample interval and over the September-March sample period less than 16% co-occurred on the experimental and less than 10% co-occurred on the control. On each grid 25% or less than 25 sites failed to capture any Microtus sps. but often caught white footed mice. On the high density, experimental grid, 34 sites caught only meadow voles, while 21 sites caught only pine voles. On the control grid 50 sites were meadow voles while 7 sites caught only pine voles. Other species co-occurring on these grids wereshorttail shrew (Blarina brevicauda), eastern chipmunk (Tamias striatus), eastern cottontail (Sylvilagus floridanus), least weasel (Mustela nivalis), and common opossum (Didelphis marsupialis).

Smith indicated pine voles were dominant to meadow voles in behavioral tests and our data indicate that an interaction does occur which results in a partial redistribution of meadow voles. Pine voles could colonize the site in the presence of a well established competitor and the historical lack of pine voles at the site is probably due to distributional problems. Over the snowfree extremely cold winter both species were reduced in total numbers with the pine voles reaching a critical low density. Analysis of site factors important to colonization and persistence on the site is currently being evaluated.

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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 ± 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 ± 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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Influence of Apples on Population Density, Body Weights, and Reproductive Organ Weights in Pine Voles

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Previous field studies at Virginia Tech have found differences in reproductive output of pine voles in abandoned and maintained orchards. Cengel et al. (1978), trapping in northern Virginia, found higher levels of reproduction in a maintained orchard than in an abandoned orchard. The breeding season of voles extended into winter in the maintained orchard but ceased in late fall and winter in the abandoned orchard. Noffsinger (1976), working in orchards near Roanoke, Virginia, found a higher natality rate in the maintained orchard and a year-round breeding season; however, the percentage of pregnant females declined in winter. Reproduction was lower in the abandoned orchard in late fall and winter with no pregnant females caught in March.

Both of these studies attributed the differences in reproduction to differences in nutrition. Both felt the quality and quantity of forage available to pine voles and the presence of apple drops in the maintained orchard contributed to more reproduction and a longer breeding season. Lochmiller et al. (1980), who worked in the same orchards as Noffsinger, found the maintained orchard had higher levels of both biomass and gross energy in summer, fall, and winter.

The objective of the present study was to test the influence of apples as a food source on the population density, body weights, and reproductive organ weights in pine voles in the fall. To achieve this objective, two experiments were conducted during the autumn of 1980. This paper is a preliminary report of the data collected from these studies.

The first experiment was conducted in a metal frame building near the Virginia Tech campus. One to two inches of soil were placed in the bottom of four concrete troughs inside the building. Each trough was then divided into four equal sections 2.3 sq. m. in area. Sunlight entered the building through skylight panels in the roof.

Pine voles used for this experiment were trapped in late July and immediately placed in the troughs. In early September, two males and five females were grouped at random in 12 of the 16 sections of the troughs. Half of these groups were fed an ad libitum amount of ground rabbit chow, while the other half were fed ad libitum amounts of both rabbit chow and apple. The commercial chow had a fiber content of 15% and a digestibility of 65-68%. In mid-September, florescent lights and black plastic were suspended from the rafters. This further subdivided the groups so that half were maintained on a constant 14L:10D photoperiod and the remaining groups were kept on a natural declining photoperiod. Thus, the four treatment groups in this experiment were

(1) ad libitum chow and declining photoperiod, (2) ad libitum apple and chow and declining photoperiod, (3) ad libitum chow and 14:10 photoperiod, and (4) ad libitum apple and chow and 14:10 photoperiod.

The experiment was run for 12 weeks. Natural photoperiod at the beginning of the experiment was about 12:12 and at the end was approximately 9.5:14.5. Body weight, body length and reproductive condition were recorded every 2 weeks. Dead or missing voles were replaced during the first half of the study but no voles were added during the last 6 weeks.

There was little difference in mean change in body weight for pine voles living through the entire study. Only two groups, females on the apple and chow diet on both constant and declining photoperiods, had a positive mean change in body weight. All other groups showed a slight loss in body weight during the 12 weeks. There was also little difference in mean change in body weight for any group during the last half of the study. Females in the 14:10 constant photoperiod and fed apple and chow were the only group having a positive mean change.

Photoperiod and nutrition had little effect on final mean body weight for adult males. These two factors did influence mean testes weight, however. Mean testes weight was higher in males on the 14:10 photoperiod than in those on the declining photoperiod and in males fed both apples and chow than in those on the chow diet only. Males on a 14:10 photoperiod and apple-chow diet had the highest mean testes weight while those on a declining photoperiod and fed only chow had the lowest mean value.

The second experiment was a field study conducted in an apple orchard near Roanoke, Virginia. During the second week of September, apples were removed from two areas of this orchard. One area was five tree rows wide by three trees long and the second area was four tree rows by 12 trees. Apples were not removed from the remainder of the orchard.

Both areas with apples removed and a third grid (6 rows x 12 trees) in the area with apples present were live-trapped from August to October. All three areas were trapped at the same time for 3 sequential days each month. The voles were weighed, sexed and aged; and reproductive condition, body length and location were recorded. The animals were then marked for later identification and released.

In November, the smaller area with apples removed and an equivalent number of trees from the area with apples were snap-trapped. The larger grid with apples removed and the control grid were live-trapped at this time. In December, the larger area with apples removed and an equal number of trees in the rest of the orchard were snap-trapped.

In November, 5.4 voles per tree were caught from the area where apples were picked and 3.0 voles per tree from the area with apples. Nearly equal numbers were captured from both areas in December. Fifty-two voles were removed from 16 trees in the larger area without apples and 53 voles from 16 trees in the area with apples.

Removing apples appeared to have little influence on monthly mean body weight for either adult females or males. Mean body weight for males was not different from those of females captured in the same month and treatment area.

Presence of apples had little effect on mean body weight or mean adrenal weight for adult males snap-trapped in November. However, there was nearly a two-fold difference in mean seminal vesicle weight and mean testes weight between voles from the two areas. The larger mean weights were from males which had apples available. In December, adult males in the area with apples had a slightly higher mean body weight and mean adrenal weight. The difference between mean seminal vesicle weight and mean testes weight from the two areas was even greater in December than in November. Males from the area with apples present had a mean seminal vesicle weight about six times greater than for males in the area with apples removed. There was a three-fold difference in mean testes weight.

Mean body weight, mean adrenal weight, and mean paried ovarian weight were not different for adult non-pregnant females in the two areas for either November or December. Mean uterine weight was slightly higher for non-pregnant females in November in the area with apples removed. In December, mean uterine weight was higher for females in the area with apples. Mean paired ovarian weight was lower in both areas in December than in November.

No pregnant females were snap-trapped in either area in November. Eight pregnant females were captured in December in the area with apples present but none was caught in the area without apples.

Results from this experiment relate well to those found in other field studies done at Virginia Tech. Cengel et al. (1978) had similar mean testes weights for adult males in the abandoned and maintained orchard. Mean testes weight in their abandoned orchard for November and January are comparable to those found in our area without apples in Nobember and December. Noffsinger (1976) found a higher mean uterine weight in an abandoned orchard in November but in January the maintained orchard had a higher mean weight. Mean uterine weight and mean testes weight reported by Valentine and Kirkpatrick (1970) for a maintained orchard in November are quite close to the values found in November in the area with apples.

In summary, the availability of apples apparently had little influence on population size in the orchard studied. Presence of apples had no effect on mean body weight during the fall in either study. The presence of apples as an additional food source may have increased mean weights of reproductive organs and reproduction. These results and additional data will be further analyzed to gain insight into the influence of apples on reproduction in pine voles.

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Survey of Pine Vole Activity in Apple Orchards near Roanoke, Virginia

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A survey of pine vole activity in apple orchards around the Roanoke, Virginia area was made in conjunction with current trapping efforts involving pine vole research. A total of 60 orchards were examined and subjectively ranked according to pine vole activity. At least 10% of the trees in each orchard were examined for signs of possible activity.

Surveys were conducted during the fall and winter 1978 seasons in a 6 county area surrounding Roanoke, Virginia. Vegetative conditions of orchards varied from a maintained orchard to an abandoned orchard. Pine vole activity was noted in each orchard: activity being defined as visible evidence of pine vole presence such as runways, holes, and partially consumed apples. Each orchard was ranked according to the extent of pine vole activity present. One of 3 activity levels was assigned to each orchard: 1) low activity, with little or no trees examined showing signs of pine vole activity, 2) medium activity, with pine vole signs scattered among trees in orchard, and 3) high activity, with pine vole signs occurring at almost every tree examined. Pine vole control methods were also noted for each orchard reviewed.

Three types of categories for pine vole control were practiced among the 60 orchards examined. These included: 1) no methods practiced, 2) annual spray applications of endrin, and 3) annual baiting of chlorophacinone (Rozol) pellets. Among the 60 orchards reviewed, 20 (33%) had no pine vole control program, 31 (52%) were treated with endrin, and 9 (15%) of the orchards were treated with chlorophacinone.

Rating of pine vole activity for the 60 orchards showed that 35 (58%) orchards were low in activity. Among these 35 orchards, 10 (29%) had no treatment program, 17 (49%) were previously treated with endrin, and 8 (22%) had previously been treated with chlorophacinone. Seventeen of the 60 orchards rated had medium pine vole activity. (Among the 17, 6 (35%) orchards had no treatment program, 10 (59%) orchards had been previously treated with chlorophacinone.) Eight (13%) of the 60 orchards reviewed had high pine vole activity. Among the 8 orchards, 4 (50%) had no treatment program, 4 (50%) were being treated with endrin and none was treated with chlorophacinone.

Digestibility and Nutritional Quality of Apple Tree Roots and Other Orchard Forages of the Pine Vole

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Analysis of the seasonal food habits of pine voles (Microtus pinetorum) by Cengel et al. (1978) revealed that apple tree root consumption occurs only during winter months. Increased root consumption in the winter has been postulated to be due to a decrease in the quantity and quality of other foods in orchards. However, the normal translocation of carbohydrates into the root systems of trees during the dormant season may improve the quality of apple tree roots as a food source for voles. One objective of the pine vole nutrition studies at Virginia Polytechnic Institute and State University is to examine the seasonal variation in the quality of the pine vole's diet and the seasonal quality of apple tree roots as a food source for pine voles.

Apple tree roots were collected from ten different trees in each of two orchards on a bimonthly basis from May to January. The moisture content of these roots was determined and was found to be relatively constant throughout the sampling period. The phloem and bark layers of the roots were then fed to pine voles in a dried and ground state in a mixture with Purina rabbit chow to determine their digestibility by the difference method. The roots were about 50% digestible throughout the sampling period. The variability in the root digestion results indicated that this method was not accurate enough to distinguish small changes in digestibilities between months. However, a nutritive analysis of the root diets by the Goering and Van Soest (1970) procedure for analyzing the nutritive quality of feeds and forages showed that there was an increase in cell solubles (the highly digestible portion of the roots) between May and January and a corresponding decrease in the acid detergent fiber levels. Compared to other forages utilized by pine voles that have been examined in the VPI&SU lab, roots were as digestible as orchard grass when fed in similar trials, but much less than clover and dandelion. Future root analyses will include bimonthly determinations of total sugars, total nonstructural carbohydrates, ether extract, and crude protein levels.

A series of digestion trials using 24 diets made up of various combinations of four commercial feeds (Wayne lab block, Purina rabbit chow, and two varities of Purina horse chows) and five orchard plants that are commonly fed upon by pine voles (orchard grass, clover, dandelion, apple tree root bark, and apple) have been completed. Stomach contents of the voles used in these trials have also been analyzed by the Goering and Van Soest (1970) procedure. These data will be used to develop a regression equation that will predict the digestibility of the pine vole's diet in the field from a Van Soest analysis of its stomach contents. In addition, data from this same experiment will be used to evaluate the lignin tracer method of determining the diet digestibility of field caught voles.

Stomach contents of pine voles snap-trapped in many different orchards over the last year will be used to determine the seasonal variation in the digestibility of the pine vole's diet using the predictive equation developed in the lab. These data, coupled with information on the seasonal changes in the nutritive quality of apple tree roots, may aid in explaining why voles turn to roots for a food source during the winter months.

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Analysis of Seasonal Dynamics of Pine Vole Populations in Two Virginia Orchards

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Presently, V. P. I. and S.U. is involved in a three year multidisciplinary project to study pine and meadow vole ecology, behavior, and control (see additional V.P.I. and S. U. papers in Proc. Fifth East. Pine and Meadow Vole Symposium). In conjunction with this research, a long-term field study has been initiated to collect seasonal data on vole densities, survivorship, and reproduction in two Virginia apple orchards. The use of these data will be fourfold: (1) to gain insight into the dynamics of Virginia vole populations; (2) to act as a reference (or control) for future field experiments involving manipulation of pine and meadow vole populations; (3) to serve as input to a computer model being developed at V.P.I and S.U. (Coyle et al., 1981); and (4) to allow comparison of our results with other vole population studies. This paper presents some preliminary results after one year of the field study (December 1979 through December 1980) and will mainly concentrate on the pine vole population data.

Two areas were selected for this study; both are located near Troutville, Virginia in the Roanoke Valley. One area is a maintained apple orchard which has had no vole control for at least two years prior to the study, but has been mowed during spring and summer. The second area is an abandoned orchard which has had no type of maintenance for three to four years. The sites are within one mile of each other; however, they differ in regard to ground vegetation, slope, and aspect.

Live-trapping was conducted on a monthly basis in each orchard beginning in December 1979. Grids were approximately 1/3 hectare in each orchard and were 6 tree rows wide and 12 or 13 trees long. Two Sherman live traps were placed at the entrance of burrows at each tree with tar paper squares covering traps. Apple pieces were used for bait. Traps were checked at least twice daily (every three to four hours) for three sequential days in each orchard. All animals captured were toe and ear clipped for identification, measured for weight and length, and examined for sex and reproductive characteristics. Pine voles were classified as juveniles, subadults, or adults by weight criteria. Juveniles were less than 15 grams. Subadults were greater than or equal to 15 grams, but less than 21 grams. And adults were greater than or equal to 21 grams. This classification was based on the weight distribution found by Miller and Getz (1969) for the three age classes.

In general during the first year of this study, voles were abundant in both orchards as indicated by the large number of animals marked and the total number of animals captured (Table 1).

Table 1. Total number of animals marked and total number of captures recorded during the first twelve months of trapping in the maintained and the abandoned orchards. Animals of questionable sex were included in TOTAL ANIMALS but not in TOTAL MALES or TOTAL FEMALES.

	MAINTAINED ORCHARD		ABANDONED ORCHARD	
	PINE	MEADOW	PINE	MEADOW
TOTAL ANIMALS	699	34	194	296
TOTAL MALES	326	10	96	121
TOTAL FEMALES	298	17	93	158
TOTAL CAPTURES	2274	61	652	814

Pine voles were the dominate small mammal trapped in the maintained orchard; however, more meadow than pine voles were marked and captured in the abandoned orchard (Table 1). Monthly capture data for male and female pine voles is presented in Table 2. In both orchards the greatest number of pine voles were captured in the winter and spring and the lowest number during the summer and early fall. Although sex ratios varied from month to month, the yearly totals do not appear to be different from a 1:1 ratio (Tables 1 and 2).

Table 2. Total number of individual male and female pine voles captured each month in each orchard type. Animals of questionable sex are not included.

	MAINTAINED ORCHARD			ABANDONED ORCHARD		
MONTH	MALE	FEMALE	TOTAL	MALE	FEMALE	TOTAL
DEC	90	78	168	23	28	51
JAN	48	67	115	9	22	31
FEB	52	70	127	14	15	29
MAR	51	59	110	25	22	47
APR	106	110	216	18	17	35
MAY	66	79	145	13	7	20
JUNE	60	62	122	17	12	29
JULY	16	14	30	8	7	15
AUG	7	7	14	1	0	1
SEPT	13	8	21	1	0	1
OCT	49	38	87	16	17	33
NOV	63	50	113	28	15	43
DEC	56	67	123	16	14	30

In Table 3 the minimum number of voles known alive (MNA) in each orchard is given. MNA was calculated for a designated month by adding the number of individual animals captured in that month and the number of individuals which were marked prior to that month, not caught in that month, but captured subsequently. Hilborn et al. (1976) concluded from computer simulations that MNA underestimated actual population size of five species of voles by 10-20%. Population estimates of pine voles using MNA in the maintained orchard ranged from 243 animals/ha in August to 798 animals/ha in April. In the abandoned orchard pine vole estimates ranged from 27 (Aug., Sept.) to 162 (Dec. 1979) animals/ha and meadow vole estimates from 30 (July) to 381 (Dec. 1979) animals/ha. Often, especially during the summer months, many more animals were known to be alive each month (Table 3) than were captured (Table 2). This result would suggest that vole trappability varied each month and drastically declined during the hot, dry summer and early fall of 1980. Perhaps, the lower number of voles indicated during July, August, and September and the higher numbers in winter and spring (Tables 2 and 3) may reflect the problem of trappability rather than true population trends.

Table 3. Minimum number of voles known alive each month on the 1/3 hectare grid in each orchard.

