SEASONAL VARIATION IN THE NATALITY, MORTALITY, AND NUTRITION OF THE PINE VOLE IN TWO ORCHARD TYPES

by

Robert E. Noffsinger

Thesis submitted to the Graduate Faculty of the
Virginia Polytechnic Institute and State University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

in

Fisheries and Wildlife Science

APPROVED:

Roy L. Kirkpatrick, Chairman

Patrick F. Scanlon

Burd S. McGinnes

November 1976

Blacksburg, Virginia 24061

ACKNOWLEDGEMENTS

I want to thank Dr. Roy L. Kirkpatrick for his encouragement and support with this study and Dr. Patrick F. Scanlon and Dr. Burd S. McGinnes for their help with the preparation of this thesis. Dr. Henry Mosby, Dr. James Whelan, Dr. Allan Tipton, and Mr. Bob Downing also gave valuable advice and criticisms on various aspects of the study. I owe many thanks to Mrs. Wanda Moorehead and Mrs. Helen Lysy for their help with laboratory work and to the many fellow graduate students, undergraduate students, and friends who helped with the trapping and laboratory work involved in this study. Special thanks is due to Mr. John Estep for his many hours of help with trapping and laboratory work. I would also like to thank the people who provided laboratory space, equipment, and/or assistance for some of the work in this study. Laboratory space, equipment, and assistance for lignin determinations were provided by Dr. Carl Polan of the Dairy Science Department and Dr. Scott Carr of the Forage Testing Laboratory of V.P.I.&S.U. Dr. Jackson Webster and Dr. Fred Benfield of the Biology Department and Dr. Albert Hendricks of the Center for Environmental Studies, V.P.I.&S.U. provided laboratory space, equipment, and assistance for gross energy determinations. Dr. Roderick Young of the Biochemistry and Nutrition Department, V.P.I.&S.U. provided equipment and time of his technicians for freeze drying of vole carcasses. Dr. Richard Dapson, Michigan State University, furnished the computer program used in his method of determining survival equations and advice and assistance on the use of the program. Ikenberry Brothers Orchards, Daleville, Virginia provided assistance in locating suitable orchards for use in this study. Most of all I want to express my appreciation for my wife Susan's encouragement and sacrifices which allowed me to complete this study.

TABLE OF CONTENTS

LIST OF TABLES

INTRODUCTION

The pine vole (Microtus pinetorum) is a semi-fossorial rodent whose natural habitat is hardwood forests. When pine voles occur in orchards, trees of all ages may be killed or weakened by the voles eating the phloem and cambium tissues from the main stem and large lateral roots. If no control measures are taken, serious losses to the orchardist may occur (LaVoie and Tietjen 1971). Hamilton (1935) estimated that pine voles and meadow voles (Microtus pennsylvanicus) caused a $500,000 annual loss to fruit trees in New York. Garbough (1944) described an orchard near Charleston, West Virginia, in which one thousand 18 year old trees were killed by pine voles. In Virginia, pine voles cause an estimated $7 million annual loss to the apple industry (Virginia Fruit 1971). This loss is considered a major contributing factor in reducing profits from Virginia apple orchards and in the declining number of growers in the state.

Byers (1974) gives a theoretical estimate of the market value loss due to pine voles to be approximately $40 million per year within the geographic range of the pine vole. This loss continues even though growers are presently spending an average of $36-74 per hectare for control (about $3,300,000 annually).

Problems with pine voles were recorded as early as 1857 (Kennicott 1857), but few attempts were made to control them until 1934 when the Fish and Wildlife Service became involved in evaluating toxicants, baits, and application techniques (LaVoie and Tietjen 1971). Later research continued along these lines. Due to the limited and temporary success achieved by such an approach, concern about the effect of pesticides on nontarget species, possible withdrawal of Endrin (the most widely used toxicant in pine vole control) from the market, and possible Endrin resistance in pine voles (Webb and Horsfall 1967), the U.S. Fish and Wildlife Service decided to change their approach. A review of the pine vole problem by LaVoie and Tietjen (1971) recommended that basic research on pine vole populations, habitats, damage patterns, and control methodology be funded at universities involved with the pine vole problem. Hopefully, from this type of research the factors which determine the occurrence and abundance of pine voles can be found. Manipulation of these limiting factors, if they can be determined, should become an important part of an integrated program to control pine vole populations to prevent damage to orchards.

Paul (1970) noted that pine vole densities were lower in abandoned orchards than in actively maintained orchards. Cengel (1975) determined the seasonal variations in pine vole reproduction and food habits in a maintained and an abandoned orchard. He found lower reproduction throughout the year and a longer cessation of breeding in winter in the abandoned orchard. Apple roots were identified in vole stomachs in the abandoned orchard in January and March (stomachs were obtained bi-monthly), while in the maintained orchard they were present only in March. Horsfall (1972) found in food choice trials with captive voles that apple roots are not a preferred pine vole food. Although no data on seasonal food availability or food quality were obtained in the study by Cengel, the use of root material in January and March suggests that roots were being consumed at this time because a diet sufficient to support the voles was not available from preferred foods. Estep (1975), in a companion study, found declining fat levels in autumn and late winter, which also suggests that winter is a period of reduced food availability and/or quality. Thus, the longer breeding season and shorter period of root consumption in the maintained orchard may be a result of better nutrition being available.

Maintained orchards are fertilized and mowed, which keeps the the vegetation in a young, vigorous growth stage. In these early growth stages, the vegetation is more digestible than when it matures, due to its being higher in protein, vitamins and mineral content and lower in fiber and lignin (Cook and Harris 1950, Campbell and Cassidy 1954, Morrison 1956, Heady 1964, Morrison 1972). In the abandoned orchard which is not fertilized or mowed, the vegetation is not kept in these early, more digestible stages, but rather matures and becomes less digestible. This decrease in digestibility of food consumed by voles could lower energy intake, which could affect the natality of vole populations by reducing reproductive hormone levels. Howland (1972) found lower levels of plasma LH in laboratory rats on a 50 percent restricted diet than in ad libitum fed rats and rats with a 50 percent restriction in food but supplemented with glucose. The rats on the 50 percent restriction also had depressed body and ovarian weights. Howland concluded that although it is unknown to what extent the reduction in ovarian weight is attributable to the low circulatory levels of LH, it is reasonable to assume that this hormonal deficiency at least partially explains the reduction in ovarian weight. A study by Kirkpatrick and Merson (1976) with captive white footed mice (Peromyscus leucopus) indicated that as little as a 10 percent reduction in ad libitum food supply can cause a marked reduction in uterine weights, ovarian weights, and the percent of females exhibiting an estrous smear, with very little change in body weight.

Reproduction may be limited by restricted nutrition well before the effects of the reduced nutrition would be noticed in decreased fat levels and weight loss. Except under severe conditions of energy restriction, most implanted embryos will be carried to parturition. However, in periods of restricted energy intakes high mortality of young would result if the high energy requirements for lactation were not met. Inadequate energy intake in young animals would also decrease growth rates which would prolong maturation, as attainment of puberty is more a function of size than age. This would mean a longer period from time to birth of a female to production of her offspring, thus reducing population natality. A reduction in energy intake of voles, either through lower digestibility and/or lower availability and consumption, could cause the reductions in natality and thus density of pine voles in abandoned orchards.

The present study was undertaken to:

1. determine if similar seasonal trends in reproduction as found by Cengel (1975) and fat content as found by Estep (1975) would be found in another maintained and another abandoned orchard in a different year, and

2. determine population densities, mortality rates and the quality of forage available in the two orchards.

Such information should show more clearly if available nutrition is important in limiting pine vole numbers in orchards.

LITERATURE REVIEW

Densities

In hardwood forest habitat, Paul (1970) found that the pine vole occurred in densities of 15-20 per hectare. In orchards, densities are much higher. Hamilton (1938) estimated densities in New York apple orchards to be as high as 490-750 per hectare. Gourley and Richmond (1972) captured 304 pine voles in a .65 hectare section of orchard which they completely trapped out. Horsfall et al. (1973) estimated 198 voles per hectare to be a maximum in the Virginia orchards which he studied.

Mortality Rates

Miller and Getz (1969) live trapped pine voles in hardwood forest habitat in Connecticut. Only 19.2 percent were recaptured more than two months after the first capture. Of the 129 voles live trapped, two males survived twelve months, and two females survived ten months. In Oklahoma (Goertz 1971) pine voles disappeared from the population in an average of 70 days after first trapping (range 2-206 days). Of 408 pine voles live trapped the first month, 50 percent were recaptured in the second month, 38 percent in the third month, 32 percent in the fourth, 23 percent in the fifth, 20 percent in the sixth, 18 percent in the seventh through ninth, and 12 percent in the tenth. Two males were present for at least 13 months, and one was present for 14 months. Since many individuals were full size adults when first captured, the estimate of maximum longevity should be considered a minimum. In South Carolina (Gentry 1968) 50 percent of animals marked were not being recaptured two months later. After six months only 23 percent were recaptured. Seven voles were recaptured for twelve months and one for 18 months. There was a trend for increased survival from the beginning to the end of the study. Twelve percent of the animals captured the first winter survived the summer, 48 percent of the animals trapped and the second winter survived the summer, and 70 percent of the animals trapped the last winter survived the summer. There was no difference in survival between age groups, as the mean survival from one season to the next was 58 percent for adults and 57 percent for juveniles. A constant number of deaths per unit time occurred after juveniles entered the trappable population.

Natality

Breeding Season

Miller and Getz (1969) found indications that the breeding season for pine voles in a natural habitat in Connecticut extended from at least mid-February to mid-November. In New York orchards (Benton 1955), a cessation of breeding occurred in September, October, and November, and there was a peak of breeding in March and April. A continuous breeding season was also found in an orchard in a mountainous area of Virginia by Horsfall (1963), with the highest numbers of pregnant females in July, August, September, and October. Cengel (1975), in two orchards near Sperryville, Virginia, found pregnant females in a maintained orchard in all months trapped except January, and in an abandoned orchard in all months trapped except November and January (each orchard was trapped bi-monthly). The peak of breeding occurred in the active orchard in July and September. Although the abandoned orchard was not trapped in July, the peak probably occurred in the abandoned orchard in July and September also. Valentine and Kirkpatrick (1970) in an orchard near Danville, Virginia found pregnant females in April through October, with a peak in July and August, and no breeding during the period from November through March. In western North Carolina (mountainous region), Paul (1970) found pregnant females in all months, with a peak of 60 percent of adult females being pregnant in July. In Piedmont areas in summer months (June to September) only 10 percent of females captured were pregnant, and from October to May, 42 percent were were pregnant. Captive voles in air-conditioned pens bred the year round in North Carolina (Boyette 1966). In natural habitat in Oklahoma, Goertz (1971) found evidence of breeding in all months of a 17 month study except for June and July, 1960, and May, 1961.

Litter Size

Horsfall (1963) found the year round average of fetuses per pregnant female pine vole in Virginia to be two, with a range of one to four. Also in Virginia, Valentine and Kirkpatrick (1970) found an average of 1.9 with a low of 1 in April, and a high in June of 3. Cengel (1975) had an average of 1.9 in a maintained orchard in Virginia, with a low in March of 1.5 and a high in September of 2.2, and an average of 1.6 in an abandoned orchard with a low of 1.4 in September and a high in March of 2 (based on only one pregnant female). In North Carolina, Paul (1970) found an average of 2.24 fetuses per pregnant female. He also found a correlation between litter size and size of female. Females less than 120 mm total length had an average litter size of 2.19. Females 121 mm to 129 mm had an average litter size of 2.20, while females greater than 130 mm total length had an average litter size of 2.48. Even with litter size down in winter, the larger females still had larger average litter sizes.

Reproductive Potential

Boyette (1966) found the modal period between successive litters in captive female pine voles to be 25 days. Kirkpatrick and Valentine (1970) determined the gestation period for captive female pine voles to be 24 days. In the same study the pine vole was shown to be an induced ovulator with a postpartum estrus occurring on the day of parturition or the day following parturition. Boyette (1966) observed 5 different females which had one litter per month for 4 months or more. One female had one litter per month over a 7 month period with 3, 3, 4, 2, 2, 2, 2 young in respective litters. Gentry (1968) studying pine voles in large outside enclosures in South Carolina found one female pregnant seven times over an 18 month period. The average for the study was 1.68 pregnancies per female per year. He thought this to be a minimum estimate, as pregnancy was determined by palpation and weight change, and these techniques probably missed many early pregnancies. Goertz (1971) in Oklahoma also used palpation and weight change in live trapped animals for checking pregnancy. Five females were trapped which had two pregnancies during the year, one female had three pregnancies during the year and one female had four pregnancies during the year.

Sex Ratios

Gourley and Richmond (1972) and Dunaway and Kay (1963) both found no significant differences from a 1:1 sex ratio in extensive trapping of pine voles. Paul (1970) found that sex ratios of trapped voles closely approximated 1:1 in all areas trapped, with the exception of one sample taken in October, 1963, on an area during a period of high density and reproductive activity. In that sample there were nearly three times as many females trapped as there were males (61:21).

Age Ratios

In North Carolina, Paul (1970) found that the proportion of the population composed of subadults and young animals (those under 115 mm) was approximately 45 percent in summer, 33 percent in spring and fall, and less than 10 percent in the winter. Cengel (1975) in a maintained orchard in Virginia found 29 percent juveniles in July, 35 percent in September, 15 percent in November, 13 percent in January, 14 percent in March, and 18 percent in May. In an abandoned orchard he found 18 percent juveniles in September, 5 percent in November, none in January and March, and 8 percent in May. (No trapping was done in the abandoned orchard in July). Goertz (1971) in Oklahoma found that young were not being added to the population from July through October, as the lower weight classes were absent. In Connecticut (Miller and Getz 1969) juveniles were captured from March until July and subadults from March to September. Approximately 50 percent of the population during this time were juveniles and subadults.

Home Range, Movements and Activity

The average minimum diameter of the home ranges of 17 pine voles captured by Burt (1940) was approximately 37 meters and that of 13 captured by Benton (1955) was 19 meters. Several of the voles were taken only around a single tree. Twenty nine voles caught by Miller and Getz (1969) had average home range diameters of 34 meters for males and 33 meters for females. In Okahoma, 71 females and 73 males captured at least two times had home range diameters of 68 meters and 87 meters respectively (Goertz 1971). In Pennsylvania orchards (Gettle 1975), movements of radio-tagged voles were usually confined to the dripline of two or three trees within a row. Voles seldom moved between rows. In South Carolina (Gentry 1968) the mean distance between captures, based on 83 voles captured four or more times, was 22.1 meters.

Boyette (1966) found that, in general, the exploratory tendencies of captive voles became obvious in infancy (during the first three weeks), increased in the juvenile period (4-8 weeks), reached a peak in late juvenile and early adult period (8-16 weeks), then waned with prime to late adulthood (greater than 16 weeks). Nearly all escapes from the lab cages involved late juveniles and young adults.

In natural habitat in Oklahoma (Goertz 1971) maximum movements were based on 73 voles travelling 60 meters or more. Age (based on weight) of 36 males and 36 females indicated that three were juveniles (10-15 grams) when first captured. Sixteen were subadults of 15-20 grams, 15 were subadults of 21-25 grams, and 39 were fully mature adults of 25 plus grams. Gettle (1975) found that voles were more mobile seasonally than during short periods within seasons. Fall was the season of greatest mobility, and spring was the season of least mobility. Gentry (1968) found that in South Carolina a significantly greater number of movements between the enclosures used in the study took place during winter. There also appeared to be no activity above ground on hot summer days. Benton (1955) also found restricted activity above ground on hot summer days. Other authors have noted lower numbers of captured animals in summer months (Horsfall 1963; Paul 1970). Benton (1955) found indications of one hour cycle of activity and rest in the pine vole throughout the day. Boyette (1966) found that his captive voles fed at all times during daylight and darkness. The pine voles radiotagged by Gettle (1975) were equally active at all hours of the day. Generally, for any 15 minute interval, 50 percent of the pine voles radio-tagged were active.

Food Habits

Cengel (1975) and Estep (1975) studied the food habits of pine voles in an abandoned and in an actively maintained orchard. They found that the relative amounts of grasses and forbs consumed by pine voles in the two orchard types varied significantly ($P < .01$) between months and between orchards. During May, stomachs of voles captured in both orchards contained over 80 percent forbs and only small amounts of grasses. In July, voles collected in the maintained orchard contained 68.4 percent forbs and 30.4 percent grasses. The abandoned orchard was not trapped at this time. In September, differences in the stomach contents of the two populations became evident; grasses were much more prevalent in the stomachs of voles collected in the maintained orchard. While forbs were the most common component in the stomachs of voles from the abandoned orchard. This trend continued through November, January, and March. The utilization of grasses and forbs was thought to be the result of both availability of plants and section by the voles. The consumption of root material varied significantly ($P < .01$) between months; however, differences between orchards were not significant.

Epidermal fragments from roots occurred most frequently in the stomachs of voles collected during January and March. Stomachs of voles from the abandoned orchard in March contained twice the percentage of roots as stomachs of voles in the maintained orchard in that month. Roots were available to voles throughout the year, but were only utilized by them in winter and early spring. This suggested that roots were consumed only when the above ground vegetation was scarce, or was unavailable or unacceptable for some reason.

Fat Content

In the same study described above, Estep (1975) compared the fat content of pine voles trapped bimonthly throughout one year. He found significant ($P < .01$) monthly fluctuations in fat content. Voles from the abandoned orchard were significantly ($P < .05$) fatter than those from the maintained orchard. There was also a significant ($P < .01$) month X orchard interaction. Food habits and vegetational data for the two orchards suggested that the voles in the maintained orchard had a more adequate diet than voles in the abandoned orchard. Thus, while the female voles in the maintained orchard had adequate energy intake to allow production of young, the energy intake in the abandoned orchard may not have been adequate to support gestation and lactation and the net energy available was deposited as fat.

