BIOENERGETICS AND NUTRITION OF THE PINE VOLE
(MICROTUS PINETORUM) IN TWO VIRGINIA APPLE ORCHARDS

by

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INTRODUCTION

The economic importance of the pine vole *(Microtus pinetorum)* has been well established (Kennicott 1857, Rhoads 1903, Hamilton 1935, Garbough 1944, Byers 1974, Anthony and Fisher 1977). Within the eastern United States pine voles have caused considerable damage to apple orchard trees due to their root and trunk girdling behavior (Hayne 1975, Byers 1976). As of yet, there has been little success in controlling this microtine rodent as pointed out by LaVoie and Tietjen (1971). Anthony and Fisher (1977) noted that the solution to pine vole control has traditionally been that of extermination by whatever means possible. Their research indicated inconsistent and ineffective control of pine voles in orchards with rodenticides, herbicides, poison baits and many cultural practices. Even though endrin was applied and mowing and herbicides were used to reduce ground cover, populations of pine voles remained at high levels (Anthony and Fisher 1977).

It is clear that traditional practices of pine vole control are often ineffective, expensive, and environmentally questionable. If pine vole populations are to be controlled effectively for long-term periods, vulnerable periods in their biology or ecology will probably have to be identified and exploited through habitat management techniques. One approach to studying this problem is through community energetics. Golley et al. (1975) noted that as man's impact on the environment increases there is a corresponding increase in mammalian pests. He further stated that while conventional control measures can be implemented, such measures are seldom successful over prolonged periods of time; in contrast, an ecosystem approach to the problem, considering all aspects of the system including energy assimilation, metabolism, and food habits, may provide the basis for successful pest management.

The food web of the community is one of the more important concepts of community organization and structure, and its complete qualitative as well as quantitative description is the ultimate goal of understanding the interrelationships which exist between animals and their habitat (Hairston 1959). Hairston (1959) made the assumption that niche or status of an animal in the community might better be defined in terms of the amount and type of food it consumes, ultimately in terms of energy consumed.

Phillipson (1975) stated that energetic parameters when used in conjunction with population density data were invaluable in the formulation of a dynamic diagram of the ecosystem. Such a detailed analysis of food, food consumption, food digestibility, food availability, respiration, and reproduction of a population would allow the incorporation of results into a complex, but meaningful, model. Such a model should provide a better explanation of the overall consequences of pine vole population control through habitat management or any other means. Such predictive and simulative capabilities should help identify the way in which a system (pine vole density) responds to various induced environmental stresses (pesticides, herbicides, cultural practices, etc.). Knowledge of this kind will hopefully highlight areas of poor comprehension or areas of great importance, and thus direct future research needs. Innis (1971) cited a characteristic example of the importance of modeling a system, "that without the model, they would never have guessed the relative sensitivities (of the various parameters) and might have wasted a great deal of money and time trying to collect data whose effect was negligible."

Thus, a bioenergetic approach to studying pine vole pest populations coupled with detailed knowledge of their population dynamics, should provide a useful approach for identifying critical or weak points in the ecology of populations as well as for assessing the effects of various management or control strategies applied to biological systems (orchards) (Schreiber and Watts 1977). Keith et al. (1959) was able to reduce pocket gopher *(Thomomys talpoides)* numbers by the application of a selective herbicide (2, 4-D), in Colorado rangelands, which took advantage and exploited a weak point in their ecology. A reduction of 80-90 percent in pocket gopher numbers was achieved by the subsequent change in the proportion of succulent forbs and grasses. A change in the diet of pocket gophers from 42 percent forbs and 18 percent grasses to 50 percent forbs and 50 percent grasses was indicated as the reason for such a large reduction in population numbers. The percent of bare ground did not change after 1 year of treatment.

This study attempted to qualify and quantify the bioenergetic parameters of the pine vole as influenced by different physiological and environmental conditions in maintained and abandoned apple orchard habitats in southwestern Virginia. Results from this research will ultimately be included as part of an overall population energetics model for simulative and predictive purposes. The approach to this bioenergetics study was a combination of both the ecological and physiological approaches as defined by Klekowski and Duncan (1975). Such an approach to ecological energetics is based mainly on laboratory studies, but with major attempts at designing and transferring experiments and results to field situations, and to interpret field events with the aid of some physiological/bioenergetic parameters.

LITERATURE REVIEW

Bioenergetics

Energy flow through a population is the sum of the energy used for maintenance plus the energy used for growth (Golley 1960, Ryszkowski and Petrusewicz 1967, Chew and Chew 1970, and Odum 1971). Of these 2 very important components of energy flow, maintenance is by far the most important in the annual energy budget of a population (Fleharty and Choate 1973, Baar and Fleharty 1976). In order to quantify and understand the ecological energetics of a population, the subject has to be approached by considering the bioenergetics of the species.

Energy flow (A) through a population of small mammals per unit area for an interval of time (T) can be calculated from the following equation:

$$A = [Kc\ (N \times C \times T) - Ke\ (N \times FU \times T)]/M$$

where:

N = number of individuals in population,

C = daily food consumption per individual ($\bar{X}$),

Kc = caloric value of food,

FU = daily egestion of feces and urine per individual ($\bar{X}$),

Ke = caloric value of rejecta,

T = time period (in days),

M = area in square meters.

Energy flow through small mammal populations has been studied in a variety of ecosystems and species, including grasslands (Golley 1960, Odum et al. 1962, French et al. 1976, Grodzinski 1966, Collins and Smith 1976), cultivated field (Trojan 1969), coniferous forests (Grodzinski 1971, Hansson 1971), deciduous forests (Grodzinski et al. 1970, Bobek 1971, Baar and Fleharty 1976), and desert shrub communities (Chew and Chew 1970).

Seasonal and Sexual Differences

Seasonal metabolic cycles exist for a number of wildlife species (Moen 1973). Such changes can be the result of seasonal differences in the body insulative index (Gorecki 1966), body weight, digestion coefficients (Gebczynska 1970, Morris 1974) or behavior patterns.

Baar and Fleharty (1976) found that the daily energy budget of *P. leucopus* was greatest in winter, lower in spring and autumn, and least during the summer. Summer values were significantly different from values during winter and spring, but not from those during autumn. In winter, the majority of the animal's time was spent inside the nest (72 percent). Temperatures within the nest of *P. leucopus* were found to be higher than the ambient temperature for all seasons except summer.

Gebczynski (1966) determined the average daily metabolic rate (ADMR) of *Apodemus flavicollis* in different seasons by the oxygen consumption method. He found that ADMR was highest in the spring, slightly lower in the autumn and considerably lower in both winter and summer.

Tieu and Stoica (1971) failed to find any statistically significant differences in seasonal metabolic rates of *Mus musculus spicilegus*.

Morris (1974) found that winter acclimatized *Peromyscus maniculatus bardii* have a lower daily metabolic rate than do summer acclimatized deer mice when compared at the same temperature. The lower winter metabolic rate was correlated with the increased insulation afforded by larger hair and greater pelage weight.

Randolph (1973) estimated that a population of *Blarina brevicada* required about 43 percent more food during the winter than during the summer. Gebczynska (1970) determined that the daily energy budget of *Microtus oeconomus* during summer was 0.581 kcal/g and 0.510 kcal/g during the winter. Grodzinski (1966) determined that the daily energy budget (DEB) of *Clethrionomys glareolus* for winter was 10.2 kcal/animal and 10.6 kcal/animal during the summer. DEB of *Microtus arvalis* was found to be 13.5 kcal during the winter and 12.6 kcal during the summer. DEB of *Apodemus flavicollis* was 11.2 kcal in winter and 12.3 kcal during the summer.

Pregnancy and Lactation

Determining the energy requirements of a small mammal during periods of pregnancy and lactation is an extremely important component for constructing a bioenergetic model of a population (Davis and Golley 1963). Two or 3-fold increases in food consumption have been observed in rats and mice during periods of lactation (Brody 1945, Nelson and Evans 1961, Barnett and Little 1965).

Kaczmarski (1966) completed an extensive study on the bioenergetics of pregnancy and lactation in *Clethrionomys glareolus*. He noted that energy requirements of females increased by 24 percent during pregnancy and 92 percent during lactation. In order to produce a litter of 5 young and raise 4 of them to weaning, it was determined that a female would have to assimilate an additional 364 kcal; 75 kcal for the pregnancy and 289 kcal for the lactation.

Millar (1975) noted similar increases in food consumption in captive female *Peromyscus leucopus*. Females supporting relatively large litters were found to consume more food than females with small litters; however, there was no difference in fat reserves between females. The survival and rate of growth of nestlings were effected by a shortage of food. On the basis of this observation, Millar (1975) suggested that of the important parameters related to the breeding-strategy of *P. leucopus* include the availability of food.

Migula (1969) determined that pregnant female *Microtus arvalis* required 32 percent more energy than control females. During lactation, energy requirements were found to be elevated by 133 percent over that of non-reproducing females. To produce and nurse 1 young vole it was determined that the mother would have to assimilate 75.9 kcal. For the entire period of pregnancy and lactation, the cost of maintenance of female common voles increased by an average of 82.5 percent. Trojan and Wojciechowska (1967) found that the cost of pregnancy and lactation in female *Microtus arvalis* increased an average of 80.5 percent.

Myrcha et al. (1969) found that *Mus musculus* required 82.3 kcal of metabolizable energy during pregnancy. The total amount of assimilated energy additionally taken by a female during 26 days of lactation was 354.2 kcal.

Periods of increased food consumption during pregnancy and lactation coincide with distinct changes in the alimentary tract of the female animal (laboratory rats, Fell et al. 1963; *Clethrionomys glareous* and *Apodemus flavicollis*, Myrcha 1964, 1965). The weight and length of areas along the alimentary tract have been found to temporarily increase (Myrcha 1964, 1965A) and hypertrophic and hyperplastic changes in the intestinal walls occur (Fell et al. 1963). Apparently, these structural changes allow pregnant and lactating animals to maintain an equivalent level of digestibility (Kaczmarski 1966).

The energetic efficiency of reproductive processes in small mammals is extremely high. The efficiency of net production during the breeding period can be determined by the ratio of the energy deposited by the litter (production) to the energy additionally metabolized by the female. Kaczmarski (1966) calculated efficiency coefficients of 13.8 percent (includes placenta and membrane) and 14.6 percent for pregnant and lactating *Clethrionomys glareolus*, respectively. Similar results were found for *Microtus arvalis*, 13.9 percent for the pregnancy and 15.4 percent over the period of lactation (Migula 1969). Randolph et al. (1977) found that lactating female *Sigmodon hispidus* had an efficiency of lactation above that found in other wild rodents. Offspring of *Sigmodon hispidus* stored energy during the period of lactation equivalent to 45 percent of the increased assimilation by the mother. When considering the utilization of stored fat reserves in the lactating female *Sigmodon hispidus*, production efficiency dropped to 34 percent, but was still nearly 2 times as high as in other rodent species.

Juvenile Growth

During the period of postweaning development, voles generally accumulate high levels of fat tissue and moderate levels of protein (Sawicka-Kapusta 1970, Drozdz et al. 1972, Miller 1974). Deposition of this high energy tissue results in dramatic increases in the gross energy content of carcass tissue. In order to sustain such a high rate of energy storage, animals require substantial amounts of metabolizable energy above their individual maintenance requirements and the ability to efficiently utilize this surplus energy.

Drozdz et al. (1972) monitored the growth requirements of *Microtus arvalis* from 20 to 50 days of life. They noted an increase in food consumption from 10 to 14 kcal/day/animal over the experimental period. Over the entire experimental period, voles consumed on the average 339 kcal of metabolized energy of which 16.1 kcal was actually deposited in the form of body tissue. The average growth efficiency (energy deposited as tissue/metabolized energy intake) during the postnatal development of *Microtus arvalis* was 4.74 percent.

Metabolic demands of growing juvenile animals, when expressed per unit of body weight, show a definite increase above the metabolic requirements of an adult (Miller 1974, Drozdz et al. 1972). Average daily metabolic rate (ADMR) of *Microtus arvalis* decreased from 25.8 kcal/kg/hr for the 20 day old group to 21.5 kcal/kg/hr for the 50 day old group (Drozdz et al. 1972). These results demonstrate a definite decrease in energy used with age per unit of body weight. The reduced metabolic demand with age can be partly explained by (1) the inverse relationship between ADMR and body weight, and (2) by the decreased growth rate with age. The caloric value of body gain was reduced from 5.7 kcal/10 days at 20 days of age to 5.0 kcal/10 days at 50 days of age in *Microtus arvalis* (Drozdz et al. 1972). Similar results were obtained by Sawicka-Kapusta (1970) on *Microtus arvalis*.

Utilization of Indicators in Determining Diet Digestibility in Small Mammals

Studies of energy flow through small mammal populations require the estimation of diet digestibility efficiencies. Determining the digestibility of each component of the diet individually by conventional feeding trials can become laborious and impractical in highly diversified consumers. As a result, alternate methods have been developed which allow the estimation of diet digestibility under field conditions (Golley 1967, Johnson and Maxell 1966, Johnson and Groepper 1970, Soholt 1973, Schreiber 1978, Kaufman et al. 1976). Ratio techniques using natural and artificial indicators in the food have been widely used. These include the use of lignin (Cook and Harris 1951), chromogen (Reid et al. 1952), and silica (Gallup and Kuhlman 1936) which occur naturally in plant cells, and substances such as chromium (Mautz and Petrides 1967) which are artificially added to the food.

Ratio techniques were originally developed for use on foods before their ingestion by the animal. However, this requirement is impractical for field conditions when the proportion of various food items making up the diet of small mammals are unknown. Compounding the problem is the possibility of selective feeding by animals which choose only those portions of plants which are high in nutritional value and digestibility. An alternative to this problem is to rely on the stomach contents of small mammals as representative samples of the food eaten.

Ecologists have employed the ash tracer technique on small mammals as the ratio of the concentration of ash in the stomach contents to the concentration of ash in the feces from the large intestine (Johnson and Maxell 1966, Johnson and Groepper 1970, Soholt 1973, Schreiber 1978, and Kaufman et al. 1976). This ratio technique assumes that : 1) the animal in question is in mineral balance, 2) the feces in the large intestine (rectum region) were formed from the same foods as those found in the stomach, and 3) the animal in question lost ash in the feces and urine in the same proportion as that determined in the laboratory (Johnson and Groepper 1970).

In addition to these three assumptions, one must assume that the ash (indicator) is not absorbed to any great extent, and that absorption, if it occurs, is independent of forage quality and composition. One must also assume that the ash (indicator) substance and nutrient under investigation (dry matter or energy) move together through the digestive tract and are not influenced by differing rates of passage (Chandler 1964).

Of the three assumptions listed above, only number two appears to be a reasonable possibility. The assumption that an animal is in mineral balance can be reasonably achieved only if stomach contents and feces are collected from mature adults in nonreproductive condition.

However, problems can arise with using adults, since some minerals are assimilated (Kaufman et al. 1976) and added to the feces by the blood (Schneider and Flatt 1975).

Assumption number three pertains to the determination of correction factors under laboratory conditions to account for the incomplete recovery of ash from the stomach in the collected feces. In theory, the correction factor accounts for the assimilation and urinary loss of minerals. However, for such a theory to be correct, one must assume that the concentration of ash in the stomach contents is identical to the concentration of ash in the food source before its ingestion. Due to the differential rate of passage of foodstuffs and the fact that some foods begin to pass through the gastrointestinal tract as early as 1 hour after ingestion (Lee and Horvath 1969), such an assumption may not always be correct. Highly digestible foodstuffs (carbohydrates) move quickly through the stomach while those high in fiber content and low in digestibility may remain for longer periods in the stomach (Wohl and Goodhart 1960). This can result in the overrepresentation (or underrepresentation) of certain foodstuffs and components of foodstuffs in the stomach when compared to the foods before their ingestion by the animal.

Ash concentrations in the stomach contents of a mammal represent both the soluble and insoluble portions as well as mineral additions from the saliva (Lesperance et al. 1960, McManus 1961, VanDyne and Torell 1964). Fecal ash concentrations represent the insoluble portion with some endogenous mineral additions from the blood. Both of these constituents will vary with respect to the nature of the food consumed (Schneider and Flatt 1975). Much of the silica in plants is incorporated into an insoluble form in the flat cell wall (Heath et al. 1973). Silica acts in combination with lignin to reduce the digestibility of this fraction of plant cell structure, which results in a longer retention time for this fraction in the digestive tract. This can result in the concentration of the insoluble ash component in the stomach. So the determination of correction factors for a tracer in the stomach contents not only accounts for its assimilation and urinary loss by an animal, but also for the increased concentration of that tracer (or dilution) in the stomach contents due to differential rates of passage.

In order to minimize the error in applying correction factors determined under laboratory conditions to field caught animals, the correction factors should be determined for diets with similar digestibilities and rates of passage as the diets comprising the stomach contents of the field caught animals. This of course requires some knowledge of the major foods comprising the diet of the animal under study for each season of interest by the researcher. Johnson and Groepper (1970) and Kaufman et al. (1976) determined correction factors for small mammals in the laboratory using a commercial rodent chow of high digestibility and applied the results directly to field caught animals without any prior knowledge as to the composition and digestibility of foods in their diet. This could have resulted in some degree of error in their estimates of digestibility. Soholt (1973) determined correction factors in the laboratory for *Dipodomys merriami* using natural foods which are commonly selected for by this species. This approach eliminates much error and results in more reliable estimates of digestibility since the rate of passage of these foods are likely to be similar to field diets.

This phase of the study reported herin was developed to evaluate the use of a lignin ratio technique as an alternative approach to the present ash tracer method of stomach content analysis. Lignin is a naturally occurring indicator in plant cell walls which is virtually indigestible by monogastric species (Van Soest and Wine 1967). Digestion of lignin by *Microtus pennsylvanicus* was found to be negligible by Johanningsmeier and Goodnight (1969). It was thought that lignin would have the advantages over ash as an internal plant indicator since it was not necessary for the animal to be in mineral balance (no age effect) for reliable results (Noffsinger 1976). Lignin itself serves as a useful index to digestibility. Digestibility varies inversely with the lignin content of the forage (Forbes and Garrigus 1948, Van Soest 1964).

Noffsinger (1976) developed laboratory procedures for conducting a lignin analysis of pine vole stomach contents. He analyzed the stomach contents of pine voles collected from orchard habitats and found significant variations in diet digestibility between habitats and seasons.

Relationship of Small Mammals to the Food Source

Quantifying the available net primary production in a habitat is a necessary step in analyzing the relationship between a population and its food resource. It has been shown that small mammals consume

1 percent or less of the total net primary production (Golley 1960, Odum et al. 1962, Grodzinski 1966, Weigert and Evans 1967, Chew and Chew 1970, Grodzinski 1971). All of the net primary production is not directly available to small mammals due to much of it being out of reach or unpalatable. When considering only the available primary production, small mammal populations have been observed to consume a much greater proportion of the food resource.

Chew and Chew (1970) found that *Dipodomys merriami* can consume up to 75 percent of the available seed production during any given year. Soholt (1973) estimated that a population of *Dipodomys merriami* consumed about 10.7 percent of the available primary production and over 95 percent of the *Erodium* production, its major food resource.

Herbivores have generally been considered as having less of an impact on their food resources than granivorous species of small mammals. Grodzinski (1966) estimated that a population of *Clethrionomys rutilus* and *Microtus oeconomus* consumed approximately 9.9 percent and 3.7 percent of the available primary production, respectively. Gebczynska (1970) found that *Microtus oeconomus* populations in a forest plantation consumed about 3.1 percent of the available production. Similarly, Hansson (1971) estimated that a population of the vole *Microtus agrestis* in a spruce plantation consumed between 1.5-2.8 percent of the available primary production.

Factors which are usually not considered when assessing the impact of small mammals on the food resource are the extra-energetic effects of rodents on their food supplies during normal feeding and nest building activities. Grodzinski et al. (1977) has shown that a population of *Microtus arvalis* in alfalfa and wheat fields had an impact which was 4 to 13 times greater than the consumption as computed from energy requirements alone. Similarly, Ryszkowski et al. (1973) determined that a population of voles destroyed plants in alfalfa cultures by a ratio of 1.8:1 (destroyed:consumed).

Another factor which can limit the available food supply even further is the nutritional quality of the resource (White 1978). Studies dealing specifically with this aspect of small mammal ecology are limited, mostly because of the difficulty involved in studying this problem. Of special concern here is whether sufficient nitrogenous materials are available to sustain growth and reproduction, and the fibrous nature of the forages available since fiber is known to decrease forage digestibility (Grodzinski et al. 1977, Keys and Van Soest 1970, Hansson 1971).

METHODS

Seasonal Energetic Requirements of Adult Pine Voles

Experimental Subjects

The pine voles used in the metabolism trials were live-trapped from apple orchards near Daleville, Virginia and placed in an outdoor holding facility located at VPI and SU. This holding pen consisted of an underground bunker-type building which contained wire-bottom cages with metal pipes leading to outside enclosures which were covered on all sides with hardware cloth. Approximately 1 foot of soil existed above the bottom layer of hardware cloth. Pine voles were allowed free access to both the bunker and outdoor enclosures at all times. They were free to breed, burrow, and nest in any location. The majority of the voles chose to nest in the outdoor enclosure instead of the wire-bottom cages.

All voles were supplied with nesting material consisting of shredded burlap. However, sufficient vegetation for nesting was also available in the outdoor enclosure. Water and purina laboratory chow were supplied *ad libitum*. Apples were occasionally given as a supplement to the laboratory chow diet.

Voles were housed in the facility for 1 to 3 months before being used in a metabolic trial. Offspring (born in the facility) of wild voles were used in metabolic trials if they were adult size at the time of capture from the outdoor holding facility. Since the outdoor facility allowed the animals to partake in most forms of activity as well as being subjected to natural temperature, photoperiod, humidity and weather conditions, the colony was able to undergo seasonal acclimatization similar to a wild population of voles.

Experimental Design

Bioenergetic parameters of adult male and female voles were measured for each of the 4 seasons (Summer, Fall, Winter, Spring) utilizing a food consumption trial (Swift and French 1954). It was felt that the food consumption method was the most accurate means of estimating field metabolisms of wild vole populations since the animals are less restrained and are observed for a longer period of time than animals whose metabolism is measured with a respirometer (Golley 1966, Golley 1968, Odum et al. 1962).

Adult pine voles were live trapped from the outdoor holding pens during the respective season of the trial and brought immediately to the laboratory environmental chamber which simulated the respective seasonal temperature and photoperiod conditions. Voles were sexed, weighed, and placed singly at random in metal metabolic cages. Two varieties of metabolic cages were utilized. In order to determine the metabolic costs of existence within the nest, voles were housed in metabolic cages (24X18X18cm) containing 50g of cotton-gauze bedding material. Purina laboratory chow and water supplies were located immediately adjacent to the nest. Activity in these cages was generally limited to feeding and watering activities with some climbing and walking. To estimate the metabolic costs of out-of-the-nest activity, voles were housed in metal metabolic cages (11.5X7.5X6.5cm) with exercise wheels having a diameter of 15.5cm. Exercise wheels were equipped with automatic counters to record revolutions traveled. No bedding material was supplied to these animals. In order to apply the results to field conditions it was assumed that activity of voles in cages equipped with exercise wheels would be similar to expenditures under natural conditions. Johnson and Groepper (1970) reported that when captive rodents were provided with exercise wheels, the maintenance energy expenditure ranged from 3.8 to 4.8 times the basal metabolic rate. In order to simulate natural energy expenditure by *Peromyscus leucopus* in the laboratory, Baar and Fleharty (1976) placed exercise wheels within respirometers for determining the daily energy budget (DEB). They then incorporated these data into an overall population model for the determination of energy flow through a wild population of *Peromyscus leucopus*.

Voles were maintained in the cages for a 1 week acclimation period prior to taking measurements on food consumption and fecal production. Nests were usually well constructed after only 3 days in confinement. Following acclimation, food consumption and fecal production were measured for each animal over a 1 week period. Purina Laboratory Chow and water were supplied to all voles *ad libitum*.

Ingestion by adult voles was measured by differences in weight of Purina Lab Chow in food bowls at 24 hour intervals. All Lab Chow was given in a ground state to minimize spillage and hoarding. Water content and energy equivalent of the food were determined for each trial. Digested energy was estimated for each animal from differences between ingestion and fecal production over a 7-day collection period, using dry weights of food eaten minus feces produced multiplied by the average energy equivalent of Lab Chow and feces. Ingestion, fecal production, and fecal energy equivalents were determined for each animal. Dry weights of food and feces were determined by oven-drying at $55^{o}C$ for a period of 72 hours. Metabolized energy was calculated as digested energy minus 2.0 percent of the gross energy ingested, the approximate energy loss in urine as determined for pine voles on a Lab Chow diet by Merson (1979).

Production

At the beginning and end of each 7-day trial voles were weighed to the nearest 0.1g. Change in body weight was determined by subtracting initial and final body weights. It is essential to know the total amount of energy metabolized by an animal which went into production in the case of weight gain, or the amount of energy derived from tissue catabolism in the case of weight loss. These data are needed for accurate determinations of maintenance energy requirements for an individual of a given body weight.

Many researchers correct for body weight changes by simply multiplying the amount of weight gained or lost by the caloric density of fat tissue and subtracting the product or adding the product to the metabolizable energy intake of the animal to compute the maintenance energy expenditure. Researchers have also used the caloric density of the whole body of an animal as a correction factor (Sawicka-Kapusta et al. 1975). This is an underestimate which will result in an inflated maintenance requirement estimate. Weight gain in an adult animal over a short period of time will be largely due to lipogenesis. Body tissue as a whole contains large amounts of other components in addition to the fat component which results in a caloric density much lower than that of fat.

The process of fat deposition is far from 100 percent efficient and likewise the process of fat metabolism yields much less energy than the energy equivalent of fat tissue. This makes using the caloric density of fat (9.3 kcal/g) as a correction factor somewhat questionable.

Estimates of efficiency of fat deposition vary among species. Pullar and Webster (1974) determined that the efficiency of fat production in laboratory rats was 65 percent of the metabolizable energy available for production. This estimate was accepted to be a reasonable estimate of pine vole efficiency of fat deposition.