	MAINTAINED		ABANDONED	
MONTH	PINE	MEADOW	PINE	MEADOW
DEC	176		54	127
JAN	184		44	115
FEB	202		46	103
MAR	209		53	90
APR	266		44	46
MAY	191		25	29
JUNE	174	5	31	49
JULY	92	2	16	10
AUG	81	5	9	20
SEPT	86	13	9	18
OCT	133	9	38	34
NOV	147	8	48	17
DEC	125	3	30	14

In general the age structure of the captured population in the maintained orchard each month was 5-10% juveniles, 15-20% subadults, and 75-80% adults (Table 4). In the abandoned orchard juveniles were frequently lacking in the monthly trapping and generally for the year, subadults and adults constituted 5-30% and 60-90% of the captured population, respectively. In August and September only one subadult male was trapped in the abandoned orchard (Table 4), consequently accounting for the 100% subadult composition of the captured population during these months. Again, low trappability, and therefore, few captures of voles during the summer and early fall of 1980 is most likely influencing these data.

Table 4. Percent on a weight basis of juvenile (JU), subadult (SA), and adult (AD) pine voles captured monthly in each orchard. Sample size is indicated in parentheses. Data for January are not included because many animals were not weighed this month.

	MAINTAINED ORCHARD			ABANDONED ORCHARD		
MONTH	JU	SA	AD	JU	SA	AD
DEC	7.7(13)	8.3(14)	84.0(142)	5.9(3)	3.9(2)	90.2(46)
FEB	5.6(7)	19.4(24)	75.0(93)		10.3(3)	89.7(26)
MAR	9.6(11)	16.5(19)	73.9(85)		15.2(7)	84.8(39)
APR	11.6(27)	25.4(59)	62.9(146)		2.9(1)	97.1(33)
MAY	6.0(9)	16.1(24)	77.9(116)		5.0(1)	95.0(19)
JUNE	13.8(19)	8.7(12)	77.5(107)	12.9(4)	3.2(1)	83.9(26)
JULY	9.7(3)	22.6(7)	67.7(21)	6.7(1)	33.3(5)	60.0(9)
AUG	7.1(1)	14.3(2)	78.6(11)		100.0(1)	
SEPT	13.0(3)	8.7(2)	78.3(18)		100.0(1)	
OCT	9.3(8)	26.7(23)	64.0(55)	9.1(3)	18.2(6)	72.7(24)
NOV	6.2(7)	39.8(45)	54.0(61)		25.6(11)	74.4(32)
DEC	4.0(5)	15.2(19)	80.8(101)	6.7(2)	10.0(3)	83.3(25)

Table 5. Mean monthly weight (g) of adult male and female pine voles in each orchard. Sample size is indicated in parentheses. Data for January are not included because many animals were not weighed this month.

MONTH	MALE	FEMALE	MALE	FEMALE
DEC	26.0(81)	27.5(61)	26.0(21)	25.7(24)
FEB	26.3(39)	26.4(53)	26.5(13)	25.8(13)
MAR	26.6(37)	26.5(48)	25.1(20)	23.6(19)
APR	25.3(68)	25.3(78)	24.6(16)	25.9(17)
MAY	26.2(52)	26.5(64)	24.6(12)	27.6(7)
JUNE	26.6(49)	29.7(56)	25.9(14)	26.3(12)
JULY	27.0(10)	28.8(11)	24.0(4)	24.0(5)
AUG	23.8(5)	27.8(6)		
SEPT	25.6(12)	23.3(6)		
OCT	24.4(30)	25.8(25)	25.0(12)	23.6(12)
NOV	24.5(33)	24.5(28)	23.7(18)	25.6(14)
DEC	24.7(49)	25.2(52)	24.1(14)	26.7(11)

Mean monthly weight by sex for adult pine voles is given in Table 5. Average weight of adult male and female pine voles in the maintained orchard during the first twelve months of this study was 25.7 g and 26.4 g, respectively. In the abandoned orchard during the same period, average adult male and female weight was 25.0 g and

25.3 g, respectively. Adult female weight in both orchards showed greater variation during the year than did adult male.

To examine aspects of pine vole survival in these orchards, the number of months between first and last capture of marked animals was calculated (Table 6). Generally, as expected, as the number of months between first and last capture increased, the number of animals in each category decreased. In the maintained and abandoned orchards, over 50% of marked pine voles were captured in only one month (see 0 months column in Table 6). However, survival appears to be higher in the maintained orchard when compared to the abandoned. Twenty (11%) of the original 176 animals captured in December 1979 were captured in December 1980. This estimate of longetivy is probably an underestimate since it is possible that animals from the original group may be captured in subsequent months as the study continues.

Table 6. Months between first and last captures of marked pine voles in the maintained (M) and the abandoned (A) orchards.

		MONTHS BETWEEN FIRST AND LAST CAPTURES												
		0	1	2	3	4	5	6	7	8	9	10	11	12	TOTAL
NUMBER	M	368	87	54	30	41	25	29	13	14	7	5	6	20	699
	A	107	29	20	8	14	6	4	4		2				194

As previously stated, these results are preliminary at this point. Computer programs are being developed to examine seasonal age and weight dynamics, survivability, trappability, reproduction, movement, and spatial distribution of pine voles. Reports of this continuing research will be given at future symposia and meetings.

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PROGRESS AND PROSPECT OF A BIOENERGETIC SIMULATION MODEL OF PINE VOLE POPULATIONS

by

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As reported previously (Coyle and Tipton 1980), we have been engaged in the development of a computerized system which outlines the basic demographic features of a pine vole population. The system, when complete, will hopefully contain four subsystems (biological, spatial, control, and economic). This paper will discuss the biological submodel, its development and validity, and prospects for its future.

A mathematical model of pine vole population dynamics was constructed using bioenergetic information supplied by Cengel et al. (1978) and Lochmiller (1980) to describe the biological relationships (Coyle 1980). Interactions within the population were described using energetic stages (i.e. a group of animals with similar daily energy requirements) instead of age classes because pine voles are very difficult to accurately age and age-specific data were scarce. Matrices of transition probabilities for transfer between the energetic stages were generated each week during the simulations.

Relative energy balance, as simulated from energy transfers, was used as the driving force in the model. Functions for weekly energy availability and digestibility of forages were derived from field data. The processes of energy requirements, energy acquisition, energy deposition, and energy mobilization were simulated based on available energy. Algorithms for these processes were developed using field and laboratory data, and personal opinion where data were lacking. The degree of weekly energy restriction was used as input for routines calculating survival, reproduction, and transfer of individuals between stages. We originally intended to use body fat level as an indicator of energy restriction, but inconsistencies between field and laboratory data required re-evaluation of its use.

Validation of the model was conducted using population data collected from the 2 apple orchards used by Lochmiller (1980) and Kukila (unpublished data). Simulations were conducted from 1 December to 1 March using vole population densities of 75 and 70 animals per 1/2 ha for the maintained and abandoned orchards, respectively. The densities, age distributions, proportions of females reproductively active were taken from data (unpublished) collected in the same orchards that Lochmiller (1980) used to determine the energy availability values. Discrepancies between simulated and observed values were attributed to several factors, including the incomplete data sets, and inaccurate program algorithms.

Sensitivity analysis, the process of varying parameter values to determine their relative importance to model output, revealed that estimates of daily energy budget, number of feeding times per day, and the degree of forage utilization were important components of the model. Further refinements of the mathematical representations of these processes, as well as additional collection of data, are needed. Simulation results indicated also that juvenile growth rates are not expressed accurately in the model, and that further refinement of that algorithm is needed. Nineteen recommendations for further study are included in Coyle's (1980) thesis.

In addition to the sensitivity simulations, two simulation experiments of a year in length (from 8 September to 1 September of the following year) were conducted. The original population level consisted of 98 animals (50 males [13 juveniles, 37 adults] and 48 females [13 juveniles, 6 nonreproductive adults, 29 pregnant adults], values from unpublished field data) on a 1/2 ha grid in an apple orchard.

During the reference simulation, population levels increased by 16 percent during the year (to 114 voles). Cohorts in spring and summer contributed significantly to the over-wintering population. Although these population levels could not be accurately verified with existing field and laboratory data, the general trend of the population dynamics appeared to be reasonable.

A second simulation was conducted (with the above-mentioned initial population levels) to examine the effect of a pesticide application in mid-October. The effect of the application was to remove 80 percent of the individuals in all stages of voles. The population level decreased by 47 percent (to 60 voles) from the previous simulation. Most over-wintering reproductively inactive females conceived and bore young during April. After sexual maturity, this strong cohort contributed to an equally strong August cohort. Although the population was reduced by 80 percent at the outset of the simulation, results indicated the potential for the population to increase prior to the following winter due to strengths of the April and August cohorts. This hypothesis confirms prior observations that pine vole populations can and do recover within 1 year after a pesticide application.

The next phase of model construction will refine the algorithms representing bioenergetic regulation of survivorship, growth, and reproduction. The biological submodel will then be nested in a larger model of intra-orchard spatial movement. This larger model will itself be nested within a control optimization routine intended to recommend optimum treatment regimes for controlling pine vole populations in individual orchards.

Possible refinements of the bioenergetic model involve determining:

1.) seasonal digestibilities and palatibilities of forages,

2.) the effects of population density and forage abundances, digestibilities, and palatibilities on utilization rates,

3.) the effects of utilization rates on the subsequent abundances of forages,

4.) how survivorship varies as a function of age, energy balance, body weight, and body fat level,

5.) how growth and body fat level vary as functions of age, energy balance, and litter size,

6.) how litter size varies as a function of maternal age, energy balance, body weight, and body fat level,

7.) how energy intake, and thus utilization, vary as functions of energy balance, with stomach size limiting only when digestibility is so low that food bulk, rather than energy balance, limits energy intake,

8.) how ambient temperature, light/dark cycle of illumination, fossorial behavior, and social strife affect survivorship, growth, and reproduction,

9.) the effects of a positive or negative energy blance achieved gradually, rather than suddenly, on survivorship, growth, and reproduction.

Evidence that pine voles live and reproduce in tree-specific demes (Stehn et al. 1977) suggests that the orchard can be treated as a matrix of subpopulations, rather than as a single population. Since some limited movement has been shown to occur between trees and rows, a corresponding matrix of movement probabilities might be computed for density differences between adjacent tree subpopulations. Both the population matrix and the spatial distribution matrix could be stacked in a third dimension to represent the different energetic stages. The total orchard population size, as simulated from the bioenergetic and spatial distribution submodels, could be computed as the three dimensional sum of the subpopulations.

The control optimization routine would operate bioenergetically at the tree subpopulation level, with effects summed to yield commercial impact at the orchard level, the level of concern to the orchardist. Control options would consider the following parameters:

1.) type of control substance,

2.) purchase cost per unit mass,

3.) cost of application,

4.) effectiveness on populations of different sizes and age structures at different times of the year under different forage conditions.

Control options would be evaluated in terms of total cost to the orchardist, with recommendations made to minimize the sum of the cost of control and of pine vole damage to current and future apple crops via apple consumption and tree damage. Benefits and costs of each control option would be present-discounted at the specified market rate to yield practical benefit-cost analysis.

Current work at VPI & SU, both in the field and in the lab will provide important information in achieving the refinements mentioned above. The present state of the model embodies the results of extensive research into pine vole population demography and nutritional needs. This knowledge has been unified in a bioenergetic format that resolves populations into the energetic stages traversed in a single male or female life history. The future effort will address what happens when those nutritional needs are not met, the importance of other environmental and social variables on population demography, the impact of voles on orchards, and the recommendation of orchard control practices. These refinements, along with additional data, may eventually be incorporated in a system that will prove useful as a management tool for pine voles.

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SOCIAL BEHAVIOR OF THE PINE VOLE (PITYMYS PINETORUM):

I. ACTIVITY PATTERNS OF MATED PINE VOLES IN SEMI-NATURAL ENVIRONMENTS

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Introduction

The root damage resulting from pine vole (Pitymys pinetorum) infestation of apple orchards remains a major vertebrate pest problem. Currently, research effort is being directed at habitat management and at toxic bait development and application as two potentially cost-effective methods for control of these rodents. Recently, investigations have begun into the detailed relationships between the pine vole's physiology and it's habitat in an effort to understand and perhaps disrupt the seemingly ideal balance achieved by the animal in apple orchard situations. In addition to these approaches, which have possible immediate application, one area of pine vole biology that is poorly understood but which holds a great deal of promise for incorporation into an integrated control program is the study of social organization of pine vole familial and non-familial social units. With the relatively recent application of Sociobiological Theory and Information Theory to the analysis of animal behavior, an understanding of the social biology of the pine vole is a necessity for the development of an integrated pest control program. Such a program, one that incorporates information not only about orchard management and toxic bait placement but also about the number of voles per famiy and the behavioral interactions occurring within pine vole social units could then take a sociomanagement approach in addressing the problem. For example, knowing i) the activity patterns of males and females, ii) the degree to which pine voles recongize kin and iii) the cohesiveness of social breeding units would undoubtedly aid in optimizing the timing of management procedures and toxic bait placements both in terms of when to manage (e.g. time of year) and where to place baits (e.g. dispersed vs. concentrated stations). Figure 1 illustrates several types of behavioral studies which might be included in the formulation of such a pest control program.

This paper presents data on pine vole social behavior derived from the activity patterns of opposite-sex pairs allowed to occupy semi-natural enclosures. Of particular interest are several questions about the time spent in various activities. For example, is there a sex or photoperiod difference in the amount of time that pine voles remain at the nest? Concomitantly, can either sex or photoperiod variables be implicated in the amount of time that pine voles engage in investigatory behavior, digging, nest building and eating? Lastly, do males and females spend a large/small amount of time in proximity to each other during the light and dark periods of the day? That is, when provided the opportunity to nest, eat, travel, etc. independently, do pine voles remain tightly bonded or loosely associated? The answers to these questions can provide insight into the behavior of orchard-dwelling animals.

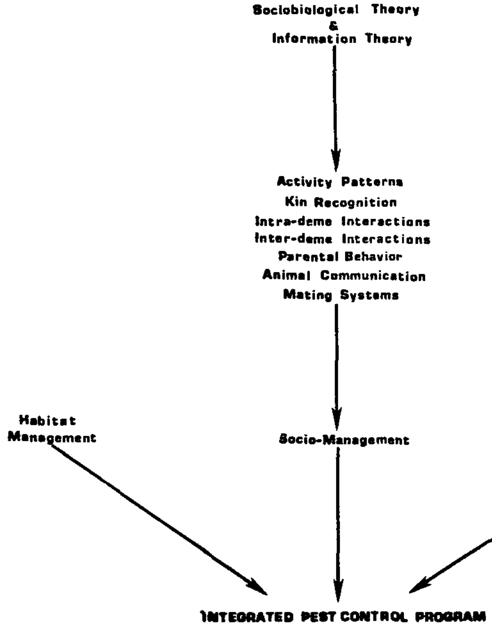

Figure 1. Flow diagram depicting the formation of an integrated pest control program from information obtained through the use of three different management strategies.

The objectives of this study are:

1) to understand social behavior of male/female pairs
2) to investigate effects of photoperiod on social behavior
3) to learn the activity patterns of males and females in semi-natural enclosures.

Methods

Adult opposite-sex pairs, established 14-15d pre-test were placed in semi-natural plexiglass enclosures (Figure 2) and allowed 24h for habituation. Both the nesting area and the tunnels were partially filled with dirt and covered with red acetate in an attempt to keep them as dark as possible at all times. Soil depth in the non-tunnel portion was approximately 8 cm. Orchard grass (Dactylis glomerata) was provided for nest material. Apple and sprouted wheat were provided ad libitum and served as food and water. Animals were kept on a 12:12 light cycle at a temperature of 15-18°C.

Each enclosure was divided into eleven key areas to facilitate the recording of an animal's location. After the habituation period, pairs were observed at separate times over both the light and dark cycles during a six day period for a total of 33h. A 4 min sampling period

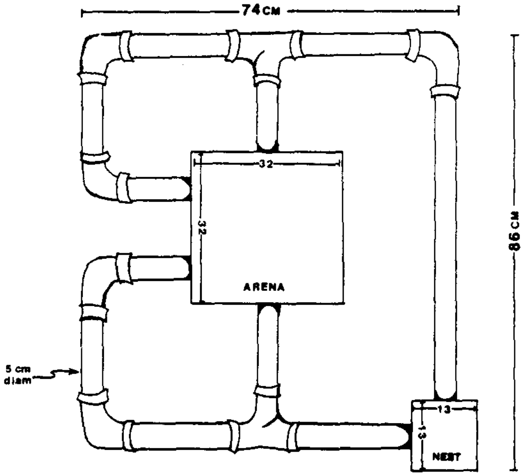

Figure 2. Diagram of the semi-natural plexiglass enclosure used in the study.

each hour was taken on all pairs, during which time sixteen scan samples of 15s each were performed. The scan samples consisted of observing the enclosure every 15s for 5-7s. The location and activity of each animal was recorded.

Results

Figure 3 shows the sum of all investigatory, digging, nesting and eating behaviors observed per hour (=frequency). This represents the hourly combined activity for each animal. The average frequency of occurrence of combined activity for males (n=8) and females (n=8) is plotted against the time of day for a 24h period. While both males and females appear more active during the dark period than during the light period, they seem to be in-phase only during the dark period. That is, the peak in light activity for males occurs early in the morning, immediately after lights are turned on. For females, this peak is shifted approximately 6h and occurs at about noon. During the dark period, peak activity for both sexes occurs between 8 pm and 11 pm. Both sexes exhibit a dramatic decrease in activity at 9 pm with a sharp increase following.