Effects of Nutrition on Small Mammal Breeding and Densities

There is evidence that breeding in consumers of secondary plant products is controlled by the amount of available food (Jameson 1953, 1955; Bendall 1957, Smyth 1966, Watts 1970, Fordham 1971, Hansson 1971, Smith 1971, Flowerdew 1972, 1973; Sadlier et al. 1973). However, Hairston et al. (1960) postulate that vegetation consuming herbivores are not usually limited by available food. Krebs and Delong (1965) provided a low density population of *Microtus californicus* with supplemental food and fertilized their natural vegetation for 11 months. There was a slow initial increase in numbers; then the population rose abruptly to a moderate density before declining rapidly. The supplemental food produced excellent individual growth rates and a sustained high reproductive rate among the adults, but did not raise survival rates. The authors concluded that some factor other than nutrition was affecting survival. Chitty et al. (1968) placed single voles (*Microtus argestis*) in enclosed outdoor areas and left them until their food supply was nearly exhausted. They then weighed herbage on control plots and the remaining herbage on the experimental plots and determined that enough food was on a 10.85 square foot plot in the area to keep a vole alive for 5.2 days. From this work they inferred that no vole need starve if 2.1 square feet of herbage was available to it each day. The conclusions drawn in these studies support the ideas of Hairston et al. (1960). However, Chitty's study failed to consider possible changes in digestible nutrients in the herbage throughout the year. Krebs and Delong (1965) did not consider that what they concluded to be low survival could have been caused by dispersal. As pointed out by Watson and Moss (1970) more than one factor can be limiting a population simultaneously. Thus, the fact that the population did not continue to expand in that area does not mean that food quality was not an important factor in the low numbers; some other important factor could have been causing dispersal.

Hairston et al. (1960:422) state that:

> There are temporary exceptions to the general lack of depletion of green plants by herbivores... This occurs when herbivores are protected either by man or natural events, and it indicated that the herbivores are able to deplete the vegetation whenever they become numerous enough, as in the cases of the Kaibab deer herd, rodent plagues, and many insect outbreaks. It therefore follows thatthe usual condition is for populations of herbivores not to be limited by their food supply.

Murdock (1966), in a critique of the paper by Hairston et al. (1960) points out that herbivores may well be limited by an insufficient supply of the necessary nutrients, and therefore, may be limited without depleting their food supply. An animal on a very indigestible diet, one which is usually high in fiber, lignin, and silica content (Campbell and Cassidy, 1954; Morrison 1956 and Morrison 1972), eats more to satisfy its energy requirements. This can cause a faster rate of passage of food through the gut and cause even less of the material to be digested (Shenk et al. 1970; Church and Pond 1974). Thus, abundant plant material can be available to a herbivore, but its nutrient requirements may still not be met. This will affect not only survival of the animals present, but will affect their reproduction and the survival of their offspring.

Hoffman (1958) found positive correlations between seasonal changes in litter size and food quality in Microtus californicus and Microtus montanus. The protein content of the food of Microtus montanus was based on actual analysis of the protein content of one of its major food plants, while the protein content of the grass in the diet of Microtus californicus was based only on a general evaluation. Miller (1946) found that on cultivated (irrigated) lands in Sacramento Valley, California, pocket gophers may breed continuously, with three periods of increased fertility in spring, summer, and early winter. Breeding in alfalfa fields, which are irrigated in the dry months, was significantly greater in summer than in non-irrigated fields, but there was no significant difference at other times of the year. Bodenheimer (1949) found that breeding of the Le Vant vole (Microtus guentheri) in Israel varied with location. In some months breeding had ceased completely or was at very low levels in nonirrigated fields, but continued at high levels in irrigated fields. The continental vole (Microtus arvalis (Pallas) breeds into winter if it is living among crops of rape and winter rye, but not if it is living on uncultivated land in the same vicinity (Stein 1953). These authors concluded that differences in diet between cultivated and/or irrigated and noncultivated areas were important factors influencing breeding. Batzli and Pielka (1970), in an enclosure study with Microtus californicus, noted that preferred food plants made up 60 percent of the vegetative volume on ungrazed areas, while non-preferred plants and litter contributed 70-80 percent of the volume on grazed areas. In another study (Batzli 1968), the frequency of Microtus californicus and pooled Peromyscus maniculatus and Reithrodontomys megalotis showed positive correlation with the percent cover of wild oats (Avena). No such correlation existed with other widespread species of grasses or with the total amount of grass cover. Distribution of cuttings suggested that Avena was the major food source of Microtus at this time, implicating food as a major factor in the control of dispersion and, therefore, of population density.

Hudson Valley trapping records (Gourley and Richmond 1972) suggest that significant pine vole populations occur only in areas where there is active farming, a symptom in common with many agricultural pests. Paul (1970) has also noted more significant densities of pine voles in actively maintained orchards than in abandoned orchards or typical hardwood forest habitat. Gentry (1968) had difficulty in explaining the low pine vole populations in natural areas as compared to the densities reached in the large outside enclosures used in his study. He thought that dispersal, food, and possibly predation were probably the most important factors controlling the pine vole population in the enclosures. During periods of high density, practically all bait was removed from the traps in less than a week, meaning that 15-20 pounds of food was added each month. This may have been instrumental in allowing the animals to achieve winter peaks. He thought predation on pine voles was probably low due to the apparently large amount of time spent underground. Restriction on dispersal by the walls of the enclosure was thought to be a factor in the relatively high densities inside the enclosures.

In contradiction to the theory of Hairston, et al. (1960) there seems to be considerable evidence that one of the major factors affecting the breeding and densities of small herbivores is the nutritional quality of the food available to them.

MATERIALS AND METHODS

Study Areas

The two areas used were near Daleville, Virginia. One area was an abandoned apple orchard which had had no type of maintenace for three to four years. The second area was an actively maintained apple orchard which had had no form of vole control for at least four years. The sites were within one mile of each other and were very similar with respect to slope, aspect, and soils. The sites were chosen as typical representations of the two orchard types. Both orchards were large enough to allow removal of the required number of voles without danger of significantly affecting the remaining parts of the orchards to be trapped.

Trapping

Pine voles were snap-trapped bimonthly for one year in the two orchards. Two or three randomly selected sites in each orchard were trapped during each trapping period. Two Victor snaptraps, baited with apple chunks were set at each tree in burrows showing recent activity. The traps were checked every two hours until approximately 15 adult voles of each sex were caught in each orchard. As each vole was captured, the number of the tree at which it was caught was recorded on a tag attached to the vole, along with capture period (first, second, or third two-hour period), sex, and age as determined by pelage characteristics and size (Paul 1970). Eye lenses were removed as soon as possible after capture and preserved in a 10 percent buffered formalin solution. Lenses were handled and dried as described by Gourley and Jannet (1975). The regression equation developed by Gourley and Jannet (1975) for aging pine voles was used to obtain an age estimation in days for each vole by use of dried, paired eye lens weights.

Density Estimates

The Leslie Method (Overton 1976:450) which uses reduction of population and rate of capture to estimate density and probability of capture was used to measure population densities in the two orchards. The method assumes that one unit of capture effort, in this instance a trap hour, has a given probability of capturing any particular vole in the area being sampled, and that additional units of effort are noninterferring. The number of animals which will be captured then is a function of the number of animals present and their probability of capture. By trapping for several periods, data are obtained on numbers of animals captured per period, trap effort per period, and the cumulative numbers caught. With these values, if there is a depletion in number of animals caught, the number of animals in the population and their probability of capture can be estimated by linear regression.

Mortality

The method of Dapson (1971 and 1972) was used to determine survival equations for cohorts from the maintained and abandoned orchards. With this method, animals, aged by days, are arranged chronologically and their relative frequencies of occurrence in the sample are accumulated from oldest to youngest. Relative cumulative frequency (RCF) is then plotted against age, which gives a survival curve. The data are then transformed to produce a rectilinear relationship and the best fitting line through these values is found by linear regression. From the equation of this line, data for the 1_x column of a life table are obtained. The point where the RCF equals zero gives an estimate of maximum ecological longevity (MAX) or the age at which probability of occurrence is zero.

The data obtained was sufficient to allow four cohorts from each population (maintained and abandoned) to be followed. Three of these cohorts were the animals born between July 15 and September 14 (i.e., animals with estimated ages of 1 to 60 days when captured on September 14), September 15 and November 14, and November 15 and January 14. Since the study was done for only one year, the voles 1 to 60 days of age from the March (January 15 to March 14 cohort) and May (March 15 to May 14 cohort) and July (May 15 to July 14, 1975 cohort) trappings could only be followed until July, which did not allow time for most of the voles of these age classes to die off.

As an example of how the cohorts were followed, the September-November cohorts for the maintained and abandoned orchards were made up of all animals captured in the respective orchard on November 14 which were 1 to 60 days of age, all animals captured on January 14 which were 61 to 120 days of age, all animals captured on March 14 which were 120 to 180 days of age, all animals captured on May 14 which were 180 to 240 days of age, etc. Since the youngest voles

(1-30 days of age) are not in the trappable population, this age group was estimated by reproductive data from the respective previous trapping period.

The fourth cohort which was followed were the voles born between the period of May 15 to July 15 (1974) before the beginning of the study on September 14, 1974. This cohort was started with animals 60-120 days old when captured on September 14. A survival equation was determined using animals 60 days and older and animals 1-60 days of age were then estimated by extending the regression line of each respective survival equation.

Necropsy of Voles

Voles were kept on ice after capture until arrival at the laboratory at VPI&SU. At this time, lengths and weights were recorded. Testes were removed from males, weighed, and frozen in .09 percent saline solution. Carcasses were then frozen. At a later date spermatozoan counts were made using the technique of Sullivan and Scanlon (1976). Carcasses were later thawed and the seminal vesicles and adrenals of males were removed and fixed in a 5 percent solution of formalin. Uteri of females were examined for number of visible fetuses and fixed in 5 percent formalin. Ovaries and adrenals of females were removed and fixed in 5 percent formalin. All organs removed were trimmed of extraneous tissue after fixing for two weeks and weighed. Stomachs, intestines and remaining organs were removed and any mesentary fat was stripped from the intestines and organs, and placed back in the carcasses. Carcasses, bare of organs and digestive tracts, were then freeze-dried and body fat was determined by standard methods (AOAC 1960). The stomach contents and feces from the lower part of the large intestines were removed and dried at 60 C for one week and weighed. Organ weights, spermatozoan counts, body weights, body lengths, stomach contents weights, and fat content were analyzed by analysis of variance using the Statistical Analysis System (Barr and Goodnight 1972).

Determination of Digestible Energy

Apparent digestible energy was determined using lignin as a tracer material (Cook and Harris 1951, Kane et al. 1953, Reid 1962:45, Golley 1967:112, Harris 1971:319, Church and Pond 1974:29, Church 1975:125). Lignin is an indigestible substance found in the cell wall of plants. Apparent digestible energy is the difference between the gross energy of food ingested and the gross energy of the feces from that food. In the classical balance technique this is done by drying, weighing, and determining the gross energy of the food ingested, collecting, drying, weighing, and determining the gross energy of the feces egested, and subtracting the gross energy of all the feces produced from the gross energy of all the food consumed. In the field, measuring total ingestion and egestion is impractical. An indigestible tracer, such as lignin, can be used to calculate the amount of feces which is produced from a given amount of food consumed. For example, if the stomach content of a vole contains 10 percent lignin, and the feces contains 15 percent lignin, then 240 mg of stomach contents will contain 24 mg of lignin and 216 mg of other cell material. All of this lignin will be passed through the intestines while some of the other cell material will be assimilated. One then needs to find the amount of feces (which is 15 percent lignin) which contains 24 mg of lignin (and will contain less than 216 mg of other cell material). If .15 X weight of feces = 24 mg lignin, then the weight of feces is 160 mg. If the gross energy of the stomach contents is 4 kcal/mg and the gross energy of the feces is 4.3 kcal/mg, then the apparent digestible energy (ADE) is:

$$\text{ADE} = (240 \text{ mg} \times 4 \text{ kcal/mg}) - (160 \text{ mg} \times 4.3 \text{ kcal/mg})$$
$$= 1.133 \text{ kcal/mg}$$

or

$$\text{ADE} = (240 \text{ mg} \times 4 \text{ kcal/mg}) - \left(240 \text{ mg} \times \frac{.10}{.15} \times 4.3 \text{ kcal/mg}\right)$$
$$= 1.133 \text{ kcal/mg}$$

For one unit of stomach content this reduces to:

$$\text{ADE} = E_{sc} - E_f \frac{L_{sc}}{L_f}$$

where

ADE = apparent digestible energy

E_{sc} = energy per unit of stomach contents

E_f = energy per unit of feces

L_{sc} = percent lignin in stomach contents

and L_f = percent lignin in feces.

The stomach contents and feces of several voles had to be pooled to obtain an adequate amount of fecal and stomach material (about .6 g of each) for the gross energy and lignin determinations. Voles caught at the same tree or at adjacent trees with similar vegetation were pooled. The pooled stomach contents and feces were then ground in a mortar and pestle and redried for three weeks at 60 C.

The gross energy of the stomach contents and the feces from the large intestine was determined in a microbomb calorimeter (Phillipson 1964, Gentry Instrument Co. 1969, Prus 1975). Only water is absorbed in the lower portion of the large intestine (Church and Pond 1974) and therefore the feces there represent undigested material from the food consumed. The gross energy of each pooled sample was determined twice. Samples were chosen randomly and a gross energy for all samples was determined before replications were begun. The percent of lignin in the food and feces were determined by the Van Soests' procedure for determining permanganate lignin (Van Soests and Wine 1968).

Seventy-five trial lignin determinations were done with bluegrass and a mixture of fall forbs prior to doing determinations on the actual stomach and fecal material from the study. Six lignin determinations could be done simultaneously with the laboratory equipment available. The final eighteen determinations for the bluegrass and fall forb mixture gave values and standard errors of $3.88 \pm .57$ and $10.64 \pm .37$ percent lignin respectively. Most of the variability was between the groups of six samples while variation within any one group of six samples was generally very small. Due to this, and because the ratio of lignin in the stomach contents and feces is more critical to estimate digestible energy than the actual percentages, stomach contents and feces for each pooled sample were done in the same group of determinations. Pooled samples were chosen randomly when doing the lignin determinations. Gross energies, digestible energies, and lignin content were analyzed by analysis of variance using the Statistical Analysis System (Barr and Goodnight 1972).

Plant Composition

The plant composition under and around each tree where traps were set was determined by taking five 400 sq cm random plots inside and outside the dripline of each tree during or soon after each trapping period. These plots were located by indiscriminately tossing a 20 cm X 20 cm wire frame onto the areas being sampled. The species present in the plot and the percent of the plot they covered were recorded. Unidentified plant species were keyed to genus or species according to Strausbaugh and Core (1970). Vegetation was analyzed by analysis of variance using the Statistical Analysis System (Barr and Goodnight 1972).

RESULTS

Densities

The number of voles caught per trap hour in each orchard for each sampling period is given in Table 1. More voles per trap hour were caught in the abandoned orchard than in the maintained orchard from September through January. In March this trend reversed, and in May essentially the same number of animals was caught in each orchard per trap hour. In July more animals were caught per trap hour in the abandoned orchard. Density estimates and probabilities of capture, based upon depletion of the population and the rate of capture (Leslie Method) are given in Table 2. For most sampling periods no real depletion occurred; either more animals were caught in the later periods or essentially equal numbers were caught in all periods. September was the only month where depletion estimates were obtained for both orchards. At this time mean estimates of density were higher in the maintained orchard than in the abandoned orchard. Animals in the abandoned orchard in September had a higher probability of capture than animals in the maintained orchard.

Mortality

Life tables, based on survival equations determined by regression of relative cumulative frequency on age (Dapson 1971 and 1972), for cohorts from both orchards both in the periods from May - July, July - September, September - November and November - January are presented in the Appendix Tables I through VIII. Table 3 is

Table 1. Number of voles caught per trap per hour in two apple orchards near Daleville, Virginia between September 1974 and July 1975.

Month	Maintained Orchard voles/trap hr	Abandoned Orchard voles/trap hr
September	0.167	0.195
November	0.331	0.377
January	0.305	0.369
March	0.204	0.138
May	0.081	0.078
July	0.093	0.106

Table 2. Density estimates and probability of capture of pine voles, based upon the depletion of population and rate cf capture (Leslie Method), in two apple orchards located near Daleville, Virginia between September 1974 and July 1975.

Month	Maintained Orchard			Abandoned Orchard		
	sampling area	voles/ hectare[a]	probability of capture	sampling area	voles/ hectare[a]	probability of capture
September	1	69	.0196	1	82	.0417
	2	111	.0123	2	77	.0183
	3	b	--	3	69	.0417
				4	b	--
	mean	90	.0160	mean	76	.0339
November	1	b	--	1	111	.02
	2	b	--	2	b	--
	mean	--	--			
January	1	168	.0064	1	b	--
	2	b	--	2	b	--
	mean	--	--	mean	--	--
March	1	b	--	1	b	--
	2	b	--	2	b	--
				3	b	--
	mean	--	--	mean	--	--
May	1	b	--	1	82	.0051
	2	b	--	2	84	.0205
	mean	--	--	mean	83	.0128

Table 2. Density estimates and probability of capture of pine voles, based upon the depletion of population and rate of capture (Leslie Method), in two apple orchards located near Daleville, Virginia between September 1974 and July 1975 (continued).

Month	Maintained Orchard			Abandoned Orchard		
	sampling area	voles/ hectare[a]	probability of capture	sampling area	voles/ hectare[a]	probability of capture
July	1	b	--	1	b	--
	2	b	--	2	b	--
	mean	--	--	mean	--	--

[a]Based on standard distance of approximately 15 m between trees

[b]No depletion occurred

Table 3. Values of mean monthly mortality, mean age class mortality, mean expectation of life at 2 months, and maximum ecological longevity of cohorts from a maintained and an abandoned orchard near Daleville, Virginia.

Cohort	Mean monthly mortality	Mean mortality per 1000 per age class	Mean expectation of life at 2 months (months)	Maximum ecological longevity (days)
Maintained Orchard				
May 15 to July 14	14.6	287	5.9	575
July 15 to Sept 14	18.9	356	4.1	829
Sept 15 to Nov 14	19.6	350	4.3	822
Nov 15 to Jan 14	19.7	350	4.3	763
Abandoned Orchard				
May 15 to July 14	29.0	298	4.3	615
July 15 to Sept 14	21.7	373	3.7	806
Sept 15 to Nov 14	20.0	334	4.2	815
Nov 15 to Jan 14	22.8	362	3.6	848

a summary of pertinent data for each cohort. Estimates of mean monthly mortality were higher in the abandoned orchard than in the maintained orchard for each pair of cohorts. The mean number of voles dying per age class per 1000 voles (1000qx) was also larger in the abandoned orchard for each pair of cohorts except for the September - November pair in which the active orchard had a larger mean death rate per 1000 per age class per month. Life expectancy at two months of age was consistently higher in the maintained orchard. Estimates of maximum ecological longevity for the abandoned orchard were higher than for the maintained orchard for the May - July and November - January cohorts, while in the July - September and September - November cohorts the maintained orchard had slightly higher estimates of maximum ecological longevity.