In order to verify this assumption a modification of the method described by Lofgreen (1965) and utilized for gray squirrels *(Sciurus carolinensus)* by Ludwick et al. (1969) was applied to bioenergetic data collected on 20 adult male and female pine voles during simulated summer conditions. Seasonal changes in the caloric value of fat tissue derived from its catabolism or needed for its deposition were considered to be nonexistent. The relationship between change in body weight of these pine voles and their metabolizable energy intake (MEI) is shown in figure 1. From this relationship, multiple regression analysis was used to partition MEI between maintenance energy requirements and change in body weight (energy retention) as follows:

$$MEI = ME_m + ME_p,$$

where ME_m is daily maintenance requirements and ME_p is daily

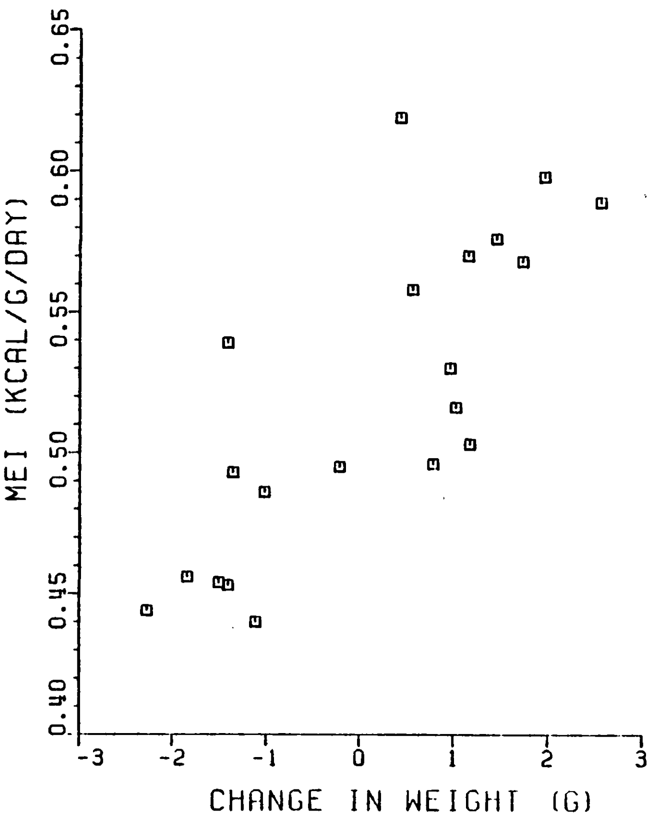

Figure 1. Relationship between total metabolizable energy intake (MEI) in kcal/g/day and change in body weight (g) in adult pine voles.

metabolizable energy available for production.

Since the process of fat deposition and fat breakdown possess different efficiencies, animals were separated into 2 groups; assignment depending upon whether the vole lost weight or gained weight during the 7-day trial. For the group of animals which lost weight the regression for predicting MEI was:

$MEI = ME_m + ME_p$ (r=0.89)

where:

$ME_m = 6.21 + 1.30X_1 - 2.32X_2$

$ME_p = 6.51CW$

X_1 = body weight in grams

X_2 = metabolic body weight in grams ($Kg^{0.75}$)

CW = change in body weight/7 days

The partial regression coefficient 6.51 for the variable CW represents the amount of MEI (kcal/day) obtained from the breakdown of 1 g of live body weight per day.

For the group of animals which gained weight the regression for predicting MEI was:

$MEI = ME_m + ME_p$ (r=0.93)

where:

$ME_m = 67.29 + 9.33X_1 - 25.82X_2$

$ME_p = 9.6CW$

The partial regression coefficient 9.60 for the variable CW represents the amount of MEI (kcal/day) required to deposit 1 g of body weight per day. Assuming that 2/3 of the body weight gain is fat and the remaining 1/3 composed of protein, carbohydrate, and water (Blaxter

1962), the efficiency of fat deposition (EF) in the pine vole can be estimated as follows:

$$EF = \frac{2/3(1) \text{ X } 9.3 \text{ kcal/g fat}}{9.6 \text{ kcal/g}} \text{ X } 100 = 65\%$$

This value of 65 percent efficiency for fat deposition is equivalent to the 65 percent efficiency determined by Pullar and Webster (1974) for the laboratory rat. Thus, if an animal gained weight during the trial the amount of 9.6 kcal/g was subtracted from MEI to obtain the maintenance energy requirements of the animal. Likewise, if an animal lost weight the equivalent of 7 kcal/g was added to MEI to obtain an estimate of maintenance energy requirements (Drozdz 1975). This value of 7.0 kcal was used since our value of 6.51 kcal/g derived from regression analysis was based on only a few animals (8) and is relatively close to the value of 7 kcal/g used and recommended by Drozdz (1975) and King (1961).

Seasonal Conditions

Mean monthly temperatures (1975-1978) in the study area were obtained from the Hydrologic Information Storage and Retrieval System (HISARS) for the Roanoke Airport weather station. Seasonal mean temperatures were determined as the mean for the period 1975-1978. Mean temperatures used to simulate seasonal conditions were 23C, 14C, 4C, and 13C for the summer, fall, winter, and spring seasons, respectively. Relative humidity was maintained at 36 percent. Photoperiods of 15L:9D, 12L:12D, 10L:14D, and 12L:12D were used during the summer, fall, winter, and spring seasons, respectively.

Sample Sizes

During the summer season trial, 28 adult pine voles were housed individually in metabolic cages. Fourteen voles (7 females and 7 males) were housed in metabolic cages with nesting material and 14 voles (6 females and 8 males) were housed in metabolic cages with exercise wheels and no nest. During the fall season, 30 adult voles were used in the trial. Seventeen (7 females and 10 males) voles were housed in metabolic cages with nests while 13 (7 females and 6 males) were housed in metabolic cages with exercise wheels and no nest. Twenty-nine adult voles were used during the winter season trial. Sixteen voles (8 female and 8 male) were housed in metabolic cages containing nesting material while 13 voles (9 females and 4 males) were housed in cages equipped with exercise wheels. During the spring season trial, 34 adult pine voles were utilized. Twenty-one voles (11 females and 10 males) were housed with nests while 13 voles (9 females and 4 males) were housed with exercise wheels.

Statistical Analysis

Linear and multiple regression techniques in the General Linear Models procedure of the Statistical Analysis System (SAS-76) were used in this study (Barr et al. 1976). Analysis of variance (Barr et al. 1976) was used to test differences in the bioenergetic parameters of voles due to sex and cage type (out-of-the-nest metabolism and in-the-nest metabolism). The statistical procedure of Graybill (p. 284, 1976) was used to test differences between regression equations.

Bioenergetics of Lactation and Neonatal Development

Experimental Design

The purpose of this phase of the study was to determine the energy costs of lactation only. These studies were carried out on wild-caught female voles which were maintained for at least 30 days in the laboratory before conception. Repeated attempts at detecting copulation by the occurrence of a vaginal plug resulted in females not breeding. The repeated handling of the animals appeared to initiate a stress response and a subsequent failure to breed. Due to this behavior, it was not possible to explore the energetic requirements for pregnancy in the pine vole. However, lactational reproductive costs are energetically the most expensive and therefore, an important phase of the annual reproductive and energy cycle in small mammal populations.

Adult female pine voles were live trapped from apple orchards in southwestern Virginia and maintained on a Purina Lab Chow diet for at least 1 month before being bred. Females were separated and paired with an adult male. Each pair was housed in wire bottom cages (24X18X18cm) which contained a separate nesting and feeding compartment. Approximately 75g of cotton gauze was supplied for nesting material to each pair. Purina Lab Chow and water was supplied to all voles *ad libitum* throughout the experimental period. Voles were maintained under controlled conditions in environmental chambers simulating a natural summer photoperiod and temperature regime of the apple orchard study area. Temperature was maintained at 23C ± 1C and the photoperiod was 14L:10D. Relative humidity was maintained at an average of 36 percent. Adult males were removed from the metabolic cages at the time of female parturition.

Metabolic measurements were collected for the entire period of lactation. Juvenile voles began to consume small quantities of solid food around 15-16 days of age and were eating substantial quantities at 18 days of age. However, they were not completely independent of the mother's milk until about 21 days of age. Therefore, measurements were made from day 1 through day 21 of lactation. Measurements were taken at 6-day intervals (1-6, 7-12, 13-18) except for the 3-day period from day 19 to 21.

A known quantity of lab chow was placed in each cage every other day. The Purina Lab Chow was ground in a Wiley Mill (40-mesh screen) and fed in this state to minimize spillage and caching. The remaining food was weighed and total food consumption determined as the difference between the amount given and the amount remaining. Samples of lab chow were oven-dried for 72 hours at 55C for determination of dry matter intake by using the percent dry matter of lab chow. Total collections of fecal waste production were made for each individual during each phase. Feces were oven-dried for 72 hours at 55C and weight of dry matter determined. Urine production was assumed to be 2 percent of the gross energy of lab chow consumed (calculated from Merson 1979).

Samples of feces from each family group for each 6-day phase were pelleted and combusted in an automatic Parr adiabatic oxygen bomb calorimeter for gross energy determination. The calorimeter was charged to 25 atmospheres and corrections were made for fuse wire and acid formation according to specifications supplied by the manufacturer. Similarly, energy equivalents for lab chow were determined. Total energy consumed, and excreted in the form of feces, was determined as the product of dry matter intake (lab chow) and dry matter production (feces) multiplied by their respective energy equivalents. Digested energy was determined by subtracting total fecal energy production from the total gross energy consumed. Metabolized energy intake (MEI) was determined by substracting the 2 percent correction factor for urine loss from the amount of energy digested. Digestive efficiency was the product of the amount of energy digested divided by the amount of energy consumed multiplied by 100.

Production

A colony of control females was housed singly with adult male voles for breeding purposes. This colony served as a source of young for the determination of gross body composition and energy equivalent changes during lactation. Adult males were removed from the cages at the time of female parturition. Lactating females were maintained on a lab chow diet and were given water *ad libitum.*

The gross body composition and energy equivalent of 41 young were determined. This included 33 neonates which were less than 24 hours old from a total of 10 different litters, and 8 weanling voles 18 days of age from a total of 4 different litters. In order to obtain a large enough sample for some analyses, it was necessary to pool neonates within a litter.

Percent water and dry matter content of the body was determined by lyophilizing preweighed carcasses for 48 hours. Dry weight was the weight of the carcass following lyophilization. The percentage of water in the body was the difference between the wet weight minus the dry weight divided by the wet weight times 100. Percentage of dry matter was equal to 100 minus percent water. Pooling was not necessary for this analysis, therefore body water and dry matter content were determined individually for all 41 young.

The percentage of body fat was determined for 10 pooled litters of neonates and 8 weanling voles. Fat content was determined by ether (anhydrous) extraction in a Soxhlet Apparatus (A.O.A.C. 1973). Samples were ground in a mortar and mixed thoroughly. The oven-dried carcass was wrapped in previously extracted filter paper, weighed, and extracted for a period of 16 hours. Following extraction, packets were dried to a constant weight and fat content was calculated as initial minus the final weight of the packet. Percent fat was determined on a dry weight basis. Lean weight was calculated as 100 minus percent fat.

Samples were ashed in a muffle furnace at 500C for 2 hours. Percent ash content was determined as weight of residue remaining divided by the lean dry weight before ashing. Body protein concentration was determined on a lean dry weight basis and was assumed to be equal to that portion of the lean tissue lost due to ashing in the muffle furnace: 100 minus percent ash.

Energy equivalents for fat and lean body tissue were determined by combustion in a Parr automatic adiabatic oxygen bomb calorimeter.

Corrections were made for fuse wire and nitric acid formation. Samples of fat for energy content determinations were obtained from the fat residue remaining after ether extraction. Body energy equivalents were calculated as the sum of the products of percent fat and percent lean tissue times their respective energy equivalents.

Statistical Analysis

Linear and multiple regression techniques in the General Linear Models procedure of the Statistical Analysis System (SAS-76) were used in this study (Barr et al. 1976). The correlation procedure of SAS-76 was used to compute correlation coefficients between various variables and an approximation to its significance probability.

Bioenergetics of Postweaning Development

Experimental Design

This experiment was designed to determine the energy requirements of pine voles for the period of postweaning development from age 22 to 46 days. Voles used were from litters consisting of 1 to 3 individuals. Voles were separated from their mothers and litter mates at age 21 days. There was no change in the temperature or light regime from conditions experienced during lactation. Temperature was maintained in an environmental chamber at 23C ± 1C with 14L:10D photoperiod which were the mean conditions observed in the field for the summer season. Relative humidity was maintained at approximately 36 percent throughout the trial. All juveniles were placed in identical wire bottom metabolism cages as were used during the lactation phase of their development. Nests were available in all cages. Watering and feeding procedures were identical to those used during the lactation developmental stage. Purina Laboratory Chow and water were supplied to all animals *ad libitum*. All juveniles were from litters of wild-caught females which were kept in captivity for at least 30 days prior to being bred by captive male voles.

Food consumption, energy utilization, and tissue deposition were monitored on a total of 28 juvenile voles from 22 to 46 days of age. Every 6 days each juvenile vole was weighed and the bioenergetic requirements determined for the previous 6 days. The experiment was begun at 22 days of age because juvenile voles did not appear to become completely independent of the mother and her milk until around 21 days of age. Growth was then monitored through the period of most intensive weight change, up to 46 days of age when the juvenile voles were molting into their characteristic sub-adult pelage (Paul 1970).

Voles were given a known amount of Purina Laboratory Chow once every 2 days. At the end of each 2-day period, uneaten food was collected and weighed. Total consumption over each 6-day period was determined by subtracting the total amount of uneaten food from the total amount of food given. Food samples were oven-dried at 55C for 72 hours to determine dry matter content. Feces were collected and dry-matter content determined by oven drying for 72 hours at 55C. Urine energy production by juvenile voles was assumed to be 4 percent of the gross energy of lab chow consumed (Drozdz et al. 1972).

Samples of feces from each vole for each 6-day period were pelleted and combusted in a Parr adiabatic oxygen bomb calorimeter for gross energy determination. Samples of lab chow were likewise bombed for gross energy determination. Total energy consumed and excreted in the form of feces was determined as the product of dry matter intake (lab chow) and dry matter production (feces) multiplied by their respective energy equivalents. Digested energy was determined by subtracting total fece energy production from the total gross energy consumed. Metabolizable energy intake (MEI_j) was determined by subtracting the 4 percent correction factor for urine loss from the amount of energy digested.

An attempt was made to separate the total metabolizable energy intake by a juvenile vole into that portion required for maintenance (M_j) and that portion which was used for tissue production (P_j). In order to separate these 2 components it was first necessary to determine the amount of energy required for growth of gross body components such as protein and fat. The caloric equivalent of weight gain in juvenile voles was determined from body composition analysis (using procedures described previously) of voles 18 and 50 days of age (Tables 9, 10 and 11). The total gain in body energy was divided by the total gain in live body weight to obtain the caloric equivalent of 1 g body weight gain. Maintenance energy (M_j) or respiration was assumed to be equal to the total metabolizable energy intake (MEI_j) of a juvenile vole minus the energy deposited as tissue growth (P_j).

Statistical Analysis

Linear and multiple regression techniques in the General Linear

Models procedure of the Statistical Analysis System (SAS-76) were used in this study (Barr et al. 1976). Two-factor Analysis of Variance of SAS-76 was used to test differences in the bioenergetic parameters of juvenile pine voles due to sex and age class.

Determining Diet Digestibility of Pine Voles Under Field Conditions Utilizing the Lignin Tracer Technique

Laboratory Study

Pine voles were live trapped from apple orchards in southwestern Virginia and maintained under laboratory conditions for at least 1 week prior to data collection. Animals were placed on either a diet of low digestibility (Purina Rabbit Chow) or high digestibility (Purina Laboratory Chow) immediately after capture. Measurements of ingestion and egestion were made over a 7-day period on 7 voles, for each diet, maintained in metabolic cages. Water was supplied *ad libitum*. Percent dry matter was determined for each chow .by oven-drying at 55C for 72 hours. The amount of uneaten food remaining after each 24-hour period was weighed and subtracted from the amount given at the beginning of the period. Consumption was then converted to a dry weight basis. Feces were collected and oven-dried at 55C for 72 hours. Gross energy determinations of food and feces was determined with a Parr adiabatic oxygen bomb calorimeter. Corrections were made for both fuse wire and nitric acid formation. Dry matter and energy digestibility of each chow was calculated from the amount of ingestion and egestion over the 7-day period for each animal.

Thirty-six voles maintained on the high digestibility diet and 28 voles maintained on the low digestibility diet were sacrificed. Stomach contents were removed and fecal pellets collected for lignin determination. Samples were lyophilized for 48 hours and weighed. Dried samples were ground in a Wiley mill (40-mesh screen) and thoroughly mixed. A portion of each sample was removed for gross energy determination in a Phillipson microbomb calorimeter (Phillipson 1964). Two or 3 determinations of gross energy were made for each sample.

Lignin concentrations were determined in chow, stomach, and fecal samples using the permanganate lignin procedure outlined by Goering and Van Soest (1970). Approximately 1 gram of material was required for both energy and lignin determinations. This necessitated the pooling of animals in order to obtain a large enough sample for the analysis.

Field Study

Pine voles were snap trapped from 2 southwestern Virginia apple orchards (a maintained and an abandoned orchard) which varied in habitat structure and composition. Seventeen to 36 voles were trapped from each orchard at bimonthly intervals between May 1978 and March 1979. Stomach contents and feces from the lower portion of the large intestine were removed from each animal. Samples were processed in the same manner as in the laboratory phase. Mean weights of extracted feces were extremely small. This required the pooling of between 11 to 25 animals to obtain a sample large enough for both lignin and gross energy determination.

Mathematical Analysis

Digestible dry matter (% DDM) and digestible energy (% DE) of rabbit chow and rodent chow was determined from

$$\text{DDM or DE} = \frac{\text{I-E}}{\text{I}} \times 100$$

where I is the dry matter (for DDM) or total energy (for DE) ingested and E is the dry matter (for DDM) or total energy (for DE) egested by the animal.

Digestible dry matter (DDM) of the stomach contents, expressed as a percent, was calculated from

$$\text{DDM} = 100 - 100 \times \frac{\text{LS}}{\text{LF}} \qquad (1)$$

where LS is the percent lignin concentration in the stomach contents and LF is the percent lignin concentration in the feces. Digestible energy (DE) is calculated by using the change in the ratio of energy concentration with reference to the concentration of lignin in the stomach contents and feces. DE expressed as a percent was calculated from

$$\text{DE} = 100 - 100 \times \frac{\text{LS} \times \text{GEF}}{\text{LF} \times \text{GES}} \qquad (2)$$

where GEF (kcal/g dry wt.) is the gross energy concentration of the feces and GES (kcal/g dry wt.) is the gross energy concentration of the stomach contents. Advantages to using equation number 2 is that the GEF:GES ratio can be substituted with the change in fece:stomach concentrations of any other nutrient to calculate the digestibility of that nutrient.

The above equations calculate the apparent digestion coefficients for dry matter and energy with respect to total particulate matter in the stomach (dry weight). This differs from the equation used by Johnson and Maxell (1966) because their equation calculates the ash-free digestibility of organic matter.

When determining digestion coefficients of nutrients by the indicator method, it is assumed that the reference indicator passes through the alimentary tract at a uniform rate. If the reference material accumulates in the stomach or passes through the stomach quickly, corrections will have to be made to account for this, since the technique assumes that the composition of the stomach contents is similar to the forage before its ingestion. A correction factor (CF) obtained from the laboratory analysis using rabbit chow and rodent chow was later applied to the feces so that CLF is equal to LFXCF.

Seasonal Changes in the Available Primary Production of An Abandoned and Maintained Apple Orchard Habitat

Study Area

The field phase of this research was conducted on the 2 apple orchards located in Daleville, Virginia, in the Roanoke Valley, which were used for the pine vole stomach analyses. The orchards selected have been the subject of periodic research by our department since 1975, so a considerable data base existed from which to work. The 2 study areas represented an abandoned and a maintained apple orchard. The abandoned orchard has been out of production and maintenance for approximately 9 years. The maintained apple orchard was actively maintained by mowing and tree pruning, however, no form of vole control had been implemented for at least 9 years. The sites were chosen on the basis of their similarity in aspect, slope, and soil characteristics and their dissimilarity in vegetative composition and structure. The abandoned apple orchard was undergoing a form of old-field succession while the maintained apple orchard was predominately a grass dominated field. The composition and structure of the habitats in each orchard was previously described by Noffsinger (1976).

Herbaceous Production

Seasonal biomass and energy production available to *Microtus pinetorum* was measured in the maintained and abandoned apple orchard. Forage phenology data were obtained from field observations in each of the orchards.

A 100 percent clip of green vegetation was made on 24 ($1m^2$) sample plots for each of the four seasons sampled. In addition, all wind-felled apples lying on the ground were collected from each plot. Within each orchard habitat, 6 unreplecated plots were randomly chosen beneath the dripline of apple tree canopies and 6 unreplecated plots were randomly chosen outside the dripline. All sample plots were located outside established trapping grids. A (1mXlm) rectangular frame was used to delineate sample plot boundaries.

Vegetation was separated by species for each plot and fresh weight determined. Forage dry matter production was determined for each plot by oven drying plant material for 48 hours at 70C. Forage moisture content was determined as the water lost from the above drying scheme. Forage samples were later ground in a Wiley mill to pass a 40-mesh screen. Gross energy for each species was determined by combustion in a Parr automatic adiabatic oxygen bomb calorimeter. Gross energy production of a species for a given sample plot was estimated by multiplying total dry matter/plot/species by its respective energy equivalent.

Subjective judgments of whether a plant was available for vole consumption were occasionally made. Woody shrubs, vines, and tall forbs which appeared to be unharvestable by voles were excluded from the total clip. Such a procedure was used to more accurately estimate production available to pine voles. Only above-ground vegetative parts were harvested with the exception of *Allium vineale* where the below ground rootstock was removed when encountered.

Sampling dates for each season were (1) Summer (mid-July, 1978), (2) Fall (late-October, 1978), (3) Winter (late-January, 1979), and (4) Spring (early-May, 1979).

Soft Mast Production

Apple production was estimated at monthly intervals for both orchard habitats. Within each orchard, 10 ($1m^2$) mast traps were randomly placed beneath the dripline of 10 apple trees. Mast traps were situated approximately 1m above the ground to prevent predation on the collected crop. Traps were checked at regular monthly intervals and samples were weighed fresh. Dry matter production for each plot was determined by oven drying at 70C for 30 days. Moisture content and gross energy production for each plot was determined as before.

Nutrient Analysis

A nutritive analysis of the major plant species was made for each of the apple orchard habitats following accepted A.O.A.C. (1975) methods. Once samples were ground to pass a 40-mesh screen they were subsampled for proximate analysis and determination of total soluble carbohydrates (%TNC). Analyses were made by the Virginia Polytechnic Institute and State University Forage Testing Lab and the Forage Analysis Lab of the Agronomy Department. Protein, fiber, ether extract, ash and nitrogen free extract (N.F.E.) were expressed as a percent of the total dry weight of the sample undergoing proximate analysis. Percent TNC was also expressed on a dry weight basis. A nutrient analysis of the major plant species was made for each of the 4 seasons.

Comparisons between the nutritional quality of foods collected in both the abandoned and maintained apple orchard were made, based on the production and corresponding nutrient profile of the major plant species.

Food Preferences

Food preferences of live-trapped voles were studied during late spring (May, 1978) using "cafeteria choice tests," similar to those used by previous researchers (Gorecki and Gebczynska 1962, Drozdz 1966, and Pinowski and Drozdz 1975). The method involves offering voles in the laboratory a choice of several kinds of foods and then estimating the degree of consumption of each food. Foods selected for this study were chosen on the basis of previous food habit information collected by Cengel (1975) and Estep (1975), as well as on the abundance and distribution of forages within the orchards under study.

Two series of "choice tests" were employed in this experiment. The first test involved housing each animal singly in standard wire-bottom laboratory cages and offering a choice of 3 foods comprised of apple fruit, bulbs, grasses, forbs, or vines. The second experiment involved placing 4 animals per cage and offering each group (3) a selection of 4 foods comprised of forbs and grasses. Since the first experiment showed small individual differences in food preferences, the second design was employed to simplify the logistics. Water was supplied to all animals *ad libitum*.

A known quantity of each food was placed daily into each cage. The food was periodically sprayed with water to keep the vegetation from wilting. The remaining food was collected after each feeding, separated to species and weighed. The degree of consumption for each forage was determined by subtracting the amount remaining from the amount given (corrections for desiccation were not made since it was kept to a minimum by spraying). All of the forages offered were clipped fresh from apple orchards under study. Estimates of consumption were made at 12 hour intervals over a 24 to 48 hour period. Forages were ranked in decreasing order of preference based on their degree of consumption.

Statistical Analysis

Data were analyzed using the Statistical Analysis System (SAS-76, Barr et al. 1976). Differences in herbaceous production between apple orchard habitats were analyzed for each season using the *t*-test procedure of SAS-76. This procedure computes an F-statistic which tests the hypothesis that the variances of the means are equal and an approximation of *t* appropriate when the variances are not equal. Monthly apple production was analyzed by Analysis of Variance using the General Linear Models procedure of SAS-76 with the appropriate model statement.

RESULTS

Seasonal Energetic Requirements Of Adult Pine Voles

Summer Season

With Nest. Bioenergetic parameters for adult female, adult male, and adult male and female pine voles combined are shown in Tables 1, 2, and 3, respectively. Voles digested 83.48 ± 0.33 (SE) percent of the gross energy in lab chow and metabolized an estimated 81.48 ± 0.33 (SE) percent.

Daily energy requirements for maintenance increased with an increase in body weight. The daily energy budget (DEB) of adult female pine voles was described by the equation:

$$\text{DEB (kcal/animal/day)} = 0.47W - 0.095$$

where W is body weight in grams. The corresponding correlation coefficient for this relationship was $r = 0.96$. The daily energy budget of adult male pine voles was described by the equation:

$$\text{DEB (kcal/animal/day)} = 0.82W - 7.80.$$

The corresponding correlation coefficient was $r = 0.97$. The average daily energy budget of all adult voles of both sexes combined was described by the equation:

$$\text{DEB (kcal/animal/day)} = 0.70W - 5.25.$$

The corresponding correlation coefficient was $r = 0.92$. Expressed on a per gram body weight basis, the DEB for maintenance was 0.470 ± 0.006 (SE) kcal/g/day for adult females, 0.513 ± 0.019 (SE) kcal/g/day

Table 1. Seasonal bioenergetic parameters (mean ± SE) of adult female pine voles in metabolic cages with nests and corresponding ambient temperatures.

Parameter	Summer	Fall	Winter	Spring
Ambient temperature (°C)	23	14	4	13
N	7	7	8	11
Body weight (g)	24.63±1.13	26.46±1.25	25.72±0.97	28.66±0.92
Consumption (kcal/day)	17.48 ± 0.91	22.02±0.98	22.22±0.72	19.58±0.53
Egested energy (kcal/day)	2.94±0.21	3.96±0.17	3.80±0.17	3.58±0.06
Digested energy (kcal/day)	14.53±0.72	18.05±0.83	18.41±0.56	16.00±0.48
Urinary energy (kcal/day)[1]	0.29±0.01	0.36±0.02	0.37±0.01	0.32±0.01
Production (g/day)	0.28±0.08	0.08±0.14	-0.20±0.03	-0.13±0.03
Production energy (kcal/day)	2.66±0.77	0.94±0.44	-1.38±0.22	-0.93±0.21
Maintenance energy (kcal/day)	11.58±0.56	16.87±0.81	19.42±0.50	16.61±0.57

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[1] Estimated from Merson (1979).