When the combined activity for each pair is graphed separately, several observations can be made. For the most part, each animal displays a characteristic pulsing of activity and non-activity rather evenly spaced throughout a 24h period. In addition, most animals show an increase in activity just after lights are turned off and a few animals show a similar activity burst just before lights come on again. These individual observations are somewhat obscured in the average graph (Figure 3). Of primary importance though, is the fact that each animal (or pair of animals) has it's own activity pulsing pattern and

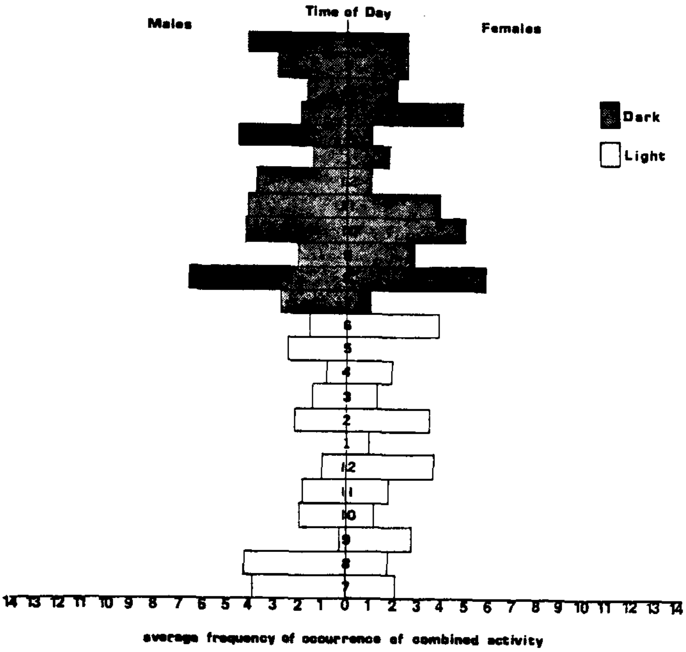

Figure 3. Average combined activity of 8 pairs of pine voles in semi-natural enclosures.

consequently, may be 1 or 2 h out of phase with other pairs. As a result, graphing the average activity patterns not only obscures this periodic pulsing but may even result in an average activity pattern that in some respects, differs dramatically from individual activity patterns.

Table 1 lists the behaviors that were monitored throughout the study, the average percent of a 24 hour day that was spent in each behavior and the total amount of activity engaged in by males and females. For all behaviors there appears to be no significant difference between male and female activity either in the light period, the dark period or the combined light/dark periods. Time period had more of an effect than did sex on pine vole activity. With all activities combined, males were significantly more active during the dark than they were during the light ($X^2 = 10.64$, 1 d.f. $p \leq .05$). Nest building, in which males engaged for a significantly longer time during the dark than during the light ($X^2 = 5.39$, 1 d.f. $p \leq .05$) probably accounts for the significant difference seen when all activities are combined. Females, on the other hand, did not show a significant difference in combined activities between dark and light periods, but, as was the case with males, they spent more time building the nest in the dark than the light ($X^2 = 12.35$, 1 d.f. $p \leq .05$).

Table 1. The percent of a 24 hour day spent in various behaviors by paired male and female pine voles in semi-natural enclosures.

	Male			Female		
Location	Dark	Light		Dark	Light	
Nest	73.07	87.07	*	80.15	81.46	ns
Arena	19.49	2.86	*	11.82	11.20	ns
Tunnel	7.44	10.07	ns	8.02	7.34	ns
Total	100.00	100.00		100.00	100.00	
Activity						
Investigating	8.59	4.47	ns	5.62	4.69	ns
Eating	7.19	3.34	ns	4.43	3.77	ns
Digging	2.65	2.78	ns	3.85	5.86	ns
Nesting	3.18	0.26	*	5.05	0.04	*
Chewing	1.19	0.13	ns	0.31	0.22	ns
Caching	0.05	<0.01	*	0.47	0.61	ns
Copulating	0.05	0.56	ns	0.05	0.56	ns
Grooming	0.26	0.04	ns	0.26	0.08	ns
Following	<0.01	0.22	*	<0.01	<0.01	ns
Contact						
naso-genital	0.31	0.22	ns	<0.01	0.09	*
naso-lateral	0.05	0.04	ns	<0.01	<0.01	ns
naso-nasal	0.05	0.04	ns	<0.01	<0.01	ns
Aggressing	<0.01	<0.01	ns	<0.01	<0.01	ns
Urinating	<0.01	<0.01	ns	<0.01	<0.01	ns
Defecating	<0.01	<0.01	ns	<0.01	<0.01	ns
Total	23.61	12.14	*	20.11	15.98	ns
Inactivity						
Total	76.39	87.86		79.89	84.02	

*Chi Square test; $p \leq .05$

ns = not significant

There was no significant difference between the amount of time that males spent in the nest and the amount of time that females spent in the nest during the light period, dark period or combined light/dark periods. However, males did remain at the nest significantly longer during the light period than during the dark periods ($X^2 = 13.04$, 1 d.f. $p \leq .05$). Conversely, females showed no preference for the nest during light or dark periods.

Three of eight pairs engaged in copulatory behavior during the course of the sampling. In each of these cases, one to three bouts of copulatory activity were observed, most occurring in the light period. These copulations plus other apparently normal interactive behaviors (see Table 1) most likely attest to the accurate representation of a semi-natural environment for studying pine vole behavior. In addition to the copulatory behavior seen, litters were born to two other pairs. Back-dating from the date of birth revealed that one pair apparently mated prior to the end of sampling (no copulations were observed, however). The other pair apparently mated during the 14d pre-test pairing period. This female therefore was pregnant during the study. Interestingly, she spent more of the dark period (97%) at the nest than any other animal. Only one other female spent more time at the nest than this female during the light period. In addition, this pair spent more time (89%) than any other pair in proximity to one another during the dark period. On average, however, males and females were together signficantly longer during the light period than during the dark period ($X^2 = 4.07$, 1 d.f. $p \leq .05$).

All eight pairs engaged in caching behavior, however, much of this activity occurred when animals were not being observed. Nonetheless, males cached for a significantly greater length of time when the lights were off than when the lights were on ($X^2 = 5.72$, 1 d.f. $p \leq .05$). In all cases, animals cached sprouted wheat (and only occasionally small apple chunks) at the corners of the plexiglass tunnels.

Discussion and Conclusion

The purpose of this study was to investigate the activity patterns of mated pine voles. None of the four prevalent behaviors (investigating, digging, nesting and eating) was engaged in for a significantly different amount of time by males and females (Table 1). However, males engaged in nest building for a significantly longer amount of time in the dark period than in the light period. The same was true for females.

The most intriguing result does not concern what constituted the animal's activity, but rather, when the animal was active. On average males achieved two activity peaks during the 24h cycle; one just at dark (between 7:00 pm and 10:00 pm) and the other beginning one hour before the lights came on and continuing on into the early light period, dropping off as the light period continued. Females showed a similar peak, but achieved no early morning peak. Instead, they displayed an activity peak in the middle of the light period (about 6h after the male peak). One can speculate on the significance of phase-shifting activity patterns in wild populations of pine voles. Phase-shifting could serve to keep one animal at the nest while the other forages thus ensuring protection of the nest and any young that might be present there. In-phase activity during the night would not appear to be as adaptive as phase-shifted day activity. While mutual night foraging may serve as added protection against predators, females risk the loss of any nest young to nocturnal predators. A reduction in home range size by pregnant and lactating females may allow such females to forage effectively and still remain close to the nest.

Further research in this area and other areas of social interaction is necessary to gain a fuller understanding of the behavior of orchard-dwelling pine voles.

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EFFECTS OF TASTANTS ON CACHING, GNAWING, GROOMING AND TASTE AVERSIONS IN PINE VOLES (MICROTUS PINETORUM) AND MEADOW VOLES (M. PENNSYLVANICUS)

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ABSTRACT: Several behaviors of pine and meadow voles were studied, specifically those affecting the role of taste in ingestion. These behaviors include: 1) caching, 2) gnawing, 3) grooming, and 4) taste aversions.

Male pine voles cached more than females, particularly when housed with females. Solitary females more than those housed in mixed sex pairs. When presented with peanuts and pine dowels in one-hour tests, pine voles cached peanuts first; the addition of flavorants did not affect the sequence in which they were cached. In six-hour tests, however, sucrose- and oil-soaked items were cached first.

Gnawing by pine voles, like caching, was enhanced by the addition of oil and fruit extract to dowels and rootstocks. However, flavoring dowels with bark homogenates did not alter the extent of gnawing.

Durations of auto- and mixed-sex pairs of voles after one vole had been unilaterally-coated with a gel. Consistently, soiled voles groomed more than did clean voles, licking the soiled side of their fur more than the clean side. The clean vole groomed the soiled partner more than himself, suggesting that soiled fur is a powerful stimulus for both auto- and hetero-grooming. Adding tastants to the gel before applying it to the fur did not alter grooming durations in either species.

A taste aversion to saccharin was induced in pine voles and meadow voles via drinking water. When voles were later coated unilaterally with a saccharin- flavored gel, grooming duration was unaffected by the taste aversion treatment. Attempts to induce a taste aversion via grooming a saccharin- flavored gel from the fur did not succeed.

Taken together, these studies demonstrate that various non-feeding behaviors can result in ingestion of a material, however, that vole responses to tastants vary with different behavioral contexts. Grooming behavior might be exploited as a means of delivering toxicants to the fur for the control of vole populations.

INTRODUCTION: Pine voles and meadow voles exhibit several behaviors that can result in ingestion of food material. Food items are cached into burrow systems. These and other items, such as tree roots, may be gnawed. Material clinging to the fur of voles or their partners may be groomed from the fur. Novel foods which are temporally associated with illness may subsequently be avoided, a phenomenon termed a taste aversion.

While these behaviors have been studied in some other species, relevant knowledge for pine voles and meadow voles is extremely limited. In the present laboratory studies we have investigated each of these behaviors, emphasizing effects, if any, of adding various tastants.

Pine voles used in this study were laboratory-born in a colony originally trapped in Beiglerville, Pennsylvania in 1972. Meadow voles were wild-caught in 1979-1980 in Winchester, Virginia. Pine voles and meadow voles were housed as heterosexual pairs in plastic cages (28 x 18 x 12 cm, 34 x 30 x 16 cm, respectively) under light/dark cycles of 12/12 hr and 18/6 hr, respectively. In each study, data were analyzed using appropriate analyses of variance, and significant differences between groups were tested with the Bonferroni t statistic (1).

CACHING: Pine voles extensively cache in the field. The present laboratory study measured caching of peanuts and dowels when flavorants had been added. Pine dowels (.5 x 3.9 cm) were soaked in corn oil, 25% apple extract, 2% quinine hydrochloride, 25% sucrose, or deionized water with identifying food colors for 4 hr and were then dried in the oven 3 hrs at 65°C. One peanut and one dowel with each flavorant were then placed in a gallon container connected to the vole cage (27 x 17 x 13 cm) by plastic tubing (16 x 32 cm). Behavioral observations were taken during the first hour. At 24 and 48 hours the locations of dowels and peanuts were noted, and at 48 hours dowels were weighed to assess damage by gnawing. One hour behavioral observations of solitary males and females and mixed-sex pairs showed that males cached more when housed with females than when housed alone, and that females cached less when males were present, $F(3,44)=4.68$, $p < .025$. Net caching was greater for vole pairs than for solitary voles. Analysis of caching sequence showed no effect of tastant, but peanuts were cached before dowels, $F(1,36)=5.09$, $p < .05$. In 6 hr behavioral observations of seven pairs, males showed a nonsignificant trend toward greater caching than females, $t = 1.52$, $p < .1$. Peanuts were cached before dowels, $F(1,48)=23.52$, $p < .025$. Sucrose items were cached before water, quinine and apple extract items, and oil items were cached before and water items, $p < .05$. The two cached materials (peanuts and dowels) significantly interacted with the five flavorants, $F(4,48)=3.22$, $p < .025$.

Gnawing of the dowels was affected by taste, replicating our earlier 24 hr tests. In week-long tests, oil soaked dowels were consumed more than all others, $F(4,20)=6.06$, $p < .005$, t-tests, $p < .05$. A similar result was found in 48 hr tests using solitary males, $F(4,50)=3.72$, $p < .025$, or mixed-sex pairs, $F(4/45)=5.51$, $p < .005$. Gnawing was so limited in solitary females that no effect was found, $F(4/40)=.42$, p = ns.

It appears that gnawing, but not caching, is demonstrably affected by addition of tastants and/or nutrients to the wood. Our data also suggest that males cache and gnaw more than females.

GNAWING: Having already demonstrated that taste additives affect the extent to which voles gnaw pine dowels (see Caching section and 2), we proceeded to test whether or not tastants alter attractiveness of rootstocks for gnawing. Pine voles preferentially gnaw "Golden Delicious " (GD) and Malling 9 (M9) and M. x sublobata P.I 286613 (613) (1,2,10). We have some evidence implicating texture as a factor in differential acceptance (3). In the present experiment, we tested whether acceptance of rootstocks could be altered by addition of a tastant.

Pine voles were housed in mixed-sex pairs (N=54). Pairs were used only once in any portion of the study. Rootstocks were cut in 15 cm lengths and 4 longitudinal slashes were cut in the bark of each. Twigs were then soaked for 2 hours in 25% fruit extract solutions; .05 M quinine hydrochloride solution; .6 M glucose solution, or water. Rootstocks were then drained, individual weights collected and each placed in a cage for a 24 hr test. After collection, twigs were again weighed, including two control twigs (as before) for each variety. In the first portion of this study, Golden Delicious and 613 were soaked in water, fruit extract or glucose, for subsequent testing. In the second portion, R5 and M9 were soaked in glucose, quinine and water for gnawing tests.

Tastants significantly affected acceptance of GD and 613 rootstocks, F(2,48)=12.208, $\underline{p} < .001$, with glucose significantly preferred to water ($\underline{p} < .01$) and to fruit extract ($\underline{p} < .0005$), and water also preferred to fruit extract ($\underline{p} < .025$) (Table 1). Acceptance of R5 and M9 was also influenced by tastants, F(2,48)=4.137, $\underline{p} < .025$, with glucose preferred to quinine ($\underline{p} < .01$). There was also a significant interaction between rootstock variety and tastant, for example, R5 treated with quinine had limited acceptance when compared with M9 given the same treatment, yet the acceptability of two rootstocks did not differ with glucose treatment, F(2,48)=7.56, $\underline{p} < .005$, quinine contrast $\underline{p} < .005$.

In this experiment, gnawing preferences for tastants on rootstocks were similar to the taste preference previously shown for solutions and different from those previously shown for flavored wooden dowels. The moisture in rootstocks may account for their having been chosen similar to solutions.

Table 1. Gnawing damage by pine voles to rootstocks soaked in water fruit extract, glucose, or quinine solutions.

Variety	Glucose	Water	Fruit Extract	Quinine
Golden Delicious	1.92 ± .21*	1.63 ± .30	.96 ± .18	
613	1.97 ± .30	1.10 ± .13	1.03 ± .10	
M9	1.35 ± .12	.74 ± .23		1.18 ± .15
R5	1.17 ± .16	1.22 ± .17		.46 ± .16

* Mean gm ± standard error

This study verifies that taste quality can alter gnawing of wood, however, we did not find evidence that rootstock flavors account for differential rootstock acceptability. In previous studies, when distinctively flavored substances were added to dowels, differences in gnawing resulted. However, when rootstock-bark homogenates were recently used as flavorants for dowels, gnawing was unaffected (4), though whole rootstocks of various varieties are gnawed differently (5,6) While voles did gnaw both dowels and rootstocks differently in response to taste cues, the effect was not a strong one when compared with ingestion of solutions.

We have found in related studies that rootstock acceptance is highly correlated with textural properties. Preferred rootstocks are less dense (2,3), more tender (3) and perhaps more open in internal structure (7). The present data, showing a limited effect of taste, are consistent with our previous suggestions that texture affects preference more than does taste.

GROOMING: The auto-grooming and hetero-grooming behavior of pine voles and meadow voles were tested by applying a carboxymethyl cellulose (CMC) gel to one side of one member of a pair, and observing subsequent grooming. Voles were tested in their home cages under red light, with all food and water removed from the cage. CMC (3% solution, 2.5 - 3.5g) was applied randomly to the right or left side of each subject, from neck to rump. The vole was then returned to the cage to interact with its unsoiled partner.

Grooming by the two voles was manually-recorded on a 20 channel Esterline-Angus event recorder by an observer who scored, for the soiled vole: head grooming, auto-grooming of the right and left sides, and hetero-grooming of the other vole; and, for the unsoiled vole: head grooming, auto-grooming of either side, hetero-grooming of the right and left sides of the soiled vole.

Data for total grooming duration at each body site for each test were extracted from all strip chart records. Also, in pine vole data from Experiment 2, the average grooming bout length for each vole within each test and the average interbout-interval for each vole within each test were also determined. Based on examination of grooming sequences, a bout interval was operationally defined as any cessation of grooming lasting at least 20 sec.