Natality

The percent of immatures captured, percent pregnant females, and number of fetuses per pregnant female for the maintained and abandoned orchards are given in Table 4. The maintained orchard had a higher percent of immatures in the population in all sampling periods except for July, when the percent of immatures was similar in the two orchards. The percent of females was similar for the two orchards in May, July, and September; in November the maintained orchard still had 83 percent of adult females pregnant, while in the abandoned orchard only 35 percent of the adult females captured were pregnant. In January, the percent pregnant females in the maintained orchard decreased to 50 percent, while in the abandoned orchard the

Table 4. Number of adult females and percent visible pregnant adult female voles, fetuses per pregnant female and numbers, and immature to adult ratios of pine voles captured in two orchards near Daleville, Virginia between September 1974 and July 1975.

	Adult Females			Immatures	
Month	(n)	Percent pregnant	Mean no. fetuses/ pregnant female	(n)	immature:adult
Maintained Orchard					
Sept.	21	81	2.2	13	27:73
Nov.	18	83	1.9	10	23:77
Jan.	14	50	1.9	10	20:80
March	17	13	2.0	3	6:94
May	15	53	1.3	2	7:93
July	13	85	2.0	4	12:88
Totals, means	98	61	1.9	42	16:84
Abandoned Orchard					
Sept.	15	80	1.9	5	13:87
Nov.	17	35	2.3	9	19:81
Jan.	17	35	1.7	4	8:92
March	20	0	--	0	0:100
May	13	46	1.2	0	0:100
July	15	87	1.6	5	13:87
Totals, means	97	47	1.5	23	9:91

percent of pregnant females remained at 35 percent. No pregnant females were captured in the abandoned orchard in March, while 13 percent (2) of the females were pregnant in the maintained orchard. The average number of fetuses per pregnant female for the maintained orchard (1.9) was greater than for the abandoned orchard (1.5).

Indicators of Reproductive Activity in Females

Mean values of several characteristics of nonpregnant and visibly pregnant adult female pine voles from the maintained and abandoned orchards are given in Tables 5 and 6. Mean squares and significance levels for a two factor (month and orchard) analysis of variance are given for paired ovarian weight, adrenal gland weight, and uterine weight of nonpregnant adult females in Table 7. Paired ovarian weights for nonpregnant females in the maintained orchard were significantly different ($P < .0001$) from nonpregnant females in the abandoned orchard. There was also a significant ($P < .04$) month-orchard interaction. Paired ovarian weights were higher in the maintained orchard than in the abandoned orchard in the months of September, January, March, and May, while higher paired ovarian weights were found in the abandoned orchard in November and July. Adrenal weights of nonpregnant females were significantly higher ($P < .02$) in the abandoned than in the maintained orchard. There were no significant differences in uterine weights.

Indicators of Reproductive Activity in Males

Mean values for several characteristics of adult male pine voles from the maintained and abandoned orchards are given in Table 8. Mean

Table 5. Mean values, standard errors, and sample sizes by collection period for selected characteristics of nonpregnant female pine voles captured in two orchards near Daleville, Virginia between September 1974 and July 1975.

Month	Paired ovarian weight (mg±SE) (n)	Adrenal glands weight (mg±SE) (n)	Uterine weights (mg±SE) (n)
Maintained Orchard			
Sept.	6.80±2.87(3)	6.70±1.82(3)	54±34(4)
Nov.	4.12±1.89(3)	9.17±1.90(3)	49±22(3)
Jan.	4.52±1.76(7)	9.03±1.25(7)	46±17(7)
March	3.15±1.16(13)	8.81±2.48(15)	51±54(15)
May	3.54±0.58(7)	7.30±1.29(7)	31±12(7)
July	4.50±2.14(2)	8.65±3.75(2)	60± 1(2)
Abandoned Orchard			
Sept.	4.70±2.74(3)	7.27±0.57(3)	39±14(3)
Nov.	4.40±1.97(11)	10.21±1.89(11)	52±28(11)
Jan.	3.65±2.08(11)	9.20±2.17(11)	31±19(11)
March	2.15±0.76(15)	8.86±2.17(20)	18±10(20)
May	2.35±1.49(7)	7.27±0.87(6)	22±21(7)
July	8.79±0.35(2)	8.05±0.64(2)	70±26(2)

Table 6. Mean values, standard errors, and sample sizes by collection period for selected characteristics of visibly pregnant female pine voles captured in two orchards near Dalesville, Virginia between September 1974 and July 1975.

Month	Paired ovarian weight (mg±SE) (n)	Adrenal glands weight (mg±SE) (n)
Maintained Orchard		
Sept.	7.64±2.48(17)	9.28±2.37(17)
Nov.	6.54±2.87(15)	10.73±1.92(15)
Jan.	8.21±3.11(7)	11.91±3.19(7)
March	8.49±6.75(2)	11.20±3.81(2)
May	8.62±1.81(8)	8.30±1.50(8)
July	6.78±2.61(11)	8.30±1.58(11)
Abandoned Orchard		
Sept.	9.41±3.88(12)	9.65±2.65(11)
Nov.	12.06±4.04(6)	10.06±1.28(6)
Jan.	5.65±1.96(6)	9.96±3.04(6)
March	a	a
May	7.89±2.67(6)	9.63±1.97(6)
July	8.65±2.79(13)	9.49±1.51(13)

[a]No pregnant females were captured in the abandoned orchard during this collection period.

Table 7. Mean squares for weights of reproductive organs of nonpregnant adult female pine voles captured in two orchards located near Daleville, Virginia between September 1974 and July 1975.

Source	df		Paired ovarian weights	Adrenal glands weight	Uterine weights
Month (M)	5	Mean square	0.13	0.51	1227.42
		P <	.82	.72	.22
Orchard (O)	1	Mean square	20.74	11.20	1388.17
		P <	.0001	.14	.02
M X O	4	Mean square	6.33	0.57	822.72
		P <	.04	.98	.42
Error	92	Mean square	2.55	3.99[a]	810.93[b]

[a]Degrees of freedom for error was 78.

[b]Degrees of freedom for error was 80.

Table 8. Mean values, standard errors, and sample sizes by collection period for selected characteristics of adult male pine voles captured in two orchards near Daleville, Virginia between September 1974 and July 1975.

Month	Testes weight (mg±SE) (n)	Seminal vesicles weight (mg±SE) (n)	Adrenal glands weight (mg±SE) (n)	Spermatozoa sperm/mg testes wt±SE X10^3 (n)
Maintained Orchard				
Sept.	117±36(13)	83±40(13)	10.4±1.9(13)	79±32(11)
Nov.	115±39(10)	77±46(10)	13.7±4.3(10)	117±21(10)
Jan.	102±18(14)	72±38(14)	9.2±2.1(14)	130±42(14)
March	105±25(18)	37±17(19)	9.3±2.3(19)	73±19(19)
May	74±16(9)	42±21(10)	8.7±1.9(10)	87±24(9)
July	80±12(11)	68±24(11)	8.8±1.3(11)	87±26(11)
Abandoned Orchard				
Sept.	131±27(13)	109±48(13)	11.8±2.1(12)	84±24(13)
Nov.	128±46(12)	82±64(12)	13.8±4.7(12)	173±34(12)
Jan.	110±34(13)	66±43(13)	12.7±4.9(13)	106±32(13)
March	63±23(15)	17±13(15)	9.3±2.5(15)	66±29(15)
May	72±18(13)	47±21(13)	10.7±2.6(13)	68±18(13)
July	107±26(16)	121±57(16)	11.6±2.1(16)	99±31(16)

squares and significance levels from a two factor (month and orchard) analysis of variance for testes weight, seminal vesicles weight, adrenal weights, and spermatozoa per mg of testes weight are given in Table 9.

There were significant ($P < .0001$) differences in testes weights due to month and a significant ($P < .0002$) month-orchard interaction. The difference in seminal vesicles weights between orchards approached significance ($P < .10$), effect due to month was significant ($P < .0001$), and there was a significant month-orchard interaction ($P < .01$). There was no significant ($P < .41$) orchard effect on sperm/mg testes weight; there was a significant month effect ($P < .0001$) and a significant month-orchard interaction ($P < .0001$). There was a significant difference in adrenal weights due to orchard ($P < .0008$) and month ($P < .0001$) with no significant month-orchard interaction ($P < .16$).

In the maintained orchard testes weights and seminal vesicles weights decreased from September through May, and then increased in July. In the abandoned orchard testes weights and seminal vesicles weights decreased from September to March, but increased in May and July. Spermatozoa/mg testes weights increased from September to November, then decreased through March, were about the same level in May as in March, and then increased in July.

Male adrenal weights were higher in the abandoned orchard in all months except March, when adrenal weights in both orchards were at the same level. In the maintained orchard, adrenal weights increased from September to November, then decreased in January and did not change through March, decreased again in May, and did not change in July. In the abandoned orchard adrenal weights increased

Table 9. Mean squares for reproductive characteristics of adult male pine voles captured in two apple orchards near Daleville, Virginia, between September 1974 and July 1975.

Source	df		Testes weights[a]	Seminal vesicles weights[b]	Adrenal weights[c]	Sperm/mg testes wts[d] x 10^5
Orchard (O)	1	Mean square	333.96	4237.02	97.56	5686.24
		P <	.52	.10	.0008	.41
Month (M)	5	Mean square	10093.51	22175.06	60.71	203231.22
		P <	.0001	.0001	.0001	.0001
M X O	5	Mean square	4417.15	4715.75	13.54	49347.30
		P <	.0002	.01	.16	.0001
Error		Mean square	790.03	1518.07	8.36	8167.87

[a]Degrees of freedom for error was 145

[b]Degrees of freedom for error was 147

[c]Degrees of freedom for error was 146

[d]Degrees of freedom for error was 144

from September to November, decreased in January and March, and increased in May and July.

Fecundity Tables

Female fetuses per female, assuming a 50:50 sex ratio, are given in Table 10. Fecundity tables are given for cohorts born between May - July, July - September, September - November, and November - January for both the maintained and abandoned orchards in the appendix (Appendix Tables IX through XVI). Table 11 gives a summary of data from the fecundity tables for each cohort. In the maintained orchard the May - July and the July - September cohorts had net reproductive rates (the number of times a population can multiply its numbers in a generation) greater than one which would indicate that they would more than replace themselves before the members of the cohort died. The September - November, and November - January cohorts had net reproductive rates (R_o's) less than 1, indicating that these cohorts would not replace themselves before the members of the cohort died. All cohorts in the abandoned orchard had R_o's of less than 1, indicating that none of the cohorts were replacing themselves.

Nutrition

Mean fat content of adult male and adult female pine voles collected in the two orchards for each sampling period is given in Table 12. Mean squares and significance levels from a three factor (month, orchard, and sex) analysis of variance of fat content are

Table 10. Mean number of female fetuses per female, assuming a 1:1 ratio, for two age classes (75-165 days old and 165+ days old) and each sampling period. Data are from pine voles captured in two orchards near Daleville, Virginia between September 1974 and July 1975.

	Number of female fetuses per female vole			
	Maintained orchard		Abandoned orchard	
Month	75-165 days	165+ days	75-165 days	165+ days
Sept.	.56	1.00	.38	.94
Nov.	.50	.91	.14	.60
Jan.	.25	.45	.17	.31
March	.00	.13	.00	.00
May	.20	.33	.13	.42
July	.50	.79	.75	.60

Table 11. Values of net reproductive rate and mean generation time of cohorts from a maintained and an abandoned orchard near Daleville, Virginia.

Cohort	Maintained Orchard: R_o Net reproductive rate $(\Sigma l_x m_x)$	Maintained Orchard: T Mean length of[a] generation $\frac{\Sigma x l_x m_x}{\Sigma l_x m_x}$ (months)	Abandoned Orchard: R_o Net reproductive rate $(\Sigma l_x m_x)$	Abandoned Orchard: T Mean length of[a] generation $\frac{\Sigma x l_x m_x}{\Sigma l_x m_x}$ (months)
May 15 to July 14	2.389	6.98	0.722	6.14
July 15 to September 14	1.255	5.61	0.533	5.64
September 15 to November 14	0.894	6.97	0.556	8.02
November 15 to January 14	0.857	8.18	0.511	7.59

[a]Mean time from birth of vole to birth of its offspring.

Table 12. Mean values of fat content (fat expressed as percent of dry body weight), standard errors, and sample size of adult male and female pine voles collected between September 1974 and July 1975 in two apple orchards near Daleville, Virginia.

Month	Maintained Orchard		Abandoned Orchard	
	Males	Females	Males	Females
September	18.0±4.1(12)	19.3±9.4(21)	17.8±4.5(13)	18.9±6.5(15)
November	17.2±3.8(10)	16.6±6.1(18)	14.7±3.2(12)	13.9±4.3(18)
January	19.5±4.8(14)	19.5±3.6(14)	17.5±6.0(13)	18.7±3.8(17)
March	14.9±5.1(18)	14.8±4.8(17)	13.3±4.1(15)	16.1±6.6(20)
May	12.8±3.4(10)	17.4±7.3(15)	14.8±5.3(12)	16.2±3.3(12)
July	16.8±2.9(11)	14.9±5.4(13)	16.7±3.6(16)	18.6±5.4(15)

given in Table 13. The only significant difference in fat content ($P < .0001$) was due to month, although the effect of sex approached significance ($P < .12$). Fat content of males in the maintained orchard decreased from September to November, increased in January, decreased through March and May, and increased in July. Males in the abandoned orchard showed essentially the same trend, except that they increased from March to May. Fat content of females in the maintained orchard decreased from September to November, increased in January, decreased in March, increased in May, and decreased in July. Females in the abandoned orchard followed the same trend from September to March, but did not change from March to May, and increased in July.

Means of fat content of nonpregnant and pregnant females are given in Table 14. Mean squares and significance levels from a three factor analysis of variance (month, orchard, and state - male, pregnant, or nonpregnant female) of fat content are given in Table 15. There were significant differences in fat levels due to month ($P < .0004$) and state ($P < .06$), and a significant month-orchard interaction ($P < .03$) and a significant month-orchard-state interaction ($P < .07$).

Body Weight and Length

Body weight and length for adult voles by orchard and month are given in Tables 16, 17 and 18. Mean squares and significance levels from a three factor (month, orchard and sex) analysis of variance for body length and weight are presented in Table 19. All adult male and female voles were used in the analysis of variance of length, while only adult male and adult nonpregnant females were used in the analysis of

Table 13. Mean squares for fat content (fat expressed as percent of dry body weight) of adult male and female pine voles collected between September 1974 and July 1975 in two apple orchards near Daleville, Virginia.

Source	df		Fat
Month (M)	5	mean square	172.9
		P <	.0001
Orchard (O)	1	mean square	12.0
		P <	.52
Sex (S)	1	mean square	68.9
		P <	.12
M X O	5	mean square	30.5
		P <	.38
M X S	5	mean square	20.7
		P <	.61
O X S	1	mean square	11.8
		P <	.52
M X O X S	5	mean square	20.4
		P <	.61
Error	327	mean square	28.5

Table 14. Mean values of fat content (fat content expressed as percent of dry body weight), standard errors, and sample size of adult pregnant and nonpregnant female pine voles collected between September 1974 and July 1975 in two orchards near Daleville, Virginia.

Month	Maintained Orchard		Abandoned Orchard	
	nonpregnant females	pregnant females	nonpregnant females	pregnant females
September	28.4±13.6(4)	17.2±7.1(17)	17.3±5.6(3)	19.3±6.9(12)
November	15.6± 0.7(3)	16.8±6.7(15)	14.2±4.5(11)	13.5±4.3(7)
January	19.2± 3.4(7)	19.7±4.1(7)	18.9±4.0(11)	18.4±3.6(6)
March	14.8± 5.0(15)	14.7±4.2(2)	16.1±6.6(20)	----
May	17.1± 8.4(7)	17.6±6.8(8)	16.4±4.2(7)	15.9±1.9(5)
July	14.4± 8.4(2)	15.0±5.3(11)	26.6±6.7(2)	17.3±4.2(13)

Table 15. Mean squares for fat content (fat expressed as percent of the dry body weight) of adult male, pregnant female, and nonpregnant female pine voles between September 1974 and July 1975 in two orchards near Daleville, Virginia. Since no pregnant females were captured in the abandoned orchard in March, data for March were deleted.

Source	df		Fat
Month (M)	4	mean square	154.3
		P	.0004
Orchard (O)	1	mean square	7.1
		P	.61
State (S)	2	mean square	75.5
		P	.06
M X O	4	mean square	74.7
		P	.03
M X S	8	mean square	27.3
		P	.55
O X S	2	mean square	0.7
		P	.98
M X O X S	8	mean square	50.7
		P	.07
Error	250	mean square	27.5

Table 16. Mean values, standard errors, and sample sizes by collection period for body length and body weight of nonpregnant female pine voles captured in two orchards near Daleville, Virginia between September 1974 and July 1975.

Month	Body length (mm±SE)	(n)	Body weight (g±SE)	(n)
Maintained Orchard				
September	95±7	4	27.0±5.9	3
November	96±2	3	25.3±0.9	3
January	100±3	7	25.5±3.3	7
March	101±6	15	24.4±4.3	15
May	99±4	7	24.9±2.2	7
July	101±1	2	29.7±	2
Abandoned Orchard				
September	95±4	3	21.6±3.2	3
November	101±6	10	25.5±3.1	10
January	98±8	11	23.6±3.9	11
March	100±6	20	22.2±3.9	11
May	94±4	7	22.0±2.1	7
July	104±6	2	26.2±4.7	2

Table 17. Mean values, standard errors, and sample sizes by collection period for body length and body weight of visibly pregnant pine voles captured in two orchards near Daleville, Virginia between September 1974 and July 1975.

Month	Body length (mm±SE)	(n)	Body weight (g±SE)	(n)
Maintained Orchard				
September	101±6	17	28.3±4.3	17
November	101±6	15	28.8±4.8	14
January	101±6	7	28.1±4.4	7
March	107±6	2	31.8±8.3	2
May	101±3	8	27.7±1.7	8
July	102±2	11	27.9±2.2	11
Abandoned Orchard				
September	98±6	12	27.7±3.4	12
November	104±6	6	31.8±4.6	6
January	100±5	6	27.7±2.9	6
March	a		a	
May	102±4	6	26.1±0.7	6
July	102±4	13	28.2±2.6	13

[a]No pregnant females were captured in the abandoned orchard during this collection period.

Table 18. Mean values, standard errors, and sample sizes by collection period for body length and body weight of male pine voles captured in two orchards near Daleville, Virginia between September 1974 and July 1975.