Table 2. Seasonal bioenergetic parameters (mean ± SE) of adult male pine voles in metabolic cages with nests and corresponding ambient temperatures.

Parameter	Summer	Fall	Winter	Spring
Ambient temperature (°C)	23	14	4	13
N	7	10	8	10
Body weight (g)	25.44±1.37	24.61±1.25	24.56±0.82	28.14±0.90
Consumption (kcal/day)	17.10±1.43	22.60±1.28	21.19±0.79	18.51±1.19
Egested energy (kcal/day)	2.78±0.23	3.96±0.22	3.64±0.15	3.56±0.16
Digested energy (kcal/day)	14.33±1.20	18.64±1.06	17.54±0.65	14.95±1.05
Urinary energy (kcal/day)[1]	0.29±0.02	0.37±0.02	0.35±0.01	0.30±0.02
Production (g/day)	0.08±0.05	0.20±0.03	-0.07±0.09	-0.28±0.09
Production energy (kcal/day)	0.87±0.47	2.12±0.26	-0.30±0.87	-1.96±0.63
Maintenance energy (kcal/day)	13.17±1.16	16.36±1.24	17.49±0.83	16.61±0.62

[1] Estimated from Merson (1979).

Table 3. Seasonal bioenergetic parameters (mean ± SE) of adult male and female pine voles in metabolic cages with nests and corresponding ambient temperatures.

Parameter	Summer	Fall	Winter	Spring
Ambient temperature (°C)	23	14	4	13
N	14	17	16	21
Body weight (g)	25.04±0.86	25.43±0.87	25.14±0.63	28.41±0.63
Consumption (kcal/day)	17.29±0.81	22.34±0.79	21.70±0.53	19.07±0.63
Egested energy (kcal/day)	2.86±0.15	3.96±0.14	3.72±0.11	3.57±0.08
Digested energy (kcal/day)	14.23±0.67	18.23±0.69	17.98±0.43	15.50±0.56
Urinary energy (kcal/day)[1]	0.29±0.01	0.36±0.01	0.36±0.01	0.31±0.01
Production (g/day)	0.18±0.05	0.16±0.03	-0.13±0.05	-0.20±0.05
Production energy (kcal/day)	1.76±0.50	1.61±0.28	-0.84±0.45	-1.42±0.33
Maintenance energy (kcal/day)	12.38±0.66	16.58±0.75	18.46±0.53	16.61±0.41

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[1] Estimated from Merson (1979).

for adult males, and 0.491 ± 0.011 (SE) kcal/g/day for all adults combined. There was a significant difference between the regression lines describing the DEB for male and female adult pine voles ($F = 8.31$, $df = (2,10)$, $P<0.01$).

With Exercise Wheel. Bioenergetic parameters for adult female, adult male, and adult male and female pine voles combined are shown in Tables 4, 5, and 6, respectively. Voles with exercise wheel equipped cages digested 82.48 ± 0.29 (SE) percent of the gross energy in lab chow and metabolized 80.48 ± 0.29 (SE) percent. Fecal and urinary excretion was significantly greater ($P<0.001$) than values for voles housed in metabolic cages with nests. Food consumption was also greater ($P<0.001$) for voles housed in exercise wheel cages. Digestive efficiency was significantly lower ($P<0.05$) for voles in exercise wheel cages. This is probably a direct result of increased food consumption and subsequent increased rate of passage of the foodstuff through the alimentary tract.

The degree of activity between individual animals varied considerably. The mean level of activity was 8428 ± 1285 (SE) rev/animal/day which converts to 4130 m/animal/day traveled. The daily energy budget of adult voles in exercise wheel cages was significantly greater ($P<0.001$) than that of voles in cages with nests. The DEB was described by the equation:

$$\text{DEB (kcal/animal/day)} = 0.73W + 0.00062D - 7.17$$

where D is the level of activity in m/animal/day traveled. The

Table 4. Seasonal bioenergetic parameters (mean ± SE) of adult female pine voles in activity wheel equipped metabolic cages and corresponding ambient temperatures.

Parameter	Summer	Fall	Winter	Spring
Ambient temperature (^{o}C)	23	14	4	13
N	6	7	9	9
Body weight (g)	27.73±0.50	23.93±0.94	26.40±0.74	28.04±0.89
Consumption (kcal/day)	20.26±0.73	30.89±1.05	31.16±1.18	31.18±0.67
Egested energy (kcal/day)	3.58±0.12	6.03±0.35	5.77±0.31	5.56±0.21
Digested energy (kcal/day)	16.67±0.62	24.86±0.73	25.39±0.98	25.62±0.61
Urinary energy (kcal/day)[1]	0.33±0.01	0.50±0.01	0.51±0.02	0.51±0.01
Production (g/day)	0.13±0.05	0.12±0.09	-0.09±0.07	-0.03±0.08
Production energy (kcal/day)	1.30±0.50	1.32±0.73	-0.52±0.58	-0.02±0.61
Maintenance energy (kcal/day)	15.04±0.58	23.04±0.89	25.40±0.84	25.12±0.86

[1] Estimated from Merson (1979).

Table 5. Seasonal bioenergetic parameters (mean ± SE) of adult male pine voles in activity wheel equipped metabolic cages and corresponding ambient temperatures.

Parameter	Summer	Fall	Winter	Spring
Ambient temperature (°C)	23	14	4	13
N	8	6	4	4
Body weight (g)	28.52±0.99	29.55±2.12	24.82±1.86	26.45±0.96
Consumption (kcal/day)	22.29±0.93	31.92±1.49	29.26±1.43	31.24±1.27
Egested energy (kcal/day)	3.90±0.15	5.82±0.35	5.37±0.22	6.16±0.14
Digested energy (kcal/day)	18.39±0.81	26.10±1.22	23.87±1.22	25.07±1.22
Urinary energy (kcal/day)[1]	0.37±0.02	0.52±0.02	0.48±0.02	0.50±0.02
Production (g/day)	0.14±0.08	0.04±0.05	-0.12±0.07	0.01±0.15
Production energy (kcal/day)	1.38±0.74	0.44±0.47	-0.82±0.49	0.34±1.31
Maintenance energy (kcal/day)	16.64±0.87	25.14±1.14	24.21±1.35	24.23±0.84

[1] Estimated from Merson (1979).

Table 6. Seasonal bioenergetic parameters (mean ± SE) of adult male and female pine voles in activity wheel equipped metabolic cages and corresponding ambient temperatures.

Parameter	Summer	Fall	Winter	Spring
Ambient temperature (°C)	23	14	4	13
N	14	13	13	13
Body weight (g)	28.22±0.63	26.52±1.33	25.92±0.75	27.55±0.69
Consumption (kcal/day)	21.51±0.68	31.36±0.86	30.58±0.93	31.20±0.57
Egested energy (kcal/day)	3.78±0.11	5.93±0.24	5.65±0.22	5.75±0.17
Digested energy (kcal/day)	17.73±0.58	25.43±0.68	24.92±0.77	25.45±0.54
Urinary energy (kcal/day)[1]	0.35±0.01	0.51±0.01	0.50±0.02	0.51±0.01
Production (g/day)	0.14±0.05	0.08±0.05	-0.10±0.05	-0.02±0.06
Production energy (kcal/day)	1.35±0.48	0.92±0.45	-0.61±0.42	-0.09±0.55
Maintenance energy (kcal/day)	16.02±0.60	24.01±0.74	25.04±0.70	24.85±0.64

[1] Estimated from Merson (1979).

corresponding correlation coefficient was r = 0.81. Expressed on a per gram body weight basis, the DEB of adult voles was 0.568 kcal/g/day. Thus, a 24g vole would require 11.78 kcal/animal/day when housed in the metabolic cage with a nest, and would require 13.63 kcal/animal/day if housed in the exercise wheel cage without a nest. Assuming that the values represent in-the-nest and out-of-the-nest activity, this results in a 15.7 percent increase in the DEB of adult pine voles during the summer season.

Fall Season

With Nest. Bioenergetic parameters for adult female, adult male, and adult male and female pine voles combined are shown in Tables 1, 2, and 3, respectively. Voles with nests during the fall season digested 82.26 ± 0.21 (SE) percent of the gross energy in lab chow and metabolized an estimated 80.26 ± 0.21 (SE) percent.

There was a definite increase in food consumption during the fall season probably due to the added cost of thermoregulation. The daily requirements for maintenance increased with an increase in body weight. The daily energy budget of adult female pine voles was described by the equation:

$$\text{DEB (kcal/animal/day)} = 2.08 + 0.56W.$$

The corresponding correlation coefficient was r = 0.87. The daily energy budget of adult male pine voles was described by the equation:

$$\text{DEB (kcal/animal/day)} = 0.90W - 5.75.$$

The corresponding correlation coefficient was $r = 0.91$. The daily energy budget of all adult voles combined was described by the equation:

$$\text{DEB (kcal/animal/day)} = 0.86W - 5.03.$$

The corresponding correlation coefficient for this relationship was $r = 0.87$. Expressed on a per gram body weight basis, the daily energy budget for maintenance was 0.638 ± 0.017 (SE) kcal/g/day for adult females, 0.660 ± 0.023 (SE) kcal/g/day for adult males and 0.652 ± 0.015 (SE) kcal/g/day for all adult voles combined. There was no significant difference between the regression lines describing the DEB of male and female adult pine voles based on body weight ($F = 1.50$, $df = (1,14)$, $P > 0.05$).

With Exercise Wheel. The bioenergetic parameters determined for out-of-the-nest activity for adult female, adult male and adult male and female pine voles combined are shown in Tables 4, 5, and 6, respectively. The increase in food consumption by these animals over that of voles in nest equipped cages resulted in a significant decrease ($P<0.05$) in digestive efficiency, similar to what occurred during the summer season. Voles in cages with exercise wheels during the fall season digested 81.13 ± 0.45 (SE) percent of the gross energy in lab chow and metabolized an estimated 79.13 ± 0.45 (SE) percent.

Food consumption by these voles was significantly greater ($P<0.001$) than that of voles housed in metabolic cages with nests. Fecal and urinary waste production was similarly greater ($P<0.001$). Digestive efficiency was also lower ($P<0.05$) for out-of-the-nest animals than for the nesting animals, once again, due primarily to the increased rate of food consumption.

The mean level of activity for voles during the fall season was 2957 ± 390 (SE) rev/animal/day which converts to 1449 ± 191 (SE) m/animal/day traveled. This was a considerable reduction in activity from what was observed during the summer season. The daily energy budget of voles for out-of-the-nest activity was significantly greater ($P<0.001$) than energy expenditures of voles with nests despite the reduction in activity. The DEB for out-of-the-nest activity was described by the equation:

$$\text{DEB (kcal/animal/day)} = 11.05 + 0.46W + 0.00042D$$

where D is the degree of activity measured in m/animal/day traveled. Expressed on a per gram body weight basis the DEB of adult voles was 0.917 ± 0.026 (SE) kcal/g/day. A 24g vole would require about 15.65 kcal/animal/day when housed with a nest while 22.01 kcal/animal/day would be required for out-of-the-nest activity. This amounts to a 40.6 percent increase in energy expenditure over that which is required for in-the-nest activity. This was a considerable increase in energy requirements for out-of-the-nest activity compared to those for the summer season (15.7%). This was probably due to the increased cost of thermoregulation at a lower temperature (14C).

Winter Season

With Nest. Bioenergetic parameters determined for adult female, adult male and adult male and female pine voles combined are shown in Tables 1, 2, and 3, respectively. Fecal and urinary waste production for the winter season was similar to that during the fall season. Voles with nests during the winter season digested 82.86 ± 0.21 (SE) percent of the gross energy of lab chow and metabolized an estimated 80.86 ± 0.21 (SE) percent.

The daily maintenance energy requirements of these voles increased with an increase in body weight. The daily energy budget of adult female pine voles was described by the equation:

$$\text{DEB (kcal/animal/day)} = 8.38 + 0.43W.$$

The corresponding correlation coefficient for this relationship was $r = 0.83$. The daily energy budget of adult male pine voles was described by the equation:

$$\text{DEB (kcal/animal/day)} = 0.33 + 0.70W.$$

The corresponding correlation coefficient was $r = 0.69$. The daily energy budget for all adult voles combined was described by the equation:

$$\text{DEB (kcal/animal/day)} = 3.23 + 0.60W.$$

The correlation coefficient for this relationship was $r = 0.72$. Expressed on a per gram body weight basis the DEB for maintenance was 0.758 ± 0.016 (SE) kcal/g/day for adult females, 0.712 ± 0.025 (SE) kcal/g/day for adult males, and 0.735 ± 0.015 (SE) kcal/g/day for all adults combined. There was no significant difference between the regression lines describing the DEB for male and female pine voles based on body weight ($F = 1.92$, $df = (2,12)$, $P > 0.05$).

With Exercise Wheel. Bioenergetic parameters determined for adult female, adult male, and adult male and female pine voles combined in exercise wheel metabolic cages during the winter season are shown in Tables 4, 5, and 6, respectively. Voles with exercise wheels during the winter season digested 81.52 ± 0.43 (SE) percent of the gross energy in lab chow and metabolized an estimated 79.52 ± 0.43 (SE) percent. This degree of digestive efficiency was similar to what was observed in the fall season. Similar to what was observed in the fall and summer season, fecal and urinary waste production for out-of-the-nest activity was significantly greater ($P<0.001$) than for voles with nests. Food consumption was also significantly greater ($P<0.001$) for these animals when compared to voles with nests. Digestive efficiency was significantly lower ($P<0.05$) for voles without nests. This same trend was observed for both the summer and fall seasons.

The mean level of activity was slightly greater than levels observed during the fall season, but still remained considerably lower than those in the summer season. The mean level of activity was 3565 ± 602 (SE) rev/animal/day which converts to 1746 ± 296 (SE) m/animal/day traveled. The daily energy budget of adult voles for out-of-the-nest activity was described by the following equation:

$$\text{DEB (kcal/animal/day)} = 5.71 + 0.83W - 0.0012D$$

where D is distance traveled in m/animal/day. The corresponding correlation coefficient for the above relationship was $r = 0.88$. The effect of increased levels of activity on an individual vole's energy budget for the winter season was in sharp contrast to what was observed during the fall and summer seasons. The above beta coefficient for the independent variable D was negative which results in an overall decrease in the daily energy budget with increased levels of activity. This was unexpected and difficult to interpret. It appeared from this relationship that moderate levels of activity could possibly result in beneficial savings in energy expenditures for thermoregulation. Expressed on a per gram body weight basis the DEB of adult voles was 0.969 ± 0.020 (S) kcal/g/day, a slight increase over that observed for the fall season. A 24g vole would require 17.64 kcal/animal/day for in-the-nest activity, while requiring 23.26 kcal/animal/day for out-of-the-nest activity. This resulted in a 31.8 percent increase in energy expenditure which is slightly lower than the 40.6 percent increase observed during the fall season.

Spring Season

With Nest. Bioenergetic parameters determined for adult female, adult male, and adult male and female pine voles combined are shown in Tables 1, 2, and 3, respectively. Mean body weight for voles during the spring season were higher than for other seasons of the year. Voles with nests during the spring season digested 81.00 ± 0.48 (SE) percent of the gross energy in lab chow and metabolized an estimated 79.00 ± 0.48 (SE) percent.

The daily energy requirements for maintenance increased with an increase in body weight. The daily energy budget of adult female pine voles for the spring season was described by the equation:

$$\text{DEB (kcal/animal/day)} = 2.15 + 0.050W.$$

The corresponding correlation coefficient for this relationship was $r = 0.81$. The daily energy budget of adult male pine voles for the spring season was described by the equation:

$$\text{DEB (kcal/animal/day)} = 2.72 + 0.49W.$$

The corresponding correlation coefficient for this relationship was $r = 0.72$. The daily energy budget of all adult voles combined was described by the equation:

$$\text{DEB (kcal/animal/day)} = 2.53 + 0.50W.$$

The corresponding correlation coefficient for this relationship was $r = 0.76$. Expressed on a per gram body weight basis, the DEB for maintenance was 0.580 ± 0.012 (SE) kcal/g/day for adult females, 0.591 ± 0.016 (SE) kcal/g/day for adult males and 0.585 ± 0.010 (SE) kcal/g/day for adult male and female pine voles combined. There was no significant difference between the regression lines describing the DEB for male and female pine voles based on body weight ($F = 0.107$, $df = (2,17)$, $P>0.05$).

With Exercise Wheel. The bioenergetic parameters determined for adult female, adult male, and adult male and female pine voles combined for out-of-the-nest activity during the spring season are shown in Tables 4, 5, and 6, respectively. Mean body weight was also higher for this group of animals when compared to previous seasons. Voles in exercise wheel cages during the spring season digested 81.54 ± 0.54 (SE) percent of the gross energy in lab chow and metabolized an estimated 79.54 ± 0.57 (SE) percent. Fecal and urinary excretion was significantly greater ($P<0.001$) for out-of-the-nest activity than for voles with nests. Food consumption was also significantly greater ($P<0.001$). There was no difference in digestive efficiency ($P>0.05$) due to cage type or sex. This differed from what was observed in previous seasonal trials.

The degree of activity was greater than fall and winter levels, but lower than summer levels. Mean level of activity observed for the spring season was 6855 ± 1187 (SE) rev/animal/day which converts to 3359 ± 582 (SE) m/animal/day traveled. The daily energy budget for out-of-the-nest activity was significantly greater than ($P<0.001$) energy expenditures by voles with nests. The daily energy budget for out-of-the-nest activity was described by the equation:

$$\text{DEB (kcal/animal/day)} = 9.93 + 0.56W - 0.00016D$$

where D is the degree of activity in m/animal/day traveled. The corresponding correlation coefficient for this relationship was $r = 0.65$. The influence of increased levels of activity in total daily energy expenditure was similar to what was observed for the winter season. The negative beta coefficient for the variable D indicates a reduced energy budget with moderate increases in the level of activity. Expressed on a per gram body weight basis the daily energy budget of adult voles for out-of-the-nest activity amounted to 0.904 ± 0.020 (SE) kcal/g/day. A 24g vole would require approximately 14.04 kcal/animal/day for maintenance with a nest and 21.70 kcal/animal/day for out-of-the-nest activity during the spring.

This amounted to a 54.6 percent increase in energy expenditure by adult voles. This percentage was higher than estimates derived for all other seasons.

Seasonal Comparisons

The linear regression lines describing the daily energy budget of adult male and female pine voles combined, based on body weight (Figure 2), were tested for significant differences between seasons. The regression describing the daily energy budget of voles during the summer season was significantly different from the regressions for the fall season ($F = 9.99$, $df = (9,27)$, $P<0.001$), the winter season ($F = 20.28$, $df = (9,26)$, $P<0.001$), and the spring season ($F = 5.14$, $df = (10,31)$, $P<0.01$). There was also a significant difference between the regression equations for the fall and spring seasons ($F = 6.87$, $df = (3,34)$, $P<0.01$). The regressions for the winter and fall seasons were also found to be significantly different ($F = 7.47$, $df = (2,29)$, $P<0.01$) from one another. Likewise, the regressions for the winter and spring seasons were significantly different ($F = 15.38$, $df = (3,33)$, $P<0.001$) from one another.

Bioenergetics Of Lactation In Female Pine Voles

Female Body Weight

The mean body weight of all lactating females was 28.9 ± 0.4 (SE) g for the whole period of lactation. The weight dynamics throughout

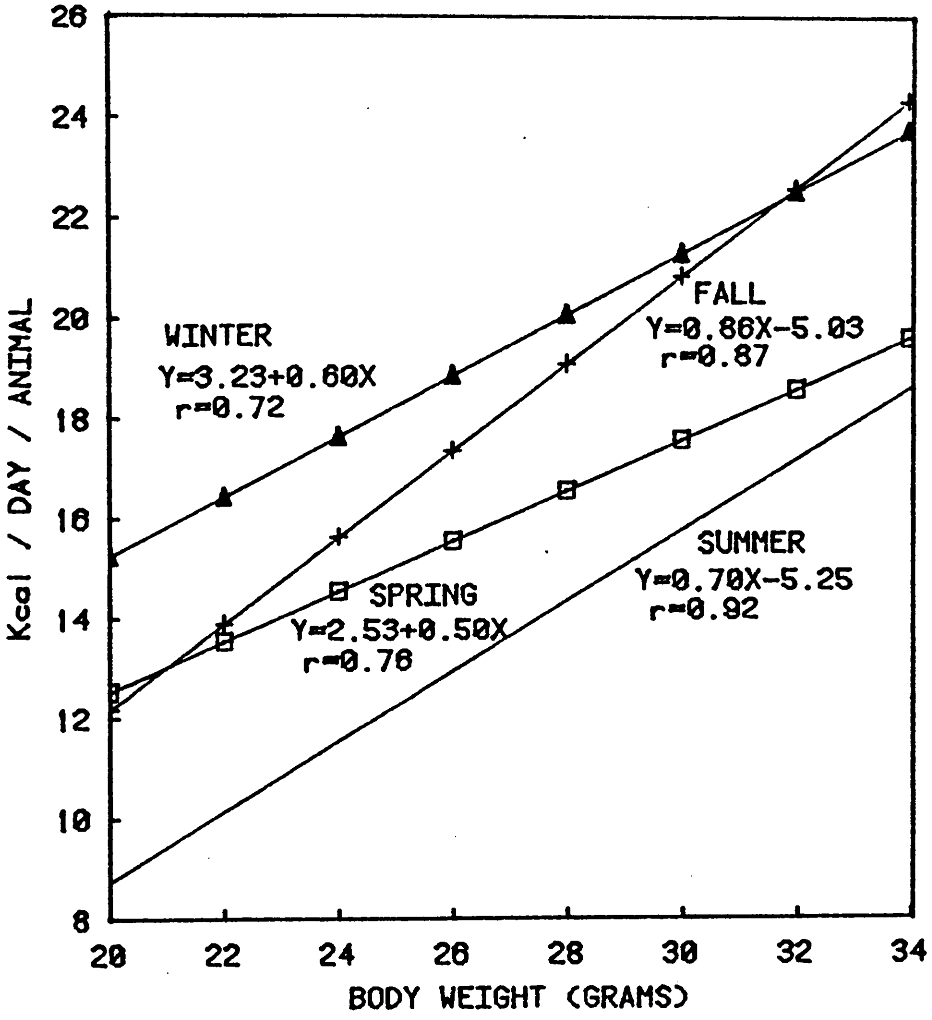

Figure 2. Relationship between the average daily maintenance energy requirement of adult pine voles and body weight in grams for the summer, fall, winter, and spring seasons.

this period was unrelated to reproductive effort. For the whole period of lactation, weight change of lactating females, measured as

$$\text{Change in body weight (g/day)} = \frac{\text{Final weight - Initial weight}}{\text{days}}$$

was equal to 0.002 ± 0.058 (SE) g/day. There was considerable variation in body weight change of individual females for any given period of lactation. A correlation analysis of the data showed no significant relationship between body weight change of lactating females and the phase of lactation ($r = 0.07$, $P>0.55$). There was also no significant relationship between litter size and body weight change ($r = 0.14$, $P>0.25$). Likewise, there was no significant correlation between the initial body weight of a female and size of the litter supported ($r = 0.10$, $P>0.42$) or weight of the litter ($r = 0.04$, $P>0.73$).

There was a slight, but significant, correlation between digested energy (kcal/day) and body weight change ($r = 0.31$, $P<0.01$). Thus, a decrease in body weight was probably due to insufficient amounts of digested energy.

Ingestion

Lactating female voles and their young ingested an average of 25.86 ± 0.85 (SE) kcal/day over the 21 days of lactation. Ingestion was not significantly correlated with female body weight ($r = -0.02$, $P>0.90$). However, there was a significant relationship between amount ingested and the phase of lactation ($r = 0.55$, $P<0.001$). Table 7 shows the mean rate of ingestion in kcal/day for each of the 4 phases of lactation. Ingestion by the mother and her young reached a peak during the phase 19-21 days of 32.40 ± 2.13 (SE) kcal/day for a mean litter

Table 7. Mean and standard error of body weight, consumption, excretion, digested energy, digestive efficiency, and metabolizable energy intake of lactating female pine voles and their young during 4 phases of lactation. Phases 1, 2, 3, and 4 represent days 1-6, 7-12, 13-18, and 19-21 of lactation, respectively. (N=19).

	Phase of lactation (Mean±S.E.)			
Parameter	1	2	3	4
Body weight (g)	28.7±0.7	29.1±0.7	28.8±0.7	29.0±0.9
Consumption (kcal/day)	20.60±0.87	24.18±0.94	26.75±1.47	32.40±2.13
Excretion (kcal/day)	3.90±0.19	4.62±0.20	4.98±0.24	5.96±0.45
Digested energy (kcal/day)	16.70±0.70	19.56±0.77	21.77±1.29	26.44±1.71
Digestive efficiency (%)	81.19±0.35	80.85±0.35	81.14±0.55	81.78±0.45
Metabolic energy intake				
kcal/female/day	16.37±0.68	19.16±0.76	21.33±1.26	25.91±1.67
kcal/g/day)	0.577±0.030	0.660±0.031	0.747±0.052	0.902±0.062
kcal/kg$^{0.75}$/day)	236.56±11.55	272.56±11.55	306.85±20.42	370.84±24.53

size of 2.2 ± 0.1 (SE) young. This was a 57.3 percent increase over the 20.60 kcal/day ingested during the first 6 days of lactation. The largest percentage increase in rate of ingestion occurred between phase 3 (13-18 days) and phase 4 (19-21 days) of lactation which amounted to a 21.1 percent increase. The smallest increase occurred between phase 2 (7-12 days) and phase 3 (10.6% increase). During the first 18 days of lactation, when the suckling young are not consuming any appreciable amounts of solid food, the largest increase in rate of ingestion occurred during the first 6 days of lactation (17.4% increase).

The rate of ingestion by lactating females and her suckling young was also highly correlated with the size of the litter ($r = 0.61$, $P<0.001$). Tables 8, 9, and 10 show the mean rate of ingestion for litter sizes of 1, 2, and 3 young, respectively for each of the 4 phases of lactation. There was a clear linear relationship between percentage increase in rate of ingestion over the duration of lactation and size of the litter. The increase between the first 6 days (phase 1) of lactation and the last 3 days (phase 4) for a litter of 1 amounted to 26.7 percent. For a litter size of 2 the percent increase was nearly double that of a litter size of 1 and amounted to 55.7 percent. For a litter size of 3 the percent increase was nearly triple that of a litter size of 1 and amounted to a 76.9 percent increase.