Experiment 1

Pine vole pairs (N = 16) and meadow vole pairs (N = 9) were initially observed in ten minute tests. In each test, one vole of the pair was coated unilaterally with CMC, and the gender given CMC was randomly alternated. Each pair was tested only once. Subsequently, pine voles (N = 9 pairs) were observed in the same paradigm during thirty minute tests.

In the 10 minute test, pine voles with soiled fur auto-groomed more than they were hetero-groomed by their cage partners, $F(1,30)=8.8$, $p < .01$ (Table 2). In both hetero- and auto-grooming, the soiled side was groomed more than the clean side, $F(1,30)=17.7$, $p < .001$. The interaction was also significant, $F(1,30)=7.7$, $p < .01$, reflecting the extensive auto-grooming on the soiled side. The soiled vole engaged in significantly more head-grooming than did the unsoiled vole, $p < .005$ (Table 3).

In the 30 minute test, there was a significant interaction between auto- vs. hetero-grooming and grooming of the unsoiled vs. the soiled side by both voles, $F(1,32)=9.5$, $p < .005$ (Table 2). Significant contrasts included: total auto-grooming by the unsoiled vole, $p < .05$, and auto- vs. hetero-grooming by the soiled vole, $p < .05$. There was no significant difference in extent of head grooming by soiled and unsoiled voles.

In the ten minute meadow vole test, extent of grooming was much less than in pine voles, and grooming of the greased side did not significantly differ from grooming of the ungreased side (Table 2). Durations of auto-grooming also did not differ significantly. However, the soiled vole groomed its head a longer duration than did the clean vole (Table 3).

Pine voles, similar to other rodents, increased auto-grooming of soiled fur and the head after being coated with a substance. Further, uncoated voles selectively hetero-groomed the coated side more than the uncoated side of their cagemates. This can reflect either social facilitation caused by grooming of the coated vole, or responding directly to the coated fur.

Table 2. Grooming of a Unilaterally-Soiled Vole by Itself and Its Partner

	Auto Groom		Hetero-Groom	
	Soiled Side	Unsoiled Side	Soiled Side	Unsoiled Side
Pine Vole				
10 min test N	16	16	16	16
	112.8 ± 30.4*	4.7 ± .6	23.2 ± 10.7	.8 ± .5
30 min test N	9	9	9	9
	237 ± 79.5	26.3 ± 10.9	5.9 ± 4.1	192.3 ± 109.5
Meadow Vole				
10 min test N	9	9	9	9
	7.8 ± 5.8	.2 ± .2	2.78 ± 2.7	0

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* Mean sec ± Standard Error

Table 3. Head Grooming in Voles Whose Back Fur Is or Is Not Unilaterally Soiled

	Soiled Vole	Clean Vole
Pine Vole		
Experiment 1		
10 min test	21.9 ± 4.3 (16)*	4.1 ± 2.0 (16)
30 min test	110.8 ± 45.0 (9)	40.3 ± 10.7 (9)
Experiment 2		
20 min test	42.4 ± 20.0 (48)	9.0 ± 3.2 (48)
Meadow Vole		
Experiment 1		
10 min test	13.8 ± 4.5 (9)	0 (9)
Experiment 2		
30 min test	33.8 ± 10.9 (24)	18.0 ± 5.9 (24)

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* Mean sec ± Standard Error (Number)

Although performance of meadow voles was consistent with that of pine voles, the grooming durations were too low to obtain significant effects, except for head-grooming. In the subsequent experiment, we increased both test duration and number of subjects to obtain more data points.

Experiment 2

In the present experiment, tastants were added to CMC to determine whether tastants affect grooming durations in pine voles and meadow voles.

Experimentally-naive pine voles (N=24 pairs) were divided into three groups. Meadow voles (N=12 pairs) were divided into two groups since additional naive animals were unavailable. One member of each pair was unilaterally coated with a CMC solution: plain; .015 M sodium saccharine: and for pine voles only, .0024 M quinine hydrochloride. Each pair was tested twice with the specified CMC solution. A single member of the pair was coated with CMC, alternated and counterbalanced with respect to gender. Pine voles were tested for 20 min. and meadow voles for 30 min.

Addition of tastants had no significant effect on grooming duration in either pine voles or meadow voles. Nor was there a gender difference in either species. Auto- and hetero-grooming by clean and soiled pine voles significantly differed, F(2,84)=32.1, $p < .01$ (Table 4). The soiled vole groomed his soiled side more than he was groomed by the clean vole, $p < .01$. The soiled vole also engaged in more head-grooming than did the clean vole, $p < .01$.

Meadow voles engaged in significantly more auto- than hetero-grooming, F(1,46)=8.35, $p < .01$ (Table 4). The coated vole was groomed by its partner more than the clean vole, F(1,46)=6.39, $p < .025$. There was also a significant interaction between the two factors, F(1,46)= 12.14, $p < .005$ since hetero-grooming exceeded auto-grooming in the clean vole, and the reverse occurred for the soiled vole. There was no significant difference in extent of head-grooming by the coated and the uncoated voles.

An analysis of bout duration in pine voles showed that the average grooming bout duration was significantly longer in soiled voles as compared with unsoiled voles, F(1,44)=12.45, $p < .005$ (Table 5). Soiled voles engaged in more grooming bouts than did clean voles, F(1,44)=7.30, $p < .025$. The inter-bout interval was unaffected by soil on the fur. Neither variable was influenced by gender.

Experiment 2 demonstrates that taste qualities do not alter grooming duration in pine voles or meadow voles, a result that is consistent with other findings. Although tastants can alter gnawing of wooden dowels, texture appears to be the primary factor accounting for preferential gnawing of apple rootstocks (3). Taste preferences in solutions are exhibited for sodium saccharin but the same tastants appear to have weak effects, if any, in the gnawing context (4).

Previous studies have noted that peripheral stimulation is a powerful stimulus to auto-grooming in mice (8), kangaroo rats (9), and rats (10). The present results demonstrate that hetero-grooming by an unsoiled vole also is increased when its partner's fur has been soiled. Remarkably, the extent of hetero-grooming exceeds auto-grooming in these voles. Further studies could elucidate whether social grooming by the clean vole is socially faciliated or is a direct response to the material on the partner's fur.

Under normal circumstances, the incidence of hetero-grooming is very low. One possible control technique is to apply a toxicant to voles' fur (perhaps via greased tubes). Such a method is successful with vampire bats, particularly since a few toxicant-coated bats returning to the home roost are then hetero-groomed by several others. Our findings suggest that, although pine voles generally hetero-groom very little, soiled fur leads to much higher levels of hetero-grooming. It seems reasonable to expect that a toxicant-soiled pine vole returning to a home burrow would, via hetero-grooming, provide toxicant to its nest partners. Radio-tracking field studies indicate that a typical living group of pine vole includes 2-3 adult males, only one of which is breeding, and 2-3 adult females (11). Soiling a single family member could thus create a toxicant system that is automatically delivered to the home nest.

Table 4. Auto- and Hetero-Grooming by a Soiled Vole And Its Clean Partner

	Auto-groom	Hetero-groom	Auto-groom	Hetero-groom
Pine Vole				
20 min test	149.4 ± 21.3* (48)	.8 ± .4	10.5 ± 3.2 (48)	28.9 ± 9.1
Meadow Vole				
30 min test	181.0 ± 59.6 (24)	.9 ± .6	11.0 ± 5.1 (24)	21.0 ± 12.2

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* Mean sec ± Standard Error (Number)

Table 5. Grooming Parameters for Voles as a Function of Whether Their Fur is Soiled

	Soiled Fur		Unsoiled Fur	
	Females	Males	Females	Males
N =	24	24	24	24
Bout duration (sec)	43.0 ± 8.6*	74.4 ± 15.3	14.7 ± 5.3	25.8 ± 11.2
Inter-bout interval (sec)	95.2 ± 20.9	97.8 ± 21.6	77.1 ± 25.1	72.3 ± 22.0
Number of bouts	3.4 ± .7	7.8 ± 4.1	2.3 ± .7	2.0 ± .6

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* Mean ± Standard Error

TASTE AVERSIONS: Many rodent species exhibit unlearned preferences for sodium saccharin solution over water, including meadow voles (.006 M; 12) and pine voles (.0035 M; 13). However, conditioned taste aversions have not been described for these species. In this experiment voles were given an initial exposure to the taste of saccharin and subsequently injected with either lithium chloride solution or sodium chloride solution. Later, the preference for sodium saccharin solution relative to water was measured in the two groups. Pine voles (25 ♂, 25 ♀) and meadow voles (22 ♂, 22 ♀) were housed individually. Peanuts, sunflower seeds, and alfalfa were available *ad lib* throughout the study.

The drinking tubes used were calibrated 10 ml syringes fitted with metal sipper tubes. Each vole was allowed to consume .5 ml of saccharin and then the drinking tube was removed. During a one-week training period, pine voles were deprived of water for 17 hours daily and meadow voles were deprived for 4 hours for a 2 1/2 week period. Following water deprivation, voles were offered water on a schedule paralleling the experiment to familiarize them with experimental procedures. Water was presented from a calibrated drinking tube for five minutes, and after a 2 1/2 hour delay, from two calibrated drinking tubes for one hour in the afternoon. Standard water bottles and fresh apple were then provided to pine voles for 3 1/2 hours and to meadow voles for 16 1/2 hours, and then water deprivation was resumed.

Meadow voles exhibited a sensitivity to water deprivation noted previously by other investigators (12,14). Therefore, meadow vole subjects were given a shorter water deprivation period than pine voles, and the training regime for inducing drinking was generally less effective for meadow voles. Consequently, they took longer to consume a specific volume of saccharin solution, and consumption on 2-choice preference tests was sometimes nil. The short water deprivation period for meadow voles was adopted when a single overnight deprivation resulted in 4 deaths.

Induction of the taste aversion was a 3-day procedure. On day 1 each vole was offered 1 sipper tube and allowed to drink .5 cc of water. One half hour after receiving the drinking tube each vole was weighed. Weighing provided handling experience for voles and was the basis for calculating injection dosages on the following day. Two hours after weighing, each vole was offered 2 drinking tubes of water simultaneously for 1 hour, as a mock preference test. On day two each vole was offered .5 cc of the actual taste solution, Na saccharin (.2% wt/vol in tap water). One half hour (pine voles) or one hour (meadow voles) later, each received an injection (ip) of either LiCl (.51% wt/vol in distilled water, autoclaved to induce sickness or NaCl (.88% wt/vol in distilled water, autoclaved) as a control, with approximately equal numbers of males and females receiving each treatment. Two hours (pine voles) or one hour later (meadow voles), each was given another mock preference test with 2 drinking tubes of water for 1 hour, and the volume of water drunk from each tube was recorded. On day three, each vole was given the actual 2-choice preference test between drinking tubes of water and saccharin for one hour. Amounts consumed of each were recorded.

A preference ratio of saccharin solution to total fluid consumption was derived for each 1 hr, 2-choice test. For pine voles, the effects of sodium vs lithium injections on subsequent preferences were analyzed using a one-way analysis of variance, with gender as the independent factor. Eleven meadow voles did not consume measurable amounts of water or saccharin. This resulted in unequal numbers of males and females. Thus, the data from both sexes were pooled and the student's t-test was used to test for differential consumption.

Animals that drank no saccharin prior to the scheduled lithium or sodium injection, or drank no liquid in the preference test were eliminated from the study and not replaced, reducing to 46 pine voles

(22 ♂, 24 ♀) and 30 meadow voles (15 ♂, 15 ♀). Two additional female pine voles were removed at random to make equal sized groups.

Voles injected with lithium chloride avoided sodium saccharin in subsequent two-choice preference test (Figure 1); pine voles, $F(1,40)=16.8$, $p < .001$; meadow voles $t\ (28)=12.5$, $p < .005$). No significant gender effect was found for pine voles. These results support the notion that voles form conditioned taste aversions. In this respect the voles are similar to numerous other species that have been studied.

TASTE AVERSION EFFECTS ON GROOMING: The previous experiment showed that voles can form conditioned taste aversions to saccharin. In the present experiment we applied sodium saccharin in a viscous vehicle to the fur of voles from Experiment 1 to determine whether the voles would avoid grooming in the presence of the conditioned stimulus.

The experiment followed the Experiment 1 preference test by 3 weeks in pine voles, and by 4 days in meadow voles. Due to the intervening time since Experiment 1 for pine voles, each was given a repeat saccharin preference test on Day 1. This step was omitted for meadow voles, since they had completed Experiment 1 only days earlier. On day 2, voles were coated on one side of the body from neck to rump, with a mixture of carboxymethylcellulose (3.0%) and saccharin (.35%) weighing 2.5-3.5 g and placed under red light in home bedding for a 25 min grooming test. Grooming bout durations were recorded manually on an Esterline-Angus event recorder and separately scored as to soiled side or unsoiled side. On day 3 a final preference test was administered, again measuring the amounts of water and saccharin the experimental voles drank in one hour.

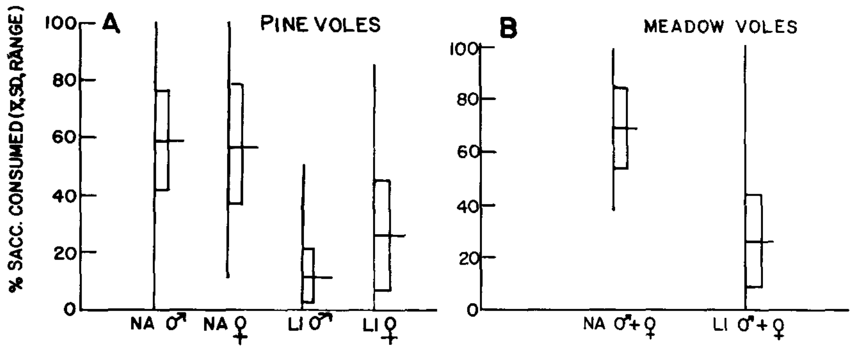

Figure 1: Saccharin consumption scores for sodium chloride and lithium chloride injected voles.

Voles which had been injected with lithium and failed to exhibit a conditioned taste aversion in either the pre-grooming or the post-grooming preference tests were eliminated from the analysis. Also, sodium injected voles failing to exhibit a preference for saccharin (less than 50%) were eliminated. Eliminated by these criteria on pre- and post-grooming tests, respectively, were: sodium-injected pine voles, lithium-injected pine voles, 8, 1; sodium-injected meadow voles, 3, 1; lithium-injected meadow voles, 3,6. In addition, one sodium-injected pine vole was removed in a random fashion from the analysis.

For data preparation, the following measures of grooming were extracted from the strip-chart record; grooming latency; total grooming duration; and grooming on the greased vs. the ungreased side. For pine voles, grooming durations and latencies were subjected to a one-way analysis of variance with gender as a factor and the soiled vs. clean sides as a subplot variable. For meadow voles, disproportionate numbers of males and females remained, so the two sexes were pooled and grooming durations, grooming latencies and grooming of soiled vs clean side were analyzed with separate student's t-tests.

Grooming duration was unaffected by treatment for both meadow voles and pine voles. The greased side was groomed longer than the un-greased side in both pine voles $F(1,24)=87.9$, $p < .001$, and in meadow voles, $t\ (22)=8.75$, $p < .0005$ (Figure 2). Female pine voles spent more time grooming than males, $F\ (1,20) = 5.68$, $p < .05$.

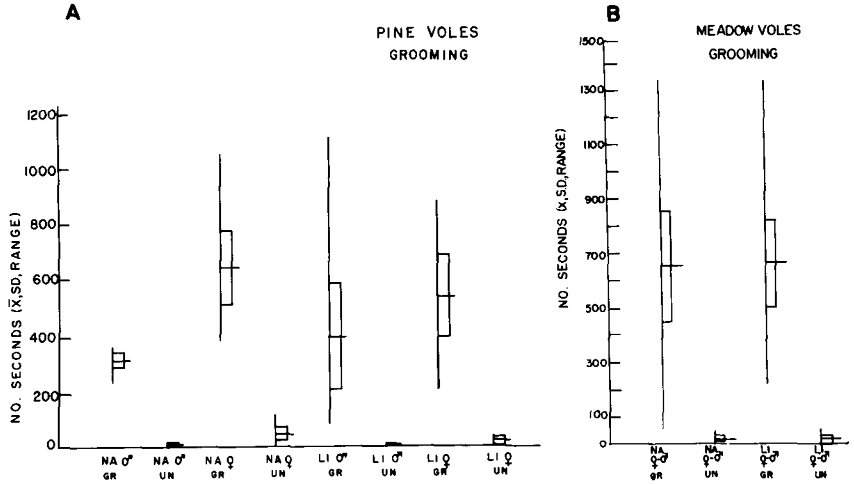

Figure 2: Grooming durations on the greased and ungreased sides of subjects that had been injected with sodium chloride or lithium chloride.

Grooming latency was affected by treatment in pine voles, as lithium-injected animals had a prolonged latency, $F(1,20)=6.69$, $p < .025$. The greased side was groomed with a shorter latency than the ungreased side in both pine voles, $F(1,24)=21.48$, $p < .001$, and in meadow voles, $t\ (22)=5.23$, $p < .0005$. Thus voles which avoid saccharin in their drink do not avoid grooming when saccharin is present.