Month	Body length (mm±SE)	(n)	Body weight (g±SE)	(n)
Maintained Orchard				
September	98±5	13	27.7±3.3	13
November	102±4	10	27.0±2.6	10
January	99±3	14	25.3±2.2	14
March	100±4	19	24.2±2.5	18
May	99±3	10	23.7±2.3	10
July	99±3	11	25.3±2.0	11
Abandoned Orchard				
September	97±3	13	26.7±1.8	13
November	102±5	12	26.8±2.7	12
January	103±6	13	27.3±2.7	13
March	100±6	15	23.3±2.5	15
May	100±7	13	24.3±3.3	13
July	101±4	16	26.2±2.0	16

Table 19. Mean squares for body length measurements for adult male and female pine voles, and body weight and adrenal weight for nonpregnant adult female and adult male pine voles captured in two orchards near Daleville, Virginia between September 1974 and July 1975.

Source	df		Body length	Body weight[a]	Adrenal weight[b]
Orchard (O)	1	mean square	3.8	60.43	29.81
		P <	.70	.0038	.04
Month (M)	5	mean square	92.8	58.78	38.18
		P <	.0036	.0001	.0002
Sex (S)	1	mean square	5.7	32.07	237.89
		P <	.64	.03	.0001
O X M	5	mean square	20.4	10.70	4.39
		P <	.55	.19	.67
O X S	1	mean square	72.8	70.61	17.85
		P <	.09	.0018	.11
M X S	5	mean square	29.8	14.54	19.00
		P <	.32	.07	.02
O X M X S	5	mean square	25.4	6.58	6.32
		P <	.58	.54	.53
Error	328	mean square	25.5	7.08	6.82

[a]Degrees of freedom for error are 222.

[b]Degrees of freedom for error are 223.

variance of weight. There was a significant difference in body length due to month ($P < .004$). Body weight was significantly different due to orchard ($P < .004$), month ($P < .0001$), and sex ($P < .03$). There were significant orchard-sex ($P < .002$) and month-sex ($P < .07$) interactions. There was no apparent trend in mean length due to month.

Mean weights of males in the maintained orchard were higher than the mean weights of males in the abandoned orchard in September, November, and March and lower than mean weights of males in the abandoned orchard in January, May, and July. Mean weights of non-pregnant females in the maintained orchard were higher than those of nonpregnant females in the abandoned orchard in all months except November when mean weights were essentially the same.

In the maintained orchard mean body weights of males were essentially equal in September and November, decreased in January, March, and May, and increased in July. Mean weights of nonpregnant females decreased from September to November, were essentially the same in January as in November, decreased in March, increased slightly in May, and increased in July.

In the abandoned orchard mean weights of males in September and November were essentially equal, increased in January, dropped dramatically in March, increased slightly in May, and increased in July. Mean weights of nonpregnant females increased from September to November, decreased in January and March, did not change from March to May, and increased in July.

Stomach Contents

Mean values for dry weight of stomach contents of adult voles are given in Table 20. Mean squares and significance levels from a three factor (month, orchard, and sex) analysis of variance of dry weight of stomach contents are given in Table 21. There was a significant difference in mean dry weight of stomach contents due to orchard ($P < .02$), month ($P < .01$), and sex ($P < .08$). The mean dry weight of stomach contents of adult voles was higher in the maintained orchard than in the abandoned orchard in all months. The mean dry weight of stomach contents of females was generally higher than that of males.

Mean values for gross energies, digestible energies and percent lignin of pooled stomach contents of adult pine voles by orchard and month are presented in Table 22. Mean squares and significance levels from a two factor (month and orchard) analysis of variance for gross energies, digestible energies, and percent lignin are given in Table 23. There was a significant difference ($P < .09$) in gross energies due to month. Gross energies declined from September to November, were lowest in November and January, increased in March, and held fairly constant through July. Apparent digestible energy was significantly different due to the orchard effect ($P < .09$). The means of digestible energy estimates were higher in the maintained orchard than in the abandoned orchard in the months of September, January, March and July, essentially equal in November, while in May the abandoned orchard had higher mean digestible energies. There were significant differences in percent lignin due to month ($P < .0001$) and orchard ($P < .003$), and a

Table 20. Mean values ± standard error and sample size for dry weight of stomach contents for adult pine voles collected in two orchards near Daleville, Virginia between September 1974 and July 1975.

Month	Maintained Orchard				Abandoned Orchard			
	Males (gm/stomach ±SE)	(n)	Females (gm/stomach ±SE)	(n)	Males (gm/stomach ±SE)	(n)	Females (gm/stomach ±SE)	(n)
Sept.	.152±.124	(11)	.178±145	(21)	.101±.058	(13)	.097±.057	(11)
Nov.	.088±.104	(10)	.176±093	(18)	.106±083	(12)	.129±.131	(17)
Jan.	.122±.090	(14)	.127±.099	(14)	.109±.082	(13)	.110±.076	(17)
March	.152±.117	(19)	.197±.146	(17)	.147±.076	(15)	.154±.120	(20)
May	.171±.093	(10)	.216±.141	(15)	.195±.136	(13)	.156±.092	(13)
July	.170±.150	(11)	.179±.131	(13)	.114±.064	(16)	.162±.136	(15)

Table 21. Mean squares for dry weight of stomach contents of adult pine voles collected from two orchards near Daleville, Virginia between September 1974 and July 1975.

Source	df		Dry weight of stomach contents
Orchard (O)	1	mean square	.0693
		P <	.02
Month (M)	5	mean square	.0362
		P <	.01
Sex (S)	1	mean square	.0374
		P <	.08
O X M	5	mean square	.0052
		P <	.83
O X S	1	mean square	.0195
		P <	.21
M X S	5	mean square	.0054
		P <	.82
O X M X S	5	mean square	.0063
		P <	.77
Error	324	mean square	.0124

Table 22. Mean values, standard errors, and sample sizes for gross energy, digestible energy, and lignin content of pooled stomach contents of adult pine voles collected in two orchards near Daleville, Virginia between September 1974 and July 1975.

Month	Gross energy kcal/gm dry weight (n)	Digestible energy kcal/gm dry weight (n)	Lignin % of dry weight (n)
<u>Maintained Orchard</u>			
Sept.	4.1191±.3081(4)	0.9820±.4423(3)	9.7± .7(4)
Nov.	4.0807±.1511(4)	0.9241±.1939(4)	9.2± .2(4)
Jan.	4.0618±.1767(4)	1.7965±.3090(4)	8.8±1.0(4)
March	4.3099±.3737(5)	1.2886±5476 (5)	11.9±2.6(5)
May	4.2495±.1970(4)	1.0484±.6270(4)	10.5±2.1(4)
July	4.2716±.1643(3)	1.3861±.5253(3)	10.4±1.0(3)
<u>Abandoned Orchard</u>			
Sept.	4.2338±.1292(4)	0.4409±.5198(4)	10.8±1.3(4)
Nov.	4.0982±.0590(4)	1.0124±.635 (4)	11.0±1.4(4)
Jan.	4.0976±.0603(4)	1.0606±.4669(4)	11.5±2.3(4)
March	4.3703±.3181(6)	1.0761±.7600(6)	16.0±0.7(6)
May	4.4041±.2331(3)	1.1360±.2545(3)	9.8±2.4(3)
July	4.1855±.0494(3)	1.0359±.4204(3)	10.4±1.5(3)

Table 23. Mean squares for gross energy, digestible energy, and lignin content of pooled stomach contents of adult pine voles collected in two orchards near Daleville, Virginia between September 1974 and July 1975.

Source	df		Gross energy	Digestible energy	Lignin
Orchard (O)	1	mean square	0.0283	0.8652	26.2015
		P <	.46	.09	.0028
Month (M)	5	mean square	0.1083	0.4364	24.0448
		P <	.09	.20	.0001
O X M	5	mean square	0.0115	0.2109	6.5258
		P <	.95	.60	.0435
Error	36	mean square	0.05	0.28[a]	2.5471

[a]Degrees of freedom for error equals 35.

significant ($P < .04$) month-orchard interaction. Percent lignin was higher in the abandoned orchard than in the maintained orchard in all months except May and July. In the maintained orchard lignin decreased from September to January, increased in March, and then decreased through July. In the abandoned orchard lignin increased from September through March, decreased in May, and increased again in July.

Plant Composition

Mean values for the percent ground cover for the major plant species beneath and outside the tree dripline for the maintained and abandoned orchards for each sampling period are presented in Tables 24 through 29. Mean squares and significance levels from a two factor (month and orchard) analysis of variance for each major plant species and uncovered ground are given in Table 30 for beneath dripline vegetation. Table 31 gives the same information for outside the tree dripline. There were highly significant differences in the percent ground cover of the major species and percent uncovered ground (beneath and outside the dripline) between months and orchards, and a significant month-orchard interaction.

The maintained orchard had less uncovered ground than the abandoned orchard. The percent uncovered ground increased greatly in both orchards from September to November, but increased more drastically in the abandoned orchard. The percent uncovered ground remained relatively constant in January in both orchards. In the maintained orchards the percent uncovered ground decreased in March, but held constant in the abandoned

Table 24. Mean values for percent ground cover of major plant species found in two orchards near Daleville, Virginia for September 1974 sampling period.

Species	Percent ground cover: Beneath tree canopies	Outside tree canopies	Combined
Maintained Orchard	33 plots	33 plots	66 plots
Dactylis glomerata (orchard grass)	40	43	42
Rhus radicans (poison ivy)	25	2	14
Poa pretensis (bluegrass)	14	13	14
Solanum carolinense (horse nettle)	9	1	5
Succulent forbs[a]	5	28	17
Abandoned Orchard	39 plots	39 plots	78 plots
Rhus radicans (poison ivy)	38	9	24
Dactylis glomerata (orchard grass)	21	15	18
Succulent forbs[a]	8	27	18
Lonicera japonica (Japanese honeysuckle)	8	1	5
Parthenocissus spp. (Virginia creeper)	5	1	5
Solanum carolinense (horse nettle)	5	7	6
Ambrosia artemisiifolia (ragweed)	4	14	9

[a]Includes *Taraxacum officinale* (dandelion), *Plantago lanceola* (narrow leaf plantain), *Plantago major* (broad leaf plantain), *Trifolium pratense* (red clover), *Trifolium repense* (white clover), *Melilotus alba* (white sweet clover), *Melilotus officinalis* (yellow sweet clover).

Table 25. Mean values for percent ground cover of major plant species and percent uncovered ground found in two orchards near Daleville, Virginia for November 1974 sampling period.

Species	Percent ground cover: Beneath tree canopies	Outside tree canopies	Combined
Maintained Orchard	25 plots	25 plots	50 plots
Dactylis glomerata (orchard grass)	31	37	34
Poa pretensis (blue grass)	10	19	15
Lonicera japonica (Japanese honeysuckle)	6	1	4
Other grasses[a]	4	15	10
Succulent forbs[b]	1	5	3
Uncovered ground	47	22	35
Abandoned Orchard	25 plots	25 plots	50 plots
Dactylis glomerata (orchard grass)	10	20	15
Lonicera japonica (Japanese honeysuckle)	4	2	3
Poa pretensis (blue grass)	1	4	3
Succulent forbs[b]	1	9	5
Uncovered ground	83	64	74

[a]Includes *Festuca* (fescue), *Muhlenbergia* (muhly grass), *Paspalum* (paspalum), *Agrostis alba* (redtop).

[b]Includes *Taraxacum officinale* (dandelion), *Plantago lanceolata* (narrow leaf plantain), *Plantago major* (broad leaf plantain), *Trifolium pratense* (red clover), *Trifolium repens* (white clover), *Melilotus alba* (white sweet clover), *Melilotus officinalis* (yellow sweet clover).

Table 26. Mean values for percent ground cover of major plant species and percent uncovered ground for two orchards near Daleville, Virginia for the January 1975 sampling period.

Species	Percent ground cover: Beneath tree canopies	Outside tree canopies	Combined
Maintained Orchard	22 plots	22 plots	44 plots
Dactylis glomerata (orchard grass)	38.2	48.0	43.1
Poa pratensis (blue grass)	12.1	24.3	18.2
Alium vineale (field garlic)	0.5	0.3	0.4
Succulent forbs[a]	0.2	0.5	0.4
Lonicera japonica (Japanese honeysuckle)	0.2	0.5	0.4
Uncovered ground	49.3	26.5	37.9
Abandoned Orchard	24 plots	24 plots	48 plots
Lonicera japonica (Japanese honeysuckle)	13.0	0.2	6.6
Dactylis glomerata (orchard grass)	3.5	21.5	12.5
Poa pratensis (blue grass)	2.6	18.5	10.6
Alium vineale (field garlic)	0.4	0.1	0.3
Succulent forbs[a]	0.3	2.1	1.2
Uncovered ground	80.1	57.6	68.9

[a]Includes *Taraxacum officinale* (dandelion), *Plantago lanceolata* (narrow leaf plantain), *Plantago major* (broad leaf plantain), *Trifolium pratense* (red clover), *Trifolium repens* (white clover), *Melilotus alba* (white sweet clover), *Melilotus officinalis* (yellow sweet clover).

Table 27. Mean values for percent ground cover of major plant species and percent uncovered ground found in two orchards near Daleville, Virginia for the March 1975 sampling period.

Species	Percent ground cover: Beneath tree canopies	Outside tree canopies	Combined
Maintained Orchard	25 plots	25 plots	50 plots
Dactylis glomerata (orchard grass)	18.9	45.5	32.2
Lonicera japonica (Japanese honeysuckle)	14.0	3.0	8.5
Poa pratensis (blue grass)	3.6	20.6	12.1
Alium vineale (field garlic)	0.6	0.8	0.7
Succulent forbs[a]	0.5	3.2	1.9
Uncovered ground	62.2	26.9	44.9
Abandoned Orchard	29 plots	29 plots	58 plots
Poa pratensis (blue grass)	7.9	18.4	13.2
Dactylis glomerata (orchard grass)	7.1	12.3	9.7
Lonicera japonica (Japanese honeysuckle)	3.7	3.1	3.4
Succulent forbs[a]	0.8	4.3	2.6
Alium vineale (field garlic)	0.1	0.4	0.3
Uncovered ground	79.8	60.1	70.0

[a]Includes *Taraxacum officinale* (dandelion), *Plantago lanceolata* (narrow leaf plantain), *Plantago major* (broad leaf plantain), *Trifolium pratense* (red clover), *Trifolium repens* (white clover), *Melilotus officinalis* (yellow sweet clover).

Table 28. Mean values for percent ground cover of major plant species and percent uncovered ground found in two orchards near Daleville, Virginia for the May 1975 sampling period.

Species	Percent ground cover: Beneath tree canopies	Outside tree canopies	Combined
Maintained Orchard	25 plots	25 plots	50 plots
Rhus radicans (poison ivy)	55	8	32
Dactylis glomerata (orchard grass)	24	39	32
Poa pratensis (blue grass)	11	15	13
Parthenocissus spp. (Virginia creeper)	4	1	3
Succulent forbs[a]	1	20	11
Uncovered ground	< 1	< 1	< 1
Abandoned Orchard	24 plots	24 plots	48 plots
Rhus radicans (poison ivy)	58	14	36
Dactylis glomerata (orchard grass)	22	20	21
Poa pratensis (blue grass)	7	12	10
Ambrosia artemisiifolia (ragweed)	4	16	10
Lonicera japonica (Japanese honeysuckle)	3	4	4
Succulent forbs[a]	2	23	13
Uncovered ground	1	2	2

[a]Include Taraxacum officinale (dandelion), Plantago lanceolata (narrow leaf plantain), Plantago major (broad leaf plantain), Trifolium pratense (red clover), Trifolium repens (white clover), Melilotus alba (white sweet clover), Melilotus officinalis (yellow sweet clover).

Table 29. Mean values for percent ground cover of major plant species and percent uncovered ground in two orchards near Daleville, Virginia for the July 1975 sampling period.

Species	Percent ground cover: Beneath tree canopies	Outside tree canopies	Combined
Maintained Orchard	25 plots	25 plots	50 plots
Rhus radicans (poison ivy)	35	4	20
Dactylis glomerata (orchard grass)	34	37	36
Poa pratensis (blue grass)	15	18	17
Parthenocissus spp. (Virginia creeper)	4	1	3
Succulent forbs[a]	1	22	12
Uncovered ground	4	1	3
Abandoned Orchard	25 plots	25 plots	50 plots
Rhus radicans (poison ivy)	51	14	33
Dactylis glomerata (orchard grass)	23	30	27
Lonicera japonica (Japanese honeysuckle)	5	2	4
Poa pratensis (blue grass)	3	10	7
Solanum carolinense (horse nettle)	3	4	4
Succulent forbs[a]	2	10	6
Ambrosia artemisiifolia (ragweed)	<1	8	4
Uncovered ground	8	2	5

[a]Includes *Taraxacum officinale* (dandelion), *Plantago lanceolata* (narrow leaf plantain), *Plantago major* (broad leaf plantain), *Trifolium pratense* (red clover), *Trifolium repens* (white clover), *Melilotus alba* (white sweet clover), *Melilotus officinalis* (yellow sweet clover).

Table 30. Mean squares for percent ground cover of nine plant species and uncovered ground beneath the tree canopies in two orchards near Daleville, Virginia from September 1974 to July 1975.

Source	df		Orchard grass	Blue grass	Poison Ivy	Virginia creeper	Horse nettle
Month (M)	5	mean square	2256	123	31700	160	487
		P <	.0001	.3565	.0001	.0001	.0001
Orchard (O)	1	mean square	21901	3840	2124	3	23
		P <	.0001	.0001	.0050	.7353	.2746
M X O	5	mean square	1498	512	702	116	52
		P <	.0001	.0007	.0231	.0005	.0181
Error	309	mean square	253	111	266	24	19

Table 30. Mean squares for percent ground cover of nine plant species and uncovered ground beneath the tree canopies in two orchards near Daleville, Virginia from September 1974 to July 1975 (continued).

Source	df		Honey-suckle	Succulent forbs	Ragweed	Field garlic	Uncovered ground
Month (M)	5	mean square	312	368	71	2.550	67190
		P <	.1706	.0001	.0002	.0017	.0001
Orchard (O)	1	mean square	398	78	73	.259	18191
		P <	.1595	.0885	.0165	.5201	.0001
M X O	5	mean square	817	28	31	1.873	3147
		P <	.0017	.3928	.0309	.0118	.0001
Error	309	mean square	200	27	13	.625	248

Table 31. Mean squares for percent ground cover of nine plant species and uncovered ground outside the tree canopies in two orchards near Daleville, Virginia from September 1974 to July 1975.