Similar to the influence of litter size, the rate of ingestion was also affected by the weight of the litter ($r = 0.90$, $P<0.001$). Corresponding to litter weight is litter weight gain which was also highly correlated with rate of ingestion ($r = 0.65$, $P<0.001$).

Table 8. Mean and standard error of body weight, consumption, excretion, digested energy, digestive efficiency, and metabolizable energy intake of lactating female pine voles with a litter size of 1 during 4 phases of lactation. Phases 1, 2, 3, and 4 represent days 1-6, 7-12, 13-18, and 19-21 of lactation, respectively. (N=3).

Parameter	Phase of lactation (Mean ± S.E.)			
	1	2	3	4
Body weight (g)	29.00±2.2	28.10±2.1	28.60±1.5	28.00±1.5
Consumption (kcal/day)	16.17±1.16	17.44±1.70	19.07±1.94	20.49±2.22
Excretion (kcal/day)	3.04±0.10	3.30±0.18	3.63±0.27	3.63±0.48
Digested energy (kcal/day)	13.13±1.06	14.13±1.56	15.44±1.67	16.86±1.78
Digestive efficiency (%)	81.10±0.81	80.87±1.12	80.80±0.61	82.40±0.91
Metabolizable energy intake				
(kcal/female/day)	12.87±1.04	13.85±1.53	15.13±1.64	16.53±1.74
(kcal/g/day)	0.431±0.017	0.500±0.070	0.533±0.059	0.571±0.036
(kcal/kg$^{0.75}$/day)	178.99±8.05	203.80±26.67	218.57±23.63	235.24±17.03

Table 9. Mean and standard error of body weight, consumption, excretion, digested energy, digestive efficiency, and metabolizable energy intake of lactating female pine voles with a litter size of 2 during 4 phases of lactation. Phases 1, 2, 3, and 4 represent days 1-6, 7-12, 13-18, and 19-21, respectively. (N=8).

Parameter	Phase of lactation (Mean ± S.E.)			
	1	2	3	4
Body weight (g)	28.20±1.0	29.20±0.6	28.80±1.1	28.40±1.7
Consumption (kcal/day)	20.42±1.13	23.83±1.13	24.92±0.97	31.80±1.33
Excretion (kcal/day)	3.83±0.30	4.55±0.25	4.83±0.28	5.90±0.61
Digested energy (kcal/day)	16.60±0.87	19.28±0.91	20.09±0.84	25.90±0.78
Digestive Efficiency (%)	81.33±0.72	80.90±0.47	80.58±0.92	81.62±1.17
Metabolizable energy intake				
(kcal/female/day)	16.26±0.86	18.89±0.89	19.68±0.83	25.38±0.76
(kcal/g/day)	0.595±0.042	0.647±0.031	0.687±0.052	0.909±0.049
(kcal/kg$^{0.75}$/day)	241.77±15.53	267.28±12.31	282.39±18.79	371.31±16.76

Table 10. Mean and standard error of body weight, consumption, excretion, digested energy, digestive efficiency, and metabolizable energy intake of lactating female pine voles with a litter size of 3 during 4 phases of lactation. Phases 1, 2, 3, and 4 represent days 1-6, 7-12, 13-18, and 19-21, respectively. (N=8).

Parameter	Phase of lactation (Mean ± S.E.)			
	1	2	3	4
Body weight (g)	28.90±1.1	29.4±1.3	29.00±1.3	30.10±1.5
Consumption (kcal/day)	22.40±1.15	27.06±0.45	32.18±1.69	39.63±1.24
Excretion (kcal/day)	4.28±0.26	5.19±0.17	5.78±0.26	7.32±0.33
Digested energy (kcal/day)	18.12±0.93	21.87±0.44	26.40±1.65	32.30±1.00
Digestive Efficiency (%)	80.93±0.50	80,80±0.61	81.80±1.00	81.53±0.49
Metabolizable energy intake				
(kcal/female/day)	17.76±0.91	21.43±0.43	25.87±1.62	31.66±0.98
(kcal/g/day)	0.618±0.046	0.732±0.046	0.907±0.082	1.086±0.065
(kcal/kg$^{0.75}$/day)	254.24±16.93	302.36±15.63	372.40±30.29	447.98±21.89

Digestible Energy

The mean energy equivalent of lab chow was 4.40 kcal/g dry weight. Fecal excretion rate (kcal/day) increased with an increase in the rate of ingestion (r = 0.92, $P<0.001$). Table 7 shows the mean fecal excretion rate of lactating females and her suckling young for each of the 4 phases of lactation. Excretion rate increased throughout lactation reaching a peak for the phase 19-21 days of lactation, when ingestion was at its peak. Excretion rate was significantly correlated with the phase of lactation with a correlation coefficient of r = 0.52 ($P<0.001$). Similar to the pattern of ingestion, fecal excretion rate was also significantly related to litter size (r = 0.59, $P<0.001$), weight of the litter (r = 0.79, $P<0.001$) and litter weight gain (r = 0.66, $P<0.001$). Tables 8, 9, and 10 show the mean excretion rates for females and litters of 1, 2, and 3, respectively, for each phase of lactation.

Digestive efficiency (DE) was determined as:

$$DE = \frac{I-F}{I} \times 100$$

where I is the amount of energy ingested (kcal/animal/day) and F is the amount of energy excreted (kcal/animal/day). Digestive efficiencies for each phase of lactation are shown in Table 7. Digestive efficiencies for lactating females and her young of litter sizes 1, 2, and 3 are shown in Tables 8, 9, and 10, respectively. Digestive efficiency was not correlated with the phase of lactation (r = 0.14, $P>0.26$). The mean excretion rate for the whole period of lactation for all females and their litters was 4.84 ± 0.16 (SE) kcal/animal/day with a energy equivalent of 3.90 ± 0.01 (SE) kcal/g dry weight of feces. The mean digestive efficiency for all females and their litters was 81.20 ± 0.22 (SE) percent for the entire 21 days of lactation.

The mean amount of energy digested by lactating females and their litters for each phase of lactation is shown in Table 7. Tables 8, 9, and 10 show the mean amount of energy digested for litters of 1, 2, and 3, respectively. Digestible energy requirements were also dependent upon the size of the litter supported ($r = 0.60$, $P<0.001$), the weight of the litter ($r = 0.88, P < 0.001$), litter weight gain ($r = 0.63$, $P<0.001$), and the period of lactation ($r = 0.58$, $P<0.001$). There was no significant correlation between weight of the lactating female and digestible energy requirements ($r = 0.03$, $P>0.78$). This is probably due to the small range in body weights among lactating females.

Metabolizable Energy Intake

Digestible energy intake was corrected for urinary loss to obtain metabolizable energy intake. Table 7 shows the metabolizable energy requirements of lactation expressed on a per animal basis, per gram body weight basis, and a metabolic body weight basis ($kg^{0.75}$) (Brody 1945). Metabolic energy requirements for lactation increased throughout the duration of lactation and was expressed by the equation:

$$\text{MEI (kcal/animal/day)} = 13.33 + 0.58T$$

where MEI is the metabolizable energy requirements of lactation and T is the day of lactation. The corresponding correlation coefficient for this relationship was $r = 0.57$ ($P<0.001$). Expressed on a metabolic body size basis ($kg^{0.75}$) (Brody 1945) the metabolizable energy requirements for lactation was described by the equation:

$$\text{MEI (kcal/kg}^{0.75}\text{/day)} = 189.23 + 8.38T$$

where T is the day of lactation. The corresponding correlation coefficient for this relationship is $r = 0.56$ ($P<0.001$).

Metabolizable energy intake for all lactating females and their litters increased by 58.3 percent from the first 6 days of lactation to the last 3 days of lactation (19-21 days). There was a 30.3 percent increase from the first 6 days of lactation to the mean requirements for the phase 13-18 days. The largest increase occurred during the phase 19-21 days, which was an increase of 4.58 kcal/animal/day (21.5%) over the 21.33 kcal/animal/day required for phase 3 (13-18 days).

Tables 8, 9, and 10 show the metabolizable energy requirements of lactating females with litters of 1, 2, and 3, respectively. Although the range of litter sizes was small (1-3 young), there was a direct influence of size of the litter on the metabolic requirements for lactation. Metabolizable energy requirements (MEI) necessary to support offspring was related to size of litter by the equation:

$$\text{MEI (kcal/female/day)} = 10.46 + 4.52N_L$$

where N_L is the litter size. The corresponding correlation coefficient for this relationship was $r = 0.60$ ($P<0.001$). Expressed on a metabolic body weight ($\text{kg}^{0.75}$) basis (Brody 1945) the metabolizable energy requirements can be expressed by the equation:

$$\text{MEI (kcal/kg}^{0.75}\text{/day)} = 153.57 + 63.21N_L$$

where N_L is again equal to litter size. The corresponding correlation coefficient for this expression was $r = 0.56$ ($P<0.001$).

For the first 6 days of lactation an average of 12.87 kcal/female/day of metabolizable energy was required to support a litter of 1 young (Table 8). The additional amount of metabolizable energy required to support a litter of 2 (over that required for a litter of 1) for the first 6 days of lactation was 3.39 kcal/female/day. However, the additional amount of metabolizable energy required to support a litter of 3 (over that required for a litter of 2) for the first 6 days of lactation was only 1.50 kcal/female/day. This pattern changed toward the end of lactation, when the additional requirements needed to support additional young became increasingly greater. For phase 3 (13-18 days) a female required an average of 15.13 kcal/female/day to support a litter of 1. An additional 4.55 kcal/female/day was required to support a litter of 2 for this phase of lactation. To support a litter of 3 a female required an additional 6.19 kcal/female/day over that required for a litter size of 2 for phase 3. The metabolic requirements necessary to support additional young was even greater between 19-21 days of lactation. This trend in energy requirements is probably the result of increasing rates of growth of litters during the latter stages of lactation.

The mean metabolizable energy requirements for the 21 days of lactation was 20.60 ± 0.69 (SE) kcal/day for a female with an average litter size of 2.2 young. This was equivalent to 0.718 ± 0.026 (SE) kcal/g/day when converted to a per gram body weight basis. On a metabolic body weight basis (Brody 1945) the mean metabolizable energy requirement for a female and her litter was 295.12 ± 10.37 (SE) kcal/kg$^{0.75}$/day for the 21 days of lactation.

Metabolizable energy requirements for lactation were also highly correlated with the total weight of the litter at any given period of lactation. Litter weight was a better predictor of lactational costs during the latter stages of lactation. This was due to a considerable amount of variation in weights between litters toward the latter stages of lactation. Obviously, the variable litter weight includes the factor of litter size which will result in heavier litters with increases in litter size. The relationship between metabolizable energy intake requirements (MEI) and litter weight is described by the equation:

$$\text{MEI (kcal/female/day)} = 10.46 + 0.68W_L$$

where W_L is the mean weight of the litter in grams. The corresponding correlation coefficient for this relationship was $r = 0.89$ ($P<0.001$).

Production

The average number of young in 19 litters born to lactating females in this study was 2.2 ± 0.1 (SE). The smallest litter was 1 and the largest was 3. Of all the young monitored in this study only 1 individual died.

The average neonatal pine vole weighed 1.95 ± 0.06 (SE) g at birth. The average weight of weaned voles at 21 days was 11.2 ± 0.43 (SE) g. The average weight of suckling voles at 18 days of lactation, which is when young voles begin to eat considerable amounts of solid food, was 8.7 ± 0.30 (SE) g. Weights of litters were directly related to the size of the litter as might be expected ($r = 0.64$, $P<0.001$). Likewise, the amount of gain in weight by a litter was directly related to the size of the litter ($r = 0.58$, $P<0.001$). Litter growth rate, expressed as weight gain (GR_L), was related to litter size (N_L) by the expression

$$GR_L \text{ (g/day)} = 0.473N_L - 0.034.$$

The corresponding correlation coefficient for this relationship was $r = 0.57$ ($P<0.001$).

Table 11 shows the growth rate statistics for all litters during the 4 phases of lactation. Tables 12, 13, and 14 show the growth rate statistics for litters of 1, 2, and 3 young, respectively. Body weight of young (W_y) can be described by the equation:

$$W_y(g) = 1.85 + 0.36T$$

where T is the age in days since birth. The corresponding correlation coefficient for the above relationship was $r = 0.93$ ($P<0.001$).

Some studies have observed that individuals in large litters each gain less weight than they would have if they had been part of a smaller litter (Randolph et al. 1977). This was not the case in this study as can be observed from Tables 12, 13, and 14. Growth rate of a litter, measured in g gain/day, was a product of the number of young in that litter. The only exception was during the phase of 7-12 days when the mean growth rates of individual voles within larger litters was less than that of individuals from smaller litters (Tables 12, 13, and 14). The average weight gain of an individual vole from a litter of 1 for the phase 7-12 days was 0.45 g/day, while only 0.35 g/day for individuals from a litter of 2 and 0.38 g/day for individuals from a litter of 3.

Table 11. Litter weight gain, production and relative growth rate during 4 phases of lactation (N=19). Phases 1, 2, 3, and 4 represent days 1-6, 7-12, 13-18, and 19-21 of lactation, respectively.

	Litter growth (Mean ± S.E.)		
Period of lactation	Weight gain (GR_L) g/day	Production kcal/day	Relative growth rate g/g litter/day
1	0.78±0.09	1.38±0.16	0.093±0.007
2	0.85±0.08	1.49±0.13	0.067±0.004
3	0.83±0.10	1.46±0.17	0.048±0.003
4	1.72±0.20	3.04±0.36	0.078±0.054
Total	1.02±0.07	1.81±0.13	0.070±0.031

Table 12. Litter weight gain, production and relative grwoth rate during 4 phases of lactation for litter sizes of 1 (N=3). Phases 1, 2, 3, and 4 represent days 1-6, 7-12, 13-18, and 19-21 of lactation, respectively.

	Litter growth (Mean ± S.E.)		
Period of lactation	Weight gain (GR_L) g/day	Production kcal/day	Relative growth rate g/g litter/day
1	0.33±0.15	0.58±0.26	0.083±0.034
2	0.45±0.04	0.79±0.08	0.073±0.003
3	0.35±0.11	0.62±0.19	0.041±0.010
4	0.69±0.19	1.22±0.34	0.067±0.012

Table 13. Litter weight gain, production and relative growth rate during 4 phases of lactation for litter sizes of 2 (N=8). Phases 1, 2, 3, and 4 represent days 1-6, 7-12, 13-18, and 19-21 of lactation, respectively.

	Litter growth (Mean ± S.E.)		
Period of lactation	Weight gain (GR_L) g/day	Production kcal/day	Relative growth rate g/g litter/day
1	0.70±0.05	1.24±0.10	0.097±0.005
2	0.70±0.07	1.24±0.13	0.063±0.006
3	0.70±0.07	1.23±0.12	0.046±0.003
4	1.65±0.26	2.91±0.47	0.085±0.014

Table 14. Litter weight gain, production and relative growth rate during 4 phases of lactation for litter sizes of 3 (N=8). Phases 1, 2, 3, and 4 represent days 1-6, 7-12, 13-18, and 19-21 of lactation, respectively.

	Litter growth (Mean ± S.E.)		
Period of lactation	Weight gain (GR_L) g/day	Production kcal/day	Relative growth rate g/g litter/day
1	1.02±0.14	1.79±0.25	0.093±0.008
2	1.14±0.08	2.01±0.14	0.068±0.006
3	1.18±0.12	2.09±0.21	0.051±0.005
4	2.37±0.13	4.18±0.22	0.080±0.004

The rate of litter weight gain (g/day) approximately doubled during the phase 19-21 days (Tables 12, 13, and 14). Individual weight gain was only slightly greater for litters of 2 and 3 when compared to a litter of only 1. This doubling in rate of weight gain is due to the change in diet from one of mostly mother's milk to one in which a larger portion of high energy solid food is consumed.

The increase in the rate of weight gain at 19-21 days was not due entirely to the larger body weight of young voles alone. The relative growth rate (RGR_L) of a litter

$$RGR_L = GR_L/W_L$$

was calculated for all litters, where GR_L is the average weight gained by a litter per day (g/day) and W_L is the mean weight of the litter in grams. As shown in Tables 12, 13, and 14 there was a considerable increase in the relative growth rate at 19-21 days for all litters. The relative rate of growth was largest during the first 6 days after birth and gradually decreased until the phase 19-21 days after birth when the notable increase occurred.

Body Composition During Growth

Changes in the body composition of 41 young voles at birth and age 18 days after birth are shown in Table 15. The 2 body components showing the most dramatic changes with age were water and fat content. There was a clear inverse relationship between water and fat concentrations in the body with age. While water concentration decreased with age, the concentration of body fat increased. Similar patterns of change were noted during the growth of other vole species

Table 15. Body composition of young pine voles at the ages of 1 day, 18 days and 50 days after birth (Mean ± S.E.).

Age (days)	N	Live body wt. (g)	Water (% live wt.)	Fat (% dry wt.)	Protein (% lean dry wt.)	Ash (% lean dry wt.)
1	33	1.95 ±	83.59 ±	7.29 ±	85.43 ±	14.57 ±
		0.06	0.20	0.39	0.16	0.16
18	8	7.69	70.90	15.28	82.49	17.51
		0.74	0.70	2.76	6.44	0.44
50	3	21.80[a]	63.21	34.98	80.54	19.46
		0.42	0.96	1.63	0.59	0.59

[a]/Mean body weight of 31 animals.

(Fedyk 1974, Sawicka-Kapusta 1974). Fat and lean tissue is probably accumulated at the expense of body water. The percentage of fat tissue more than doubled during the period 1-18 days of age.

The tissue remaining after removal of water and fat represents the lean dry portion of the body. This portion is composed of mainly protein and ash. As seen in Table 15 the percentage of body protein (lean tissue minus the ash component divided by the amount of lean tissue) decreased with age. Although the amount of the decrease was much smaller than the changes which occurred in the water and fat components, there was a distinct depression with age. While protein concentration decreased, the ash concentration (weight of ash divided by the weight of lean tissue) increased. This was due to the increased growth of the skeleton with age, resulting in a larger percentage of the lean dry tissue composed of the mineral ash component.

The percentage of each body component was converted in Table 16 to show the weight of young voles. All components increased from 1 day to 18 days of age. The largest portion of weight change was attributed to the accumulation of body water. Protein content increased from 0.25g to 1.56g during the period, a 6-fold increase. The amount of fat and ash which accumulated during the 18 days of growth were very similar. Fat increased from 0.02g at 1 day of age to 0.34g at 18 days of age, a 17-fold increase. Likewise, the weight of ash in the body increased from 0.04g to 0.33g during the 18 days of growth, an 8-fold increase.

Table 16. The amount of body water, dry tissue, fat, lean dry tissue, protein, and ash by weight in young pine voles at ages 1 day, 18 days, and 50 days after birth.

Age (days)	N	Water (g)	Dry body weight (g)	Fat (g)	Lean dry (g)	Protein (g)	Ash (g)
1	33	1.63	0.32	0.02	0.30	0.25	0.04
18	8	5.45	2.24	0.34	1.90	1.56	0.33
50	3	13.78	8.02	2.80	5.22	4.20	1.02

Energy Deposition During Growth

At 1 day after birth the energy equivalent of lean dry tissue was equal to 4.58 ± 0.01 (S) kcal/g. At 18 days after birth, the caloric equivalent of lean dry tissue was 4.52 ± 0.06 (SE) kcal/g. The caloric value of fat tissue was double that of lean tissue. The caloric equivalent of fat at 1 day of age was equal to 9.22 kcal/g (N = 1). This decreased to 9.15 kcal/g (N = 2) at age 18 days.

The weights of fat and lean dry tissue in the body of young voles ages 1 day and 18 days were multiplied by their respective caloric equivalents to obtain the total body energy content (Table 17). Over the 18 days of growth monitored, voles accumulated 1.31g of body protein and 0.32g of body fat (19.6% of the total weight of energy yielding tissues). However, fat tissue comprised 28.8% of the total energy content deposited as tissue. A total of 10.13 kcal of additional energy was deposited as growth over the 18 days after birth. This was a 7.4-fold increase in total carcass energy. Also, the energy equivalent per gram of live body tissue (Table 17) reflected the increased concentration of fat tissue in growing voles. The caloric equivalent of live body tissue increased from 0.80 kcal/g at age 1 day to 1.52 kcal/g live body tissue at 18 days of age, an increase of 0.72 kcal/g or 88.9 percent.

The change in body weight from 1 to 18 days of age in the suckling voles monitored for body compositional changes amounted to 5.74g. This was equivalent to an additional 10.13 kcal of energy deposited as fat

Table 17. The distribution of total body energy in growing pine voles at ages 1 day, 18 days, and 50 days after birth.

Age (days)	N	Fat energy (kcal)	Protein energy (kcal)	Total body energy kcal	Total body energy kcal/g live weight
1	33	0.212	1.360	1.572	0.805
18	8	3.128	8.570	11.698	1.521
50	3	25.178	23.666	48.844	2.240

and protein. To determine the energy concentration of a 1 gram change in body weight due to suckling growth, the additional energy deposited as tissue growth was divided by the total change in body weight over the 18 days after birth. This gave a value of 1.76 kcal/g live weight change due to growth. To determine the amount of energy deposited as growth in the experimental litters monitored for metabolizable energy requirements, the rate of growth (GR_L) (g/day) was multiplied by 1.76 kcal/g gain.

Effect Of Growth On Metabolizable Energy Requirements

The rate of growth of a litter had a strong relationship to the total metabolizable energy requirements of a lactating female. This relationship was expressed by the equation:

$$\text{MEI (kcal/female/day)} = 12.47 + 7.93GR_L$$

where GR_L is the rate of growth of the litter in g/day. The corresponding correlation coefficient for the above relationship was $r = 0.86$ ($P<0.001$).

The amount of energy deposited as growth was significantly correlated with both litter size and day of lactation. The equation describing the relationship between litter production (P_L) (kcal/day) and size of the litter (N_L) was:

$$P_L \text{ (kcal/day)} = 0.834N_L - 0.061.$$

The corresponding correlation coefficient for this relationship was $r = 0.58$ ($P<0.001$). The equation describing the relationship between P_L and day of lactation (T) was:

$$P_L \text{ (kcal/day)} = 0.710 + 0.087T.$$

The correlation coefficient for the above equation was $r = 0.45$ ($P<0.001$).

The metabolizable energy requirements of a lactating female was also highly correlated with the energy demands of the suckling litter for tissue deposition, as might be expected. Inherent to this parameter is the growth rate of the litter as well as the size of the litter. This explains why litter tissue deposition is so highly correlated with the energy requirements of lactation to support that litter. The metabolizable energy requirements of a lactating female was related to litter production by the equation:

$$\text{MEI (kcal/day)} = 12.47 + 4.49\ P_L$$

where P_L is the rate of tissue deposition by a litter in kcal/day. The corresponding correlation coefficient for this equation was $r = 0.86$ ($P<0.001$).

Cost Of Lactation

The energetic costs of lactation were determined by comparing metabolizable energy requirements of lactating females to the maintenance requirements of nonreproductive adult females. Maintenance energy requirements of adult nonreproductive females was described by the equation:

$$\text{DEB (kcal/female/day)} = 0.47W - 0.10$$

where DEB is the daily energy budget for maintenance and W is the female body weight in grams. Total metabolizable energy costs of lactating females for each phase of lactation are shown in Table 18. Two major periods were evident from these data; the first distinguishing

Table 18. Energetic costs of lactation (kcal) in *Microtus pinetorum*. Total MEI is the metabolizable energy requirement of lactation, ♀ maintenance requirements are based on energy requirements of nonbreeding females of similar body weight, offspring costs are based on total MEI costs minus ♀ maintenance requirements, offspring production is the energy deposited as tissue growth, and offspring respiration is based on the offspring costs minus offspring production. These data represent means ± S.E. for 19 litters (mean litter size of 2.2).

Period of lactation (days)	Total MEI	♀ maintenance requirements	Offspring costs		Offspring production		Offspring respiration	
			Per litter	Per offspring	Per litter	Per offspring	Per litter	Per offspring
1-6	98.22±4.08	80.46±2.04	17.76±1.11	7.76±0.48	8.28±0.96	3.62±0.42	9.48±0.59	4.14±0.26
7-12	114.96±4.56	82.20±2.10	32.76±1.90	14.49±0.84	8.94±0.78	3.96±0.34	23.82±1.38	10.54±0.61
13-18	127.98±7.56	81.00±1.98	46.98±3.50	21.26±1.58	8.76±1.02	3.96±0.46	38.22±2.85	17.29±1.29
19-21	77.73±5.01	40.50±1.14	37.23±2.94	17.00±1.34	9.12±1.08	4.14±0.22	28.11±1.50	12.84±0.68
Total								
1-18	341.16±16.20	243.66±6.12	97.50±6.51	43.51±2.90	25.98±2.76	11.54±1.22	71.52±4.82	31.97±2.16
1-21	418.89±21.21	284.16±7.26	134.73±9.45	60.54±4.24	35.10±1.85	15.95±1.68	99.63±6.76	45.29±1.29

the period of dependence 1-18 days after birth and the second period was of incomplete dependence on the mother's milk, 19-21 days. During the period of dependence (18 days) lactating females with an average litter of 2.2 young required 341.16 ± 16.20 kcal of metabolizable energy. For the period of incomplete dependence an additional 77.73 ± 5.01 kcal of energy was metabolized for a total requirement of 418.89 ± 21.21 kcal of metabolized energy over the entire 21 days of lactation.

Maintenance requirements of lactating females varied slightly from one phase to the next due to slight fluctuations in body weight of lactating females. This was probably due to either increased deposition of energy reserves or the increased mobilization of stored energy to support the litter. Maintenance energy requirements of nonreproductive females were subtracted from the total metabolizable energy requirements of a lactating female of identical body weight to obtain the costs of supporting offspring (Table 18). For an average litter of 2.2 offspring, 97.50 ± 6.51 kcal of additional metabolizable energy was required above maintenance requirements of nonreproductive females to support the litter during the first 18 days of lactation. An additional 37.23 kcal were required by the mother and her litter over the 3 day phase, 19-21 days, for a total metabolizable energy requirement above nonreproductive requirements of 134.73 ± 9.45 kcal (47.5% above the nonreproductive maintenance requirements) over all 21 days of lactation.

The average litter incorporated 25.98 ± 2.76 kcal of energy into production during the 18 days of dependence. An additional 9.12 kcal were deposited as tissue growth by the average litter during the period of incomplete dependence which resulted in a total of 35.10 ± 1.85 kcal of energy deposited as tissue growth over the 21 days monitored. This was equivalent to 11.54 ± 1.22 kcal per offspring, for the period of dependence (1-18 days) and 15.95 ± 1.68 kcal deposited per offspring over the entire 21 days.