Data for the post-grooming preference tests of Experiment 2 subjects are shown in Figure 3. Pine voles exhibited a significant effect of injection treatment, $F(1/20)=155.0$, $p < .001$, as did meadow voles, $t(14)=59.4$, $p < .001$.

Pine voles and meadow voles appear similar to many other species in forming a taste aversion to saccharin when also injected with lithium chloride. Animals in whom an aversion was induced subsequently avoided drinking saccharin solutions. However, when saccharin was applied to animal's fur, the average duration and latency of their grooming remained unaffected by the aversion. The similar grooming data from animals with and without the aversion show that the taste aversion was ineffective as a deterrent to grooming and, presumably, ingestion.

Applying material to the fur resulted in increased grooming on the soiled as compared with the clean side of the fur. Changes in local peripheral input have been shown in earlier studies to alter grooming duration. Various disturbances, including applying mild peripheral irritants to the posterior surface of the animal, increase face grooming in mice (8). Cohen and Price (10) report that undisturbed rats spent significantly more time grooming a side soiled with agar than the unsoiled side and Griswold *et al.* (9) found similar effects when they applied

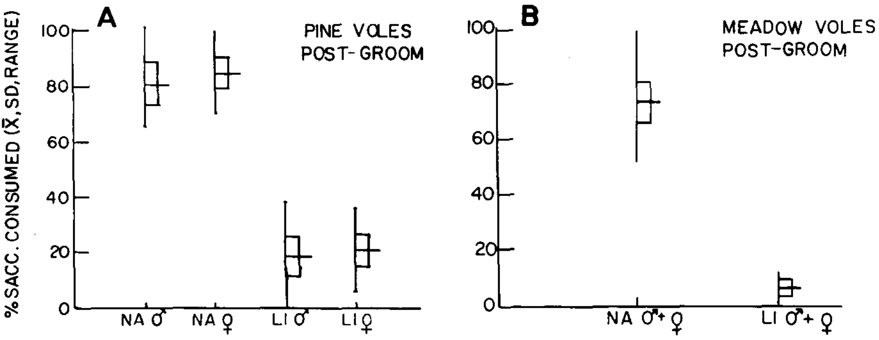

Figure 3: Saccharin consumption scores subsequent to grooming saccharin from fur in voles exposed (Li) and not exposed (Na) to the taste aversion treatment.

lanolin to one side of kangaroo rats (*Dipodomys merriami*). Further preferential grooming of soiled fur may extend to social grooming: both pine voles and meadow voles heterogroom the soiled side of a cage partner more than the ungreased side (15). The presence of material on the fur appears to be a powerful stimulus to groom.

While voles formed taste aversions to saccharin, rats in our laboratory exhibit far greater avoidance, longer retention, and less variability in their aversions as tested in similar paradigms (16).

Voles as a group formed a significant aversion after lithium injection but numerous individuals did not. Thus, 38% of pine voles and 64% of meadow voles were eliminated from experiment 2 because they did not exhibit saccharin avoidance in both preference tests. Furthermore, the preference for saccharin was not exhibited by several sodium-injected individuals, 36% of pine voles and 25% of meadow voles. This may have been a neophobia effect.

Female pine voles exhibited a significantly higher grooming duration than did males. Since we do not see this gender difference when one vole in a mixed-sex pair is coated with carboxymethylcellulose we would need more information to interpret the difference. Delivering material to fur has multiple effects, which may synergize to override the normal defenses of rodents against ingesting toxicants: 1) grooming is potentiated by the substance on the fur; 2) even if the substance would be rejected for feeding or drinking, grooming (and presumably ingestion) proceeds space; and 3) in rats but not pine voles) material tasted while grooming, if associated with an illness, may then reduce ingestion of the material via eating and drinking. This last point could result in an animal avoiding a food it normally prefers, as has occurred with coyotes after they have fed on lithium-treated sheep (17). Grooming offers an alternate means of delivery which does not require that the animal feed or drink the material, simply that it clean its fur. Our results suggest that this method could be used in vole control to increase acceptance of an avoided toxicant, perhaps administered in greased tubes. Further studies would be needed to determine: the retention curve over time for taste aversions in voles, and 2) the retention curve for a conditioned taste aversion when follow-up exposures to the tastant are unaccompanied by illness, as in the grooming experience.

CONCLUSIONS: Taken together, these experiments highlight contextual influences on ingestion by voles. Tastants exert a marked effect on the quantity of liquid voles consume in two bottle preference tests, both in direct tests and in taste aversion paradigms. Tastants appear to have less effect on gnawing, and in caching the tastant effect is barely discernible or even absent. Finally tastants did not influence grooming durations of mixed-sex pairs when one vole was unilaterally coated with a flavored gel. The flexibility of voles' taste responses in various behavioral contexts can perhaps be exploited, and needs to be considered, in the development of new control techniques.

ACKNOWLEDGMENTS: We gratefully acknowledge the support of the US Fish and Wildlife Service, Contract 14-16-0009-79-102, Our Monell colleagues J. Russell Mason, Irwin Martin, and Russell Reidinger offered constructive suggestions. We also appreciate the able technical assistance provided by Evelyn K. Meyer, William Moore, and Durke Nichols.

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Social Context Affects Expression of Conditioned Taste Aversions During Grooming By Pine Voles: Implications for Animal Damage Control

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Abstract

Rodents typically show conditioned aversions to substances previously associated with illness. Aversions can be observed when the tastant is presented in food, water and, for rats, when the tastant is smeared unilaterally on the animal's flank and ingested during autogrooming. Such results have important implications for rodent control. For that reason, others have investigated whether voles and mice continue to groom when tastants associated with sickness are smeared on their fur. Investigations have shown that grooming persists in the presence of the conditioned stimuli even though strong aversions are shown toward the same tastants in a drinking context. The question remains, however, whether conditioned aversions would be expressed in special situations. The present experiments clearly demonstrate that taste aversions can be observed during heterogrooming of a cagemate, but not during autogrooming of self. Such results suggest that social variables may modulate expression of conditioned taste aversions for some gregarious and/or communal species. Also, they are consistent with the notion that various species show specialized adaptive systems which may not obey conventional laws of learning.

Introduction

Rodents typically show conditioned taste aversions to substances previously associated with illness. Aversions can be demonstrated when the tastant is presented in food (Milgram, Krames & Alloway, 1977), water (Riley & Clarke, 1977) and, for rats, when the tastant is smeared unilaterally on the animal's flank and ingested while autogrooming (Reidinger & Beauchamp, submitted for publication). Taste aversions formed during grooming are robust and will transfer from the grooming context to other contexts, such as drinking. These results have important implications for rodent control and other workers have investigated whether voles (Geyer, Kornet & Reidinger, submitted for publication) and mice (Stewart, unpublished data) continue to groom when tastants are smeared on their fur. The investigations have shown that grooming does persist in the presence of conditioned stimuli even though strong aversions are shown toward the same tastants in a drinking context. Given the stereotypic quality of grooming (Fentress, 1977), such results reflect the possibility that voles (and mice) need to groom whenever a peripheral irritant is applied (Griswold, Borchelt, & Bensko, 1977; Fentress, 1977). The question remains, however, whether voles taste substances ingested from the fur while grooming, and if so, whether conditioned aversions would be expressed in some special situations.

In Experiment 1, taste aversions were induced after voles drank saccharin solution. To test whether the taste aversions affected ingestion of tastants while grooming, saccharin in CMC was placed on one flank and plain CMC on the other. In a manner analogous to a one versus two-choice drinking test, this procedure provided a more sensitive measure of tastant effects on grooming.

Method

Subjects. Ten male-female pairs of voles were used as subjects. These animals were laboratory -born from stock trapped near Beiglerville, Pennsylvania in 1972. Each pair of voles was housed and tested in a plastic shoe-box cage (27 cm long x 17 cm wide x 13 cm high). Animals were maintained under a 12/12 light-dark cycle and permitted *ad lib* access to alfalfa, peanuts, sunflower seeds and apple slices.

Procedure. Each pair of voles was adapted to handling and to a 14 hr water deprivation schedule. Then they were trained to drink water from a 10 ml syringe fitted with a sipper tube (Robbins, 1978). Training continued for three days. On the fourth day, the pairs of voles were separated for about two hours. One vole in each pair was selected randomly and allowed to drink 1 ml of 0.015 *M* sodium saccharin (.2% wt/vol in tapwater). Thirty minutes later, each of these voles was given an injection (ip) of either lithium chloride (LiCl: .51% wt/vol in distilled water) or distilled water as a control. Lithium-injected voles and their cagemates were subsequently referred to as group A while water-injected voles and their cagemates were referred to as group B. Sixty minutes after the injections, the pairs of voles in both groups were reunited in their home cages. On the next day (Day 5) and three and five days later, the injected vole in each pair was smeared with .5 ml of carboxymethylcellulose (CMC: 3.5% wt/vol in distilled water) and 0.15 *M* saccharin solution on one flank and .5 ml of CMC alone on the other. Counterbalancing was used to determine which side of each animal was smeared with saccharin and CMC. The cagemate of the injected vole in each pair was not smeared. Then, each pair of voles was observed for 15 minutes by two observers whose mean inter-rater reliability coefficient exceeded 0.95. Frequencies and durations of the following behaviors were scored on an Esterline-Angus event recorder for both members of each pair in both groups: (a) body washes (Bolles, 1960) of own left and right flank; (b) body washes of cagemate's left and right flank.

Results

Two-way analyses of variance (ANOVAs) and the Bonferroni post-hoc t-test (Games, 1977) were used to identify significant differences among means. While there was no difference ($p > .25$) between groups in the total amount of autogrooming and heterogrooming, the smeared injected animals in both groups groomed more than their cagemates ($F(1,19)=8.5$, $p < .05$) (See Appendix 1). While smeared injected voles in group A failed to groom one flank more than the other ($p > .25$), those in group B showed a slight but significant preference for grooming the flank smeared with saccharin ($p < .05$). Heterogrooming by cagemates of the smeared injected voles in both groups was greater in frequency and duration than autogrooming ($p < .05$) although it was not significantly differential, i.e., the saccharin-smeared flank was not preferred. There were no sex differences in autogrooming or heterogrooming on any of the test days ($\underline{p} > .25$). Frequency and duration of grooming bouts were positively correlated in every instance.

Discussion

On the one hand, the results of Experiment 1 do not clearly demonstrate the existence of conditioned taste aversions during autogrooming for smeared voles injected with lithium (Group A). On the other hand, because voles given pairings of LiCl and saccharin showed no grooming preferences between the flank smeared with saccharin and the flank smeared with CMC alone while, smeared water-injected voles (Group B) did, suggest: (a) that the presence of conditioned taste aversions may have been masked by the rigid behavioral quality of autogrooming; or (b) that generalization to the grooming context was weak. Experiment 2 aimed to test these hypotheses.

Experiment 2

Introduction

Previous work (Geyer, et al., submitted for publication) and the results of Experiment 1 suggest that a vole whose partner is smeared with CMC heterogrooms more than it autogrooms. Such heterogrooming appears to be under the control of peripheral, social cues and might permit sensitive expression of conditioned taste aversion if the aversion readily generalized from the drinking to the grooming context. Experiment 2 investigated heterogrooming by voles toward cagemates after the former had been given pairings of LiCl and saccharin and the latter had been smeared with the conditioned stimulus on one flank and vehicle on the other.

Method

Subjects. Twenty-two male-female pairs of pine voles were used as subjects. The animals were experimentally naive, from the same stock as animals used in Experiment 1 and were housed and maintained as previously described.

Procedure. The procedure of Experiment 2 was identical to that of Experiment 1, except that the non-injected, rather than the injected, voles were smeared with saccharin and CMC. As before, voles injected with lithium were assigned to group A; the other injected voles were assigned to group B, and cagemates of each sort were assigned to the same group as their injected partners.

Results

Repeated measures ANOVAs and the Bonferroni procedure were used to isolate significant differences among means. As in Experiment 1, there were no differences ($\underline{p} > .25$) between groups in the total amount of grooming (See Appendix 2). However, for both groups, heterogrooming (but not autogrooming) by injected voles was differential

($F(1,35)=34.8$, $p < .05$). Voles in Group A consistently groomed the flank of their partners smeared with CMC alone ($p < .05$) while voles in group B groomed the flank of their partners covered with saccharin CMC. Smeared voles groomed the flank covered with saccharin CMC regardless of whether their partners had been injected with LiCl or water ($p < .05$). Animals showed stronger preferences on some days than others ($F(3,160)=4.32$, $p < .05$), the strongest being on the second of the three test days ($p < .05$). By the third test, differential grooming by voles injected with LiCl or water had disappeared although differential behavior remained strong for the smeared uninjected voles in both groups ($p < .05$). There were no sex differences in autogrooming or heterogrooming on any of the test days ($p > .25$).

Discussion

Experiment 2 clearly demonstrated that voles will show conditioned aversions during heterogrooming towards substances smeared on a cagemate's flanks. The positive correlations between the frequencies and durations of various grooming behaviors suggests that both measures give essentially the same information about the presence (or absence) of conditioned aversions. Together such results are consistent with the notion that heterogrooming is more controlled by situational or social cues than is autogrooming. The fact that aversions were strongest during the second preference test suggest that the animals were neophobic toward saccharin when it was first encountered during grooming.

General Discussion

Experiments 1 and 2 are consistent with previous findings that grooming is increased when substances are applied to the animal's fur. Likewise, the results are consistent with the notion that even if the substance would be rejected while feeding or drinking, autogrooming and therefore ingestion is largely unaffected (Reidinger & Beauchamp, unpublished data). However, the present studies demonstrate that heterogrooming is affected and animals reject substances smeared on the fur of conspecifics as they would if the substance was presented in water.

Grooming could offer an alternative means for presenting toxicants to pests and insuring ingestion of pharmacological amounts. The method of delivery has the advantage of not requiring animals to drink or eat poisoned water or food. The sole requirement is that the animals groom. The results of Experiment 1 provide support for the notion that ingestion of toxicants during autogrooming could be used in the control of vole populations to increase intake of otherwise avoided toxicants, perhaps administered through greased tubes (Fiedler, personal communication; Pank, personal communication) or tracking powders (Marsh, 1972). However, the finding in Experiment 2 that pine voles will show conditioned taste aversions during heterogrooming suggests that ingestion of toxicants will occur in pharmacological amounts when the animal is presented with substances on its own fur but only in lesser amounts when one member of the colony is affected and groomed by other colony members. Thus, control of vole populations through measures similar to those used for vampire bat populations who show communal grooming is questionable (Thompson, Mitchell & Burns, 1972) and deserves further investigation.

Overall, the results of the present experiment suggest that social variables may modulate the expression of conditioned taste aversions for some social species. If so, then this is the first demonstration that social factors are important for modulating the plasticity of so-called fixed action patterns (Fentress, 1977). Moreover, the present demonstration that social factors are important for the expression of conditioned behaviors is consistent with suggestions by Rozin and Kalat (1971) and others that various species show specialized adaptive systems which may not obey the conventional laws of learning derived from typical laboratory studies of learning.