Source	df		Orchard grass	Blue grass	Poison Ivy	Virginia creeper	Horse nettle
Month (M)	5	mean square	400	1405	1179	4.94	185
		P<	.1774	.0001	.0001	.0070	.0001
Orchard (O)	1	mean square	37693	4244	1235	1.32	131
		P<	.0001	.0001	.0001	.3507	.0010
M X O	5	mean square	1099	299	273	1.74	114
		P<	.0013	.0571	.0002	.3315	.0001
Error	309	mean square	260	138	49	1.51	12

Table 31. Mean squares for percent ground cover of nine plant species and uncovered ground outside the tree canopies in two orchards near Daleville, Virginia from September 1974 to July 1975 (continued).

Source	df		Honey-suckle	Succulent forbs	Ragweed	Field garlic	Uncovered ground
Month (M)	5	mean square	50	6247	861	3.44	27397
		P<	.1051	.0001	.0001	.0004	.0001
Orchard (O)	1	mean square	167	19	2330	2.66	22199
		P<	.0144	.6902	.0001	.0501	.0001
M X O	5	mean square	29	430	608	0.76	5600
		P<	.3867	.0035	.0001	.3544	.0001
Error	309	mean square	28	117	44	.69	111

orchard. Both orchards had very little uncovered ground in May and July.

Orchard grass, which seems to be a preferred species of the pine vole (Cengel 1975) made up a larger percent of the ground cover in the maintained orchard throughout the year. The percent ground cover of orchard grass is fairly constant outside the driplines of the trees in both orchards. However, within the driplines of the trees the percent orchard grass decreased into the winter months.

The percent ground cover of succulent forbs was generally higher in the abandoned orchard throughout the year. Succulent forbs were most abundant in both orchards in the months of May, July, and September and were relatively scarce in the months of November, January and March.

DISCUSSION

Densities

Paul (1970:7) found that pine vole densities in abandoned orchards in North Carolina typically were much lower than those in maintained orchards. The data obtained on densities in this study are not sufficiently adequate to compare the densities of the pine vole populations in the maintained and in the abandoned orchards. The only data obtained which allows comparison of the two populations in all periods are the numbers of voles caught per trap hour (Table 1). These data seem to indicate higher vole densities in the abandoned orchard in September, November, January, and July, essentially equal densities in May and lower densities in the abandoned orchard only in March. However, the number of voles caught per trap is a function of the number of voles in the habitat and their probability of capture. Therefore, a higher number of voles caught per trap hour in the abandoned orchard than in the maintained orchard does not necessarily mean a higher density in the abandoned orchard. The higher rate of capture could just as well indicate lower or equal densities in the abandoned orchard with a higher probability of capture. The density estimates from September, the only month where estimates of density by the Leslie Method were obtained in both orchards, supports the alternative that there was a lower density in the abandoned orchard with a higher probability of capture. In September, although the rate of capture was higher in the abandoned orchard than in the maintained orchard (.195 voles/trap hour and .167 voles/trap hour, respectively), the mean density estimate was less in the abandoned orchard than in the maintained orchard (76 voles per hectare and 90 voles per hectare, respectively) and the mean probability of capture was higher in the abandoned orchard (.0339 and .0160, respectively). Since no other data were obtained for both orchards in any other month which would allow use of the Leslie Method no other comparable estimates of probability of capture are available to determine if the probability of capture was consistently higher in the abandoned orchard. Observations in the two areas indicate that there may have been a higher probability of capture in other months also. In November, January, and March the mean percent of uncovered ground both within and outside of the driplines of the apple trees was much higher in the abandoned orchard than in the maintained orchard (see Tables 24 through 31). At some individual trees in the abandoned orchard there was no green vegetation whatsoever within the driplines. Such conditions should necessitate further movements by the voles in the abandoned orchard to obtain food and such increased movement would mean a greater probability of encountering a trap, and possibly a greater likelihood of being lured to the apple bait. Surface burrows outside the driplines of the trees were seen frequently in November, January, and especially March in the abandoned orchard, but few were seen in the maintained orchard. If there was a higher probability of capture in the abandoned orchard in other months as well as in September, which seems to be the case, then densities were probably consistently lower in the abandoned orchard.

Mortality

Due to the assumptions and manipulations used in obtaining the survival equations determined by the method of Dapson (1971 and 1972) and the life tables derived from them (Appendix Tables I through VIII), these tables may not represent exact numerical values; however, relative differences between the two populations should be meaningful. The number of voles in the 1-30 day age class was estimated using reproductive data from the preceding trapping period, i.e., the number of fetuses from the previous trapping period were assumed to represent the number of young for the 1 - 30 day age class. This is not completely accurate, as voles were not trapped every month. For example, September reproductive data were used to estimate numbers of voles 1 - 30 days of age in November, whereas data actually should have come from October. This also assumes that all females that are pregnant have visible uterine swellings. Pregnant female pine voles probably have visible uterine swellings only after day 10 (Paul 1970), so there is an underestimation of the number of voles 1 - 30 days of age. However, this bias should be equal for both populations.

Also, the data are treated as dynamic data, which may not be completely valid. Actual dynamic data would be obtained by following a given group of voles until the last one was known to be dead, whereas these data are following the same population through time by sampling different segments of the population, not the same animals. Since an equal number of voles was not captured in each orchard during each trapping period (although numbers were very similar) over-representation of some age classes occurred. However, for any one month similar numbers were caught in each orchard. Because of this, any over-representation should be comparable in each population. Using age in days for each animal within each 60 day group implies that each 60 day group represent time specific data. Thus, for each segment to represent mortality, natality and immigration and emigration must be constant for that 60 day period. This is not a completely valid assumption, as natality is not constant for all 60 day periods and there is no way to determine what effects, if any, immigration and emigration has had on population structure. This further emphasizes that values obtained should not be interpreted as exact numerical values for survival, but that relative differences between the two populations should be meaningful. The data indicate higher mortality rates in the abandoned orchard. The mean monthly mortality was higher in the abandoned orchard than in the maintained orchard for all four cohorts. Mortality rate per 1000 per age class was consistently higher in the abandoned orchard in both old and young age classes. Mean life expectancies were consistently lower in the abandoned orchard. Generally, maximum ecological longevities in the two orchards were similar, which would seem to indicate extended survival of the few animals in both orchards who reach the older age classes. Mortality rates in both populations show a rapid turnover of voles. An average of 95 percent of animals born in both orchards were dead after twelve months.

Natality

The data collected indicate a higher natality in the maintained orchard than in the abandoned orchard. In the maintained orchard a higher percentage of adult females were pregnant, there were more fetuses per pregnant female, and there was a larger ratio of immature to adult voles. The abandoned orchard had been abandoned for three years and the natality was higher than that of the orchard studied by Cengel (1975) which had been abandoned for six years. This indicates that natality is decreasing gradually after orchards are abandoned. This fits well with the data of Paul (1970) which showed much lower densities in older abandoned orchards. The lower relative natality and higher mortality in the abandoned orchard very likely indicate a decreasing population density, whereas the higher natality and lower mortality in the maintained orchard would indicate a population decreasing less than that in the abandoned orchard, a stable population, or an increasing population. It is possible that the population in the abandoned orchard could simply be increasing at a lower rate than the maintained orchard. However, the net reproductive rates of the cohorts examined support the idea of a decreasing population in the abandoned orchard and a stable or increasing population in the maintained orchard. In the maintained orchard two of the cohorts had a net reproductive rate (R_o) greater than 1, and two had R_o's slightly less than 1, which would indicate a stable or possibly increasing population. None of the cohorts examined in the abandoned orchard had R_o's greater than 1, indicating a decreasing population.

Adrenal Weights

In some species stressful situations, such as increased social conflict or competition, have been considered to have increased ACTH output from the anterior pituitary increasing adrenal cortical function (Christian and Davis 1964). Higher adrenal cortical function increases circulating levels of adrenal androgens and these and ACTH itself are hypothesized to have a negative feedback on gonadotrophin releasing factors, thus decreasing FSH and LH secretion, shutting down reproduction and limiting populations intrinsically.

Adult male adrenal weights were significantly higher ($P < .001$) in the abandoned orchard than in the maintained orchard. Adrenal weights were higher in the abandoned orchard in the months of September, January, May and July. In three of these four months testes weights were higher in the abandoned orchard than in the maintained orchard. In two of these four months seminal vesicle weights and spermatozoan counts were higher in the abandoned orchard. Adrenal weight is not necessarily synonymous with adrenal cortical function (Christian and Davis 1964). Other factors such as age, sex, maturity, reproductive state and accumulation of lipids in the adrenal with cessation of ACTH stimulation can affect adrenal weights.

Adrenal weights of nonpregnant adult females were significantly higher ($P < .02$) in the abandoned orchard than in the maintained orchard. The only month where adrenal weights were higher in the abandoned orchard was November. The sample size for nonpregnant adult females in the maintained orchard at this time (3) was probably inadequate for a valid comparison between orchards. Cengel (1975) found no significant differences between adrenal weights in an abandoned and a maintained apple orchard. In the present study the paired ovarian weights and uterine weights of nonpregnant adult females were slightly higher in the abandoned orchard in November. The higher reproductive organ weights in both sexes in the abandoned orchard when adrenal weights are higher in the abandoned orchard do not represent increased adrenal cortical function or the effects of such increased adrenal cortical function hypothesized by Christian are not occurring.

Digestible Energy

The figures obtained for apparent digestible energy using the lignin tracer technique are considerably lower than most estimates of digestibility by small mammals reported in the literature. Grodzinski and Wunder (1975:184) gave an extensive listing of previous digestible energy and digestible dry matter work with small mammals. The average digestibility (digestible energy expressed as a percent of gross energy) in two orchards was 29 percent for the maintained and 23 percent for the abandoned orchard. Most work on digestible energy has been done in the laboratory using commercial laboratory food and the balance method. In such studies the average digestible energy or dry matter digestibility has ranged from 50 to 92 percent for small mammal herbivores. Much higher digestibility would be expected from concentrated foods than from more bulky natural foods, especially in dry periods or mature stages of plant growth. Drozdz (1968) fed several small mammal species natural foods in the laboratory and found that diets with low fiber content (shelled oats, hazel nuts, and beechmasts with 1.56 to 2.1 percent fiber) had 88 to 93 percent dry matter digested, while diets with high fiber content (green corn and herb layer vegetation with 15 to 33 percent fiber) had lower digestibility (74 - 80 percent). Work done in the field, with the ash tracer method with small mammal herbivores has given dry matter digestibility from 24.6 percent for the white-tailed prairie dog (Cynomys leucirus, Maxwell 1973) to 74.2 percent for the meadow vole (Microtus pennsylvanicus, Johnson and Gropper 1970). In laboratory comparisons (Kaufman et al. 1976) it was found that the ash tracer technique gave lower digestible energy values than did the balance method (average for balance method was 82 percent while the ash tracer method gave an average digestible energy of 62 percent). They found that 53.4 percent of ash was digested. Therefore, depending on the mineral balance of animals used, estimates may be inaccurate. For example, a pregnant female would be assimilating more minerals for use in production of young and digestible energy estimates would be lower.

The high variability and low values obtained for digestible energy by the lignin tracer technique in the present study suggests some possible error in the technique. Some variability within orchards was expected, especially within the abandoned orchard where the variability in plant species available to voles in different areas was quite high. There are several possibilities that might cause inaccuracies in the technique. This technique makes the assumption that lignin is indigestible, that the same material is represented in the food and feces, that lignin is passed through the digestive tract at the same rate as other cell material, and that lignin recovery from stomach contents and feces is equal.

Although lignin has been thought to be slightly digested in some instances in ruminant animals (Kane et al. 1951; Ely et al. 1953), it should be indigestible in the monogastric pine vole. If lignin is partially digestible by the pine vole, then the values for digestible energy obtained would be underestimated, but would still be valuable for relative comparisons. Likewise, if the rate of passage of lignin is different than other cell material, the determined values for digestible energy will not be accurate, but would be valid for relative comparisons. Different recovery rates from stomach contents and feces would again bias values, but would be valid for comparisons. The remaining assumptions that the same material is represented in the stomach contents and feces may present problems. Differential feeding on above or below ground portions of plants influenced by time of day and/or temperature, if it does occur, could lead to bias, as some plant parts contain more or less lignin than others. Coprophagy in the pine vole (Boyette 1966:35,50,133), depending on the extent to which it is practiced, could also lead to errors. If a vole were captured after reingesting cecal feces, the lignin content of the stomach contents would be higher (depending on amount ingested), giving a lower digestible energy value. If this were the case, it is probably equally likely that it happened in both orchards, and digestible energy values obtained should still be valid for relative comparisons. A laboratory comparison of the lignin tracer technique and balance method using natural foods is needed to help determine the accuracy of the technique.

Also unexpected was the very high value obtained for digestible energy in the maintained orchard in January. Digestible energies are generally considered to decrease as plants mature and to continue to decrease into winter when plants are relatively dormant. A study on pine vole food habits (Cengel 1975) indicated that root consumption increased sharply in January. This was thought to take place due to lower availability or suitability of other material. No digestibility studies are available concerning the digestible energy of roots and rhizomes of grasses and forbs by small mammals in winter. Golley (1961) found that highest gross energy values for below ground plant parts occurred in fall and winter. He thought that this was due to storage of energy in roots, tubers and rhizomes. Such energy is in the form of starch and sucrose (Garrison 1971:271). Presumably such stored energy would present a highly digestible food source which might account for the high digestible energies in the maintained orchard in January. It is likely that this energy storage would be greater in the maintained orchard where production due to fertilization would be higher. This change in diet may represent preference rather than lack of availability of above ground plant parts.

The energy intake of an animal is a function not only of digestibility but also of consumption. A lower digestible energy does not necessarily mean lower energy intake, as up to a point, animals can make up for lower digestibility by consuming more if extra food is available. However, as consumption increases, rate of passage also increases and thus, the percent of material digested decreases even more (Brody 1945). Also, highly indigestible food usually causes a reduction in consumption.

Work with Sigmodon hispidus (Gentry et al. 1975) showed a linear relationship between dry weight of stomach contents and food consumed over a four hour period. By trapping animals throughout a 24 hour cycle, daily consumption could be estimated. The mean dry weight of stomach contents of the pine voles captured, although representing feeding activities for only 6 to 8 hours of the 24 hour cycle, should give a rough index to the relative consumptions of the two populations. Seasonally, higher periods of consumption might come at different times of day and thus, since voles were captured during only part of the 24 hour cycle, may not be valid for relative comparisons between months. Both digestible energy ($P < .09$) values obtained, and mean dry weight of stomach contents ($P < .02$), which can be used as a rough index of consumption within months, were significantly higher in the maintained orchard than in the abandoned orchard. This indicates that voles in the maintained orchard were on a higher nutritional plane than voles in the abandoned orchard.

To prove that this difference in nutrition is a factor in the difference in natality between the two populations would require establishing that voles in the abandoned orchard were not obtaining adequate energy intake to meet the increased requirements of pregnancy and lactation in the periods when natality was lower than in the maintained orchard. Theoretical energy requirements for different seasons and physiological condition for the pine vole can be calculated from data available in the literature. Pearson (1947) found that the pine vole over a twenty-four hour period used on the average 4.3 cm^3 of oxygen per gram of body weight per hour. Since one cm^3 of oxygen represents approximately .0048 kcal/hr then the ADMR (average daily metabolic rate) is .4953 kcal/gm/day. From this figure daily energy budget (DEB) can be estimated by the equation below (from Grodzinski and Wunder 1975:198).

$$DEB = ADMR + TC\ (t_k - t_a) \text{ where:}$$

f = fraction of day spent outside of the nest

TC = thermal conductance

t_k = lower critical temperature (assumed to be 20 C)

t_a = ambient temperature.

Gettle (1975) found that at any one time 50 percent of his radiotagged pine voles were active at any one 15 minute interval; therefore, f will be taken as .5. The thermal conductance can be estimated from the following formula by Hart (1971):

Thermal conductance = $0.1094w^{-.499}$ with thermal conductance in kcal/gm/day C and w in grams.

Sadlier (1972) found, overa twelve month period in his study on energetics of _Peromyscus maniculatus_, that the mean monthly soil temperatures at 20 cm, which can be taken as burrow temperature (Hayward 1965), were the same as the mean monthly air temperature for the area, except when temperatures were below 0 C. When this occurred, burrow temperatures were above the mean monthly temperatures. Mean monthly temperatures recorded at Woodrum Field, Roanoke, Virginia (which is within ten miles of the study areas) can be used then as estimates of mean temperatures in pine vole burrows. Using these data, a seasonal DEB can be calculated. Gestation and lactation in two small mammal species have been found to cause an average increase in energy needs of 24 and 92 percent, respectively (Kaczmarski, 1966; Migula 1969). By using these correction factors for pregnancy and lactation, then a DEB by season and physiological state can be calculated. These data are presented in Table 32.

Without accurate measures of consumption and digestible energy there is no way of determining when energy requirements for pregnancy and lactation are not met in the two orchards. The data presented for requirements, however, gives some insight into critical periods for meeting pregnancy and lactation energy requirements. The largest increase in energy requirements due to thermoregulation between any two consecutive trapping perids was from September to November, when theoretical energy requirements would increase 27

Table 32. Theoretical energy requirements by season and physiological state for pine voles near Daleville, Virginia between September 1974 and July 1975.

	Daily energy budget (for 24 gm pine vole)		
Month	Nonpregnant female kcal/day	Pregnant female kcal/day	Lactating female kcal/day
September	11.9	14.7	22.8
November	15.1	18.7	29.0
January	16.5	20.4	31.6
March	15.1	18.7	29.0
May	12.2	15.1	23.3
July	11.9	14.7	22.8

percent due to temperature changes. This large increase in energy requirements coincided with the large drop in natality in the abandoned orchard and came between the lowest digestible energy estimates (September) and the next to lowest (November). There was also a large decrease in fat content of females in the abandoned orchard during this period. In the maintained orchard the digestible energies were also at their lowest level of the year in September and November; however, for September the digestible energy value for the maintained orchard was almost twice that of the abandoned orchard. Relative consumption (using mean dry weight of stomach contents as an index) was greater in the maintained orchard for females for both September and November.