Respiration by the offspring within a litter was determined by subtracting the energy incorporated into production from the additional amount of metabolizable energy required to support a litter of offspring. Table 18 shows the amount of energy respired by an average litter of 2.2 offspring. Respiration by a litter averaged 71.52 ± 4.82 kcal during the 18 days of dependence. For the period of incomplete dependence a litter respired an average of 28.11 kcal. This resulted in a total of 99.63 ± 6.72 kcal of energy lost through respiration of the litter over the 21 days of lactation monitored. Per individual offspring, this amounted to 31.97 ± 2.16 kcal of energy lost to respiration during the period 1-18 days and 45.29 ± 1.29 kcal of respirational losses over the 21 days monitored.

The costs of supporting a litter of 1, 2, and 3 offspring through lactation are shown in Tables 19, 20, and 21, respectively. The amount of additional metabolizable energy required increased with litter size ($r = 0.56$, $P<0.001$) and phase of lactation ($r = 0.56$, $P<0.001$). Table 19 shows that only 9.24 kcal of additional metabolizable energy was required to support a litter of 1 offspring

Table 19. Energetic costs of lactation (kcal) in *Microtus pinetorum*. Total MEI is the metabolizable energy requirement of lactation, ♀ maintenance requirements are based on energy requirements of nonbreeding females of similar body weight, offspring costs are based on total MEI costs minus ♀ maintenance requirements, offspring production is the energy deposited as tissue growth, and offspring respiration is based on the offspring costs minus offspring production. These data represent means ± S.E. for 3 litters of 1 young.

Period of lactation (days)	Total MEI	♀ maintenance requirements	Offspring costs		Offspring production		Offspring respiration	
			Per litter	Per offspring	Per litter	Per offspring	Per litter	Per offspring
1-6	77.22±6.24	83.58±5.76	---	---	3.48±1.56	3.48±1.56	---	---
7-12	83.10±9.18	78.60±6.54	4.50±0.49	4.50±0.49	4.74±0.48	4.74±0.48	---	---
13-18	90.78±9.84	79.68±3.72	11.10±1.20	11.10±1.20	3.72±1.14	3.72±1.14	7.38±0.80	7.38±0.80
19-21	49.59±5.22	40.29±2.31	9.30±0.98	9.30±0.98	3.66±1.02	3.66±1.02	5.64±0.59	5.64±0.59
Total								
1-18	251.10±25.26	241.86±16.02	9.24	9.24	11.94±3.18	11.94±3.18		
1-21	300.69±30.48	282.15±18.33	18.54	18.54	15.60±4.20	15.60±4.20		

Table 20. Energetic costs of lactation (kcal) in *Microtus pinetorum*. Total MEI is the metabolizable energy requirement of lactation, ♀ maintenance requirements are based on energy requirements of nonbreeding females of similar body weight, offspring costs are based on total MEI costs minus ♀ maintenance requirements, offspring production is the energy deposited as tissue growth, and offspring respiration is based on the offspring costs minus offspring production. These data represent means ± S.E. for 8 litters of 2 young.

Period of lactation (days)	Total MEI	♀ maintenance requirements	Offspring costs		Offspring production		Offspring respiration	
			Per litter	Per offspring	Per litter	Per offspring	Per litter	Per offspring
1-6	97.56±5.16	77.34±3.18	20.22±1.07	10.11±0.54	7.44±0.60	3.72±0.30	12.78±0.68	6.39±0.34
7-12	113.34±5.34	82.08±2.34	31.26±1.47	15.63±0.74	7.44±0.78	3.72±0.39	23.82±1.12	11.91±0.56
13-18	118.08±4.98	81.48±3.24	36.60±1.54	18.30±0.77	7.38±0.72	3.69±0.36	29.22±1.23	14.61±0.62
19-21	76.14±2.28	39.42±1.80	36.72±1.80	18.36±0.55	8.73±1.41	4.36±0.70	27.99±0.84	14.00±0.42
Total								
1-18	328.98±15.48	240.90±8.76	88.08±4.08	44.04±2.05	22.26±2.10	11.13±1.05	65.82±3.03	32.91±1.52
1-21	405.12±17.76	280.32±10.56	124.80±5.18	62.40±2.60	30.99±3.51	15.49±1.75	93.81±3.87	46.91±1.94

Table 21. Energetic costs of lactation (kcal) in *Microtus pinetorum*. Total MEI is the metabolizable energy requirement of lactation, ♀ maintenance requirements are based on energy requirements of nonbreeding females of similar body weight, offspring costs are based on total MEI costs minus ♀ maintenance requirements, offspring production is the energy deposited as tissue growth, and offspring respirations is based on the offspring costs minus offspring production. These data represent means ± S.E. for 8 litters of 3 young.

Period of lactation (days)	Total MEI	♀ maintenance requirements	Offspring costs		Offspring production		Offspring respiration	
			Per litter	Per offspring	Per litter	Per offspring	Per litter	Per offspring
1-6	106.56±5.46	81.66±3.12	24.90±1.27	8.30±0.42	10.74±1.50	3.58±0.50	14.16±0.72	4.72±0.24
7-12	128.58±2.58	83.76±4.02	44.82±0.90	14.94±0.30	12.06±0.84	4.02±0.28	32.76±0.66	10.92±0.22
13-18	155.22±9.72	81.30±3.54	73.92±4.63	24.64±1.54	12.54±1.26	4.18±0.42	61.38±3.84	20.46±1.28
19-21	94.98±2.94	41.40±1.98	53.58±1.66	17.86±0.55	12.54±0.66	4.18±0.22	41.04±1.27	13.68±0.42
Total								
1-18	390.36±17.76	246.72±10.68	143.64±6.80	47.88±2.26	35.34±3.60	11.78±1.20	108.30±5.22	36.10±1.74
1-21	485.34±20.70	288.12±12.66	197.22±8.46	65.74±2.81	47.88±4.26	15.96±1.42	149.34±6.49	49.78±2.16

during the first 18 days of lactation and 18.54 kcal over the entire 21 days monitored. These estimates appeared extremely low when compared to the costs required to support litters of 2 and 3 offspring. A litter of 2 offspring required an additional 88.08 ± 4.08 kcal during the first 18 days of lactation and a total of 124.80 ± 5.18 kcal over the entire 21 days. This equated to an individual offspring requirement of 44.04 ± 2.05 kcal over the first 18 days and 62.40 ± 2.60 kcal of additional energy over the entire 21 days. A litter of 3 required an average of 143.64 ± 6.80 kcal of additional metabolizable energy over the first 18 days and 197.22 ± 8.46 kcal over all 21 days (Table 21). Per individual offspring, metabolizable energy requirements amounted to 47.88 ± 2.26 kcal over the 18 days of dependence and 65.74 ± 2.81 kcal for all 21 days monitored. These estimates were very similar to the individual offspring requirements for litter sizes of 2, indicating that there was little difference between the energetic efficiency at which a female produces a litter of 2 or a litter of 3 offspring. However, when comparing the costs of producing a litter of 1 offspring to those of litter sizes of 2 and 3, the results appeared puzzling at first glance. During the first 6 days of lactation a female supporting a litter of 1 (Table 19) metabolized far less energy than what was required for her own body maintenance. Likewise, on subsequent phases of lactation, females with 1 young per litter appeared to be requiring less energy than females with litters of 2 and 3 young. This indicated that these females were drawing upon stored reserves of energy to support their 1 offspring through lactation and is supported by the following calculations. The average female with a litter of 1 lost an average of 0.3 g/day during the first 6 days of lactation. This amounted to an estimated 12.6 kcal of energy stores mobilized by an average female (assuming 7 kcal/g live body weight lost X 0.3 g/day X 6 days). Little change in weight occurred during the period 7-12 days, however, a slight gain in weight of 0.05 g/day occurred during the period 13-18 days of lactation. Another substantial decrease in weight occurred during the last 3 days (19-21 days) of monitoring which amounted to 0.54 g/day. This was equivalent to an estimated 11.34 kcal of stored energy mobilized. For the entire 21 days the average female supporting a litter of 1 mobilized an estimated 21.84 kcal of stored energy in the form of fat. This tends to clarify the discrepancy between energetic costs of supporting a litter of 1 and the costs of supporting a litter of 2 or 3 offspring. The corrected cost of supporting a litter of 1 offspring was 46.74 kcal for the 21 days monitored.

Referring to the overall partitioning of energy metabolized by a lactating female, 7.6 percent was deposited as production of offspring during the period 1-18 days (Table 18). Of the additional metabolizable energy required for supporting a litter above nonreproductive maintenance costs over the first 18 days of lactation, 26.6 percent was deposited on offspring production. Over the 21 days of lactation monitored, 8.4 percent of the metabolizable energy required by a lactating female was deposited as production of offspring, and of the additional metabolizable energy above nonreproductive maintenance costs 26.0 percent was deposited as production of offspring.

Considering all lactating females and their litters, the average percent increase in metabolizable energy requirements above maintenance requirements was 47.5 percent for the 21 days of lactation monitored; a 21.3 percent increase per offspring. During the first 6 days of lactation, the average percent cost per litter over maintenance requirements was 22.1 percent. From days 7-12 the mean cost of lactation was 59.9 percent over the cost of maintenance alone. During the period 13-18 days of lactation the average lactating female and her litter required a 58.0 percent increase in metabolizable energy requirements over the maintenance costs. Considering the last 3 days, the period of incomplete dependency (19-21 days), the average female and her litter expended 92.0 percent more metabolizable energy than for the maintenance requirements of the nonlactating mother.

Bioenergetics Of Postnatal Development

Growth

There was a high degree of correlation between the age of a juvenile vole and its corresponding body weight. The relationship between age of an animal (T) in days and body weight (W) in grams was expressed by the equation:

$$W(g) = 2.57 + 0.45T.$$

The corresponding correlation coefficient for this relationship was $r = 0.85$ ($P<0.001$). Growth statistics for each of the 4 age classes are shown in Table 22. Initial body weight (IBWT)(g) is the body weight of an animal at the time he enters the age class. The final body weight (FBWT)(g) of a vole is the weight of the vole at the end of the age class. This is also equal to IBWT(g) of the next higher age class (Table 22). Growth rates (GR_j) of each vole were determined as:

$$GR_j(g/day) = (FBWT - IBWT)/Days$$

where Days is the length of the age class (6 days) (Table 22). The relative rates of growth (RGR_j) of each vole was determined as:

$$RGR_j(g/day/g) = GR/IBWT$$

(Table 22).

Voles increased in body weight by an average of 9.8g between 22 and 46 days of age. This converted into an average rate of growth of 0.41 ± 0.02 (SE) g/day for the 24 day period of growth. Growth rates decreased with age, being highest between the ages of 22-28 days (Table 22). The relationship between age in days (T) and growth rate (GR_j) was described by the equation:

Table 22. Growth statistics for juvenile pine voles in 4 age classes. Values represent means ± S.E. (N=28) of body weight at the start of the age class (IBWT)(g), body weight at the end of the age class (FBWT)(g), rate of growth (GR_j) (g/day), and relative rate of growth ($RGR_j=GR_j/IBWT$).

Age class (days)	IBWT	FBWT	GR_j	RGR_j
22-28	12.0±0.3	15.9±0.3	0.65±0.03	0.056±0.003
29-34	15.9±0.3	18.9±0.4	0.50±0.03	0.032±0.002
35-40	18.9±0.4	20.9±0.4	0.33±0.03	0.018±0.002
41-46	20.9±0.4	21.8±0.4	0.15±0.02	0.007±0.001

$$GR_j(g/day) = 1.27 - 0.027T.$$

The corresponding correlation coefficient for this relationship was $r = -0.83$ ($P<0.001$). The coefficient of variation of GR between animals became increasingly greater with age. The coefficients of variation (CV) of GR were 24 percent, 28 percent, 42 percent, and 87 percent for the age classes 22-28, 29-34, 35-40, and 41-46, respectively. Drozdz et al. (1972) also found that the difference between the body weight of larger and smaller animals increased with age due to differing rates of growth. There was no significant correlation between rate of growth and size of the litter from which they were born. There was also no significant correlation between the sex of a juvenile and rate of growth.

Consumption and Digestibility

Food consumption increased from 13.99 ± 0.31 (SE) kcal/animal/day at age 22-28 to a high of 15.30 ± 0.42 (SE) kcal/animal/day at age 35-40 days. A slight reduction in food consumption occurred for the age class 41-46 days (14.81 ± 0.27 (SE) kcal/animal/day). Table 23 shows the caloric value of food and feces and the coefficients of food utilization for each age class. A 2-factor analysis of variance showed a significant difference ($P<0.05$) in the caloric equivalent of feces with age. The Duncans Multiple Range Test revealed that the caloric equivalent of feces for juvenile voles in age class 22-28 was significantly higher ($P<0.05$) than all other age classes. There was no difference in percent digestible energy with age.

The mean consumption of food by juvenile voles over the duration

Table 23. Caloric value (kcal/g dry wt.) of food, feces and coefficients of food utilization for growing pine voles. (Mean ± S.E.)

Item	Age Class							
	22-28		29-34		35-40		41-46	
	Caloric value	Percent of gross energy	Caloric value	Percent of gross energy	Caloric value	Percent of gross energy	Caloric value	Percent of gross energy
Food	4.39	100.0	4.39	100.0	4.39	100.0	4.39	100.0
Feces	3.76±0.01	17.74	3.69±0.02	17.39	3.70±0.02	17.26	3.68±0.02	17.28
Digested energy		82.26±0.20		82.61±0.22		82.74±0.24		82.72±0.28
Urine[1]		4.00		4.00		4.00		4.00
Metabolizable energy		78.26±0.20		78.61±0.22		78.74±0.24		78.72±0.28

[1] Drozdz et al. (1972)

of the experimental trial amounted to 14.81 ± 0.23 (SE) kcal/animal/day with the percent digestible energy equal to 82.58 ± 0.12 (SE) percent. Fecal production rates averaged 0.70 ± 0.01 (SE) g/animal/day or 2.58 ± 0.03 (SE) kcal/animal/day over the 24 day trial.

Metabolizable Energy Intake

Metabolizable energy intake (MEI_j) by juvenile voles was found to be a function of age, body weight, and rate of growth. Table 24 shows the mean metabolizable energy intake of juvenile voles for each of the 4 age classes expressed on a per animal, per g body weight and per metabolic body weight basis ($kg^{0.75}$)(Brody 1945). The most dramatic change in metabolizable energy intake occurred between days 22-34. Metabolizable energy requirements increased by nearly 1 kcal/animal/day (Table 24). There was a slight decrease of 0.39 kcal/animal/day which occurred during the 4th 6-day period. A similar reduction was noted by Drozdz et al. (1972) in *Microtus arvalis* during 40 days of age and could have possibly been the result of sexual maturation of the animal. Metabolizable energy intake expressed on a per animal basis showed little relationship to age of the animal. However, expressed on the basis of metabolic body size (Brody 1945) ($kg^{0.75}$), metabolizable energy intake decreased with age. This relationship was described by the equation:

$$MEI_j(kcal/kg^{0.75}/day) = 426.70 - 4.94T$$

where T is age in days (T and MEI_j represented means for their respective age classes). The corresponding correlation coefficient for this relationship was $r = -0.85$ ($P<0.001$). MEI_j was also expressed

Table 24. Metabolic parameters for growing juvenile pine voles.

Parameter	Age class (days)			
	22-28	29-34	35-40	41-46
N	28	28	28	28
Body wt. at start of age class	11.97±0.33	15.92±0.29	18.91±0.38	20.91±0.42
Metabolizable energy intake (MEI_j)				
(kcal/animal/day)	11.05±0.25	12.04±0.19	12.16±0.34	11.77±0.22
(kcal/g/day)	0.935±0.025	0.759±0.012	0.645±0.016	0.568±0.016
(kcal/kg$^{0.75}$/day)	307.54±6.80	269.20±3.72	238.69±5.83	215.31±5.18
Maintenance energy (M_j)				
(kcal/animal/day)	9.34±0.29	10.72±0.20	11.28±0.30	11.73±0.17
(kcal/g/day)	0.788±0.017	0.676±0.013	0.599±0.014	0.549±0.012
(kcal/kg$^{0.75}$/day)	211.88±5.56	211.08±4.23	204.47±4.99	200.66±3.79
Production energy (P_j)				
(kcal/animal/day)	1.71±0.08	1.32±0.07	0.88±0.07	0.39±0.07
(kcal/g/day)	0.147±0.009	0.083±0.004	0.046±0.004	0.019±0.003
(kcal/kg$^{0.75}$/day)	48.25±5.25	29.51±1.53	17.31±1.46	7.23±1.18

on a per gram body weight basis;

$$MEI_j(\text{kcal/g/day}) = 1.446 - 0.020T.$$

The corresponding correlation coefficient for this relationship was $r = 0.81$ ($P<0.001$).

Metabolizable energy intake was also significantly correlated with body weight (W). MEI_j was described by the equation:

$$MEI_j(\text{kcal/day/animal}) = 3.34 + 0.37W$$

where W is body weight in grams. The correlation coefficient for this relationship was $r = 0.80$ ($P<0.001$). This relationship was also described by the equation:

$$MEI_j(\text{kcal/g/day}) = 1.42 - 0.039W$$

where W is body weight in grams. The corresponding correlation coefficient for this equation was $r = -0.87$ ($P<0.001$).

Metabolizable energy intake was also significantly correlated with rate of growth (GR_j) of juvenile voles. Metabolizable energy intake (MEI_j) was described by the following equation:

$$MEI_j(\text{kcal/g/day}) = 0.495 + 0.572\ GR_j$$

where GR_j is rate of growth in g/day. The corresponding correlation coefficient for this relationship was $r = 0.81$ ($P<0.001$). Substituting a value of 1g/day for the growth rate in the above equation, the MEI_j of a juvenile vole is increased by 0.572 kcal/g/day, for a total metabolizable energy requirement of 1.067 kcal/g/day. For a typical 24g vole this amounts to a metabolizable energy requirement of 25.61 kcal/animal/day. For a 24g vole with a growth rate of 0, the metabolizable energy requirement is simply 0.495 kcal/g/day X 24g which is equal to 11.88 kcal/animal/day. By subtraction it is found that a juvenile vole must metabolize an additional 13.73 kcal/animal per 1g increase in body weight. Metabolizable energy intake (MEI_j) can also be expressed on the basis of metabolic body size for a given growth rate (GR_j) by the equation:

$$MEI_j(\text{kcal/kg}^{0.75}/\text{day}) = 196.15 + 151.55\ GR_j$$

where GR_j is the rate of growth in g/day. The metabolizable energy intake (MEI_j) of juvenile voles can be regressed against both body weight (W) in grams and rate of growth (GR_j) in g/day. This relationship was expressed as:

$$MEI_j(\text{kcal/g/day}) = 1.116 + 0.263\ GR_j - 0.028W.$$

The corresponding correlation coefficient for this relationship was $r = 0.90$ ($P<0.001$). MEI_j can also be regressed against body weight (W) in grams and age of the juvenile vole (T) in days:

$$MEI_j(\text{kcal/g/day}) = 1.477 - 0.029W - 0.006T.$$

The corresponding correlation coefficient for this relationship was $r = 0.88$ ($P<0.001$).

The mean metabolizable energy requirements for the entire period of growth between 22 and 46 days of age were 11.74 ± 0.13 (SE) kcal/animal/day, 258.77 ± 4.39 (SE) kcal/kg$^{0.75}$/day, or 0.731 ± 0.016 (SE) kcal/g/day.

There was no significant difference between multiple regression equations describing the metabolizable energy intake of male and female juvenile voles with metabolic body weight (MW) (kg$^{0.75}$) and growth rate (GR_j) (kg/day) as independent variables:

Females - $MEI_j(\text{kcal/kg}^{0.75}/\text{day}) = 351.08 - 2966.46\ MW + 18688.32\ GR_j$

Males - $MEI_j(\text{kcal/kg}^{0.75}/\text{day}) = 318.38 - 2229.93\ MW + 17689.37\ GR_j$

Combined - $MEI_j(\text{kcal/kg}^{0.75}/\text{day}) = 329.42 - 2533.46\ MW + 19151.16\ GR_j$

($F = 0.498$, $df = (5,102)$, P 0.05). A 2-factor analysis of variance also revealed no significant difference due to sex ($P>0.05$). However, there was a significant difference in metabolizable energy requirements due to age ($P<0.05$).

Production

The average caloric value of 1g of live body weight gain for the period 18 to 50 days of age was determined to be equal to 2.63 kcal from body composition analysis (Tables 15, 16, and 17). This estimate was lower than the 3.43 kcal/g body weight gain determined for laboratory reared bank voles between the ages 20-40 days (Fedyk 1974). Values calculated from the data given by Drozdz et al. (1972) on *Microtus arvalis* indicated a value for tissue growth equal to 2.15 kcal/g, 2.45 kcal/g, and 2.53 kcal/g live body weight gain for the periods 20-30 days, 30-40 days, and 40-50 days of age, respectively. This converted to an average value during the period 20-50 days of age equal to 2.38 kcal/g live body weight gain for juvenile *Microtus arvalis*. These comparisons indicated a wide degree of variability between species.

Table 24 shows the maintenance energy requirements of juvenile pine voles (M_j) and the amount of energy which was incorporated into tissue production (P_j) for the 4 periods of growth. Production was greatest during the age class 22-28 days, being equal to 1.71 ± 0.08

(SE) kcal/animal/day. The amount of energy incorporated into tissue production continued to decrease with age, reaching its lowest value during the period 41-46 days of age when tissue production was equal to 0.39 ± 0.07 (SE) kcal/animal/day. Production estimates for *Microtus arvalis* was reported by Drozdz et al. (1972) to be equal to 5.68 kcal/10-days (0.568 kcal/day) during the period 20-30 days of age, 5.46 kcal/10-days (0.546 kcal/day) during the period 30-40 days, and 4.98 kcal/10-days (0.498 kcal/day) for the period 40-50 days. For the entire 30-day period of growth, these values convert to an average value for juvenile *M. arvalis* production of 0.54 kcal/day. The average value for juvenile pine vole production over the 24 days of growth monitored was twice that reported for *Microtus arvalis* and was equal to 1.08 kcal/day.

Maintenance Energy Requirements

The maintenance energy requirements (M_j) of growing juvenile pine voles were determined by subtracting the energy incorporated into tissue production (P_j) from the total metabolizable energy intake (MEI_j) (Table 25). The energy required for maintenance gradually increased with an increase in body weight, reaching its highest level during the period 41-46 days of age (11.73 ± 0.17 (SE) kcal/animal/day).

When expressed on a metabolic body size basis (Brody 1945) the energy requirement for maintenance showed the typical inverse relationship with body weight. Maintenance energy requirements decreased from 211.88 ± 5.56 (SE) kcal/kg$^{0.75}$/day during the period 22-28 days to a low of 200.66 ± 3.79 (SE) kcal/kg$^{0.75}$/day during the period 41-46 days of age.

Maintenance energy requirements of juvenile pine voles were compared to those of an adult pine vole of equivalent body weight. Maintenance energy requirements of adult pine voles (M_A) was described by the equation,

$M_A = 0.70W - 5.25 = M_A$ (DEB-summer)(kcal/animal/day)

where W is body weight in grams. The difference between M_j and M_A was assumed to be an indication of the additional energy used by an immature vole above what would be expected from its smaller body size alone (M_g). This relationship is expressed as,

$$M_g = M_j - M_A.$$

The additional respiration due to growth (M_g) was added to the energy incorporated into tissue production (P_j) to estimate the total amount of metabolizable energy which was available for tissue production (M_{jp}). This relationship is expressed as,

$$M_{jp} = M_g + P_j.$$

The mean estimates for M_j, M_A, M_g, and M_{jp} are shown in Table 25.

Over the entire period of growth, the difference between adult and juvenile respiration, M_g, amounted to an average of 4.13 ± 0.19 (SE) kcal/animal/day. The largest portion of M_g was the result of the growth process. However, it should be emphasized that other factors could have attributed to the magnitude of M_g. Insulative qualities increase with the age of an animal due to better and thicker pelage as well as increased deposits of body fat. The ratio of metabolically active tissues (such as heart, liver, brain) to supportive tissues with

Table 25. The determination of juvenile pine vole tissue production efficiencies (mean ± S.E.).

Age class (days)	MEI_j 1/	M_j 2/	M_A 3/	M_g 4/	M_{jp} 5/	P_j/M_j 6/	P_j/MEI_j 7/
22-28	11.04±0.25	9.34±0.26	3.13±0.23	6.21±0.20	7.92±0.23	18.8±1.0	15.5±1.0
29-34	12.04±0.19	10.72±0.18	5.89±0.20	4.83±0.18	6.14±0.18	12.4±0.7	11.0±0.7
35-40	12.16±0.34	11.28±0.32	7.99±0.27	3.30±0.27	4.18±0.30	7.8±0.7	7.2±0.7
41-46	11.77±0.22	11.38±0.19	9.39±0.30	1.99±0.32	2.38±0.36	3.3±0.6	3.3±0.6
22-46	11.74±0.13	10.66±0.14	6.52±0.26	4.13±0.19	5.22±0.24	10.7±0.6	9.2±0.6

1/Metabolizable energy intake (kcal/animal/day).

2/Juvenile respiration (kcal/animal/day).

3/Adult respiration of equivalent juvenile body weight (kcal/animal/day).

4/Additional energy respired above what would be expected from smaller body size alone (M_j-M_A) (kcal/animal/day).

5/Metabolizable energy available for growth (M_g+P_j)(kcal/animal/day).

6/Production efficiency ((P_j/M_j)X100).

7/Production efficiency ((P_j/MEI_j)X100).

a lower metabolic rate (such as bone, inactive muscle, water) is much higher in the younger animal and decreases with age. The surface: volume ratio which is a major factor determining the thermoneutral temperatures of voles also has a role in determining the magnitude of M_g. The exact impact each of these factors have on M_g is not known and would be extremely difficult to determine.

Production Efficiency

Production efficiency can be expressed using a number of different ratios. Tissue growth efficiency expressed as a ratio of tissue production to maintenance respiration (P_j/M_j X 100) for each age class is shown in Table 25. The efficiency of production decreased with an increase in the age of the animal ($r = -0.83$, $P<0.001$). The average production efficiency for the 24 days of growth monitored when expressed as P_j/M_j X 100 was equal to 10.7 ± 0.6 (SE) percent.

Another approach to examining the efficiency of tissue production was a ratio of tissue production to metabolizable energy intake (P_j/MEI_j X 100). Efficiency expressed in this manner also decreased with an increase in age and was slightly less than the P_j/M_j ratio. For the 24 days of growth the average efficiency expressed as P_j/MEI_j X 100 was equal to 9.2 ± 0.6 (SE) percent. This was about twice as efficient as the 4.74 percent growth efficiency observed in *Microtus arvalis* by Drozdz et al. (1972).