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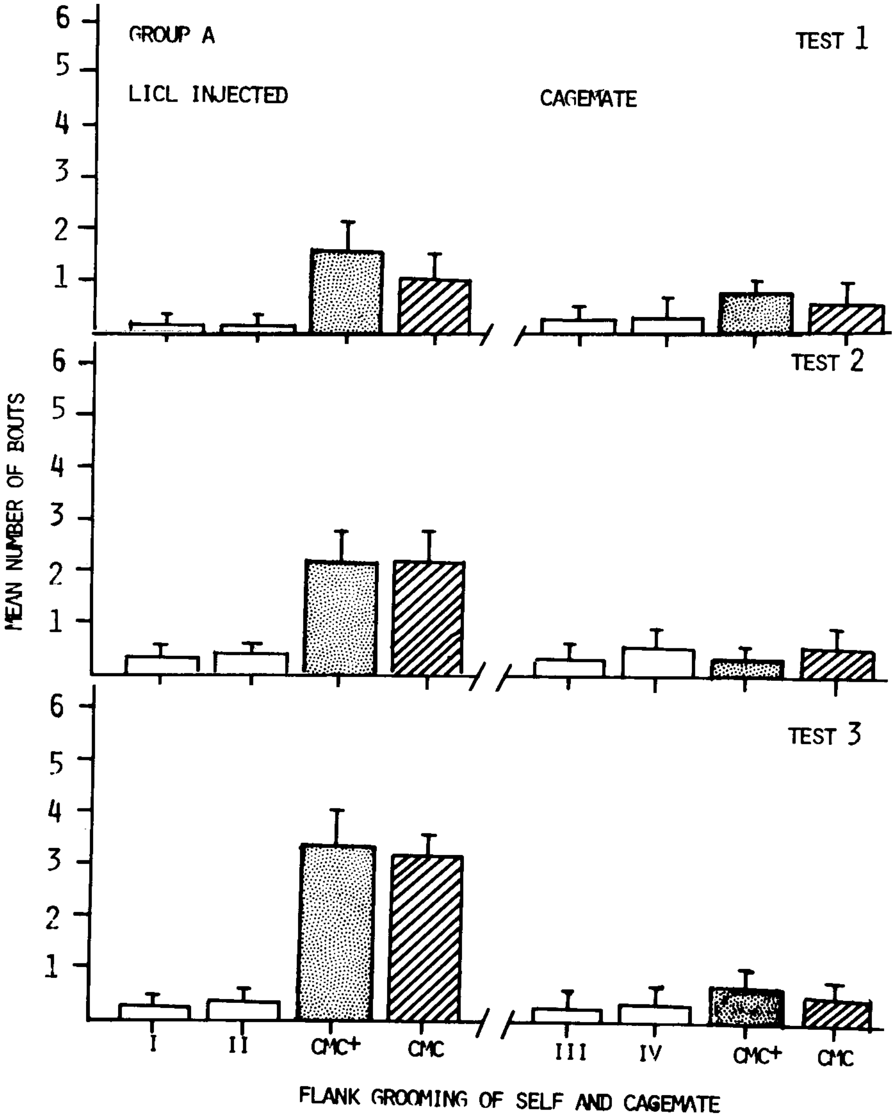
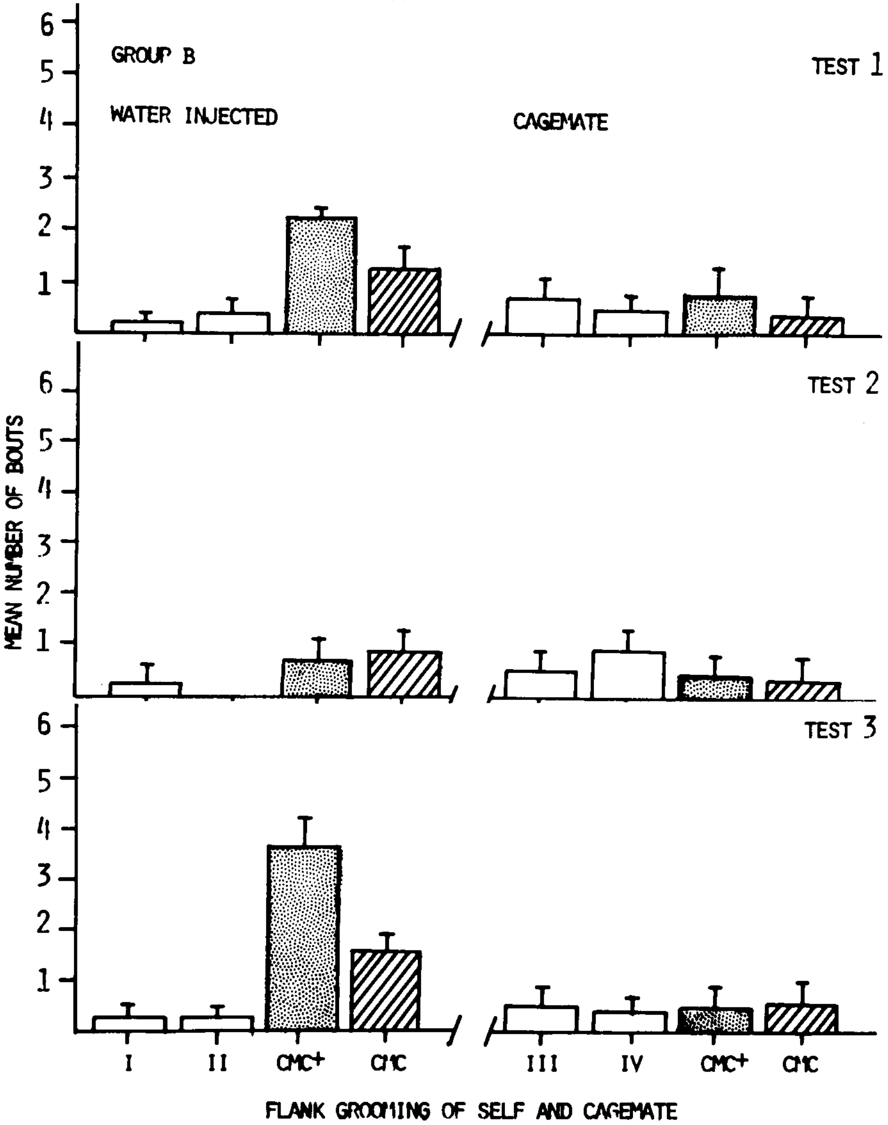
Appendix 1



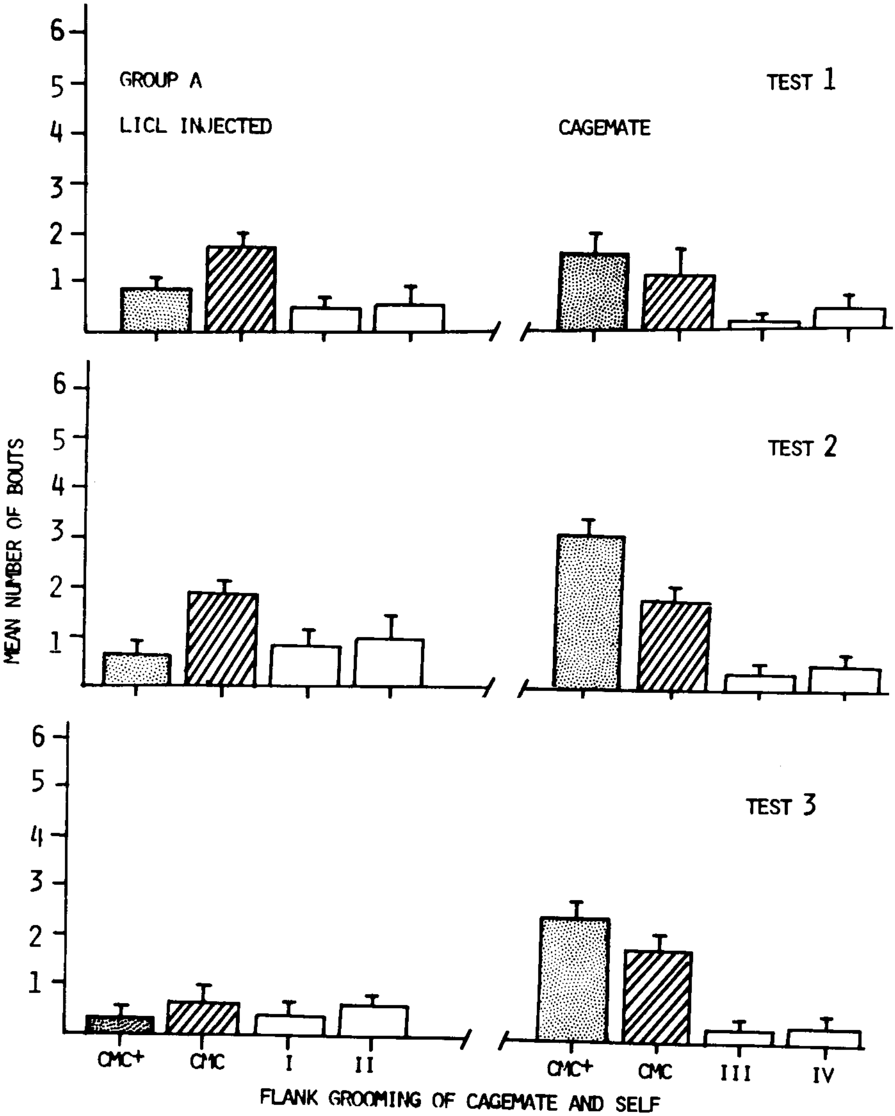
(Group A). (Left) LiCl-injected smeared voles do not show differential heterogrooming of cagemates (I,II) or autogrooming of themselves (CMC+, CMC). (Right) Cagemates of LiCl-injected voles do not show differential autogrooming (III,IV) or heterogrooming (CMC+, CMC). However, heterogrooming bouts were more frequent and for longer durations than autogrooming.

Appendix 1



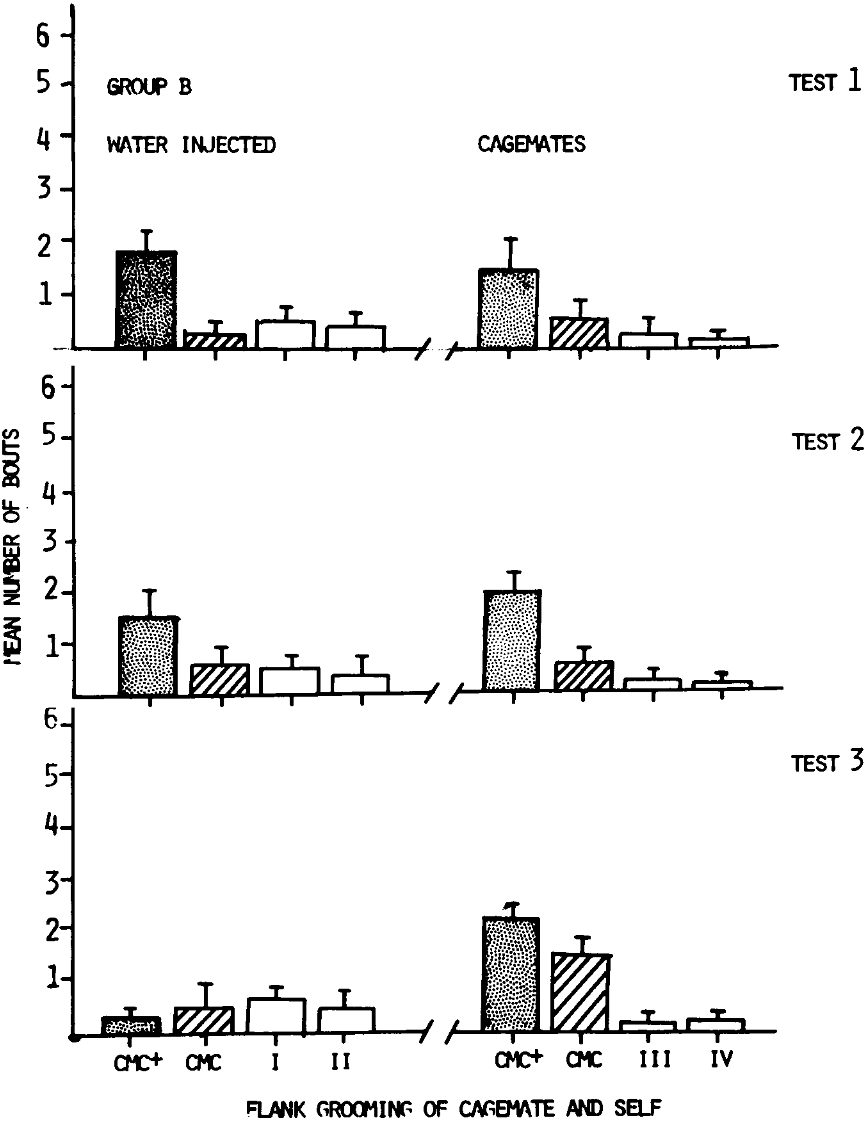
(Group B). (Left) Water-injected smeared animals do not show differential heterogrooming of cagemates (I,II) but do differentially autogroom their own flank smeared with saccharin CMC (CMC+). (Right) Cagemates of the injected smeared voles do not show differential autogrooming (III,IV) or heterogrooming (CMC+, CMC).

Appendix 2



(Group A). (Left) LiCl-injected voles show differential heterogrooming of cagemates' flanks smeared with CMC (CMC) and avoid the flank smeared with saccharin CMC (CMC+). They do not show differential autogrooming (I,II). (Right) Smeared cagemates of injected voles show differential autogrooming of the flank smeared with saccharin CMC (CMC+). They do not show differential heterogrooming of the injected voles' flanks (III,IV).

Appendix 2



(Group B). (Left) Water-injected voles heterogroom the flank of a cagemate smeared with saccharin CMC (CMC+) more than the flank smeared with CMC alone (CMC). No differential autogrooming by injected voles was observed (I,II). (Right) Non-injected smeared voles groom the saccharin CMC (CMC+) flank more than the flank smeared with CMC alone (CMC). No differential heterogrooming by these voles of the flanks of the injected voles was observed (III,IV).

SOCIAL ORGANIZATION AND REPRODUCTION IN FREELY REPRODUCING COLONIES OF PINE VOLES IN THE LABORATORY

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Freely reproducing colonies of pine voles reared in confined laboratory enclosures have a definite social organization and a predictable pattern of reproduction which results in limitation of population size. Colonies that were established in the laboratory with a single breeding pair showed that: 1) populations were self-limiting, 2) rank order existed with the founding female occupying a dominant position in the hierarchy, 3) reproduction was generally confined to the founding female and 4) the non-reproducing members of the colony showed that they did become reproductive when they were paired with normal mates. This paper is a preliminary report of the above events as they were recorded in a study of six colonies in my laboratory.

Six freely growing populations were established in metal enclosures one meter square in size. Enclosures were equipped with covers consisting of two metal trays, 22x36 cm in size, that were raised 5 cm from the floor of the enclosure. Animals were maintained on a photoperiod of 12L:12D at a temperature of 16-18 C. Wood shavings were provided for litter and nesting material and animals were fed Wayne Rat Lab Blox, Wayne Guinea Pig Pellets, apple and water.

Each colony was started with a founding pair in which the female was pregnant with her first or second litter. Populations were permitted to reproduce without disturbance except for cage cleaning and necessary handling until they ceased growing. The end point for cessation of growth was set at 60-90 days after the birth of the last surviving litter except in the case of Pen E. In this pen all the animals died over a weekend because they ran out of water. Colonies were observed 3-5 times a week to record births and deaths and to note behavior.

The six populations showed different growth curves and they varied considerably in their final population size (see Figure 1). In Pens A, B, C, and F the populations ceased growing because as density increased, newborn litters did not survive. Births continued but infant mortality was 100%. In Pen D, births of new litters ceased and the population leveled off. Adult mortality was not a factor except in Pens E and F in which animals died of thirst.

A breakdown by enclosure shows the following:

Pen A leveled off at 11 adults. The largest number was 16 including infants that did not survive to weaning age.

Pen B had 16 adults with a maximum of 20 including infants that died.

Pen C had 28 adults with a maximum of 31 including infants.

Pen D had 8 adults. Growth in size in this cage ceased because the reproductive female stopped having litters.

Pen E lost all its animals at 150 days because the water bottles were emptied over a weekend. At that time there were 16 adults and 5 juveniles that were 36 days of age. Four days before the disaster, two infants were born that survived only two days. Thus Pen E had 21 adults and juveniles with a maximum of 23 individuals including infants.

Pen F lost animals over the same weekend in which Pen E animals died and again the water bottles were empty. Before the disaster, the colony numbered 23 animals ten of which survived. Afterward, numbers leveled off at 17 animals with a maximum of 21 including litters that did not survive to weaning age.

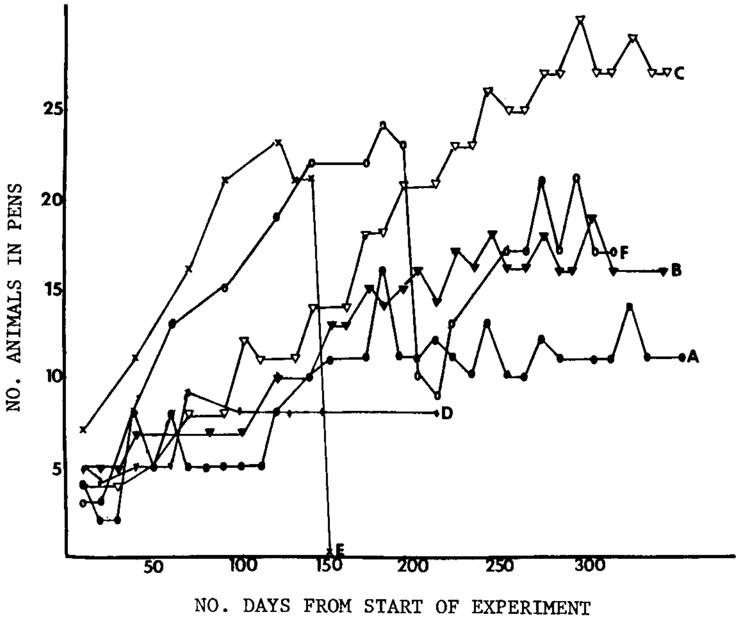

Figure 1. Growth of populations in six experimental pens.

Despite the fact that colonies showed different growth patterns, many generalizations are possible. They are discussed below.

REPRODUCTION

In all pens the surviving animals were post pubertal at the time the experiments were terminated. Only a few, however, participated in reproduction. The following observations were made on the reproducing animals.

Males - mating was not observed. Thus, in the absence of genetic markers it was not possible to tell which males were reproducing.

Females - observations of pregnancy and nursing showed that in all pens except Pen B, only the founding female gave birth. In Pen B, one female from the first generation of offspring had four litters but only two animals survived from these litters. Thus in the laboratory the reproductive patterns are structured with most births being limited to the oldest female.

After the experiments were completed, non-reproducing animals from four pens were checked to determine their state of sexual maturity. Voles from Pens A,B, and C were sacrificed and their gonads examined histologically. Animals from Pen D were paired with normal, mature mates to check for fertility.

Data show that all of the females born into experimental colonies A, B, and C had tertiary (mature) ovarian follicles (Type 7). Six had preovulatory follicles (Graafian follicles) and two had corpora lutea indicating they had ovulated. Despite the obvious maturity of the gonads, these animals did not reproduce. Testes, on the other hand were not all mature. Most of the males had depressed testicular weights and lowered numbers of mature sperm. All pens contained some males with mature testes. In Pens A and B the founding male had mature testes but in Pen C the testes of the founder had regressed. Pen D voles (four males and four females) were paired with normal mates to check fertility. Three of the females and one of the males had successful copulations within two to four days of pairing and the fourth female conceived fourteen days afterward. Young were delivered after a nomal gestation period. Clearly in Pen D the suppression of reproduction was behavioral rather than maturational.