The percent ground cover also went down more drastically in the abandoned orchard from September to November (from 0 to 83 percent uncovered ground within the driplines) relative to the maintained orchard (from 0 to 47 percent uncovered ground within the driplines. In some instances 98 percent of the ground beneath the driplines of the trees in the abandoned orchard was bare of any green vegetation. This would drastically reduce availability and presumably, consumption. It would also mean increased activity on the part of voles in the abandoned orchard to obtain food outside the driplines of the trees. A twenty percent increase in activity would, according to the equation for DEB, increase energy needs by almost ten percent. Although cause and effect cannot be shown, it seems likely that in the abandoned orchard the low digestible energies from the period of September through November, lower relative consumption, increased energy needs for foraging activity, and the 27 percent increase in energy requirements for thermoregulation did not allow sufficient net energy for pregnancy and lactation into November. In November the immature to adult ratio was high in the abandoned orchard (19:81) indicating successful production of young through lactation and weaning. The females pregnant in September would have faced the high energy demands of lactation in addition to the energy cost of increased activity, thermoregulation, a low food consumption and low digestible energy of food consumed in late September and October. This would very likely be a time when energy intake would be less than energy requirements. The drastic declines in fat content in females in the abandoned orchard at this time support this hypothesis. If circulating levels of LH are decreased due to an inadequate energy intake, resulting in a decline in reproduction, (as indicated by the work of Howland (1972) with lab rats and Kirkpatrick and Merson (1976) with *Peromyscus leucopus*), this would explain the reduction in percent females pregnant from 80 percent pregnant in September to 35 percent pregnant in November.

Females in the maintained orchard met the energy requirements for pregnancy and lactation through November, as the immature to adult ratio remained high in November (23:77). Fat content dropped but not to the extent that it dropped in the abandoned orchard. The higher relative digestible energies and consumption during September and November, in the maintained orchard, allowed sufficient energy intake to maintain pregnancy in 83 percent of the adult females.

The abandoned orchard studied by Cengel (1975) and Estep (1975) had a similar decrease in vole fat content and a drastic decrease in reproduction by November with a subsequent increase in fat content in January. In the maintained orchard they studied, female fat content also decreased from September to November but not as sharply as in the present study. The percent of adult females pregnant in that study, unlike that of the present study, decreased from September to November (from 75 to 46 percent). This would indicate that females in the maintained orchard in the previous study had experienced an energy restriction between September and November although not as severe a restriction as the females in the abandoned orchard experienced. Such a restriction could have been due to colder fall temperatures in the year of their study (no weather data were available) and/or a lower digestible energy in their maintained orchard relative to the maintained orchard of this present study. Such differences could be associated with such factors as different species compositions of the orchards, amounts of rainfall, frequency of mowing in the orchards and/or stage of succession.

Male testes weights, seminal vesicles weights, and spermatozoa per mg of testes weight generally remained high or increased from September through January, in both orchards. They then decreased rather drastically in March, especially in the abandoned orchard. Male fat contents in both orchards generally followed the same trend as the fat contents of females in the respective orchards but did not decrease as greatly. Consumption was generally lower than for females. Although no estimates are available in the literature for the increase in energy requirements for males due to reproductive activity, these requirements were probably lower than for females and the males could meet the extra energy requirements longer into the year than the females.

Digestible energy remained constant from November to January in the abandoned orchard. Relative consumption was still lower in the abandoned orchard than in the maintained orchard. Extra energy requirements for thermoregulation increased by only 9 percent from November. The immature to adult ratio for January (8:92) was high relative to the percent pregnant females for November indicating successful pregnancy and lactation. Fat content increased in females in the abandoned orchard and the same percent of adult females were pregnant from November to January. This indicates that females pregnant in November were capable of supporting pregnancy and lactation and further pregnancy into January on the energy levels obtainable.

In the maintained orchard digestible energy increased greatly from November to January, relative consumption for females was higher than in the abandoned orchard and fat content increased more. The immature to adult ratio (20:80) was high indicating that pregnancy and lactation were successful. However the percent pregnant females dropped to 50 percent in January. This is difficult to explain with respect to energy intake, as in the abandoned orchard on a lower energy intake, the same percent of females were pregnant in January as in November, while in the maintained orchard, with higher digestible energy and consumption, the percent of pregnant females dropped from November to January.

It would be ecologically naive to expect nutritional intake (or any other single factor) to be the sole factor influencing reproduction. Although no work has been done on the effect of photoperiod on reproduction in pine voles, some work has been done with other microtines. Studies on the effect of photoperiod on reproduction in microtines have indicated that changing daylength affects reproduction (Baker and Ranson 1932, Lecyk 1962 and 1963, Pinter and Negus 1965, and Thibault et al. 1966). Generally, increasing light seems to have a positive effect on reproduction while decreasing light seems to have a negative effect with the degree of these effects differing from study to study. There is some contradiction, however, as Marshall and Wilkinson (1956) found no significant differences in reproduction of voles (<u>Microtus orcadensis</u>) on long and short daylength when abundant food was given. Pinter and Negus (1965) found that both photoperiod and feeding of supplementary sprouted wheat had effects on reproduction in <u>Microtus montanus</u>. A total of 140 pairs of voles were used in an experiment which lasted 18 weeks. One group was kept on 18 hours of artificial light daily and another group was kept on 6 hours of artificial light daily. Within each group half of the pairs received a dietary supplement of sprouted wheat every three days and the other half received the supplement every 15 days. Diet and photoperiod were found to be interactive in their influence on reproduction. The group on 18 hour light and diet supplement every three days produced the most young. The group on six hour light and the diet supplement every 15 days produced the least young. The authors postulated 'plant estrogens' as the cause of the increased reproduction. However the sprouted wheat would have a high content of vitamins and protein due to germination and thus better nutrition and/or increased appetite could as well have been the factor involved.

Thus, while nutritional intake alone does not seem to explain the changes in natality for the two orchards from November to January, an interactive effect of energy balance (which would involve temperature, consumption, activity, and digestible energy), and effect of photoperiod could explain the discrepancies. In the maintained orchard, even though energy intake was high due to higher relative consumption and higher digestible energy, the energy intake may not have been sufficient at this time to override the effects of short daylength and to keep a higher percentage of females in a reproductive state. Myers and Poole (1962) postulated a similar interaction of nutrition, temperature, and photoperiod to explain the large differences in duration and magnitude of the breeding season of the European rabbit (Oryctolagus cuniculus) in different parts of the world.

In the abandoned orchard in March no females were pregnant, no immatures were captured, ovarian weights were down, and male testes weights, seminal vesicles weights, and spermatozoan counts were at their lowest points. Digestible energy was the same as in January, and consumption continued below that in the maintained orchard.

Fat content dropped to its lowest point in males, and fat content in females dropped from levels in January, indicating less ability to keep energy intake above maintenance requirements. Fat content of females in the abandoned orchard was higher than that of females in the maintained orchard. The immature to adult ratio indicates that there was no successful lactation past February, and also no animals less than 79 days of age were captured, indicating no survival of young after January. Females in the abandoned orchard, then, did not have extra energy requirements for gestation and lactation after February and were able to retain higher fat content than females in the maintained orchard.

In the maintained orchard in March digestible energy declined, relative consumption was still higher, and female fat content dropped rather drastically. The immature to adult ratio dropped more than expected, indicating high juvenile mortality, probably due to inability to meet lactation requirements. The percent of females pregnant also dropped to 13 percent at this time.

In the abandoned orchard from March to May the digestible energy had increased slightly, relative consumption was still lower, energy requirements for thermoregulation decreased 19 percent from March, and fat content of females remained constant. The percent of females pregnant increased from 0 to 46 percent, but no immatures were captured in May, indicating no successful gestation and lactation through April. Testes and seminal vesicles weights increased. This was the only period when relative consumption of males was higher in the abandoned orchard than in the maintained orchard. Digestible energy estimates were also higher in the abandoned orchard at this time, and male fat contents were higher in the abandoned orchard.

In the maintained orchard from March to May digestible energy continued a decreasing trend and relative consumption was still higher than in females in the abandoned orchard. Fat content of females increased and the percent of females pregnant increased to 53 percent. Some immature voles were present in the population (immature to adult ratio was 7:93), indicating some successful gestation and lactation during April, and thus voles were recruited throughout the year into the population in the maintained orchard. Male testes weights decreased, seminal vesicles weights were increasing only slightly, while spermatozoa per mg of testes weight went up from March to May in the maintained orchard. Fat content in males decreased from March to May in the maintained orchard while during this period in the abandoned orchard fat content of males increased. This occurred in the only period where digestible energy and relative consumption of voles in the maintained orchard was lower than in the abandoned orchard. Bailey (1969) found that forbs in their early growth stages were highly digestible foods for young cottontail rabbits. Cengel's study (1975) of pine vole food habits in a maintained and abandoned orchard indicated that voles were selecting forbs over grasses in spring when forbs are in their early, more digestible, growth stages. The percent ground cover of succulent forbs in the abandoned orchard was 2 percent, while in the maintained orchard it was only 1 percent. Also at this time ragweed was in its early growth stage when it is low-growing and succulent. This species made up 4 percent of the ground cover in the abandoned orchard, but was not present in the maintained orchard. Thus, greater availability of forbs in the abandoned orchard in May, when they are in highly digestible stages of growth, could account for the higher digestible energy in the abandoned orchard at this time.

In July the reproduction in both orchards was high. The percent females pregnant and the immature to adult ratio were essentially equal in both orchards. There was adequate energy intake in both orchards in this period to support pregnancy and lactation.

SUMMARY AND CONCLUSIONS

Higher densities of pine voles were indicated in the maintained orchard than in the abandoned orchard in the one month where density estimates by the Leslie method were obtained for both orchards. There was higher natality and lower mortality in the maintained orchard. Net reproductive rates (R_o's) were greater than 1 in two of the four cohorts examined in the maintained orchard, while the other two cohorts had R_o's less than 1. In the abandoned orchard R_o's were less than 1 for all cohorts examined. This indicated that the population in the abandoned orchard was decreasing while the population in the maintained orchard was stable or increasing.

The digestible energy of the food consumed by the voles in the maintained orchard was significantly higher ($P < .09$) than that of the food consumed by voles in the abandoned orchard. The mean dry weight of the stomach contents of adult voles, which was used as an index of consumption, was significantly higher ($P < .02$) in the maintained orchard than in the abandoned orchard in all months. The lowest digestible energy values for both orchards occurred in September and November. However the digestible energy value for the maintained orchard in September was twice that of the abandoned orchard. The females in the maintained orchard had greater stomach content weights than females in the abandoned orchard in all months. The largest difference between orchards in apparent consumption of females was found in September. The greatest increase in energy requirements for thermoregulation (27 percent) also was estimated to occur between September and November. Ground cover decreased more drastically in the abandoned orchard than in the maintained orchard at this time. This indicated that voles in the abandoned orchard would expend more energy in activity obtaining food than voles in the maintained orchard. The large increase in energy requirements, the lower digestible energies and the lower apparent consumption rates in the abandoned orchard from September to November coincide with the drastic decline in reproduction and sharp declines in female fat content in the abandoned orchard. Although cause and effect cannot be shown, it seems likely that the female voles in the abandoned orchard underwent a severe energy restriction at this time. It is postulated that such an energy restriction would lower circulating levels of LH which would result in a decline in reproduction in the voles. In the maintained orchard during this period the higher relative digestible energies and consumption allowed sufficient energy intake for reproduction to remain high.

From November to January the energy intake in the maintained orchard was much greater than the energy intake in the abandoned orchard. However, the percent of females pregnant dropped in the maintained orchard while it remained constant in the abandoned orchard. It is postulated that energy intake and photoperiod have an interactive effect on reproduction in the pine vole and that the higher energy intake in the maintained orchard in this period was not sufficient to override the effect of decreasing daylength and keep a high proportion of females in a reproductive state.

The data obtained in this study suggest that the mowing done in maintained orchards provides a very digestible food source for voles into summer and fall which allows sufficient energy intake for reproduction late into the year. In abandoned orchards, which are not mowed, plant composition shifts from grasses to forbs. Forbs, while they are highly digestible in their early growth stages, become less digestible earlier in the growing season than grasses. The forages in the abandoned orchards, since they are not reverted to their earlier more digestible growth stages by mowing, lose much of their digestibility. This low digestibility decreases energy intake in the voles in the abandoned orchard and reproduction ceases earlier in the year.

RECOMMENDATIONS

Better data on the digestible energy of food consumed by voles, the amount of food consumed and energy requirements are needed to better understand the effect of energy intake on reproduction. A laboratory comparison of the lignin tracer technique and the balance technique for determining digestibility of natural foods is needed to determine the accuracy of the lignin tracer technique. Once the accuracy of the lignin tracer technique is determined, the amount of food consumed by voles in the field daily can be estimated from daily fecal production. An estimate of daily fecal production can be obtained by using livetraps which record time of capture. By capturing voles throughout a 24 hour period and weighing the feces they produce while in the traps, daily fecal production and thus consumption can be estimated. Determinations of seasonal daily activity patterns and burrow temperatures on the study areas would refine theoretical energy requirements.

The interaction of energy restriction and photoperiod on reproduction in the pine vole can best be studied in the laboratory. Energy restriction, which was postulated to cause a decrease in circulating levels of reproductive hormones which in turn results in a cessation of reproduction, occurs when energy intake is less than energy requirements. By varying energy intake, energy requirements (by changes in temperatures), and photoperiod, the effects of energy restriction and photoperiod on reproduction (as measured by the number of young produced) should be more clearly seen. Laboratory experiments should also be done to determine whether an increase in energy intake and/or daylength is necessary to bring voles back into a reproductive condition after cessation of breeding in fall or winter.

If the data and interpretations of this study are correct, it would appear that allowing the vegetation to mature in maintained orchards, by not mowing in the summer months, would decrease the digestible energy available to pine voles. This reduction of digestible energy would greatly reduce the energy intake of pine voles which would cause an earlier cessation of breeding in the number of voles the orchards would have to support over winter. Planting of winter hardy plant species which provide rhizomes, roots and tubers, a preferred food source, should decrease the necessity of pine voles using apple tree roots as a food source in winter. Habitat management such as this may not completely eliminate the need for toxicants to reduce pine vole populations even further in the early winter months. However, it should reduce the need for their application considerably.

LITERATURE CITED

A.O.A.C. 1960. Official methods of analysis. 9th ed. Assoc. of Official Agric. Chemists. Washington, D.C. 832pp.

Bailey, J. A. 1969. Exploratory study of nutrition of young cottontails. J. Wildl. Manage. 33(2):346-353.

Baker, J. R. and R. M. Ranson. 1932. Factors affecting the breeding of the field mouse (Microtus argestis). Part I light. Roy. Soc. London Proc. 110B:313-322 (as cited in Sadlier 1969).

Barr, A. J. and J. H. Goodnight. 1972. A user's guide to the Statistical Analysis System. Student Supply Stores, North Carolina State Univ. 260pp.

Batzli, G. O. 1968. Dispersion patterns of mice in California annual grassland. J. Mammal. 49(2):239-250.

______________ and F. A. Pitelka. 1970. Influence of meadow mouse populations on California grasslands. Ecol. 51(4):1027-1039.

Bendall, J. F. 1959. Food as a control of a population of white footed mice, Peromyscus leucopus noveboracensis (Fischer). Can. J. Zool. 37(2):173-209.

Benton, A. H. 1955. Observations on the life history of the northern pine mouse. J. Mammal. 36(1):52-62.

Bodenheimer, F. S. 1949. Problems of vole populations in the Middle-east: Report on the population dynamics of the LeVant vole (Microtus guentheri D. et A.). Res. Counc. Israel. Jerusalem. 77pp. (as cited in Sadlier 1969).

Boyette, J. G. 1966. A behavioral study of the pine mouse, Pitymys pinetorum pinetorum (LeConte). Ph.D. Thesis. North Carolina State Univ. 142pp.

Brody, S. 1945. Bioenergetics and growth. Rheinhold Publishing Co. Inc., New York. 1023pp.

Burt, W. E. 1940. Territorial behavior and populations of some small mammals in southern Michigan. Misc. Publ. Mus. Zool. Univ. Michigan (as cited by Goertz 1971).

Byers, R. E. 1974. Pine mouse control in apple orchards. The Mountaineer Grower 335:3-13.

Campbell, R. S. and J. T. Cassidy. 1954. Moisture and protein in forage on Louisiana forest ranges. J. Range Manage. 7(1):41-42.

Cengel, J. C. 1975. Seasonal comparison of food habit patterns and reproductive attainment of the pine vole, in two northern Virginia orchards. M.S. Thesis. Virginia Polytechnic Institute and State University. 60pp.

Chitty, D., D. Pimentel and C. J. Krebs. 1968. Food supply of over-wintered voles. J. Anim. Ecol. 37(1):113-120.

Christian, J. J. and D. E. Davis. 1964. Endocrines, behavior and population. Science 146:1550-1560.

Church, D. C. 1985. Digestive physiology and nutrition of ruminants. Published by author. Corvalis, Oregon. 350pp.

______________ and W. G. Pond. 1974. Basic animal nutrition and feeding. Published by authors. Corvalis, Oregon. 300pp.

Cook, C. W. and L. E. Harris. 1950. The nutritive value of range forage as affected by vegetation type, site, and stage of maturity. Utah Agr. Exp. Sta. Bull. 344 (as cited in Heady 1964).

______________ and ______________. 1951. A comparison of the lignin ratio technique and the chromagen method of determining digestibility and forage composition of desert range plants by sheep. J. Anim. Sci. 10(3):565-573.

Dapson, R. W. 1971. Quantitative comparison of populations with different age structures. Ann. Zool. Fennici 8(1):75-79.

______________. 1972. Age structure of six populations of old field mice, Peromyscus polionotus. Res. Popul. Ecol. 13(2): 161-169.

Drozdz, A. 1968. Digestibility and assimilation of natural foods in small rodents. Acta Theriol. 13(21):367-389.

Dunaway, P. B. and S. V. Kaye. 1963. Effects of ionizing radiation on small mammal populations on the White Oak Lake Bed. Pages 333-338 in V. Schultz and A. W. Klement eds. Proc. First Nat. Symp. Radioecology. Radioecology Rheinhold Publishing Co. Inc., New York. AIBS, Wash., D.C.

Ely, R. E., E. A. Kane, W. C. Jacobson and L. A. Moore. 1953. Studies on the composition of lignin isolated from orchard grass hay cut at four stages of maturity and of corresponding feces. J. Dairy Sci. 36(4):346-355.

Estep, J. E. 1975. Seasonal variation in body fat and food habits of pine voles from two Virginia orchards. M.S. Thesis. Virginia Polytechnic Institute and State University. 72pp.

Flowerdew, J. R. 1972. The effect of supplemetary feeding on a population of wood mice (Apodemus sylvaticus). J. Anim. Ecol. 41(3):553-556.

______________. 1973. The effect of natural and artificial changes in food supply on breeding in woodland mice and voles. J. Reprod. Fert., Suppl. 19:259-269.

Fordham, R. A. 1971. Field populations of deermice with supplemental food. Ecol. 52(1):138-146.

Garbough, F. E. 1944. Control of destructive mice. U.S. Dept. Int. Fish and Wildl. Serv. Conserv. Bull. 36. 37pp. (as cited in LaVoie and Tietjen 1971).