The total metabolizable energy available for tissue growth, above that required for maintenance metabolism, M_{jp}, was deposited as tissue production with an efficiency equal to P_j/M_{jp} X 100. Efficiency when expressed in this manner was consistent through the period 22-40 days of age being equal to 21.6 percent, 21.5 percent, and 21.0 percent for the age classes 22-28, 29-34, and 35-40, respectively. However, during the last age class (41-46 days) the efficiency with which M_{jp} was deposited as tissue growth dropped to 16.4 percent. These estimates for the pine vole were similar to those obtained by Bull et al. (1976) in laboratory rats (12.6-27.2% efficiency) and by Drozdz et al. (1972) in *Microtus arvalis* (13-22%).

Determining Diet Digestibility Of Pine Voles Under Field Conditions Utilizing The Lignin Tracer Technique

Laboratory Phase

Table 26 shows the digestible dry matter (% DDM) and digestible energy (% DE) coefficients for the high digestibility rodent chow and the low digestibility rabbit chow as determined by the conventional feeding trial. The mean lignin concentration in rabbit chow was determined to be 5.618 percent (N=6) while the mean lignin concentration in the stomach contents was found to be 7.168 percent (N=4) (Table 27). The mean lignin concentration in rodent chow was determined to be 2.108 percent (N=6) while the mean lignin concentration in the stomach contents was found to be 3.144 percent (N=7) (Table 27). Therefore, it appeared that the lignin components of cell walls were remaining in the stomach for longer periods resulting in a slower rate of passage through the alimentary tract. The amount of lignin remaining in the stomach when compared to the concentrations in the chow was

Table 26. Digestible dry matter (%DDM) and digestible energy (% DE) coefficients of a commercial rabbit chow and rodent chow for pine voles. Measurements of consumption and egestion were a 5-day trial. Values represent means for 7 animals.

Parameter	Rabbit chow	Rodent chow
Number animals	7	7
Consumption (g)	32.29	19.98
Consumption (kcal)	138.79	87.40
Egestion (g)	12.59	3.92
Egestion (kcal)	52.66	14.75
% DDM (± S.D.)	61.01 ± 1.80	80.38 ± 0.01
% DE (± S.D.)	62.06 ± 1.69	83.12 ± 0.01

Table 27. Mean values for parameters used in the determination of correction factors to account for the amount of lignin which was not recovered in the feces of pine voles fed a commercial diet of rabbit chow and rodent chow.

Parameter	Rabbit chow	Rodent chow
% Lignin in feed	5.618	2.108
% Lignin in stomach (± S.D.)	7.168 ± 0.537	3.144 ± 0.505
Consumption (g)	32.29	19.98
Lignin consumed (g)[a]	2.31	0.63
% Lignin in feces (± S.D.)	10.654 ± 0.280	5.258 ± 0.328
Egestion (g)	12.59	3.92
Lignin egested (g)[b]	1.34	0.21
Unaccounted lignin (g)[c]	0.97	0.42
% Lignin unaccounted[d]	42.0	67.0
Correction factor[e]	1.7	3.0

[a] Lignin consumed (g) = % Lignin in stomach X consumption (g).

[b] Lignin egested (g) = % Lignin in feces X egestion (g).

[c] Unaccounted lignin (g) = Lignin consumed (g) - Lignin egested (g).

[d] % Lignin unaccounted = Unaccounted lignin (g)/lignin consumed (g).

[e] Correction factor = 100%/(100-%lignin unaccounted).

related to the digestibility of the chow. The rodent chow which had a higher digestibility had the highest concentration of lignin in the stomach in relation to the chow before ingestion. This is the result of higher rates of passage for the more digestible components of the chow.

Table 27 shows the parameters and procedure used to calculate correction factors for the differential rates of passage of lignin with respect to digestibility of the chows. The correction factors were then applied to the stomach and the fece samples of voles on laboratory chow diets (Table 28).

Field Phase

The laboratory experiment demonstrated the need for some prior knowledge of the quality of foods consumed by a small mammal before reliable correction factors can be applied to determine digestibilities. Pine voles consume largely forbs and apples throughout the year. In the spring and early summer when they are succulent and in great abundance voles will consume up to 80 percent forbs in their diet (Cengel et al. 1978). About mid-August voles will begin to consume apples as they mature and fall off the trees in the orchard. They will continue to eat large quantities of apple throughout the fall and into mid to late winter. In a digestion trial pine voles were found to digest 62 percent of the dry matter in a highly preferred forb species (*Taraxacum offincinule*) and 91 percent of the dry matter in apple (Lochmiller et al. 1979). With this knowledge of seasonal pine vole food habits and digestibility, correction factors were applied to the stomach lignin concentrations accordingly.

Table 28. Mean digestible energy coefficients (% DE), of a commercial rabbit chow and rodent chow fed to pine voles, as determined by stomach analysis. (Means and means ± S.D.).

Parameter	Rabbit chow	Rodent chow
% Lignin in stomach (LS)	7.168	3.144
Uncorrected % lignin in fece (LF)	10.654	5.258
Corrected % lignin in fece (CLF)	18.112	15.774
Stomach content energy (GES=kcal/g)	4.182 ± 0.085	4.339 ± 0.098
Fece energy (GEF=kcal/g)	3.864 ± 0.062	3.434 ± 0.103
GEF/GES ratio	0.924 ± 0.016	0.792 ± 0.024
LS/CLF ratio	0.396 ± 0.039	0.199 ± 0.030
% DDM	60.4 ± 3.9	80.1 ± 3.0
% DE	63.4 ± 3.8	84.2 ± 2.3

Table 29 shows the number of animals collected, number of pooled samples and the gross energy concentrations of stomach and fece samples from each apple orchard at bimonthly intervals. Lignin concentrations in the stomach contents, correction factors applied, and uncorrected and corrected lignin concentrations in the feces are shown in Table 30. This information was used to calculate digestible dry matter (DDM) and digestible energy (DE) coefficients of the stomach contents for each orchard. Correction factors were applied uniformly for each apple orchard.

There was a definite relationship between the lignin concentration in the stomach contents and the digestibility of the stomach contents. This inverse relationship between lignin content of forages and digestibility has been reported by other researchers with ruminants (Richards et al. 1958, Forbes and Garrigus 1948, Phillips et al. 1939, Ely et al. 1953).

The highest lignin concentrations occurred during the months of January and March for both orchards. This could indicate a period of food stress since animals appear to be reverting to highly lignified food materials which lowers the digestibility of the foods. This observation was also supported by food havits work conducted in similar orchards (Cengel et al. 1978, Estep 1975). Lignin concentrations in the stomach contents of voles for these two months were lower in the voles from the maintained apple orchard. This is

Table 29. Number of pine voles collected, number of pooled stomach and fece samples and the mean gross energy concentration (± S.D.) of the stomach contents and feces of voles collected at bimonthly intervals from the maintained and abandoned apple orchard.

Orchard/month	No. of animals collected	No. of pooled samples	Gross energy (kcal/g) Stomach	Gross energy (kcal/g) Feces
Maintained				
May	24	2	4.226±0.239	3.832±0.331
July	20	1	4.215	4.798
September	25	1	4.445	4.365
November	26	2	4.068±0.117	4.439±0.206
January	39	2	4.178±0.040	4.299±0.230
March	36	3	4.321±0.205	4.072±0.016
Abandoned				
May	25	2	4.733±0.004	4.380±0.311
July	20	1	4.495	4.050
September	17	1	4.385	4.526
November	22	2	4.273±0.101	4.528±0.193
January	25	2	4.341±0.345	4.392±0.058
March	30	3	4.317±0.212	4.461±0.098

Table 30. Lignin concentrations in stomach contents, and uncorrected and corrected lignin concentrations in feces of pine voles collected at bimonthly intervals from the maintained and abandoned apple orchard. (Means ± S.D.).

Orchard/month	% Lignin stomach contents	Feces		
		Correction factor	% Lignin uncorrected	% Lignin corrected
Maintained				
May	6.404±0.082	1.7	10.062±0.930	17.307±1.600
July	7.128	1.7	11.200	19.264
September	6.048	3.0	13.159	39.477
November	6.710±0.329	3.0	13.781±1.401	41.343±4.203
January	8.620±0.330	3.0	14.359±0.911	43.077±2.733
March	11.245±1.580	1.7	18.859±2.965	32.437±5.100
Abandoned				
May	7.898±1.620	1.7	13.354±0.721	22.969±1.240
July	5.748	1.7	15.605	26.841
September	6.726	3.0	14.504	43.512
November	9.898±0.169	3.0	20.027±1.053	60.081±3.159
January	12.114±1.530	3.0	14.170±1.845	42.510±5.535
March	13.127±2.997	1.7	17.907±0.464	30.800±0.798

probably due to the availability of highly digestible apples in the orchards. Apple availability was significantly less in the abandoned apple orchard in mid-January. The few apples which were available were concentrated in only a few areas in the abandoned orchard, making their availability to all voles limited. This finding is supported by the magnitudes of the standard deviation of mean lignin concentrations in stomach contents from the 2 orchards (Table 30).

In the maintained apple orchard, digestibility of stomach contents was lowest in May and July when forbs comprised a major portion of the diet (Table 31). Increasing maturity and subsequent lignification of plant material undoubtedly accounted for the decreases in digestibility from May to July. Digestibility began to increase where it remained above 82 percent through September and November. Digestibility began to decrease slightly in January when food supplies became increasingly lignified, however still remaining relatively high for a herbivore due probably to the plentiful supplies of apples remaining on the ground. Digestibility continued to decrease into March, but still remained higher than estimates for May and July.

A similar seasonal pattern in diet quality was noted for the abandoned apple orchard. The major difference occurred in July when digestibility continued to increase whereas the opposite occurred in the maintained orchard. Lignin concentrations in the stomach contents were at their lowest for this month (Table 30). When apples became increasingly abundant, digestibility increased accordingly in a manner and degree similar to that of the maintained orchard animals.

Table 31. Mean digestible dry matter (% DDM) and digestible energy (% DE) coefficients, as calculated from gross energy ratios (GEF/GES) and corrected (LS/CLF) and uncorrected (LS/LF) lignin ratios, for stomach contents of pine voles collected at bimonthly intervals in the maintained and abandoned apple orchard. (Means ± S.D.).

Orchard/month	GEF/GES ratio	LS/LF ratio	LS/CLF ratio	% DDM		% DE	
				Uncorrected	Corrected	Uncorrected	Corrected
Maintained							
May	0.928±0.156	0.639±0.050	0.372±0.029	36.1±5.0	62.8±2.9	42.2±3.7	66.4±2.1
July	1.138	0.636	0.370	36.4	63.0	27.6	57.9
September	0.982	0.460	0.153	54.0	84.7	54.8	85.0
November	1.091±0.019	0.491±0.074	0.164±0.024	50.9±7.4	83.6±2.4	46.6±7.1	82.2±2.4
January	1.029±0.065	0.602±0.061	0.201±0.061	39.8±6.1	79.9±2.0	38.2±2.4	79.4±0.8
March	0.943±0.042	0.603±0.108	0.350±0.063	39.7±10.8	65.0±6.3	43.2±9.3	67.0±5.4
Abandoned							
May	0.925±0.066	0.589±0.089	0.342±0.052	41.1±8.9	65.8±5.2	45.9±4.4	68.6±2.6
July	0.901	0.368	0.214	63.2	78.6	66.8	80.7
September	1.032	0.464	0.155	53.6	84.5	52.1	84.0
November	1.060±0.020	0.495±0.018	0.165±0.006	50.5±1.8	83.5±0.6	53.3±2.5	82.5±0.3
January	1.014±0.097	0.869±0.222	0.290±0.074	13.1±22.2	71.0±7.4	13.0±14.1	71.0±4.7
March	1.035±0.054	0.734±0.176	0.427±0.102	26.6±17.6	57.3±10.2	24.5±14.1	56.2±8.2

Seasonal Changes In The Available Primary Production Of An Abandoned and Maintained Apple Orchard Habitat

Production

Net primary production estimates of above ground herbaceous vegetation for areas beneath apple tree canopies and for areas outside the tree canopies within both the maintained and abandoned apple orchards are shown in Tables 32 and 33 for each season. The species composition and net primary production was distinctly different between areas beneath the apple tree canopies and areas outside the shading influence of the trees. This difference was characteristic of both apple orchards. A *t*-test revealed that the maintained orchard had a much larger standing crop (biomass and gross energy) of herbaceous plants than did the abandoned apple orchard during the summer ($P<0.01$), fall ($P<0.01$), and winter ($P<0.01$) seasons. There was no difference between orchards during the spring season ($P>0.05$).

Biomass (g dry weight/m^2) and available gross energy (kcal/m^2) of each species of plant occurring beneath the canopies of apple trees and in areas outside the tree canopies in the maintained and abandoned apple orchard during the summer, fall, winter and spring seasons are shown in Appendix Tables I, II, III, and IV, respectively (production estimates of poison ivy, *Rhus radicans*, are included in these tables).

During the period from August to January, maturing apples accumulated on the ground offering an additional food source to supplement the herbaceous vegetation available to pine voles. Biomass

Table 32. Biomass estimates (g dry wt./m^2) for herbaceous forage in a maintained and an abandoned apple orchard during each season. Estimates do not include poison ivy (*Rhus radicans*). (Mean ± S.E.).

Orchard type/area		Summer	Fall	Winter	Spring
Maintained					
Beneath canopy	6	38.2±7.0	14.6±4.2	2.7±2.0	6.2±4.6
Outside canopy	6	233.2±23.6	192.6±25.9	19.3±2.6	109.8±13.7
Abandoned					
Beneath canopy	6	6.3±2.3	2.2±0.6	1.8±1.5	17.9±10.9
Outside canopy	6	49.4±17.4	15.2±3.7	11.2±6.3	67.1±23.7

Table 33. Gross energy estimates (kcal/m^2) of herbaceous forage in a maintained and abandoned apple orchard during each season. Estimates do not include poison ivy *(Rhus radicans)*. (Mean ± S.E.).

Orchard type/area	N	Summer	Fall	Winter	Spring
Maintained					
Beneath canopy	6	163.5±30.6	64.2±18.9	11.9±9.1	27.3±20.3
Outside canopy	6	1007.3±104.7	893.0±117.9	84.9±11.4	489.5±60.7
Abandoned					
Beneath canopy	6	26.7±9.9	9.5±2.4	7.8±6.6	80.8±49.7
Outside canopy	6	209.9±76.7	66.9±16.4	47.9±27.0	303.6±107.4

and gross energy estimates of apples which accumulated on the ground in the maintained and abandoned orchards during each season are shown in Tables 34 and 35, respectively. The importance of apple to the available food supply of pine voles in each orchard during the fall and winter seasons can be easily seen by comparing with Tables 32 and 33. Apples comprised 78.8 percent of the total energy production available in the maintained orchard and 33.9 percent in the abandoned orchard during the winter season. A *t*-test showed that during the winter season, the apple production (biomass and energy) on the ground was significantly greater in the maintained orchard ($P<0.01$) than in the abandoned apple orchard. There was no difference in available apple production on the ground between orchards during the other seasons.

Results from the monthly collection of apples from soft-mast traps situated within each apple orchard are shown in Table 36. An analysis of variance revealed significant monthly variations in total dry biomass ($P<0.001$) and gross energy ($P<0.001$) production of apples in both orchards (Table 37). Peak apple drop occurred in September when an estimated 340.6 ± 91.1 (SE) kcal/m^2 and 307.8 ± 84.6 (SE) kcal/m^2 of gross energy became available to voles in areas beneath the canopies of apple trees in the maintained and abandoned apple orchard, respectively. Apple drops began to decrease by November in the abandoned apple orchard; however, apples continued to drop into December, January, and February in the maintained apple orchard. There was a large amount of variability in production between individual trees. An analysis of variance indicated that differences in production between the maintained

Table 34. Biomass estimates (g dry wt./m^2) for apple drops in a maintained and an abandoned apple orchard during each season. (Mean ± S.E.).

Orchard type/area	N	Summer	Fall	Winter	Spring
Maintained					
Beneath canopy	6	0.4±0.2	57.4±24.2	73.6±18.2	16.1±3.7
Outside canopy	6	0.0	2.5±1.5	0.9±0.6	2.3±1.6
Abandoned					
Beneath canopy	6	0.2±0.1	61.8±36.4	1.4±0.8	8.3±5.2
Outside canopy	6	0.0	8.4±4.9	5.0±3.3	2.6±2.3

Table 35. Gross energy estimates (kcal/m^2) for apple drops in a maintained and an abandoned apple orchard during each season. (Mean ± S.E.).

Orchard type/area	N	Summer	Fall	Winter	Spring
Maintained					
Beneath canopy	6	1.9±1.1	246.4±104.1	355.1±87.8	84.7±19.5
Outside canopy	6	0.0	10.9±6.6	4.3±3.1	12.3±8.5
Abandoned					
Beneath canopy	6	1.2±0.6	262.6±155.0	7.0±4.1	43.5±27.1
Outside canopy	6	0.0	35.6±20.9	25.6±16.9	13.4±12.2

Table 36. Monthly apple production in the maintained and abandoned apple orchard from July 1978 to February 1979. Values represent means ± S.E. for areas beneath the tree canopy.

Month	Production			
	Maintained orchard		Abandoned orchard	
	Dry biomass (g/m^2)	Gross energy ($kcal/m^2$)	Dry biomass (g/m^2)	Gross energy ($kcal/m^2$)
July	3.23 ± 1.10	14.55 ± 4.96	5.46 ± 1.90	24.00 ± 8.33
August	3.75 ± 1.58	16.13 ± 6.81	6.73 ± 2.62	29.48 ± 11.48
September	78.98 ± 21.13	340.58 ± 91.13	70.98 ± 19.50	307.82 ± 84.61
October	63.98 ± 21.05	273.79 ± 90.09	32.63 ± 12.16	140.66 ± 52.42
November	43.95 ± 14.17	195.52 ± 63.05	11.01 ± 5.08	48.47 ± 22.37
December	7.37 ± 7.37	33.52 ± 33.52	0.41 ± 0.41	2.06 ± 2.06
January and February	4.38 ± 3.09	21.04 ± 14.84	0	0
Total production/year	205.64	895.13	127.22	552.49

Table 37. Mean squares for dry biomass (g/m^2) and gross energy (kcal/m^2) of apple drops beneath apple tree canopies in two orchards near Daleville, Virginia, from July 1978 to February 1979.

Source	*df*		Dry biomass	Gross energy
Month (M)	6	mean square	13889	257678
		P	.001	.001
Orchard (O)	1	mean square	3450	65590
		P	.100	.098
M X O	6	mean square	934	17758
		P	.616	.607
Error	99	mean square	1255	23534

and abandoned apple orchards approached significance for dry biomass ($P<0.10$) and gross energy ($P<0.10$) (Table 37).

Quality

The results of a proximate and soluble carbohydrate analysis of the major plant species occurring in each orchard during each season are shown in Appendix Tables V-XII. In general, these analyses showed that crude protein concentrations were highest in forb species while lower in the grasses. The stem portion of forbs generally had lower protein levels than the leaf portion. Crude fiber estimates were generally lower in forbs than in the grasses. The stem portions of forbs and vines were higher in crude fiber content than the leaves. Apples had very low protein and crude fiber concentrations, but high levels of soluble carbohydrates.

Preference

A total of 14 forages were tested in a series of 9 feeding trials. Food items were ranked overall in order of decreased preference based on these choice tests (Table 37). There was not a large amount of variation between individual voles with respect to preference or degree of consumption. Thompson (1965) also noted nonsignificant variation between individual *Microtus pennsylvanicus*.

Apple fruit was a highly preferred food item among all voles tested. Apple was completely consumed before substantial amounts of other forages being tested with it were consumed. Analyses of the remaining 13 food items tested indicated that pine voles were extremely diverse in their feeding habits. This was especially apparent for

Table 38. Estimated order of preference of major forages utilized by pine voles from orchard habitats (L = leaves, S = stem, bulb = root portion).

Decreasing order of preference	Forage species
1	Apple fruit
2	Dandelion (L) *(Taraxacum officinale)*
3	Broad-leaved plantain (L) *(Plantago major)*
4	Clover (L & S) *(Trifolium sp.)*
5	Narrow-leaved plantain (L) *(Plantago lunceolata)*
6	Goldenrod (L) *(Solidago sp.)*
7	Onion (bulb) *(Allium vineale)*
8	Dock (L) *(Rumex crispus)*
9	Strawberry (L) *(Fragaria virginiana)*
10	Virginia creeper (L) *(Parthenocissus quinquifolia)*
11	Wire-grass *(Muhlenbergia schreberi)*
12	Honeysuckle (L) *(Lonicera japonica)*
13	Orchard grass *(Dactylis glomerata)*
14	Onion (L) *(Allium vineale)*

forbs; voles consumed to some degree all 7 forb species tested. This was an important characteristic because it provided for flexibility in diet and ease of transition between seasonal food supplies. Overall, forbs were found to be distinctly preferred over the grasses tested in this study.

DISCUSSION

Seasonal, Reproductive, and Developmental Energetics of the Pine Vole

Digestive efficiencies of pine voles in this study compared favorably with those reported by Merson (1979) for pine voles and by Johnson and Groepper (1970) for *Microtus pennsylvanicus*, McManus (1974) for *Clethrionomys gapperi*, and other researchers for a laboratory rodent chow. Voles which were subjected to the increased thermoregulatory and activity costs of out-of-the-nest exposure consumed greater amounts of laboratory chow than those voles with nesting material. This resulted in a significant reduction in the digestive efficiency of voles during the summer, fall, and winter season. This indicated increased rates of passage of food stuffs through the alimentary tract with the increased rate of consumption.

Lactating females maintained a level of digestive efficiency equal to that of nonbreeding adults despite their increased rates of food consumption during the period of lactation. This has been observed in other species of pregnant and lactating voles (Kaczmarski 1966). The weight and length of various parts of the alimentary tract are temporarily increased during pregnancy and lactation (Myrcha 1964, Myrcha 1965, Gebczynska and Gebczynski 1971). This permits the maintenance of digestive efficiencies which are equivalent to those of nonbreeding adults.

Juvenile pine voles had a digestive efficiency which was slightly higher than adult voles; however, this was not significant. Miller (1974) working with *Microtus ochrogaster* and Drozdz et al. (1972) with

Microtus arvalis observed that digestibility did not change with age in growing juveniles.

The daily metabolic requirements for maintenance in adult pine voles showed a definite seasonal cycle. This cycle was a reflection of the thermoregulatory costs associated with seasonal changes in ambient temperature. The average daily metabolic requirements of adult voles housed in cages with nests represented the energetic sum of energy expenditures during the time spent by an animal in the nest, plus the time spent outside the nest. Inherent to both of these activities is the thermoregulatory costs of a vole when below the zone of thermoneutrality (Morrison 1960). The lower critical temperature (T_{1c}) of a small mammal can be predicted from the equation of Morrison (1960) as modified by Wunder (1975):

$$T_{1c} = 38 - 4W^{0.25}$$

where W is body weight in grams. Substituting the weight of an adult pine vole into the above equation resulted in an estimate for T_{1c} ranging from 28-29C, depending on the body weight of the vole. If this is an accurate estimate for the pine vole, then thermoregulatory costs were a factor during all seasons. However, at temperatures above 20C, thermoregulatory costs are probably very small (Grodzinski and Wunder 1975). McManus (1974) estimated the zone of thermoneutrality in *Clethrionomys gapperi* to be 28C which was close to the calculated value for the pine vole.

Daily metabolic requirements for maintenance increased by 33 percent from the summer to fall season. The increase from the summer to winter season amounted to 50 percent. The increase from fall to winter amounted to only 13%. This was probably a result of the increased insulation afforded by hair growth and fat deposits between the fall and winter season, as well as decreased levels of activity. The fall and spring seasons appeared to be periods of transition to the winter and summer levels. This is conceivable since voles are actively molting and mobilizing fat tissues during these seasons.

The importance of the nest for its insulatory qualities was clearly demonstrated by the increased daily metabolic requirements of adult voles housed in metabolic cages with activity wheels. These voles required about 16 percent, 41 percent, 32 percent, and 55 percent more energy per day than did voles with nests during the summer, fall, winter, and spring seasons, respectively. Levels of activity decreased from the summer to the winter season and increased again during the spring trial. Similar trends of activity have been observed in other species of voles (Hansson 1970). Heat exchange in homeotherms is generally governed by insulative qualities of the body surface and by the body postures assumed (McManus 1974). The minimum thermoconductance of an animal is usually achieved when at rest in a heat conserving posture which, in the pine vole, appeared to be a huddled posture with head and feet tucked under an arched body. When a vole becomes active and its heat conserving posture changes, heat losses increase. Therefore, reduced activity levels during the fall and winter seasons appeared to be energetically conserving. The difference between the summer metabolic requirements of adult voles with nests and those without nests was probably a good estimation of the additional metabolic costs for out-of-the-nest activity (16%). This is assuming that temperatures above 20C require little correction for thermoregulation (Grodzinski and Wunder 1975, Beck and Anthony 1971).

Lactation is the most energy demanding reproductive process in all mammals, mainly because of the thermoregulatory, growth, and activity costs of the young. The energetic costs of lactation in the pine vole were extremely high in comparison with the daily maintenance requirements of nonbreeding adult females. The length of lactation in female pine voles was determined to be 21 days. Two distinct periods of lactation were evident. The period between 1-18 days of lactation was characterized by almost complete dependence on the mother's milk by the suckling young. During the period between 19-21 days of lactation appreciable amounts of solid food was being consumed by the suckling young. Suckling voles began consuming small amounts of solid food as early as 15 or 16 days of age.

During the 21 days of lactation the average lactating female and her litter required an estimated 47.5 percent more metabolizable energy than a nonbreeding female of equivalent body weight (mean litter size of 2.2 young). To nurse a litter of 2 offspring, a female pine vole and her litter (due to sucklings consuming food) required a 36.6 percent increase in energy requirements during the first 18 days of lactation, and a 44.5 percent increase during the 21 days of lactation. Millar (1978) reported that lactating female *Peromyscus leucopus* supporting a litter of 2 offspring required a 74 percent increase in ingested energy during 21 days of lactation. To support a litter of 3 offspring to weaning, a female *Peromyscus leucopus* required a 94 percent increase. A lactating female pine vole and her litter of 3 offspring required a 58.2 percent increase in metabolizable energy requirements during the period 1-18 days, and 68.4 percent during the 21 days of lactation. Migula (1969) reported that the metabolic cost of lactation in female *Microtus arvalis* with an average litter of 4 offspring, exceeded the requirements of control females by 133 percent over 16 days of lactation. Lactating female *Clethrionomys glareolus* required a 92 percent increase in energy to bring 4 out of 5 offspring born to weaning.