BEHAVIOR

Pine voles are social and when they are at rest, they cluster in large groups in a preferred spot under cover. Enclosures were equipped with two covers in order to determine if all animals would group under one shelter or if they would disperse and occupy both covers. Colonies had a preferred cover and about 65% of the time all colony members rested under the same cover. If the second cover was used, a minimum of one or two animals used it. The second cover appeared to have more value as a temporary shelter for foraging animals than as a colony resting spot.

Rank order was examined in Pens A, B, and C. Pen A had one dominant female, the founding female and two dominant males, one of which was the founder. Pen B had two dominant females, the founder and one female from the first generation of offspring. This female was the one offspring that became reproductive. Pen B also had two dominant males. Pen C had a single dominant animal, the founding females. The founding male in this cage occupied a very subordinate position. In all cases founding females were dominant. Observations on reproduction showed that all of the dominant females had litters.

The subordinate females showed mature gonads but they did not give birth to litters. The dominant males and in some cases the subdominant males had mature testes but the lowest ranking males had small testes and depressed sperm production.

Activity levels changed as populations grew more crowded. When numbers were low, pens were quiet and activity was restricted to feeding and cacheing. As numbers increased, animals were observed in apparent aimless running outside of the shelters. Threatening sounds and boxing, but not actual fighting and wounding, were common. Food and water were consumed in large quantities and containers were emptied rapidly. In the case of Pens E and F the animals died of thirst, because extra water bottles were not added to compensate for the increase in activity with the result that existing bottles were emptied over a weekend.

When populations were low, young were well cared for. Nursing mothers clustered with other members of the group but this did not appear to disrupt parental care. Infants were firmly attached to the mother's nipples and they had a high rate of survival. If infants were detached from the mother and removed from the cover, they were retrieved by the mother or by other members of the colony.

As population densities grew, parental care was disrupted. Infants were often observed detached from the mother. If they wandered from the shelter or were removed from it, they were not retrieved or if they were retrieved, members of the colony carried them around the exposed areas of the enclosure and occasionally pulled them from each other's mouths. Adults did not wound or kill infants, but when parental care was disrupted, infants did not survive.

In summary, pine vole colonies are self-limiting because: 1) infants die before they reach weaning age or 2) the reproducing female ceases to deliver young. Establishment of rank order limits the number of reproductive females. Social organization that dictates that animals crowd together regardless of the available space keeps the reproductive female in constant contact with all colony members. As crowding increases and normal activity is disrupted, reproduction and parental care is affected and population growth ceases.

A system for the observation of voles under semi-natural conditions with applications to: social interactions, competition, food habits, habitat preference and bait acceptance.

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Abstract:

A laboratory system to study microtine rodents has been developed that avoids many of the intrinsic restrictions of earlier laboratory and field studies. The system is composed of two interconnected plexiglas tables with a soil substrate and hay cover. The system permits unconstrained visual observation of voles as they move within a runway network of their own construction. The flexibility of the system facilitates its use in various avenues of microtine research.

Introduction:

Social behavior of microtines has been of interest to investigators for many years. However, the study of these rodents under natural conditions is difficult. Microtines are small, elusive animals that live in subterranean tunnels or surface runways under dense cover.

Previous studies have gone only part way in solving these inherent problems of visibility. Field studies must rely solely on remote sensing methods, as unrestricted visual observation of microtines is impossible. Thus, althought trapping grid (Koplin 1968, Krebs 1977), dropping board (Brown and Conway 1961, Justice 1961), remote photography (Pearson 1960) and radio-telemetric studies (Chute et al. 1974, Madison 1980) have been able to investigate some attributes of vole social behavior they fail completely to examine the propinquitous behavior of two or more individuals. Laboratory studies (Banks et al. 1979, Gets 1962, Novak 1980, Turner and Iverson 1973) permit the unrestricted observation of vole interactions. However encounters are usually examined within glass aquaria, which are small and offer no cover or means for mutual avoidance. Laboratory studies are therefore highly artificial and conclusions from these studies must remain tentative.

It is clear that a system which combines, ease of observation within a naturalistic environment would contribute considerably to the study of microtine social behavior.

The system we developed was an attempt to combine the best of field and laboratory studies with as few of their intrinsic compromises.

The system:

The system at its simplest is composed of two 4'x4'x1/4" plexiglas tables joined by two unidirectional plexiglas tunnels (Figure 1). Each table is filled with a soil/peat substrate to a depth of one inch.

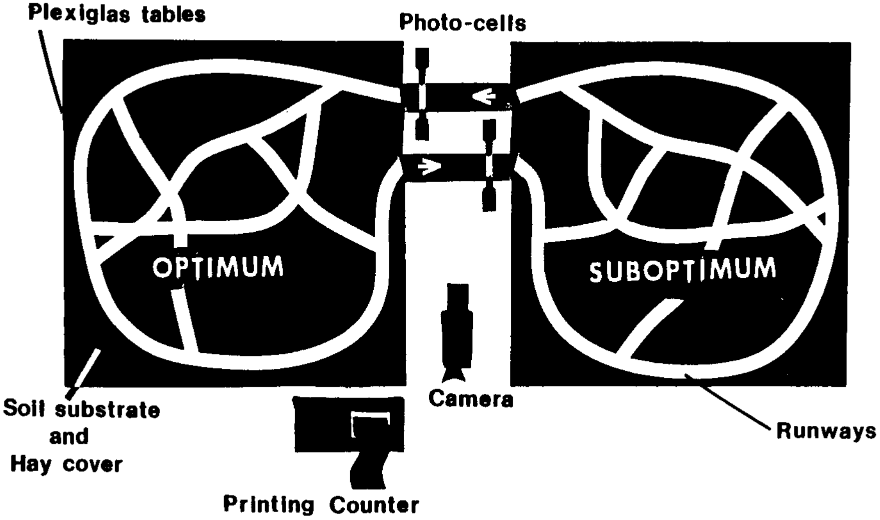

Figure 1: A system for observation of microtines under semi-natural conditions.

In each table, runways, (modelled on those built by two voles over a 21 day period), are constructed and covered with hay. In current experiments in our laboratory, the system is being used to assess competition within and between two microtine species. This is accomplished by varying the quality of the habitat in the two tables. One table is designated optimum and has a dense covering of hay and a variety of food. The suboptimum table has sparse hay cover and only rat chow as food.

Unrestricted observation of animals is possible from beneath the tables. Individuals can be easily seen through the plexiglas and identified by toe or fur clipping.

Movement of individuals between habitats (tables) is monitored using photo-cells (placed across each tunnel) connected to a single frame 8mm movie camera and a printing counter. In this way social behavior can be observed and duration of residency of individuals in each habitat can be continuously recorded.

Applications:

This system constitutes a naturalistic habitat for microtines and facilitates continuous unconstrained visual and remote monitoring of their social behavior.

At present, intraspecific and interspecific social behaviors of meadow and pine voles are being examined within the system as described. However, the system is very adaptable and with minimum alterations could be used to study a variety of microtine research topics.

Habitat preference could be readily examined by altering, for example, substrate texture and moisture or by varying the depth and type of cover. Effects of, light duration and intensity, temperature variation, and humidity on vole behavior, fecundity, and longevity could easily be examined using this controllable laboratory system. Food preference and caching behavior could be examined by regulating the quality and availability of food sources between otherwise identical tables. Study of bait acceptance would obviously follow the same basic design and would be invaluable in determining field consumption of poison bait in the presence of alternative food sources.

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WATER METABOLISM IN THE PINE VOLE, *PITYMYS PINETORUM*

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Orchard substrates, in general, provide excellent conditions for pine vole (*Pitymys pinetorum*) growth and reproduction as indicated by the distribution and abundance of pine voles within orchard situations in the eastern United States (Gourley and Richmond, 1972). However, the specific characteristics which are attractive to pine voles and facilitate their proliferation are poorly understood. The basis for selection of any particular habitat component by the pine vole is in large part a function of the vole's physiological requirements, because the physiological needs of the animals must be met by appropriate habitat resources. Thus, information on specific habitat parameters critical to pine vole survival can be obtained from an understanding of pine vole physiology. In this investigation, we present evidence that pine voles have very high water requirements and suggest that one habitat component of some importance to their survival is a high level of water availability.

Water metabolism of laboratory reared pine voles was assessed during 5 days exposure to 15° or 30°C. Ten adult voles assigned to each treatment group were weighed and then housed singly in plastic cages equipped with hardward cloth bottoms. Water, in inverted graduated cylinders, and food (Big Red rabbit food) were provided *ad libitum*. After the voles were exposed to 15° or 30° for 24 hr, the cage was placed over a pan of mineral oil and a urine sample collected for measurement of concentration. A second concentration determination was made on day 5 of temperature exposure for some voles, but because the early and late samples did not differ in concentration a single sample was collected for most voles. The voles were then transferred to clear, plexiglas metabolism chambers through which air was pumped for measurement of evaporative water loss. Hardware cloth partitions in the bottom of the chambers suspended the animals over a layer of mineral oil; this prevented evaporation of water from urine and feces. After the voles equilibrated for 1 hr, a preweighed tube of silica gel was placed in the air outlet of the chamber for 1 hr. If an animal became particularly active, as assessed by visual observation, the tube was disconnected and then reinserted into the airline after activity ceased. Subsequently, the voles were removed from the chambers, weighed and injected intraperitoneally with 50 ul^3H_2O (15 uCi). Urine samples were collected once or twice daily for 4 days and analyzed for ^3H_2O concentration. Using standard regression techniques, an expression for loss of tritiated water with increasing time was developed for each vole; biological half-life of ^3H_2O was calculated as ln 2/k where k is the slope of the associated regression line (Richmond et al., 1960).

Food and water consumption were measured during the last 3 days of temperature exposure. Daily preformed water intake was determined by calculating the amount of food consumed and the moisture content of the food. Similarly, oxidative water intake was calculated from daily food consumption which was corrected for fecal loss, and the manufacturer's suggested food composition.

Fecal water loss was determined from the weight of daily dried fecal material and the moisture content of 2 fresh fecal samples. Lastly, daily urinary water loss was calculated as the numerical difference between total daily water inputs and outputs. Data were analyzed by means of Student's t test.

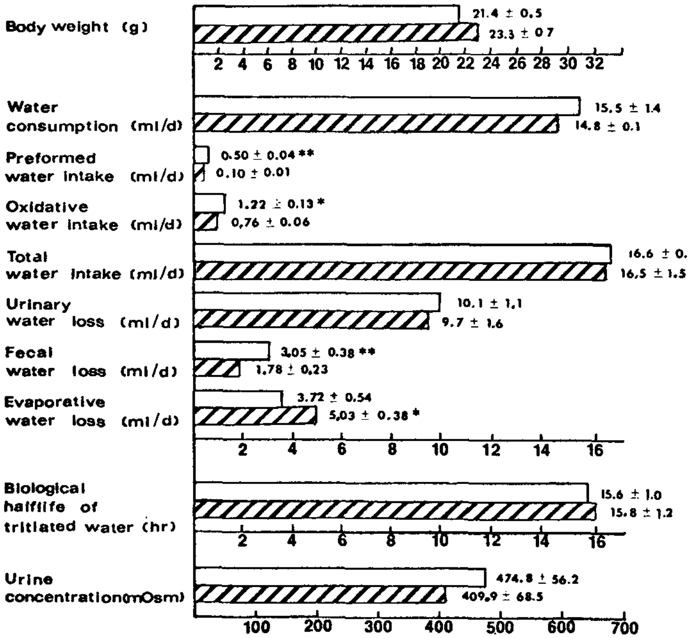

Figure 1. Summary of water metabolism in the pine vole, *Pitymys pinetorum*. Clear bars represent 15° treatment and striped bars represent 30° treatment. Values represent means ± one standard error of the mean. (*P <0.05; **P <0.01)

High rates of water use by voles were observed in both temperature treatments (Fig. 1); total daily water inputs represented 77% and 71% of the average body weight at 15° and 30°, respectively. Cold exposed mice exhibited increases in food consumption relative to voles maintained at 30° and, as a result, obtained significantly more water from food moisture and from oxidation of food components than did mice kept at 30°. Fecal loss of water was significantly elevated in cold exposed mice, whereas evaporative water loss was significantly greater in voles maintained at 30°. Daily water consumption and urinary output were high relative to other similar sized microtine and non-microtine rodents (Church, 1966; Deavers and Hudson, 1977). Urine concentrating ability was also similar between temperature treatments, but indicated a poor ability to conserve water. Similarly, the biological halflife of tritiated water did not differ between temperature treatments but indicated a very rapid turnover of body water in pine voles.

The results from this investigation indicate that pine voles have very poor mechanisms for water conservation and that high levels of water availability are critical to their survival. Furthermore, these results suggest that pine voles may require very moist habitat conditions as has been suggested for other voles (Odum, 1944; Chew, 1951). This requirement may be particularly pronounced in pine voles not only because of their physiological need for large amounts of water, but also because moist soil adds to the integrity of the vole's tunnel system. Thus, two potential methods for pine vole control are suggested by this study: 1) management of pine vole physiology with substances such as diuretics which could elevate water losses to the point of exceeding water inputs, and 2) management of orchard substrate first to reduce moisture content thereby achieving a decrease in free water availability and second to render the soil drier and less amenable to tunnel formation. Future studies will be concerned with the investigation of each of these possibilities.

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GROWTH AND DEVELOPMENT RATES OF MICROTUS PINETORUM UNDER DIFFERENT PHOTOPERIODS

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Photoperiod and nutrition are important variables affecting reproductive activity and growth in many rodents. Field and laboratory studies indicate that long photoperiod (spring-summer) cause increased growth while short photoperiods (fall-winter) inhibit these processes. In the montane vole (Microtus montanus) recently weaned animals gain weight at a much lower rate under short photoperiods or in total darkness than under long photoperiods (Vaughan et al., 1973; Peterborg, 1978). Adult M. montanus had more offspring and larger mean litter sizes under LD 18:6 than LD 6:18 (Pinter & Negus, 1965). Similarly, long (LD 16:8) or increasing photoperiods stimulated the onset of puberty in M. arvalis, while short (LD7:17) or decreasing photoperiods inhibited the onset of puberty (Lecyk, 1962). Short photoperiods caused reduced spermatogenesis and seminal vesicle weights in male M. arvalis, while long photoperiods induced increased ovulation in females. In contrast, photoperiod had no effect on the reproductive rates of M. orchadensis (Marshall & Wilkinson, 1956). Dicrostonyx groenlandicus reared on LD 6:18 grew faster than those on LD 20:4, but the latter group had larger testes (Hasler, 1975). In M. agrestis, long photoperiods stimulated male reproduction and caused greater body weight gain than did short photoperiod. Females produced fewer young, had lower ovarian and uterine weights, and fewer, smaller Graafian folicles under short photoperiods as compared to long. However, there was no effect on female body size (Clark & Kennedy, 1967; Breed & Clarke, 1970; Baker and Ranson, 1932). Microtus pennsylvanicus juveniles and adults had higher body weights under LD 18:6 than LD 6:18 (Pistole, 1980). M. oregoni reproductive activity is stimulated by long photoperiod, but due to fossorial habits this species appears to be less sensitive to light than more terrestrial forms (Cowan & Arsenault, 1958). There have been no reports of winter breeding in Clethrionomys gapperi possibly because of their behavioral avoidance of light during the winter (Evernden & Fuller, 1972).

Field reports of reproduction in pine voles vary greatly. Several studies report breeding all year (Rhoades, 1903; Linsdale 1928; Glass, 1949; Noffsinger, 1967; Paul, 1970; Goertz, 1971; Cengel et al., 1978) while others report the occurrence of breeding from February or March through November (Hamilton, 1938; Benton, 1955; Miller and Getz, 1969; Cengel et al., 1978). Noffsinger (1976) found significantly reduced body weights in males and females from January to May and significant differences in body length due to month. Molt to adult pelage began at 3 weeks of age and field data has shown that molting individuals can be found during any season of the year (Benton, 1955).

There are few laboratory studies characterizing growth, development, and reproductive activity in young and adult *M. pinetorum*. Hamilton (1938) found an increase of approximately 6g/wk in juvenile body weights whereas Paul (1970) reports an increase of 2-3g/wk. Growth rates of individuals from litters of 1 under LD 14:10 were only slightly less than those for individuals from litters of 2 or 3, with weight gain showing a sharp increase just prior to weaning (days 19-21) (Lockmiller, 1979).

Compounds present in plants which have antigonadotrophic effects may inhibit reproduction in many rodents. Two such compounds, Paracoumaric acid (PCA) and Ferulic acid (FA), are found at low concentrations in young plants but increase as plants reach senescence. These compounds caused significant reductions in uterine weight in *M. montanus* at a dose of 4 mg/g of chow when administered for 12 days (Berger et al., 1977) and in *M. pennsylvanicus* significant differences in uterine weights and mean number of follicles per female occurred with 12 mg FA/g of chow over a 21 day test period (Cranford et al., 1980; Pistole, 1980). There was no effect of FA at any reasonable dosage on uterine weights of juvenile *M. pennsylvanicus*.