Garrison, G. A. 1971. Carbohydrate reserves and responses to use. Pages 271-278 in C. M. McKell, J. P. Blaisdell and J. R. Goodin eds. Wildland shrubs; their biology and utilization. U.S.D.A. Forest Service. General Technical Report INT-1. 494pp.

Gentry Instrument Company. 1969. Assembly and operating instructions for the Phillipson oxygen microbomb calorimeter. Aiken, S.C. 5pp.

Gentry, J. B. 1968. Dynamics of an enclosed population of pine mice, Microtus pinetorum. Res. Popul. Ecol. 10(1):21-30.

______________, L. A. Briese, D. W. Kaufman, M. H. Smith and J. G. Weiner. 1975. Elemental flow and standing crop for small mammal populations. Pages 205-221 in F. B. Golley, K. Petrusewicz and L. Ryszkowski eds. Small mammals: their productivity and population dynamics. Cambridge Univ. Press. London. 451pp.

Gettle, A. S. 1975. Activities and movements of pine voles (Microtus pinetorum) in Pennsylvania. M.S. Thesis. Pennsylvania State Univ., University Park, Pa. 66pp.

Goertz, J. W. 1971. An ecological study of Microtus pinetorum in Oklahoma. Am. Midl. Natur. 86(1):1-12.

Golley, F. B. 1961. Energy values of ecological materials. Ecol. 42(3):581-584.

______________. 1967. Methods of measuring secondary productivity in terrestial vertebrate populations. Pages 99-124 in K. Petrusewicz ed. Secondary productivity of terrestial ecosystems. Vol. I. Panstwowe Wydawnictwo Naukowe, Warsaw. 379pp.

_______________, K. Petrusewicz and L. Ryszkowski (eds.) 1975. Small mammals: their productivity and population dynamics. Cambridge Univ. Press. London. 451pp.

Gourley, R. S. and F. J. Jannett. 1975. Pine and montane vole age estimates from eye lens weights. J. Wildl. Manage. 39(3): 550-556.

_______________ and M. E. Richmond. 1972. Vole populations in New York orchards. Pages 61-71 in J. E. Forbes ed. Proc. New York Pine Mouse Symp. Bur. Sport Fish. and Wildl. New York. 75pp.

Grodzinski, W. and B. A. Wunder. 1975. Ecological energetics of small mammals. Pages 173-204 in F. B. Golley, K. Petrusewicz and L. Ryszkowski eds. Small mammals: their productivity and population dynamics. Cambridge Univ. Press. London. 451pp.

Hairston, N. C., F. E. Smith and L. B. Slobodkin. 1960. Community structure, population control and competition. Am. Natur. 94(879):421-425.

Hamilton, W. J. 1935. Field mouse and rabbit control in New York orchards. Cornell Ext. Bull. 338. 23pp. (as cited in LaVoie and Tietjen 1971).

_______________. 1938. Life history notes on the northern pine vole. J. Mammal. 19(2):163-170.

Hansson, L. 1971. Small rodent food, feeding and population dynamics; a comparison between granivorous and herbivorous species in Scandinavia. Oikos 22(2):183-198.

Harris, L. E. 1971. Physiological problems in animal use of shrubs as forage. Pages 319-330 in C. M. McKell, J. P. Blaisdell and J. R. Goodin eds. Wildland shrubs; their biology and utilization. U.S.D.A. Forest Service. General Technical Report INT-1. 494pp.

Hart, J. S. 1971. Rodents. Pages 1-149 in G. C. Whitton ed. Comparative physiology of thermoregulation Vol. II: mammals. Academic Press. New York (as cited in Grodzinski and Wunder 1975).

Hayward, J. S. 1965. Microclimatic temperature and its adaptive significance in six geographic races of Peromyscus. Can. J. Zool. 43(2):341-350.

Heady, H. F. 1964. Palatability of herbage and animal preference. J. Range Manage. 17(1):76-82.

Hoffman, R. A. 1958. The role of reproduction and mortality in population fluctuations of voles (Microtus). Ecol. Monogr. 28(1):79-109.

Horsfall, F. J. 1963. Observations on fluctuating pregnancy rate of pine mice and mouse feed potential in Virginia orchards. Proc. Am. Soc. Hort. Sci. 83:276-279.

______________. 1972. Chlorophacenone and herbage as potentials for pine mouse damage control. Pages 32-46 in J. E. Forbes ed. Proc. New York Pine Mouse Symp. Bur. Sport Fish. and Wildl., New York. 75pp.

______________, R. E. Webb and R. E. Byers. 1973. How to successfully meet pine voles on their terms. Virginia Fruit 61(1): 3-15.

Howland, B.E. 1972. Effect of restricted feed intake on LH levels in female rats. J. Anim. Sci. 34(3):445-447.

Jameson, E. W. 1953. Reproduction of deermice (Peromyscus maniculatus and Peromyscus boylei) in Sierra Nevada, California. J. Mammal. 34(1):44-58.

______________. 1955. Some factors affecting fluctuations of Microtus and Peromyscus. J. Mammal. 36(2):206-209.

Johnson, D. R. and K. L. Groepper. 1970. Bioenergetics of North Plains rodents. Am. Midl. Natur. 84(2):537-548.

Kaczmarski, F. 1966. Bioemergetics of pregnancy and lactation in the bank vole. Acta Theriol. 11(19):409-417.

Kane, E. A., R. E. Ely, W. C. Jacobson and L. A. Moore. 1951. Comparative digestion studies on orchard grass. J. Dairy Sci. 34(6):492.

______________, W. C. Jacobson, R. E. Ely and ______________. 1953. A comparison of various digestion trial techniques with dairy cattle. J. Dairy Sci. 36(4):325-333.

Kaufman, D. W., M. J. O'Farrell, G. A. Kaufman and S. E. Fuller. 1976. Digestibility and elemental assimilation in cotton rats. Acta Theriol. 21(9):147-156.

Kennicott, R. 1857. The quadrupeds of Illinois injurious and beneficial to the farmer. U.S. Pat. Office Dept. Agric. 72-107 (as cited in Hamilton 1938).

Kirkpatrick, R. L. and M. H. Merson. 1976. Influence of varying degrees of nutritional restriction on vaginal estrus and reproductive organs of whitefooted mice. Va. J. Sci. 27(2):46.

______________ and G. L. Valentine. 1970. Reproduction in captive pine voles, Microtus pinetorum. J. Mammal. 51(4):779-785.

Krebs, C. J. and K. T. Delong. 1965. A Microtus population with supplemental food. J. Mammal. 46(4):566-573.

LaVoie, G. K. and H. P. Tietjen. 1971. Pine vole research: a problem analysis. Denver Wildl. Res. Center. 17pp.

Lecyk, M. 1962. The effect of the length of daylight on reproduction in the field vole Microtus arvalis (Pall.). Zool. Pol. 12:198-221 (as cited in Sadlier 1969).

______________. 1963. The effect of short daylength on sexual maturation in young individuals of the vole Microtus arvalis (Pall.). Zool. Pol. 13:77-86 (as cited in Sadlier 1969).

Marshall, A. J. and O. Wilkinson. 1956. Reproduction in the Orkney vole (Microtus orcadensis) under a six hour daylength and other conditions. Proc. Zool. Soc. Lond. 126:391-395 (as cited in Sadlier 1969).

Maxwell, M. H. 1973. Rodent ecology and pronghorn relations in the Great Divide Basin of Wyoming. Ph.D. Thesis. Univ. of Wyoming (as cited by Grodzinski and Wunder 1975).

Migula, P. 1969. Bioenergetics of pregnancy and lactation in the European common vole. Acta Theriol. 14(13):167-179.

Miller, M. A. 1946. Reproductive rates and cycles in the pocket gopher. J. Mammal. 27(4):335-338.

Miller, D. H. and L. L. Getz. 1969. Life history notes on Microtus pinetorum in central Connecticut. J. Mammal. 50(4):777-784.

Morrison, F. B. 1956. Feeds and feeding. A handbook for the student and stockman. 22nd ed. Morrison Publishing Co., Ithaca. 1165pp.

Morrison, I. M. 1972. A semimicro method for the determination of lignin and its use in predicting the digestibility of forage crops. J. Sci. Fd. Agric. 23(4):455-463.

Murdoch, W. W. 1966. Community structure, population control and competition - a critique. Am. Natur. 100(912):455-463.

Myers, K. and W. E. Poole. 1962. A study of the biology of the wild rabbit (Oryctolagus cuniculas L.) in confined populations. III. Reproduction. Aust. J. Zool. 10(2):225-267.

Overton, W. S. 1969. Estimating the numbers of animals in wildlife populations. Pages 403-455 in R. H. Giles ed. Wildlife Management Techniques, 3rd ed. The Wildlife Society, Wash., D.C. 633pp.

Paul, J. R. 1970. Observations on the ecology, populations and reproductive biology of the pine vole, Microtus pinetorum, in North Carolina. Ill. State Mus., Repts. of Invest. No. 20:1-28.

Pearson, O. P. 1947. The rate of metabolism of some small mammals. Ecol. 28(2):127-145.

Phillipson, J. 1964. A minature bomb calorimeter for small biological samples. Oikos 15(1):130-139.

Pinter, A. J. and N. C. Negus. 1965. Effects of nutrition and photoperiod on reproductive physiology of Microtus montanus. Am. J. Physiol. 208(4):633-638.

Prus, T. 1975. Measurement of caloric value using Phillipson microbomb calorimeter. Pages 149-160 in W. Grodzinski, R. Z. Klekowski and A. Duncan eds. Methods for Ecological Energetics, IBP Handbook No. 24. Blackwell Scientific Publications, London. 367pp.

Reid, J. T. 1962. Indicator methods in herbage quality studies. Pages 45-56 in G. O. Mott, H. L. Lucas, W. K. Kennedy, J. T. Reid, M. L. Peterson and D. E. Cloud eds. Pasture and Range Research Techniques. Comstock Publishing Associates, New York. 242pp.

Rhoades, S. N. 1903. The mammals of Pennsylvania and New Jersey. Published by author. Philadelphia. 266pp. (as cited in Horsfall 1963).

Sadlier, R. M. F. S. 1969. The ecology of reproduction in wild and domestic animals. Methuen and Co., London. 321pp.

_______________, K. D. Casperson and J. Harling. 1972. Intake and requirements of energy and protein for the breeding of wild deermice, Peromyscus maniculatus. J. Reprod. Fert., Suppl. 19:237-252.

Shenk, J. S., F. C. Elliot and J. W. Thomas. 1970. Meadow vole nutrition studies with semi-synthetic diet. J. Nutr. 100(12): 1437-1446.

Smith, M. H. 1971. Food as a limiting factor in the population ecology of Peromyscus polionotus. Ann. Zool. Fennici 8(1): 109-112.

Smyth, M. 1966. Winter breeding in woodland mice, Apodemus sylvaticus, and voles, Clethrionomys glareolus and Microtus argestis, near Oxford. J. Anim. Ecol. 35(3):471-485.

Stein, G. H. W. 1953. Uber Umweltabhangihkeiten bei der Vermehrung der Feldmaus, Microtus arvalis. Populations anayltische Untersuchungen an deutschen kleinen Saugetieren IV. Zool. Jb. (Abst. Syst.) 81:527-547 (as cited in Smyth 1966).

Strausbaugh, P. D. and E. L. Core. 1970. Flora of West Virginia, parts I-IV. West Virginia University Bulletin. 1075pp.

Sullivan, J. A. and P. F. Scanlon. 1976. Effects of grouping and fighting on the reproductive tracts of male white-footed mice (Peromyscus leucopus). Res. Popul. Ecol. 17(2):164-175.

Thibault, C., M. Courot, L. Martinet, P. Mauleon, F. du Mesnil du Buisson, R. Ortevant, J. Pelletier and J. Signoret. 1966. Regulation of breeding season and estrous cycles by light and external stimuli in some mammals. J. Anim. Sci., Suppl. 25:119-139.

Valentine, G. L. and R. L. Kirkpatrick. 1970. Seasonal changes in the reproductive and related organs in the pine vole, Microtus pinetorum, in southwestern Virginia. J. Mammal. 51(3):553-560.

Van Soests, P. J. and R. H. Wine. 1968. Determination of lignin and cellulose in acid detergent fiber with permanganate. J. Assoc. Official Anal. Chem. 51(4):780-785.

Virginia Fruit. 1971. 59(10):2. Virginia State Hort. Soc. Staunton, Virginia.

Watson, A. and R. Moss. 1970. Dominance, spacing behavior and aggression in relation to population limitation in vertebrates. Pages 167-220 in A. Watson ed. Animal populations in relation to their food resources. Blackwell Scientific Publ., Oxford and Edinburgh.

Watts, C. H. S. 1970. Effect of supplementary food on breeding in woodland rodents. J. Mammal. 51(1):169-171.

Webb, R. E. and F. Horsfall. 1967. Endrin resistance in the pine mouse. Science 156(3783):1762.

APPENDIX

Appendix Table I. Life table for a cohort of pine voles born between May 15 and July 14[a] in a maintained orchard near Daleville, Virginia. The l_x column was derived from a survival equation (determined by the method of Dapson 1971 and 1972) of pine voles snap trapped between September 1974 and July 1975.

Month	Age in months x	Number surviving at the beginning of age interval l_x	Number dying in age interval d_x	Mortality rate per 1000 at beginning of age interval 1000_{qx}	Avg. no. living between two age intervals L_x	Mean expectation of life remaining at age x e_x
May	0	1000	113	113	944	6.4
June	1	887	105	118	835	6.1
July	2	782	96	123	734	5.9
August	3	686	88	128	642	5.6
September	4	598	80	134	558	5.4
October	5	518	72	139	482	5.1
November	6	446	66	148	413	4.9
December	7	380	58	153	351	4.6
January	8	322	52	161	296	4.4
February	9	270	46	170	247	4.1
March	10	224	41	183	204	3.9
April	11	183	36	197	165	3.6
May	12	147	30	204	132	3.4
June	13	117	26	222	104	3.1
July	14	91	22	242	80	2.9
August	15	69	18	261	60	2.7
September	16	51	14	275	44	2.4
October	17	37	12	324	31	2.1
November	18	25	9	360	21	1.9

Appendix Table I. Life table for a cohort of pine voles born between May 15 and July 14[a] in a maintained orchard near Daleville, Virginia. The l_x column was derived from a survival equation (determined by the method of Dapson 1971 and 1972) of pine voles snap trapped between September 1974 and July 1975 (continued).

Month	Age in months	Number surviving at the beginning of age interval	Number dying in age interval	Mortality rate per 1000 at beginning of age interval	Avg. no. living between two age intervals	Mean expectation of life remaining at age x
	x	l_x	d_x	1000_{qx}	L_x	e_x
December	19	16	6	375	13	1.7
January	20	10	4	400	8	1.5
February	21	6	4	667	4	1.1
March	22	2	1	500	2	1.3
April	23	1	1	1000	0.5	0.5
		$\Sigma = 6868$	$\Sigma = 1000$	$\Sigma = 6597$		

[a]The survival equation for this cohort was determined starting with animals 60-120 days old when captured on September 15, and animals 0-60 days old were determined by an extension of the regression line.

Appendix Table II. Life table for a cohort of pine voles born between May 15 and July 14[a] in an abandoned orchard near Daleville, Virginia. The l_x column was derived from a survival equation (determined by the method of Dapson 1971 and 1972) of pine voles snap trapped between September 1974 and July 1975.

Month	Age in months	Number surviving at the beginning of age interval	Number dying in age interval	Mortality rate per 1000 at beginning of age interval	Avg. no. living between two age intervals	Mean expectation of life remaining at age x
	x	l_x	d_x	1000_{qx}	L_x	e_x
May	0	1000	464	464	768	3.0
June	1	536	140	261	466	4.1
July	2	396	89	225	352	4.3
August	3	307	63	205	276	4.5
September	4	244	49	201	220	4.5
October	5	195	37	190	177	4.5
November	6	158	30	190	143	4.4
December	7	128	25	195	116	4.3
January	8	103	19	184	94	4.2
February	9	84	17	202	76	4.1
March	10	67	13	194	61	3.9
April	11	54	11	204	49	3.8
May	12	43	9	209	39	3.6
June	13	34	8	235	30	3.4
July	14	26	6	231	23	3.3
August	15	20	5	250	18	3.1
September	16	15	4	267	13	3.0
October	17	11	3	273	10	2.9
November	18	8	2	250	7	2.7

Appendix Table II. Life table for a cohort of pine voles born between May 15 and July 14[a] in an abandoned orchard near Daleville, Virginia. The l_x column was derived from a survival equation (determined by the method of Dapson 1971 and 1972) of pine voles snap trapped between September 1974 and July 1975 (continued).

Month	Age in months	Number surviving at the beginning of age interval	Number dying in age interval	Mortality rate per 1000 at beginning of age interval	Avg. no. living between two age intervals	Mean expectation of life remaining at age x
	x	l_x	d_x	1000_{qx}	L_x	e_x
December	19	6	2	333	5	2.4
January	20	4	1	250	4	2.4
February	21	3	1	333	3	1.8
March	22	2	1	500	2	1.3
April	23	1	1	1000	0.5	0.5
		$\Sigma = 6868$	$\Sigma = 1000$	$\Sigma = 6597$		

[a]The survival equation for this cohort was determined starting with animals 60-120 days old when captured on September 15, and animals 0-60 days old were determined by an extension of the regression line.

Appendix Table III. Life table for a cohort of pine voles born between July 15 and September 14 in a maintained orchard near Daleville, Virginia. The l_x column was derived from a survival equation (determined by the method of Dapson 1971 and 1972) of pine voles snap trapped between September 1974 and July 1975.

Month	Age in months	Number surviving at the beginning of age interval	Number dying in age interval	Mortality rate per 1000 at beginning of age interval	Avg. no. living between two age intervals	Mean expectation of life remaining at age x
	x	l_x	d_x	1000_{qx}	L_x	e_x
July	0	1000	148	148	926	4.8
August	1	852	133	156	786	4.6
September	2	719	118	164	660	4.3
October	3	601	105	175	549	4.1
November	4	496	92	185	450	3.8
December	5	404	80	218	364	3.6
January	6	324	68	210	290	3.3
February	7	256	58	227	227	3.1
March	8	198	49	247	174	2.8
April	9	149	39	262	130	2.6
May	10	110	33	110	94	2.3
June	11	77	25	333	65	2.1
July	12	52	19	365	43	1.8
August	13	33	14	424	26	1.6
September	14	19	9	474	15	1.4
October	15	10	6	600	7	1.1
November	16	4	3	750	3	0.8
December	17	1	1	1000	0.5	0.5
		Σ =5305	Σ = 1000	Σ = 6048		

Appendix Table IV. Life table for a cohort of pine voles born between July 15 to September 14 in an abandoned orchard near Daleville, Virginia. The l_x column was derived from a survival equation (determined by the method of Dapson 1971 and 1972) of pine voles snap trapped between September 1974 and July 1975.