It is clear from the above discussion that larger litters require correspondingly more energy through the period of lactation. The female pine vole has a fairly constant litter size which averages about 2 offspring. In this study, the average litter consisted of 2.2 offspring. Noffsinger (1976) reported that female pine voles in southwest Virginia supported 1.9 and 1.5 offspring in a maintained and an abandoned apple orchard, respectively. Valentine and Kirkpatrick (1970) found an average of 1.9 offspring per litter in Virginia, while Paul (1970) found an average of 2.24 offspring per litter in North Carolina. Compared to those species of small mammals with litters of 4 or 5 offspring, the female pine vole has the ecological advantage of requiring less total energy to nurse a litter to weaning. This conservative strategy probably results in minimal wastage of reproductive effort and the energy resource. The probability of producing a successful litter during the winter season, when thermoregulatory costs are high and available energy limited, would be much higher for the pine vole.

The net conversion of metabolized energy into tissue growth during the period of lactation was extremely high in pine voles. Production efficiency (measured as Ps/Msp X 100, where Ps is the amount of energy incorporated into suckling tissue growth and Msp is the increased metabolized energy of a lactating female pine vole) was estimated to be 26.6 percent during the first 18 days of lactation and 26.0 percent during the 21 days of lactation. These estimates were lower than the 34-45 percent efficiency in *Sigmodon hispidus* (Randolph et al. 1977) but were higher than the estimated 14.6 percent efficiency in *Clethrionomys glareolus* (Kaczmarski 1966) and 15.4 percent in *Microtus arvalis* (Migula 1969).

The higher production efficiency observed in the pine vole was unexpected since other vole species averaged 15 percent. Some of the difference might be the result of differences in experimental conditions. The studies of Kaczmarski (1966) and Migula (1969) were conducted at 20C while pine voles in this study were subjected to 23C. More energy would be available for production instead of maintenance at the higher temperature; however, as already mentioned, thermoregulatory costs are minimal at temperatures above 20C. Another possibility is that pine voles used in this study averaged about 3-4 g larger than the voles from the other studies. Smaller voles have higher metabolic rates which would result in less energy available for production. Litter sizes were much smaller in the pine vole, but it is unknown whether this could have affected the efficiency of production. The caloric value of tissue growth was higher in the pine vole (1.76 kcal/g) in comparison to *Clethrionomys glareolus*, 1.4 kcal/g (Kaczmarski 1966) and *Microtus arvalis*, 1.2 kcal/g (Migula 1969). Randolph et al. (1977) attributed the higher production efficiency in *Sigmodon hispidus* to its larger body size, shorter duration of lactation, and storage of energy through fat deposition.

The high production efficiency observed in the pine vole is ecologically significant because it reduces the total ingestion requirement considerably for producing a litter. This could be a significant advantage during periods of intense competition and limited food availability. The combination of small litters and high production efficiency are probably important factors enabling the pine vole to breed throughout the winter season.

The period of most intensive juvenile growth occurred during the period between 22-46 days of age in the pine vole. During the period of growth the cost of energy deposition increased over what was observed before weaning. Although production efficiency was lower after weaning, it still remained relatively high in comparison to that of other vole species (Drozdz et al. 1972). Production efficiency continued to decrease with age.

Drozdz et al. (1972) found that juvenile *Microtus arvalis* deposited the metabolized energy with an efficiency of 5.6 percent, 4.8 percent, and 3.9 percent during the periods between 20-30 days of age, 30-40 days, and 40-50 days, respectively. The pine vole was nearly twice as efficient in depositing metabolized energy as tissue growth. Juvenile pine vole production efficiency was equivalent to 15.5 percent, 11.0 percent, 7.2 percent, and 3.3 percent during the periods of growth between 22-28 days, 29-34 days, 35-40 days, and

41-46 days, respectively. Pine vole and *Microtus arvalis* production efficiencies were very similar during the period between 40-50 days of age. The overall efficiency of tissue production averaged 9.2 percent in the growing juvenile pine vole. This was considerably higher than the overall efficiency of 4.74 percent reported for *Microtus arvalis* (Drozdz et al. 1972).

The physiological ability of juvenile pine voles to convert net metabolized energy into tissue growth with a minimal of energy expense is ecologically important. This provides the juvenile pine vole with an energy advantage over those species of small mammals which are unable to efficiently convert energy into growth. This advantage would probably become most important during periods of intense competition with other species of small mammals for the food resource. Periods such as this could occur during the winter season when food supplies are limited.

The average adult pine vole (25g) required 12.38 kcal/day during the summer season. The average juvenile pine vole, which was substantially smaller in body size, had an average metabolic requirement of 11.74 kcal/day, a difference of only 0.64 kcal/day. The growth process is so energy demanding that juvenile voles probably compete with adults for near equivalent amounts of energy to meet their daily requirements. The high efficiency with which juveniles deposit energy could be a physiological adaptation for improving their ability for competing with adults. During periods of food restriction, growing juvenile voles could have difficulty in acquiring daily energy requirements in the event of adult competition. Similarly, if adults continue to breed into periods of food shortages, it could become detrimental to their own survival since they will be forced into competition with their own offspring for the limited energy supplies available.

The average juvenile pine vole required 282 kcal of metabolizable energy over the 24 days of intensive postnatal development, of which 25.8 kcal was deposited as tissue growth. During this period, juvenile voles increased in weight from 11.97g to 21.78g, an increase of 9.8g.

Determining Diet Digestibility Using a Lignin Tracer

The digestibility estimates for pine voles on the commercial rodent chow (80% for DDM, 83% for DE) were similar to previously reported values for other rodents (Kaufman et al. 1975, Johnson and Groepper 1970). Digestibility estimates for rabbit chow by rodents could not be found in the literature. Rabbit chow was considerably less digestible (61% for DDM and 62% for DE) than rodent chow. Comparison of lignin concentrations in the food and stomach revealed discrepancies probably due to the differential rate of passage between the more digestible (cell contents) and less digestible (cell walls) portions of the food. To correct this concentration of lignin in the stomach contents, the concentration of lignin in the feces was multiplied by a correction factor of 1.7 for the low digestibility rabbit chow and by 3.0 for the high digestibility rodent chow. Kaufman applied a correction factor of 2.15 when applying the ash-tracer method on stomach contents and feces of cotton rats

(Sigmodon hispidus). The correction factor was determined in the laboratory for animals consuming a commercial rat chow. Application of a correction factor determined for a single diet of high digestibility as rat chow could result in serious errors in estimates of field digestibility for especially diversified foliage-eating rodents. Soholt (1973) determined separate correction factors for 3 different diets consisting of natural foods of *D. merriami*, but found no significant differences between assimilation efficiency estimates based on the average correction factor for all 3 foods and the estimates determined by using each food's respective correction factor. Thus, the ash-tracer appeared to be a reliable indicator of digestibility for *D. merriami*. Digestibility of all 3 foods was very high (84-96%) which could account for the reliability of a single correction factor.

Using a mean correction factor of 2.34 to determine digestibility of stomach contents for rabbit chow and rodent chow produced estimates which were significantly different from the estimates determined using each food's respective correction factor. Using the mean correction factor (instead of 1.7 or 3.0) gave digestibility estimates which were 6 percent higher for rabbit chow and 10 percent lower for rodent chow. This discrepancy made it necessary to use separate correction factors when they were applied to field caught animals. Knowledge of the relative quality (food habits (Cengel et al. 1978); digestibility (Lochmiller 1979)) of the foods consumed by the animals in the field was the criteria used for selecting an appropriate correction factor during any given season.

There was distinct seasonal change in the digestibility of foods consumed by the voles in the field. The highest digestibilities coincided with the maturation of the apple crop, a highly preferred forage. This high energy yielding food source was available to voles through mid- to late-winter at which time a decrease in diet digestibility was noted. With the added costs of thermoregulation under winter conditions, voles may have had difficulties in consuming and extracting enough energy from the low digestible food supply available to them for maintenance purposes. Pine voles from the abandoned apple orchard were probably more limited in their ability to meet body maintenance energy requirements under late winter conditions than voles from the maintained orchard population due to the lower digestibility of foods.

Utilization of lignin as an indigestible indicator for determining digestibility of field caught animals has certain advantages over other tracers such as ash. Lignin alone acts to decrease the digestibility of plant material. So lignin concentration in stomach material have the potential to serve as an index to the digestibility or quality of forage. In this study, stomach lignin concentration was found to be inversely proportional to digestibility ($r = -0.72$, $P<0.01$).

The major limitation to using lignin as an indicator substance is the need for 0.7-1.0g of material for chemical analysis. Working with species as small as the pine vole (24g) requires a large number of animals for a single pooled sample. The average quantity of feces extracted from an individual vole was around 68mg. The technique could be easily used on larger sized mammals without the sample size problems encountered with this small rodent. Despite the small number of pooled samples, it is felt that the results are indicative of the field conditions since each pooled sample is comprised of many individual voles. The total contribution (by weight) to the whole sample by an individual vole was extremely small.

Further refining of the techniques and understanding of the digestive processes of small mammals should enable a wider application of the lignin tracer method for determining digestibility under field conditions.

Availability of Primary Production in Orchard Habitats

The most evident finding from this part of the study was that optimal quality forage was certainly not as abundant as the superficial examination of the habitat indicated. Much of the primary production was either out of the reach of voles or was too woody and fibrous to be considered a major palatable food source. Apple was shown to be the most preferred food item tested from the orchard habitat and its low fiber concentration and high digestibility made it an important food item during the fall and winter seasons. This was most advantageous because the apple crop became available at a time when temperatures began to drop and thermoregulatory costs increased. Assuming a digestibility estimate of 90.1 percent for apple which has not yet deteriorated by lying exposed on the ground (Lochmiller et al. 1979), the estimated yearly digestible energy production of apple in the maintained orchard was 403.26 kcal/m^2 (4,032,600 kcal/ha/yr) and 248.90 kcal/m^2 (2,489,000 kcal/ha/yr) in the abandoned apple orchard. The above estimates were derived from Table 36 using an ocular estimate for apple tree canopy coverage of 50 percent.

The nutrient analysis indicated that apple had extremely low protein levels but high carbohydrate concentrations. The protein concentrations in apple were well below the maintenance requirements of meadow voles (NRC 1978). Due to this inadequacy, and the fact that reproduction and growth was observed to continue during the winter, voles must have been obtaining their nitrogen requirements from either (1) consuming additional apple above their daily maintenance requirements for energy (Meyer 1958), or (2) by consuming alternate food items which were naturally high in protein content such as many of the forb species tested. Under the first strategy voles would have deposited the excess energy derived from the increased consumption of apple as body fat. This would have resulted in a greater proportion of the body gain to be fat as opposed to protein or ash. Since forbs do occur in the fall and winter diets of pine voles (Cengel 1975), the second strategy of obtaining daily protein requirements was a possibility. Pine voles probably incorporated a combination of the 2 above strategies since fat levels were observed to increase during the fall season.

Forbs were observed to be preferred over the grass species tested. The apparent reason for the low palatability of grasses appeared to be the higher fiber concentrations. In maintained apple orchards which are continually mowed, a greater supply of low fiber forage becomes available from regrowth of grasses and forbs.

The most preferred forage species, forbs, made up only a very small portion of the net primary production available in each orchard habitat. This indicated that voles were probably selective in what they ate, consuming the more highly palatable species of forbs first. Cengel et al. (1978) found grasses in the diet of pine voles which tends to indicate an ability by pine voles to select those parts of plants which are low in fiber content. Orchard grass, which was the most abundant plant species in the maintained apple orchard, was extremely low in preference and digestibility. The most preferred plant species such as clover, dandelion, and plantain are characteristic of open field habitats because they have the distinct disadvantage of being shaded out by the more erect species of plants. The prolific nature of poison ivy was mainly responsible for the near complete elimination of these preferred forbs from the abandoned apple orchard, while mowing operations in the maintained habitat provided for the survival of these preferred forages.

It appeared from the quantitative and qualitative analysis of the seasonal primary production in both orchard habitats that the vole population inhabiting the abandoned apple orchard was generally surviving in a lower quality habitat. It would probably be correct to assume that if an apple crop failure would occur in the abandoned orchard, a noticeable decline in reproductive effort and population size would occur. Since apple crop failures naturally occur during some years, a continual monitoring of the vole populations in each orchard habitat would probably reveal more dramatic fluctuations in population demographic parameters in the abandoned apple orchard from year to year.

The quality of habitats was lowest and the differences between the 2 orchards were at their greatest during the winter season. The abundant energy source which was available from apples during the fall season was much depleted by mid-winter due to both pine vole consumption and decomposition. This was especially true within the abandoned apple orchard. Total available primary production was lowest of all seasons during the winter in both apple orchards. Appendix Tables XIII-XVI show the seasonal biomass and gross energy available from preferred herbaceous and apple primary production in each orchard habitat when assuming an estimated 50 percent (ocularly estimated) canopy coverage by apple trees. It was estimated that available primary production amounted to 47.33 g/m^2 (223.68 $kcal/m^2$) in the maintained orchard habitat and 8.39 g/m^2 (38.54 $kcal/m^2$) in the abandoned orchard habitat during the winter season (Appendix Table XV).

It was estimated from the lignin analysis of stomach contents collected during the winter season (determined as the mean of the calculated values for stomach contents collected during January and March) that the digestibility of winter diets was 73.2 percent and 63.6 percent in the maintained and abandoned apple orchards, respectively. Utilizing these estimates of digestibility, the total amount of digestible energy (TDE) available during the winter season can be calculated:

Maintained orchard:

$$\text{TDE (kcal/ha)}=((223.68\ \text{kcal/m}^2)(10{,}000\ \text{m}^2/\text{ha}))0.732$$

$$\text{TDE} = 1{,}637{,}338\ \text{kcal/ha}$$

Abandoned orchard:

$$\text{TDE (kcal/ha)}=((38.54\ \text{kcal/m}^2)(10{,}000\ \text{m}^2/\text{ha}))0.636$$

$$\text{TDE} = 245{,}114\ \text{kcal/ha}$$

Further calculations can be made to obtain an estimate of the potential number of adult voles which can be maintained on the available digestible energy reserves in each orchard habitat. The mean adult body weight for the winter season (Appendix Tables XVII-XVIII) was estimated to be 24.5g and 24.7g in the maintained and abandoned apple orchards, respectively. Substituting these estimates for body weight (W) into the following equation derived for the winter season,

$$\text{DEB (kcal/animal/day)} = 3.23 + 0.60W$$

the average maintenance energy requirements of an adult pine vole was estimated to be 17.93 kcal/day and 18.05 kcal/day in the maintained and abandoned apple orchards, respectively.

The number of vole-days (VD) of metabolizable energy available in each orchard can be calculated by assuming a 2 percent energy loss in urine and dividing the available metabolizable energy by the daily maintenance energy requirements of an average adult pine vole:

Maintained orchard:

$$\text{VD (vole-days/ha)} = \frac{((1{,}637{,}338\ \text{kcal/ha})(0.98))}{17.93\ \text{kcal/vole/day}}$$

$$\text{VD} = 89{,}492\ \text{vole-days/ha}$$

Abandoned orchard:

$$\text{VD (vole-days/ha)} = \frac{((245{,}114\ \text{kcal/ha})(0.98))}{18.05\ \text{kcal/vole/day}}$$

$$\text{VD} = 13{,}308\ \text{vole-days/ha}$$

The estimated number of adult pine voles (N) which could potentially be sustained on the available metabolizable energy in each orchard during the winter season can be calculated by dividing the number of vole-days/ha by the number of days in the season (January, February, March):

Maintained orchard:

$$N \text{ (voles/ha)} = \frac{89{,}492 \text{ vole-days/ha}}{90 \text{ days}}$$

$$N = 994 \text{ voles/ha}$$

Abandoned orchard:

$$N \text{ (voles/ha)} = \frac{13{,}308 \text{ vole-days/ha}}{90 \text{ days}}$$

$$N = 147 \text{ voles/ha}$$

It became apparent from the above derivations that energy availability in the abandoned orchard habitat was considerably limited in comparison to that which was available in the maintained orchard habitat. Reproduction was observed to occur to a limited extent during the winter in each apple orchard and has been reported by Noffsinger (1976) in the same orchards. The increased demands for energy by pregnant and lactating pine voles would result in a corresponding reduction in the estimate for N. Continual depletion of food reserves will ultimately require animals to spend correspondingly more time searching for palatable foods, thereby increasing their thermoregulatory and activity costs which will also cause a further reduction in the estimate for N.

A factor which was not considered in the above discussion was the extra-energetic destruction of the food resource which results during the normal foraging and nest building activities of pine voles. Ryszkowski et al. (1973) estimated that *Microtus arvalis* in cultivated fields destroyed 1.8 times as much as was consumed. Assuming a similar ratio for the pine vole, the estimate for N would be reduced to 552 voles/ha in the maintained apple orchard and 82 voles/ha in the abandoned apple orchard during the winter season.

SUMMARY AND GENERAL CONCLUSIONS

Adult pine voles showed a seasonal cycle in daily maintenance energy requirements. The observed cycle was a reflection of the thermoregulatory costs associated with seasonal changes in ambient temperature. Winter was energetically the most expensive season, requiring an average of 0.735 kcal/g/day for voles housed with nests and 0.969 kcal/g/day for those with exercise wheels. Requirements during the summer season were lowest of all seasons. Daily maintenance requirements of adult voles during the summer amounted to 0.491 kcal/g/day with nests and 0.568 kcal/g/day with exercise wheels. There was no significant difference in the daily energy requirements between male and female adult pine voles. Nesting material was an important insulatory asset which significantly decreased daily energy demands of adults. Adult voles housed in cages with only exercise wheels required 16 percent, 41 percent, 32 percent, and 55 percent more energy than adult voles with nests during the summer, fall, winter, and spring seasons, respectively.

The period of lactation among female pine voles was energetically very demanding. During 21 days of lactation the average lactating female and her litter required an estimated 47.5 percent more metabolizable energy than a nonbreeding adult female of equivalent body weight. The mean litter size among 19 litters studied was 2.2 young. Energetic requirements for weaning a litter of young increased with size of the litter, weight of the litter, and growth rate of the litter. The average lactating female and her litter had an additional metabolizable energy requirement above nonreproductive requirements of 134.73 kcal over 21 days of lactation. The average litter incorporated 35.10 kcal of energy into tissue production. This was equivalent to 15.95 kcal per offspring.

The net conversion of metabolized energy into tissue growth during the period of lactation was extremely high among pine voles. Production efficiency was estimated to be 26.0 percent over 21 days of lactation. Lactating female pine voles had production efficiencies which were considerably higher than estimates derived for other species of vole. The small litter size (1-3 young) and the extremely high production efficiency among lactating female pine voles are ecologically important because they result in a lower total energy requirement for producing and weaning a litter. This ecological advantage over other species of vole can become very important during periods of energy restriction. Such conditions could very well occur during winter food shortages in apple orchard habitats.

Juvenile pine voles between the ages 22-46 days had very high energy demands for maintaining the growth process. Over this 24-day period, the average juvenile pine vole metabolized 282 kcal of energy of which 25.8 kcal was deposited as tissue growth. Juvenile voles increased in body weight from 11.97g to 21.78g over the 24-day period. Similarly to the lactating female, the juvenile pine vole possessed a physiological ability to deposit energy in the form of tissue growth with an efficiency above that reported for other species of vole. The overall efficiency of production averaged 9.2 percent in the growing juvenile. This high efficiency can provide the juvenile pine vole with an energy advantage over other species. This also can be an important factor in the realm of competition. The average juvenile pine vole had a metabolic requirement of 11.74 kcal/day over the 24 days of intensive postnatal development.

A lignin analysis of stomach contents showed a distinct seasonal change in the digestibility of foods consumed by voles from the maintained and abandoned apple orchards. The highest digestibilities coincided with the maturation of the apple crop which was shown to be a highly preferred and digestible forage among pine voles. Digestibilities were very low during the winter when apple supplies diminished; this was especially true for the abandoned orchard population. Given the elevated thermoregulatory costs of winter, voles from the abandoned apple orchard habitat may have had difficulties in securing and digesting sufficient amounts of energy for maintenance.

Yearly energy production of apple in the maintained orchard was estimated to be 403.26 kcal/m^2 and 248.90 kcal/m^2 in the abandoned orchard; however, there was no significant difference between apple orchards. Quality of orchard habitats were lowest during the winter season. The quantity of available primary production amounted to only 38.54 kcal/m^2 in the abandoned orchard compared to the 223.68 kcal/m^2 in the maintained apple orchard. It was estimated that the amount of primary production available to pine voles during the winter season could support 994 nonreproducing adult voles per hectare in the maintained orchard and 147 nonreproducing adult voles per hectare in the abandoned apple orchard habitat.

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APPENDIX

Appendix Table I. Biomass (g dry wt./m^2) and available gross energy (kcal/m^2) of grasses, forbs, apple fruit, and bulbs in areas beneath the tree canopy and areas outside the tree canopy in the maintained and abandoned apple orchard. Summer 1978.

	Maintained Orchard				Abandoned Orchard			
	Beneath canopy		Outside canopy		Beneath canopy		Outside canopy	
Species[1]	Biomass	GE	Biomass	GE	Biomass	GE	Biomass	GE
Grasses								
Setaria sp.			14.96	65.46				
Poa pratense	3.11	13.69	19.80	87.23			3.70	15.86
Dactylis glomerata	23.41	100.67	110.58	475.48	0.05	0.19	0.51	1.99
Muhlenbergia schreberi			42.13	189.22			0.81	3.56
Unknown	2.08	9.03	4.02	17.43			1.36	5.86
Subtotal	28.60	123.39	191.41	834.82	0.05	0.19	6.38	27.27
Total (orchard as a whole)	100.00 (g/m^2)		479.19 (kcal/m^2)		3.21 (g/m^2)		13.73 (kcal/m^2)	
Forbs								
Rubus flagellaris (L)					0.82	3.54	0.82	3.54
Rubus flagellaris (S)	0.12	0.52			0.31	1.33	0.56	2.41
Cichorium intybus (L)			2.81	11.13				
Cichorium intybus (S)			1.81	6.83				
Trifolium sp. (L)			1.03	4.68				
Trifolium sp. (S)			1.17	4.77				
Taraxacum officinale			3.45	13.68				
Desmodium sp. (L)			0.26	1.18				
Desmodium sp. (S)			0.12	0.51				
Solidago sp. (L)	0.07	0.32	0.05	0.21			1.66	7.84
Allium vineale (L)	0.51	2.18	3.25	13.79			0.71	3.05
Plantago sp. (L)			13.75	57.67			5.13	21.03
Plantago sp. (S)			10.51	44.48			2.66	11.34
Ambrosia artesimiifolia (L)			0.23	1.04			0.67	2.96
Ambrosia artesimiifolia (S)			0.10	0.38			0.67	2.59

Appendix Table I. Biomass (g dry wt./m^2) and available gross energy (kcal/m^2) of grasses, forbs, apple fruit, and bulbs in areas beneath the tree canopy and areas outside the tree canopy in the maintained and abandoned apple orchard. Summer 1978 (continued).

	Maintained Orchard				Abandoned Orchard			
	Beneath canopy		Outside canopy		Beneath canopy		Outside canopy	
Species	Biomass	GE	Biomass	GE	Biomass	GE	Biomass	GE
Oxalis europaea (L)	0.04	0.16	0.04	0.18			0.41	1.90
Oxalis europaea (S)	0.03	0.11	0.03	0.14			0.54	2.18
Fragaria virginiana (L)					1.93	8.33	1.59	6.88
Fragaria virginiana (S)					1.08	4.27	1.02	4.03
Miscellaneous forbs (L)	0.29	1.27	0.23	1.00	0.28	1.17	1.76	7.34
Miscellaneous forbs (S)					0.04	0.16	0.87	3.39
Subtotal	1.06	4.56	38.84	161.67	4.46	18.80	19.07	80.48
Total	19.95 (g/m^2)		83.12 (kcal/m^2)		11.76 (g/m^2)		49.64 (kcal/m^2)	
Woody Vines								
Parthenocissus quinquifolia (L)	5.98	25.30			0.84	3.59	2.75	9.01
Parthenocissus quinquifolia (S)	1.69	6.54			0.34	1.35	1.44	5.75
Lonicera japonica (L)					0.07	0.33	16.33	72.51
Subtotal	7.67	31.84			1.25	5.27	20.52	87.27
Total	3.84 (g/m^2)		15.92 (kcal/m^2)		10.88 (g/m^2)		46.27 (kcal/m^2)	
Bulbs and roots								
Allium vineale	0.18	0.69	2.40	8.91			0.13	0.53
Subtotal	0.18	0.69	2.40	8.91			0.13	0.53
Total	1.29 (g/m^2)		4.80 (kcal/m^2)		0.06 (g/m^2)		0.26 (kcal/m^2)	
Fruit								
Fragaria virginiana					0.05	0.22	0.06	0.26
Apple	0.41	1.86			0.23	1.15		
Subtotal	0.41	1.86			0.28	1.37	0.06	0.26
Total	0.20 (g/m^2)		0.93 (kcal/m^2)		0.17 (g/m^2)		0.82 (kcal/m^2)	

Appendix Table I. Biomass (g dry wt./m^2) and available gross energy (kcal/m^2) of grasses, forbs, apple fruit, and bulbs in areas beneath the tree canopy and areas outside the tree canopy in the maintained and abandoned apple orchard. Summer 1978 (continued).

	Maintained Orchard				Abandoned Orchard			
	Beneath canopy		Outside canopy		Beneath canopy		Outside canopy	
Species	Biomass	GE	Biomass	GE	Biomass	GE	Biomass	GE
Others								
Rhus radicans (L)	48.67	221.80	0.60	2.72	24.61	110.08	48.40	216.44
Rhus radicans (S)	12.70	53.91	0.23	0.98	7.10	30.38	18.98	81.26
Solanum carolinense (L)	0.18	0.82	0.24	1.09	0.21	0.98	1.56	7.25
Solanum carolinense (S)	0.16	0.66	0.19	0.81	0.28	1.19	1.65	6.87
Subtotal	61.71	277.19	1.26	5.60	32.20	142.63	70.59	311.82
Total	31.48 (g/m^2)		141.40 (kcal/m^2)		51.40 (g/m^2)		227.22 (kcal/m^2)	

[1] L = leaves, S = stems, b = bulb, W = whole plant.

Appendix Table II. Biomass (g dry wt./m^2) and available gross energy (kcal/m^2) of grasses, forbs, apple fruit, and bulbs in areas beneath the tree canopy and areas outside the tree canopy in the maintained and abandoned apple orchard. Fall, 1978.