Animals often use environmental cues for the initiation and termination of reproduction, such that production of offspring occurs during optimal seasons (Reynolds and Turkowski, 1972; Petterborg, 1978). Due to the fossorial nature of *M. pinetorum* this species may be less sensitive to photoperiodic cues than more terrestrial rodents. Since most evidence indicates year round breeding it is improbable that pine voles respond to green or dead vegetation as a reproductive cue.

This study investigated the effects of 3 photoperiodic regimes on growth and maturation in juvenile and adult *M. pinetorum*, while the effect of litter size on growth of juvenile pine voles was determined under two photoperiodic regimes. The role of the inhibitor compound FA on animals under different photoperiodic regimes was determined for juvenile *M. pinetorum* and adult and juvenile *M. pennsylvanicus*.

MATERIALS AND METHODS

To determine the effect of litter size and photoperiod on body weights of pine voles from birth to 50 days of age, five litters each, of size 4,3,2, and 1 young were maintained under LD 16:8, four litters of 2 young and five litters of 3 were maintained under LD 8:16. Individuals were weighed every 3 days using a Ohaus triple beam balance (± 0.01 g) and age of molt noted.

The effects of photoperiod on body weights of young adults (7 wks. of age) were determined using 43 animals (27♂, 19♀)

maintained under LD 16:8, and 28 animals (13♂, 15♀) under LD 12:12. At 11 weeks of age one third of the LD 16:8 group was switched to LD 12:12 and the other one-third to LD 8:16. One half of the LD 12:12 group was switched to LD 16:8. All animals were then weighed weekly on an electronic balance (± 0.1g) for a total of 14 weeks. To determine the effect of photoperiod on reproductive development of juvenile *M. pinetorum*, groups of 4 to 7 individuals were raised under LD 8:16, LD 12:12, or LD 16:8 until 5 weeks of age. At this time all individuals were sacrificed and body, adrenal, uterine, and ovarian weight were determined for females, while body, adrenal, seminal vesicle, and testes weights were recorded for males.

All experimental pine voles were first or second generation offspring of wild-caught adults, and were housed as pairs after weaning. Water and food (Wayne lab blox) supplemented with sunflower seeds, apples, and oat sprouts were available *ad libitum*.

The inhibitor substance FA, obtained from Aldrich Chem. Corp., was used to determine the effects of plant inhibitory compounds on reproduction in juvenile *M. pinetorum* and adult and juvenile *M. pennsylvanicus*. The bioassays for effects on sexual maturation were wet uterine weights and testes weights. Additionally, body and adrenal weights were assayed as an indicator of the general condition of the test individuals. Previous tests have shown that total food consumption does not differ between control and experimental animals.

M. pennsylvanicus juveniles were selected randomly from a colony of lab animals at 16-21g and approximately 20 days of age, while adults were selected at 47-55g. All individuals were caged individually for the 21 day test periods, with food and water available *ad libitum*. The test chemical was dissolved in methanol, coated on to ground lab blox at a dose of 12 or 24 mg FA/g chow, and the chow air dryed for 24 hours. Control chow was treated in the same manner but without the test chemical. Tests were performed under LD 18:6, LD 16:8, and LD 12:12.

M. pinetorum juveniles were tested as described above but were randomly selected at 22 days of age (weaning). Due to their slower maturation rate, tests were run for 30 days rather than 21 days, under LD 16:8 and LD 12:12.

RESULTS

Among litters of 1,2,3 and 4 young in LD 16:8 there was a consistent trend for small litters to weigh more than large ones (1>2>3>4). Litters of 2 were significantly heavier than those of 4 (2 sample Z test, $p \leq 0.05$) at 11 and 17-23 days of age while litters of 3 and 4 were not statistically different. Under LD 12:12 litters of 2 were significantly heavier ($p \leq 0.05$) than those of 4 at 14 and 17 days of age. Though litters of 3 were consistently lighter than those of 2 under LD 8:16 no significant differences occurred. Growth rates of individuals from litters of

4 (0.45g/individual/day) were lower than those for individuals from litters of 1,2, or 3 (0.52g/individual/day). Under LD 16:8 this difference occurred from days 2-20 and under LD 12:12 from day 2-14.

Comparisons between litters of the same size but raised under different photoperiods show that photoperiod affects body weights and reproductive development of young animals. The average weight of pine voles just prior to weaning (day 20) were 13.77 ± 1.7 gms under LD 16:8, 14.72 ± 1.89 under LD 12:12, and 14.70 ± 2.04 under LD 8:16. Additionally in LD 8:16 animals from litters of 3 were significantly heavier (2 sample Z test, $p \leq 0.05$) than those raised under LD 16:8. Litters of 2 under LD 8:16 exhibited higher growth rates than those under LD 16:8 or LD 12:12 from day 29 to 44 postpartum. Other data show that under all 3 photoperiodic regimes juvenile to subadult molt began about 28 days postpartum.

The increased growth of M. pinetorum raised under LD 8:16 as compared to that of juveniles raised under LD 12:12 and LD 16:8 is correlated with increased reproductive development in females but not in males. Juvenile females at 5 weeks of age who were raised under LD 8:16 and LD 12:12 had significantly heavier uterine tracts (Wilcoxon rank sum test, $p \leq 0.015$) than those raised under LD 16:8. Juvenile females maintained under LD 12:12 had greater ovarian and adrenal weights ($p \leq 0.02$) than individuals tested under LD 8:16. Among juvenile males there were no significant differences in testes, seminal vesicle or adrenal weights for any photoperiod group. Photoperiod effects were principally limited to reproductive organs as neither males or females differed in body weight at 5 weeks of age.

Body weights of adult animals switched between photoperiodic regimes showed changes similar to juveniles. Switching from LD 12:12 to LD 16:8 (spring summer) or vice versa (summer fall) caused no change in body weights. However a switch from LD 16:8 to LD 8:16 (summer to winter) resulted in a sharp increase in body weights, but the sample is highly variable.

All experimental M. pennsylvanicus fed FA showed a decrease in reproductive organ weight though this effect was not significant due to high variances within experimental groups. No consistent trends occurred with respect to change in adrenal weights. Experimental and control adults maintained on LD 12:12 lost weight (6-8g) whereas those on LD 16:8 gained weight (2g) (significant effect of photoperiod, Wilcoxon rank sum test, $p \leq 0.005$); but there was no synergistic effect between the inhibitor substance and short photoperiod on reproductive organ weights. Juveniles showed no effect of photoperiod on body weight.

Male juvenile M. pinetorum showed a reduction in testes weight when fed FA under LD 16:8 and LD 12:12 while females showed a decrease in wet uterine weights under LD 16:8 but not LD 12:12. Body weights of pine voles under LD 12:12 did not differ from those tested under LD 16:8 at the beginning or end of experimentation.

DISCUSSION

Photoperiod has the opposite effect on growth in M. pinetorum as compared to M. pennsylvanicus where juveniles have higher body weights under long photoperiod (Pistole, 1980), and M. pinetorum juveniles have lower body weights. Higher growth rates under short photoperiods may be of adaptive value for M. pinetorum since they result in earlier reproductive development of females and probably earlier reproduction. Additional studies are being conducted to determine whether increases in body weight are correlated with increased reproductive development in subadult and adult M. pinetorum (i.e. 10, 15 and 20 weeks of age).

Average weight gains for M. pinetorum in this study were slightly higher than those reported by Paul (1970) and Lockmiller (1979) but much lower than those reported by Hamilton (1938). Though weight gains were similar for young from litters of 1, 2 and 3, young from litters of 4 had significantly lower weight gain rates before and after weaning which probably results from the increased energy drain on the adult lactating female (Hasler & Banks, 1975; Lockmiller, 1979).

No significant effect of FA occurred in M. pinetorum as expected because they appear to be continuous breeders. The results for M. pennsylvanicus do not show the significant effects reported by Pistole (1980) though there are consistent trends which support his data. In M. pennsylvanicus, photoperiod is an ultimate factor whereas plant compounds act as proximate factors affecting growth and reproduction. The variance among the response of individuals fed FA suggests that a population may be composed of responsive and nonresponsive individuals, indicating a genetic component. In M. pinetorum photoperiod may be a proximate factor whereas plant compounds are of no importance in cueing reproduction. The different responses of these 2 species may be due to differences in their habitats, as M. pennsylvanicus are more exposed to light (surface dweller) and its changes, than are M. pinetorum. Because photoperiod and plant compounds appear to play a minor role in cueing pine voles to environmental conditions, other factors such as nutrition may be of major importance for this species.

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EFFECT OF PHOTOPERIOD ON ACTIVITY PATTERNS IN PINE VOLES (*MICROTUS PINETORUM*)

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Light is an environmental variable which has considerable effect on small mammal activity patterns. This constantly repeating 24 hour signal provides information on a daily basis and has been shown to synchronize all physiological patterns in an animals existance. Laboratory studies have shown that pine voles are slightly nocturnal (Pearson, 1947) or confined their activity to the hours of twilight and darkness (Werner, 1951). Both authors indicate that activity occurs in bouts of about 1 hour duration followed by an hour of rest. Benton (1955) observed from trapping that more activity occurred at night but cautioned that due to the fossorial habits of pine voles activity could occur below ground during the day and bias the data. Continious trapping data from both above and below ground sources indicate that there is activity both above and below ground at night but only below during the day. Activity is restricted to the burrow system. Gettle (1975) radiotelemeted pine voles and found that during any 15 minute period of the day (24 hour period), 50% of the experimental animals were moving actively. He presumed that these animals fed continuously as Boyette (1966) had previously demonstrated that they fed at all times of day or night.

Airoldi (1979) has demonstrated changes in activity patterns of water voles (*Arvicola terrestris*) which are synchronized by the natural photoperiod. The activity patterns are polyphasic and are distributed throughout the 24 hour period. In winter, activity is principally during the day while it is more equally distributed during other seasons. During all seasons the active cycles are entrained by the current photoperiod and demonstrate a good circadian organization. Seasonal shifts in activity patterns have been reported for red backed voles (Clethrionomys glareolus) (Elbl-Eibesfeldt, 1958) but the influence of ambient temperature could not be determined from these data.

This research will report on activity patterns of pine voles under 5 different photoperiods and two different ambient temperature conditions. The photoperiods (LD) used, except for continious darkness (DD), were comparable to the seasonal changes in day length and the two temperatures were to evaluate the influence of low winter and moderate summer temperatures on activity patterns.

METHOD AND MATERIALS

Adult pine voles from first generation laboratory reared animals were used in all photoperiod experiments. Animals were reared under LD 16:8 at 19 ± 1°C and were acclimated to the experimental photoperiods and temperatures for 30 days prior to a 30 day activity monitoring period. Activity patterns were recorded on two 8 channel Esterline Angus event recorders from a minimum of 10 pine voles of the same sex individually housed in wheel running cages. Experimental animals had food (Wayne Lab Blocks) and water available ad libitum with fresh apple slices given daily. Data on age, sexual condition and body weight dynamics were recorded weekly over the 60 day acclimation - experimental period.

Experimental photoperiods were LD 18:6, LD 16:8, LD 12:12, LD 8:16 and DD 0:24 with temperatures maintained at a constant 6 ± 1°C or 18 ± 1°C in environmental chambers. As the recorders monitored the wheel running activity as single events both circadian pattern and a total distance analysis was performed. Trap revealed activity patterns from field study grids will be compared to laboratory determined activity patterns.

RESULTS

Activity patterns showed no significant differences between sexes but were significantly different between photoperiods. Pine voles under any LD photoperiod demonstrate entrainment to the light-dark transition with activity restricted to the dark phase (Figure 1). In DD (continuous darkness) the pattern is polyphasic with activity distributed throughout the 24 hour circadian day.

The amount of activity distributed in each phase of the active cycle clearly shows changes from unimodal in LD 18:6 to biomodal in LD 12:12 and trimodal under LD 8:16 photoperiods (Figure 2). The DD results (Figure 1) show periods of activity of 1 to 2 hours followed by approximately 1 hour periods of rest. The amount of activity in any 15 minute period changes between all LD photoperiods but in DD the total amount of activity is drastically reduced and redistributed over the 24 hour circadian day (Figure 2). Activity patterns were not significantly different between the experimental temperatures used but did differ significantly in the total amount of activity.

The mean distance traveled by pine voles in running wheels differed between all photoperiods. At 18°C in LD 18:6 they traveled 1512 meters (M) per night while at 6°C they traveled 1280 M per night. At 18°C in LD 12:12 the mean running distance was 755 M and under LD 6:18 it was 376 M but reduced to 267 in the 6°C environment. In the DD environment the voles ran only 89 M at 18°C during a 24 hour day. The amount of activity in each of the photoperiods were significantly different from each other (Wilcoxan rank sum tests) and the reduction of activity in cold environments were significantly different (Duncans Multiple Range Tests) in each of the photoperiod treatments.

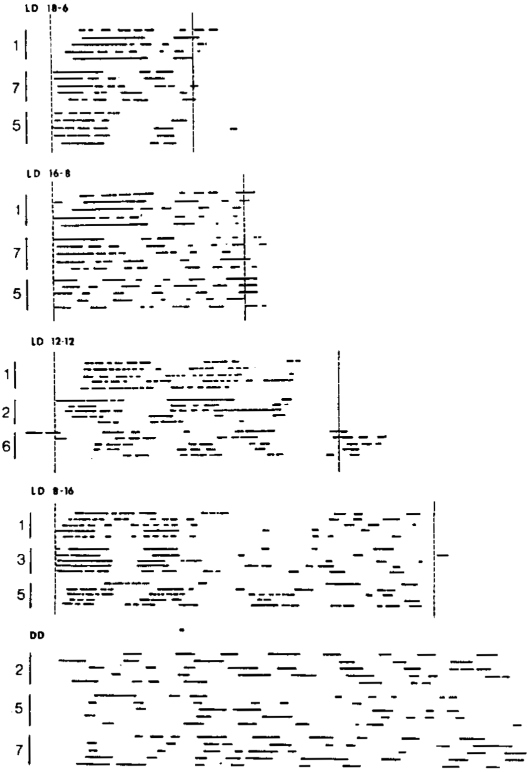

Figure 1. Distribution of activity of 3 individuals in each of the experimental photoperiods. In the LD cycles the area between dashed vertical lines indicate the dark period.

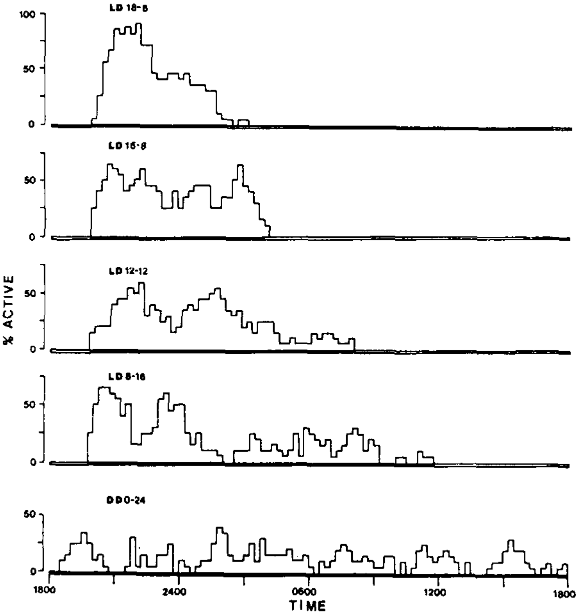

Figure 2. Percent of activity in 15 minute increments across the active cycle under all experimental photoperiods.

DISCUSSION

The overall circadian patterns indicate that pine voles entrain to all experimental photoperiods but lacking a Zeitgeber the activity pattern does not show the typical free running pattern of most rodents. The animals in DD did show a clear pattern going from the entrained to the free running state with a mean T=23.4 hrs. which is typical for a nocturnal rodent. After 5 to 10 days all animals in DD had a polyphasic pattern with periods of activity and rest distributed throughout the 24 hour circadian day. Previous reports have varied in describing activity patterns of pine voles but these data clearly show that pine voles avoid the light but do have activity distributed throughout a 24 hour day. More than 60% of the total activity in DD was distributed in the former dark phase of the previous entrainment(LD 12:12)cycle. This generally agrees with field observation based on trap recapture and telemetry data that more activity occurs at night both above and below ground while day activity is restricted to the burrow system.

All other parameters measured did not show any significant changes from the last 15 days of the acclimation phase through the experimental period. Changes in body weight and food consumption did occur as animals were switched to different photoperiods and temperatures. In general total activity decreased with increasing night length and decreasing temperature. The activity pattern and amount of activity in DD probably represents the best laboratory measure of what pine voles do in an orchard setting. The distribution of activity would permit above and below ground feeding bouts throughout the 24 hour day. The amount of activity would be equivalent to 50-60 trips through a linear home range of 35 meters or from 3-6 foraging bouts per hour within the home range. The decrease in activity with temperature points out perhaps why more subsoil root damage occurs in winter. The overall decrease in activity means energy is conserved and also that roots being available and close by would be foraged on at higher rates.

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Prairie vole - Microtus ochrogaster (Wagner)

Pine vole - Microtus Pitymys pinetorum (LeConte)

Meadow vole - Microtus pennsylvanicus (Ord)