Month	Age in months	Number surviving at the beginning of age interval	Number dying in age interval	Mortality rate per 1000 at beginning of age interval	Avg. no. living between two age intervals	Mean expectation of life remaining at age x
	x	l_x	d_x	1000_{qx}	L_x	e_x
July	0	1000	181	181	910	4.1
August	1	819	156	190	714	3.9
September	2	663	133	201	600	3.7
October	3	530	111	209	475	3.5
November	4	419	93	222	373	3.3
December	5	326	76	233	288	3.1
January	6	250	62	248	219	2.9
February	7	188	50	266	163	2.7
March	8	138	39	283	119	2.5
April	9	99	30	303	84	2.3
May	10	69	23	333	58	2.1
June	11	46	17	370	38	1.9
July	12	39	11	379	24	1.8
August	13	18	8	444	14	1.5
September	14	10	5	500	8	1.3
October	15	5	3	600	4	1.0
November	16	2	2	1000	1	0.5
December	17	0	0		0	0
		$\Sigma = 4611$	$\Sigma = 1000$	$\Sigma = 5962$	$\Sigma = 4119$	

Appendix Table V. Life table for a cohort of pine voles born between September 15 to November 14 in a maintained orchard near Daleville, Virginia. The l_x column was derived from a survival equation (determined by the method of Dapson 1971 and 1972) of pine voles snap trapped between September 1974 to July 1975.

Month	Age in months	Number surviving at the beginning of age interval	Number dying in age interval	Mortality rate per 1000 at beginning of age interval	Avg. no. living between two age intervals	Mean expectation of life remaining at age x
	x	l_x	d_x	1000_{cx}	L_x	e_x
September	0	1000	169	169	916	4.6
October	1	831	145	174	759	4.5
November	2	686	124	181	624	4.3
December	3	562	105	187	510	4.1
January	4	457	88	193	413	4.0
February	5	369	75	203	332	3.8
March	6	294	62	211	263	3.6
April	7	232	51	220	207	3.5
May	8	181	42	232	160	3.3
June	9	139	33	237	123	3.1
July	10	106	27	255	93	2.9
August	11	79	21	266	69	2.8
September	12	58	17	293	50	2.6
October	13	41	11	268	36	2.5
November	14	30	10	333	25	2.2
December	15	20	7	350	17	2.0
January	16	13	5	385	11	1.7
February	17	8	4	500	6	1.4
March	18	4	2	500	3	1.4
April	19	2	1	500	2	1.3
May	20	1	1	1000	0.5	0.5
		Σ = 5116	Σ = 1000	Σ = 6657		

Appendix Table VI. Life table for a cohort of pine voles born between September 15 and November 14 in an abandoned orchard near Daleville, Virginia. The l_x column was derived from a survival equation (determined by the method of Dapson 1971 and 1972) of pine voles snap trapped between September 1974 and July 1975.

Month	Age in months	Number surviving at the beginning of age interval	Number dying in age interval	Mortality rate per 1000 at beginning of age interval	Avg. no. living between two age intervals	Mean expectation of life remaining at age x
	x	l_x	d_x	1000_{qx}	L_x	e_x
September	0	1000	173	173	914	4.5
October	1	827	148	178	753	4.3
November	2	679	126	186	616	4.2
December	3	553	107	193	500	4.0
January	4	446	88	197	402	3.8
February	5	358	76	212	320	3.7
March	6	282	61	216	252	3.5
April	7	221	50	226	196	3.3
May	8	171	41	239	151	3.2
June	9	130	33	254	114	3.0
July	10	97	25	258	85	2.8
August	11	72	20	278	62	2.7
September	12	52	15	288	45	2.5
October	13	37	12	324	31	2.3
November	14	25	8	320	21	2.2
December	15	17	6	353	14	2.0
January	16	11	4	364	9	1.9
February	17	7	3	429	6	1.6
March	18	4	2	500	3	1.4
April	19	2	1	500	2	1.3
May	20	1	1	1000	0.5	0.5
		$\Sigma = 4992$	$\Sigma = 1000$	$\Sigma = 6688$	$\Sigma = 4496.5$	

Appendix Table VII. Life table for a cohort of pine voles born between November 15 and January 14 in a maintained orchard near Daleville, Virginia. The l_x column was derived from a survival equation (determined by the method of Dapson 1971 and 1972) of pine voles snap trapped between September 1974 and July 1975.

Month	Age in months	Number surviving at the beginning of age interval	Number dying in age interval	Mortality rate per 1000 at beginning of age interval	Avg. no. living between two age intervals	Mean expectation of life remaining at age x
	x	l_x	d_x	1000_{qx}	L_x	e_x
November	0	1000	169	169	916	4.6
December	1	831	146	176	758	4.4
January	2	685	126	184	622	4.3
February	3	559	105	188	507	4.1
March	4	454	89	196	410	3.9
April	5	365	74	203	328	3.8
May	6	291	62	213	260	3.6
June	7	229	51	223	204	3.4
July	8	178	41	230	158	3.3
August	9	137	34	248	120	3.1
September	10	103	27	262	90	3.0
October	11	76	20	263	66	2.8
November	12	56	15	268	49	2.7
December	13	41	13	317	35	2.5
January	14	28	9	321	24	2.3
February	15	19	5	263	17	2.2
March	16	14	6	429	11	1.8
April	17	8	3	375	7	1.7
May	18	5	2	400	4	1.3
June	19	3	2	667	2	0.8
July	20	1	1	1000	0.5	0.5
		$\Sigma = 5083$	$\Sigma = 1000$	$\Sigma = 6595$	$\Sigma = 4588.5$	

Appendix Table VIII. Life table for a cohort of pine voles born between November 15 and January 14 in an abandoned orchard near Daleville, Virginia. The l_x column was derived from a survival equation (determined by the method of Dapson 1971 and 1972) of pine voles snap trapped between September 1974 and July 1975.

Month	Age in months	Number surviving at the beginning of age interval	Number dying in age interval	Mortality rate per 1000 at beginning of age interval	Avg. no. living between two age intervals	Mean expectation of life remaining at age x
	x	l_x	d_x	1000_{qx}	L_x	e_x
November	0	1000	202	202	916	4.6
December	1	798	167	209	716	3.8
January	2	631	136	216	563	3.6
February	3	495	111	224	440	3.5
March	4	384	89	232	340	3.3
April	5	295	72	244	259	3.2
May	6	223	56	251	195	3.1
June	7	167	44	263	145	2.9
July	8	123	34	276	106	2.8
August	9	89	25	281	77	2.6
September	10	64	19	297	55	2.5
October	11	45	15	333	38	2.3
November	12	30	10	333	25	2.2
December	13	20	7	350	17	2.0
January	14	13	5	385	11	1.8
February	15	8	4	500	6	
March	16	4	1	250	4	1.6
April	17	3	2	667	2	0.8
May	18	1	1	1000	0.5	0.5
June	19					
July	20					
		$\Sigma = 4393$	$\Sigma = 1000$	$\Sigma = 6513$	$\Sigma = 3897.5$	

Appendix IX. Fecundity table for a cohort of pine voles born between May 15 and July 14 in a maintained orchard near Daleville, Virginia. The l_x column is from Appendix Table I, and data for the m_x column is taken from Table 10.

Month	x	l_x	m_x	$l_x m_x$	$x\, l_x m_x$
May	0	1000	0	0	0
June	1	887	0	0	0
July	2	782	0	0	0
August	3	686	.50	343	1029
September	4	598	.56	335	1340
October	5	518	.91	290	1450
November	6	446	.91	406	2435
December	7	380	.45	346	2421
January	8	322	.45	145	1159
February	9	270	.13	122	1094
March	10	224	.13	29	291
April	11	183	.33	24	262
May	12	147	.33	49	582
June	13	117	.79	39	502
July	14	91	.79	72	1006
August	15	69	1.00	55	818
September	16	51	1.00	51	816
October	17	37	.91	37	629
November	18	25	.91	23	410
December	19	16	.45	15	297
January	20	10	.45	5	90
February	21	6	.13	3	57
March	22	2	.13	0.3	6
April	23	1		0.1	3
				2389.4	16,677

x - age in months
l_x - no. surviving at beginning of age interval
m_x - no of females born per female of age x
$l_x m_x$ - no. of female offspring from age class x

Appendix Table X. Fecundity table for a cohort of pine voles born between May 15 and July 14 in an abandoned orchard near Daleville, Virginia. The l_x column is from Appendix Table II and the data for the m_x column is taken from Table 10.

Month	x	l_x	m_x	$l_x m_x$	$x l_x m_x$
May	0	1000	0	0	0
June	1	536	0	0	0
July	2	396	0	0	0
August	3	307	.75	230	691
September	4	244	.38	93	371
October	5	195	.38	74	371
November	6	158	.60	95	569
December	7	128	.60	77	538
January	8	103	.31	32	255
February	9	84	.31	26	234
March	10	67	0	0	0
April	11	54	0	0	0
May	12	43	.42	18	217
June	13	34	.42	14	186
July	14	26	.60	16	218
August	15	20	.60	12	180
September	16	15	.94	14	226
October	17	11	.94	10	176
November	18	8	.60	5	86
December	19	6	.60	4	68
January	20	4	.31	1	25
February	21	3	.31	1	20
March	22	2	0	0	0
April	23	1	0	0	0
				722	4431

x - age in months
l_x - no. surviving at beginning of age interval
m_x - no. of females born per female of age x
$l_x m_x$ - no. of female offspring from age class x

Appendix Table XI. Fecundity table for a cohort of pine voles born between July 15 and September 15 in a maintained orchard near Daleville, Virginia. The l_x column is from Appendix Table III, and data for the m_x column is taken from Table 10.

Month	x	l_x	m_x	$l_x m_x$	$x l_x m_x$
July	0	1000	0	0	0
August	1	852	0	0	0
September	2	719	0	0	0
October	3	601	.56	337	1010
November	4	496	.50	248	992
December	5	404	.50	202	1010
January	6	324	.45	146	875
February	7	256	.45	115	806
March	8	198	.13	26	206
April	9	149	.13	19	174
May	10	110	.33	36	363
June	11	77	.33	25	280
July	12	52	.79	41	493
August	13	33	.79	26	339
September	14	19	1.00	19	266
October	15	10	1.00	10	150
November	16	4	.91	4	58
December	17	1	.91	1	15
				$1255=R_o$	7039

x - age in months
l_x - no. surviving at beginning of age interval
m_x - no. of females born per female of age x
$l_x m_x$ - no. of female offspring from age class x

Appendix Table XII. Fecundity table for a cohort of pine voles born between July 15 and September 15 in an abandoned orchard near Daleville, Virginia. The l_x column is from Appendix Table IV, and data for the m_x column is taken from Table 10.

Month	x	l_x	m_x	$l_x m_x$	$x l_x m_x$
July	0	1000	0	0	0
August	1	819	0	0	0
September	2	663	0	0	0
October	3	530	.38	201	603
November	4	419	.14	59	236
December	5	326	.14	46	230
January	6	250	.31	78	476
February	7	188	.31	58	406
March	8	138	0	0	0
April	9	99	0	0	0
May	10	69	.42	29	290
June	11	46	.42	19	209
July	12	29	.60	17	204
August	13	18	.60	11	143
September	14	10	.94	9	126
October	15	5	.94	5	75
November	16	2	.60	1	16
December	17	0	0	0	0
				533	3006

x - age in months

l_x - no. surviving at beginning of age interval

m_x - no. of females born per female of age x

$l_x m_x$ - no. of female offspring from age class x

Appendix Table XIII. Fecundity table for a cohort of pine voles born between September 15 to November 14 in a maintained orchard near Daleville, Virginia. The l_x column is from Appendix Table V, and data from the m_x column is taken from Table 10.

Month	x	l_x	m_x	$l_x\ m_x$	$x\ l_x\ m_x$
September	0	1000	0	0	0
October	1	831	0	0	0
November	2	686	0	0	0
December	3	562	.50	281	843
January	4	457	.25	114	457
February	5	369	.25	92	461
March	6	294	0	0	0
April	7	232	0	0	0
May	8	181	.33	60	478
June	9	139	.33	46	413
July	10	106	.79	84	837
August	11	79	.79	62	687
September	12	58	1.00	58	696
October	13	41	1.00	41	533
November	14	30	.91	27	382
December	15	20	.91	18	273
January	16	13	.45	6	94
February	17	8	.45	4	61
March	18	4	.13	0.5	9
April	19	2	.13	0.3	5
May	20	1	.33	0.3	7
				894.1	6236

x - age in months
l_x - no. surviving at beginning of age interval
m_x - no. of females born per female of age x
$l_x\ m_x$ - no. of female offspring from age class x

Appendix Table XIV. Fecundity table for a cohort of pine voles born between September 15 and November 14 in an abandoned orchard near Daleville, Virginia. The l_x column is from Appendix Table VI, and the data for the m_x column is taken from Table 10.

Month	x	l_x	m_x	$l_x m_x$	$x l_x m_x$
September	0	1000	0	0	0
October	1	827	0	0	0
November	2	679	0	0	0
December	3	553	.14	77	232
January	4	446	.17	76	303
February	5	358	.17	61	304
March	6	282	0	0	0
April	7	221	0	0	0
May	8	171	.42	72	575
June	9	130	.42	55	491
July	10	97	.60	58	582
August	11	72	.60	43	475
September	12	52	.94	49	587
October	13	37	.94	35	452
November	14	25	.60	15	210
December	15	17	.60	10	153
January	16	11	.31	3	55
February	17	7	.31	2	37
March	18	4	0	0	0
April	19	2	0	0	0
May	20	1	.42	0.4	8
				556.4	4464

x - age in months
l_x - no. surviving at beginning of age interval
m_x - no. of females born per female of age x
$l_x m_x$ - no. of female offspring from age class x

Appendix Table XV. Fecundity table for a cohort of pine voles born between November 15 and January 14 in a maintained orchard near Daleville, Virginia. The l_x column is taken from Appendix Table VII, and data for the m_x column is taken from Table 10.

Month	x	l_x	m_x	$l_x m_x$	$x l_x m_x$
November	0	1000	0	0	0
December	1	831	0	0	0
January	2	685	0	0	0
February	3	559	.25	140	419
March	4	454	0	0	0
April	5	365	0	0	0
May	6	291	.33	96	576
June	7	229	.33	76	529
July	8	178	.79	141	1125
August	9	137	.79	108	974
September	10	103	1.00	103	1030
October	11	76	1.00	76	136
November	12	56	.91	51	612
December	13	41	.91	37	485
January	14	28	.45	13	176
February	15	19	.45	9	128
March	16	14	.13	2	29
April	17	8	.13	1	18
May	18	5	.33	1.7	30
June	19	3	.33	1	19
July	20	1	.79	0.8	16
				856.5	7002

x - age in months
l_x - no. surviving at beginring of age interval
m_x - no. of females born per female of age x
$l_x m_x$ - no. of female offspring from age class x

Appendix Table XVI. Fecundity table for a cohort of pine voles born between November 15 and January 14 in an abandoned orchard near Daleville, Virginia. The l_x column is taken from Appendix Table VIII, and the data for the m_x column is taken from Table 10.

Month	x	l_x	m_x	$l_x m_x$	$x l_x m_x$
November	0	1000	0	0	0
December	1	798	0	0	0
January	2	631	0	0	0
February	3	495	.17	84	252
March	4	384	0	0	0
April	5	295	0	0	0
May	6	223	.42	94	562
June	7	167	.42	70	491
July	8	123	.60	74	590
August	9	89	.60	53	481
September	10	64	.94	60	602
October	11	45	.94	42	465
November	12	30	.60	18	216
December	13	20	.60	12	156
January	14	13	.31	4	56
February	15	8	0	0	0
March	16	4	0	0	0
April	17	3	.42	0.4	8
				511.4	3879

x - age in months
l_x - no. surviving at bdginning of age interval
m_x - no. of females born per female of age x
l_x m_x - no. of female offspring from age class x

VITA

Robert Edwin Noffsinger was born on May 28, 1948 in Clifton Forge, Virginia. He attended public schools in Alleghany County, Virginia and graduated from Alleghany County High School in June, 1966. He then attended Virginia Polytechnic Institute and State University for two years as a co-operative education student with the U.S. Forest Service. He resigned from V.P.I.&S.U. in April 1968 and was drafted into the U.S. Army in August 1969. He served in Viet Nam from January 1970 to December 1970 and was honorably separated from active duty in June 1971. He returned to V.P.I.&S.U. in April 1972 and received a B.S. degree in Forestry and Wildlife Management in June 1974. He married Miss Susan Jane Persinger on January 19, 1973. They have two children, Daniel Lyle born July 25, 1974 and Keely Jean, born February 12, 1976. The author became a candidate for the Master of Science degree in Fisheries and Wildlife Science at V.P.I.&S.U. in July 1974 and was employed as a Graduate Research Assistant.

Robert E. Noffsinger

Robert E. Noffsinger

SEASONAL VARIATION IN THE NATALITY, MORTALITY, AND NUTRITION OF THE PINE VOLE IN TWO ORCHARD TYPES

by

Robert E. Noffsinger

(ABSTRACT)

Pine voles (Microtus pinetorum) were collected for one year in a maintained and an abandoned orchard. Higher densities of voles were indicated in the maintained orchard. Estimates of mortality were lower and reproduction was higher in the maintained orchard. Net reproductive rates indicated a stable or increasing population in the maintained orchard and a decreasing population in the abandoned orchard. Digestible energies and consumption indexes were higher in the maintained orchard.

A drastic decline in reproduction occurred in the abandoned orchard in November while reproduction remained high in the maintained orchard. The largest increase in theoretical energy requirements for thermoregulation occurred from September to November. At this time the digestible energy in the abandoned orchard was much lower than in the maintained orchard, there was a larger reduction in ground cover, a lower consumption index, and a sharp decline in female fat content in the abandoned orchard. Although cause and effect cannot be shown it seems likely that the lower energy intake, the higher energy demands for thermoregulation and for pregnancy and lactation would cause energy requirements to be greater than energy intake. It is postulated that such an energy restriction would lower

ciculating levels of LH which would result in a decline in reproduction in the abandoned orchard. It is also postulated that energy intake and photoperiod have an interactive effect on reproduction in the pine vole and that energy intake in the maintained orchard in the November to January period was not sufficient to override the effect of decreasing daylength and to keep a high proportion of females in a reproductive state.