	Maintained Orchard				Abandoned Orchard			
	Beneath canopy		Outside canopy		Beneath canopy		Outside canopy	
Species[1]	Biomass	GE	Biomass	GE	Biomass	GE	Biomass	GE
Grasses								
Tridens flavus			21.85	97.48				
Setaria sp.	0.44	2.00	1.56	7.00				
Poa pratense			15.21	68.40			0.89	3.88
Dactylis glomerata	2.68	12.16	36.36	164.80			0.08	0.35
Muhlenbergia schreberi	3.86	17.44	53.37	241.24			0.06	0.29
Unknown	1.35	5.88	1.17	5.10				
Paspalum sp.			20.23	87.82				
Subtotal	8.33	37.48	149.75	671.84			1.03	4.52
Total (orchard as a whole)	79.04 (g/m^2)		354.66 (kcal/m^2)		0.52 (g/m^2)		2.26 (kcal/m^2)	
Forbs								
Rubus flagellaris (L)					0.08	0.36	0.14	0.62
Rubus flagellaris (S)					0.08	0.36	0.20	0.87
Cichorium intybus (L)			0.58	2.46				
Cichorium intybus (S)			0.36	1.34				
Trifolium sp. (L)			0.09	0.41				
Trifolium sp. (S)			0.08	0.32				
Desmodium sp. (L)			0.04	0.17				
Desmodium sp. (S)			0.13	0.55				
Solidago sp. (L)			0.11	0.45				
Solidago sp. (S)			0.08	0.34				
Allium vineale (L)							0.08	0.34
Plantago sp. (L)			9.41	41.17			0.02	0.11
Plantago sp. (S)			0.78	3.19				
Ambrosia artesimiifolia (L)			0.77	3.65				
Ambrosia artesimiifolia (S)			7.70	35.52				

Appendix Table II. Biomass (g dry wt./m^2) and available gross energy (kcal/m^2) of grasses, forbs, apple fruit, and bulbs in areas beneath the tree canopy and areas outside the tree canopy in the maintained and abandoned apple orchard. Fall, 1978 (continued).

	Maintained Orchard				Abandoned Orchard			
	Beneath canopy		Outside canopy		Beneath canopy		Outside canopy	
Species	Biomass	GE	Biomass	GE	Biomass	GE	Biomass	GE
Oxalis europaea (L)			1.69	8.03			0.16	0.74
Oxalis europaea (S)			6.65	28.28			0.50	2.07
Fragaria virginiana (L)							0.20	0.92
Fragaria virginiana (S)							0.12	0.47
Polygonum aviculare (L & S)			0.05	0.22				
Aster sp. (L)			0.81	3.84				
Aster sp. (S)			3.39	15.29				
Acalypha rhomboidea (L)					0.03	0.14	0.94	4.02
Acalypha rhomboidea (S)							0.82	3.32
Miscellaneous forbs (L)			0.16	0.67				
Miscellaneous forbs (S)			0.15	0.62				
Subtotal			33.03	146.52	0.19		3.18	
Total (orchard as a whole)	16.52 (g/m^2)		73.26 (kcal/m^2)		1.68 (g/m^2)		7.17 (kcal/m^2)	
Woody Vines								
Parthenocissus quinquifolia (L)	1.79	7.96			0.32	1.31	0.34	1.40
Parthenocissus quinquifolia (S)	0.68	2.62			0.19	0.72	0.15	0.59
Lonicera japonica (L)			8.13	37.54	0.86	3.92	1.76	8.05
Vitis sp. (L)	0.10	0.44						
Smilax sp. (L)					0.11	0.49		
Subtotal	2.57	11.02	8.13	37.54	1.48	6.44	2.25	10.04
Total (orchard as a whole)	5.35 (g/m^2)		24.28 (kcal/m^2)		1.86 (g/m^2)		8.24 (kcal/m^2)	
Fruit								
Apple	57.43	246.45	2.53	10.86	61.75	262.62	8.38	35.61
Subtotal	57.43	246.45	2.53	10.86	61.75	262.62	8.38	35.61
Total (orchard as a whole)	29.98 (g/m^2)		128.66 (kcal/m^2)		35.06 (g/m^2)		149.12 (kcal/m^2)	

Appendix Table II. Biomass (g dry wt./m^2) and available gross energy (kcal/m^2) of grasses, forbs, apple fruit, and bulbs in areas beneath the tree canopy and areas outside the tree canopy in the maintained and abandoned apple orchard. Fall, 1978 (continued).

	Maintained Orchard				Abandoned Orchard			
	Beneath canopy		Outside canopy		Beneath canopy		Outside canopy	
Species	Biomass	GE	Biomass	GE	Biomass	GE	Biomass	GE
Others								
Rhus radicans (L)	10.57	46.45	0.04	0.18	1.98	9.03	4.80	21.95
Rhus radicans (S)	3.76	15.55	0.02	0.09	0.85	3.69	1.24	5.36
Solanum carolinense (L)	1.91	8.44	0.91	4.02	0.22	1.01	2.58	11.68
Solanum carolinense (S)	1.76	7.24	0.75	3.08	0.27	1.21	6.18	27.50
Subtotal	18.00	77.68	1.72	7.37	3.32	14.94	14.80	66.49
Total (orchard as a whole)	9.86 (g/m^2)		42.52 (kcal/m^2)		9.06 (g/m^2)		40.72 (kcal/m^2)	

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[1] L = leaves, S = stems, b = bulb, W = whole plant.

Appendix Table III. Biomass (g dry wt./m^2) and available gross energy (kcal/m^2) of grasses, forbs, apple fruit, and bulbs in areas beneath the tree canopy and areas outside the tree canopy in the maintained and abandoned apple orchard. Winter 1979.

	Maintained Orchard				Abandoned Orchard			
	Beneath canopy		Outside canopy		Beneath canopy		Outside canopy	
Species[1]	Biomass	GE	Biomass	GE	Biomass	GE	Biomass	GE
Grasses								
Setaria sp.			0.24	0.35				
Poa pratense	0.003	0.01	6.70	29.73			0.01	0.05
Dactylis glomerata	0.17	0.75	5.84	25.36			0.08	0.36
Muhlenbergia schreberi	0.12	0.52	0.44	1.98			0.04	0.18
Subtotal	0.29	1.28	13.22	57.42			0.13	0.59
Total (orchard as a whole)	6.76 (g/m^2)		29.35 (kcal/m^2)		0.06 (g/m^2)		0.30 (kcal/m^2)	
Forbs								
Trifolium sp. (L)			0.04	0.17				
Trifolium sp. (S)			0.12	0.53				
Taraxacum officinale			0.007	0.03				
Allium vineale (L)	0.14	0.65	0.72	3.24	0.05	0.23	1.42	6.43
Plantago sp.			4.17	18.34				
Oxalis europaea			0.007	0.03				
Fragaria virginiana (L)							0.14	0.65
Fragaria virginiana (S)							0.05	0.20
Miscellaneous forbs							0.13	1.15
Subtotal	0.14	0.65	5.06	22.34	0.05	0.23	1.74	7.78
Total	2.60 (g/m^2)		11.50 (kcal/m^2)		0.90 (g/m^2)		4.00 (kcal/m^2)	
Woody Vines								
Lonicera japonica (L)	0.41	1.87			0.67	2.97	2.14	9.44
Lonicera japonica (S)	1.46	6.63			0.83	3.78	3.45	15.68
Subtotal	1.87	8.50			1.50	6.75	5.59	25.12
Total	0.94 (g/m^2)		4.25 (kcal/m^2)		3.54 (g/m^2)		15.94 (kcal/m^2)	

Appendix Table III. Biomass (g dry wt./m^2) and available gross energy (kcal/m^2) of grasses, forbs, apple fruit, and bulbs in areas beneath the tree canopy and areas outside the tree canopy in the maintained and abandoned apple orchard. Winter, 1979 (continued).

	Maintained Orchard				Abandoned Orchard			
	Beneath canopy		Outside canopy		Beneath canopy		Outside canopy	
Species	Biomass	GE	Biomass	GE	Biomass	GE	Biomass	GE
Bulbs and Roots								
Allium vineale			1.05	4.35	0.08	0.34	5.56	22.40
Subtotal			1.05	4.35	0.08	0.34	5.56	22.40
Total	0.52 (g/m^2)		2.18 (kcal/m^2)		2.82 (g/m^2)		11.37 (kcal/m^2)	
Fruit								
Apple	73.62	355.13	0.89	4.30	1.39	7.04	5.05	25.65
Subtotal	73.62	355.13	0.89	4.30	1.39	7.04	5.05	25.65
Total	37.25 (g/m^2)		179.72 (kcal/m^2)		3.22 (g/m^2)		16.34 (kcal/m^2)	
Other								
Solanum carolinense (Fruit)							0.10	0.49
Subtotal							0.10	0.49
Total					0.05 (g/m^2)		0.24 (kcal/m^2)	

[1] L = leaves, S = stems, b = bulb, W = whole plant.

Appendix Table IV. Biomass (g dry wt./m^2) and available gross energy (kcal/m^2) of grasses, forbs, apple fruit, and bulbs in areas beneath the tree canopy and areas outside the tree canopy in the maintained and abandoned apple orchard. Spring 1979.

	Maintained Orchard				Abandoned Orchard			
	Beneath canopy		Outside canopy		Beneath canopy		Outside canopy	
Species[1]	Biomass	GE	Biomass	GE	Biomass	GE	Biomass	GE
Grasses								
Tridens flavus	0.07	0.34	2.65	12.22				
Setaria sp.	1.00	4.40	1.33	5.84			1.34	6.11
Poa pratense	0.98	4.34	17.95	80.05			2.34	10.69
Dactylis glomerata	3.10	13.80	61.38	272.89	tr	0.02	tr	0.02
Muhlenbergia schreberi			8.67	40.85			1.64	7.17
Paspalum sp.			0.29	1.33				
Subtotal	5.15	22.88	92.27	413.18	tr	0.02	5.32	23.99
Total (orchard as a whole)	48.71 (g/m^2)		218.03 ($kcal/m^2$)		2.66 (g/m^2)		12.00 ($kcal/m^2$)	
Forbs								
Rubus flagellaris (L)					0.25	1.15	2.72	12.32
Rubus flagellaris (S)					0.22	1.03	4.41	20.15
Cichoriumintybus (W)			1.47	6.13				
Trifolium sp. (L)			0.65	2.97				
Trifolium sp. (S)			0.62	2.64				
Taraxacum officinale	0.01	0.03	0.92	3.86			tr	0.01
Allium vineale (L)	0.33	1.50	0.16	0.72	0.02	0.07	0.39	1.75
Plantago sp. (W)	tr	tr	10.69	46.78			tr	tr
Ambrosia artesimiifolia (W)			0.14	0.63			0.06	0.25
Oxalis europaea (L)			tr	tr			0.02	0.10
Oxalis europaea (S)			tr	tr			0.02	0.08
Cirsium vulgare (W)			0.39	1.57				
Asclepias syriaca (W)	tr	tr			0.03	0.13	0.03	0.12
Barbarea vulgaris (L)			0.21	0.93				
Barbarea vulgaris (S)			0.79	3.52				
Rumex crispus (L)			0.81	3.50				

Appendix Table IV. Biomass (g dry wt./m^2) and available gross energy (kcal/m^2) of grasses, forbs, apple fruit, and bulbs in areas beneath the tree canopy and areas outside the tree canopy in the maintained and abandoned apple orchard. Spring 1979 (continued).

	Maintained Orchard				Abandoned Orchard			
	Beneath canopy		Outside canopy		Beneath canopy		Outside canopy	
Species	Biomass	GE	Biomass	GE	Biomass	GE	Biomass	GE
Rumex crispus (S)			0.36	1.54				
Miscellaneous forbs (W)			0.16	0.70	0.02	0.08	0.08	0.35
Subtotal	0.34	1.53	17.37	75.49	0.54	2.46	7.73	35.13
Total	8.86 (g/m^2)		38.51 (kcal/m^2)		4.14 (g/m^2)		18.80 (kcal/m^2)	
Woody Vines								
Parthenocissus quinquifolia (L)	0.10	0.46	0.04	0.18	0.14	0.69	0.47	2.25
Parthenocissus quinquifolia (S)	0.09	0.38	0.04	0.18	0.09	0.37	0.38	1.57
Lonicera japonica (L)	0.06	0.28			8.20	36.90	18.28	82.25
Lonicera japonica (S)	0.06	0.27			8.86	40.32	33.95	154.42
Subtotal	0.31	1.39	0.08	0.36	17.29	78.28	53.08	240.49
Total	0.20 (g/m^2)		0.88 (kcal/m^2)		35.18 (g/m^2)		159.38 (kcal/m^2)	
Bulbs and Roots								
Allium vineale	0.38	1.55	0.10	0.41	0.02	0.09	0.99	3.95
Subtotal	0.38	1.55	0.10	0.41	0.02	0.09	0.99	3.95
Total	0.24 (g/m^2)		0.98 (kcal/m^2)		0.50 (g/m^2)		2.02 (kcal/m^2)	
Fruit								
Apple	16.07	84.72	2.33	12.26	8.32	43.52	2.56	13.41
Subtotal	16.07	84.72	2.33	12.26	8.32	43.52	2.56	13.41
Total	9.20 (g/m^2)		48.49 (kcal/m^2)		5.44 (g/m^2)		28.46 (kcal/m^2)	

Appendix Table IV. Biomass (g dry wt./m^2) and available gross energy (kcal/m^2) of grasses, forbs, apple fruit, and bulbs in areas beneath the tree canopy and areas outside the tree canopy in the maintained and abandoned apple orchard. Spring 1979 (continued).

	Maintained Orchard				Abandoned Orchard			
	Beneath canopy		Outside canopy		Beneath canopy		Outside canopy	
Species	Biomass	GE	Biomass	GE	Biomass	GE	Biomass	GE
Others								
Rhus radicans (L)	3.46	16.83	0.53	2.57	2.38	11.60	3.70	18.11
Rhus radicans (S)	2.37	10.88	0.32	1.48	1.88	8.50	3.21	14.56
Solanum carolinense (W)			0.02	0.07			0.01	0.06
Subtotal	5.83	27.71	0.87	4.12	4.26	20.10	6.92	32.73
Total	3.35	(g/m^2)	15.92	(kcal/m^2)	5.59	(g/m^2)	26.42	(kcal/m^2)

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[1] L = leaves, S = stems, b = bulb, W = whole plant.

Appendix Table V. Results of proximate and soluble carbohydrate (TNC) analysis of some major plant species for the summer season, 1978, in the maintained apple orchard.

Species[1]	Percent dry weight					
	Protein	Ether extract	Crude fiber	Ash	N.F.E.	TNC
Setaria sp.	8.50	2.24	30.32	5.61	64.07	12.1
Dactylis glomerata	11.63	3.06	30.42	8.84	46.05	7.5
Muhlenbergia schreberi	10.25	1.42	28.60	5.83	53.90	7.9
Unknown grass	9.00	2.80	28.50	7.58	52.12	12.0
Rubus flagellaris (S)	6.88	1.84	15.72	3.46	72.10	---
Cichorium intybus (L)	17.38	4.56	20.08	14.57	43.41	9.0
Cichorium intybus (S)	6.00	2.10	33.20	11.35	47.35	---
Trifolium sp. (L)	22.63	2.66	17.44	9.64	47.63	7.7
Trifolium sp. (S)	11.88	1.58	27.80	9.98	48.76	8.8
Taraxacum officinale	12.88	3.98	21.46	---	---	9.1
Allium vineale (L)	7.63	1.42	31.38	3.33	56.24	30.4
Plantago sp. (L)	12.25	4.00	16.80	12.51	54.44	10.1
Plantago sp. (S)	8.13	1.22	26.76	7.51	56.38	10.6
Ambrosia artesimiifolia (L)	25.50	3.68	12.76	12.13	45.93	9.8
Parthenocissus quinquifolia (L)	16.13	4.20	19.58	7.57	52.52	7.7
Parthenocissus quinquifolia (S)	7.50	1.68	32.26	10.68	52.12	7.0
Allium vineale (bulb)	7.75	0.22	11.94	14.32	65.77	42.1
Rhus radicans (L)	19.63	2.45	22.24	7.95	47.73	---
Rhus radicans (S)	6.25	2.27	33.40	6.14	51.94	---

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[1] L = leaves, S = stems, b = bulb, W = whole plant.

Appendix Table VI. Results of proximate and soluble carbohydrate (TNC) analysis of some major plant species for the summer season, 1978, in the abandoned apple orchard.

Species[1]	Percent dry weight					
	Protein	Ether extract	Crude fiber	Ash	N.F.E.	TNC
Poa pratense	13.00	2.26	32.72	6.54	45.48	4.7
Muhlenbergia schreberi	11.88	4.06	15.56	---	---	5.9
Unknown grass	11.38	---	---	---	---	8.2
Rubus flagellaris (L)	13.25	2.67	16.42	6.15	61.51	12.9
Rubus flagellaris (S)	5.50	1.56	35.89	3.58	53.47	---
Allium vineale (L)	9.25	1.52	31.98	3.33	53.92	22.2
Plantago sp. (L)	13.00	1.66	21.72	12.40	51.22	9.5
Plantago sp. (S)	8.58	2.43	27.04	6.34	55.61	12.8
Ambrosia artesimiifolia (L)	22.25	3.28	14.28	12.13	48.06	9.3
Ambrosia artesimiifolia (S)	7.13	1.28	31.88	12.09	47.62	---
Fragaria virginiana (L)	13.13	4.88	18.24	8.05	55.70	14.2
Fragaria virginiana (S)	5.63	2.09	43.26	8.60	40.42	11.5
Miscellaneous forbs (L)	16.75	3.30	16.42	10.85	52.68	9.4
Miscellaneous forbs (S)	5.50	1.50	30.01	10.34	52.65	8.7
Lonicera japonica (L)	11.63	2.72	19.88	8.92	56.85	18.1
Parthenocissus quinquifolia (L)	16.75	4.58	16.90	7.01	54.76	10.5
Parthenocissus quinquifolia (S)	8.13	1.52	33.28	7.65	49.42	10.2
Solanum carolinense (L)	25.75	3.43	18.85	6.36	45.61	---
Solanum carolinense (S)	12.50	1.55	33.63	8.08	55.76	---
Rhus radicans (L)	17.38	3.49	22.12	7.44	49.57	---
Rhus radicans (S)	8.63	2.25	33.11	5.96	50.05	---

[1] L = leaves, S = stems, b = bulb, W = whole plant.

Appendix Table VII. Results of proximate and soluble carbohydrate (TNC) analysis of some major plant species for the fall season, 1978, in the maintained orchard.

Species[1]	Percent dry weight					
	Protein	Ether extract	Crude fiber	Ash	N.F.E.	TNC
Triodia flavus	7.50	1.93	34.11	4.76	51.70	8.4
Setaria sp.	18.38	4.44	22.34	9.49	45.35	12.4
Poa pratense	11.13	3.36	27.12	5.58	52.81	15.5
Dactylis glomerata	14.50	3.55	27.25	8.20	46.50	11.1
Muhlenbergia schreberi	10.13	1.62	28.75	4.86	54.64	9.6
Unknown grass	8.25	1.82	21.60	2.65	65.68	34.6
Paspalum sp.	7.88	1.68	31.46	6.15	52.83	10.8
Cichorium intybus (L)	15.63	4.86	18.77	14.30	46.44	13.0
Cichorium intybus (S)	6.75	2.35	30.53	15.09	45.28	13.4
Trifolium sp. (L)	23.63	4.20	14.59	8.36	49.22	12.3
Trifolium sp. (S)	11.38	2.45	24.00	9.55	52.62	14.0
Plantago sp. (L)	13.25	2.15	15.69	9.60	59.31	17.1
Plantago sp. (S)	7.88	2.12	19.82	9.14	61.04	19.6
Ambrosia artesimiifolia (L)	15.75	8.66	13.26	11.89	50.44	11.5
Ambrosia artesimiifolia (S)	9.88	7.30	27.76	7.47	47.59	9.3
Oxalis europaea (L)	20.38	7.70	11.09	7.91	52.92	17.6
Oxalis europaea (S)	9.75	5.25	24.74	9.12	51.14	14.0
Aster sp. (L)	14.13	5.19	12.65	8.16	59.87	16.4
Aster sp. (S)	8.75	2.68	20.82	5.86	61.89	22.9
Parthenocissus quinquifolia (L)	13.38	7.75	16.79	10.49	51.59	11.1
Parthenocissus quinquifolia (S)	6.00	1.71	33.31	11.64	47.34	9.1
Lonicera japonica (L)	11.88	4.01	15.32	7.54	61.25	19.5
Apple fruit	3.13	3.60	8.38	4.07	80.82	43.6
Rhus radicans (L)	16.25	3.98	19.06	11.10	49.61	12.2
Rhus radicans (S)	7.13	1.94	32.02	9.65	49.26	11.0
Solanum carolinense (L)	23.75	4.01	17.63	12.05	42.56	8.1
Solanum carolinense (S)	11.63	2.28	33.31	10.22	42.56	8.7

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[1] L = leaves, S = stems, b = bulb, W = whole plant.

Appendix Table VIII. Results of proximate and soluble carbohydrate (TNC) analysis of major plant species for the fall season, 1978, in the abandoned orchard.

	Percent dry weight					
Species[1]	Protein	Ether extract	Crude fiber	Ash	N.F.E.	TNC
Poa pratense	10.63	3.13	27.63	6.53	52.08	16.9
Dactylis glomerata	13.38	4.26	24.60	8.58	49.18	16.8
Rubus flagellaris (L)	14.00	3.64	13.40	5.18	63.78	18.0
Rubus flagellaris (S)	8.00	2.01	30.24	4.00	55.75	15.3
Plantago sp. (L)	14.25	2.30	13.19	11.13	59.13	18.4
Oxalis europaea (L)	21.50	5.72	8.18	7.66	56.94	23.7
Oxalis europaea (S)	9.63	3.43	23.21	8.33	55.40	21.2
Fragaria virginiana (L)	15.13	5.24	11.27	6.37	61.99	23.2
Fragaria virginiana (S)	6.25	2.38	27.60	7.54	56.23	19.4
Acalypha rhomboidea (L)	23.25	2.95	13.87	12.31	47.62	14.4
Acalypha rhomboidea (S)	17.38	3.98	22.50	10.52	45.62	12.7
Parthenocissus quinquifolia (L)	12.63	5.04	17.70	10.18	54.45	12.6
Parthenocissus quinquifolia (S)	5.88	1.71	33.43	11.64	47.34	9.6
Lonicera japonica (L)	13.25	3.18	17.42	8.88	57.27	17.7
Apple fruit	2.63	4.60	9.37	3.21	80.19	43.6
Rhus radicans (L)	18.13	4.91	15.05	8.81	53.10	14.9
Rhus radicans (S)	9.63	2.92	28.09	8.42	50.94	12.5
Solanum carolinense (L)	22.75	4.37	17.43	10.58	44.87	7.8
Solanum carolinense (S)	10.88	3.87	32.31	7.87	45.07	9.3

[1] L = leaves, S = stems, b = bulb, W = whole plant.

Appendix Table IX. Results of proximate and soluble carbohydrate (TNC) analysis of some major plant species for the winter season, January 1979, in the maintained apple orchard.

Species[1]	Percent dry weight					
	Protein	Ether extract	Crude fiber	Ash	N.F.E.	TNC
Setaria sp.	21.50	---	---	---	---	24.5
Poa pratense	17.75	2.42	20.23	5.79	53.81	24.3
Dactylis glomerata	15.88	2.42	17.69	7.42	56.59	27.2
Muhlenbergia schreberi	12.63	0.70	20.84	2.96	62.87	18.2
Allium vineale (L)	19.75	2.94	15.00	5.49	56.82	23.9
Plantago sp.	12.63	0.96	12.03	6.39	67.99	14.2
Miscellaneous forbs (L & S)	11.00	1.15	17.77	---	---	6.01
Lonicera japonica (L)	13.13	2.04	13.96	7.22	63.65	17.9
Lonicera japonica (S)	7.50	0.49	26.98	3.07	61.96	14.5
Apple fruit	6.00	7.85	27.20	2.40	56.55	9.7
Allium vineale (b)	15.13	0.08	10.77	6.34	67.68	31.7

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[1] L = leaves, S = stems, b = bulb, W = whole plant.

Appendix Table X. Results of proximate and soluble carbohydrate (TNC) analysis of some major plant species for the winter season, January 1979, in the abandoned apple orchard.

	Percent dry weight					
Species[1]	Protein	Ether extract	Crude fiber	Ash	N.F.E.	TNC
Poa pratense	18.25	---	---	---	---	20.1
Fragaria virginiana (L)	14.13	3.31	12.58	4.76	62.22	19.1
Allium vineale (L)	20.50	3.29	14.90	5.73	55.58	26.9
Miscellaneous forbs (L & S)	11.00	1.15	17.77	---	---	6.01
Lonicera japonica (L)	12.75	1.34	12.30	7.45	66.16	19.8
Lonicera japonica (S)	6.38	0.65	28.17	3.21	61.59	14.4
Allium vineale (b)	13.88	0.15	11.17	10.49	64.31	24.7
Apple fruit	5.75	8.94	24.17	1.77	59.37	14.3

[1] L = leaves, S = stems, b = bulb, W = whole plant.

Appendix Table XI. Results of proximate and soluble carbohydrate (TNC) analysis of some major plant species for the spring season, May 1979, in the maintained apple orchard.

Species[1]	Percent dry weight					
	Protein	Ether extract	Crude fiber	Ash	N.F.E.	TNC
Tridens flavus	16.63	1.93	26.14	6.02	49.28	4.2
Setaria sp.	17.75	3.60	22.75	8.31	47.59	8.2
Poa pratense	12.38	2.80	26.67	5.52	56.63	1.6
Dactylis glomerata	13.13	3.45	26.30	8.10	49.02	1.7
Muhlenbergia schreberi	15.00	2.05	25.66	6.03	51.26	6.0
Paspalum sp.	17.38	---	---	---	---	4.3
Taraxacum officinale	15.13	4.19	17.87	12.99	49.82	6.6
Allium vineale (L)	19.63	4.59	24.87	7.01	43.90	6.8
Trifolium sp. (L)	24.75	2.16	15.44	8.76	48.89	1.5
Trifolium sp. (S)	13.75	1.05	23.64	---	---	6.0
Cichorium intybus (L)	20.75	2.84	16.93	13.93	45.55	5.0
Rumex crispus (L & S)	19.88	2.26	15.62	10.55	51.69	6.9
Plantago sp.	14.75	1.58	14.57	9.78	59.32	8.4
Barbarea vulgaris (L & S)	13.50	1.41	29.59	9.66	45.84	3.6
Miscellaneous forbs (L & S)	18.50	3.35	17.82	13.43	46.90	6.0
Allium vineale (b)	9.13	0.00	8.30	4.98	77.59	29.0
Apple fruit	8.00	11.29	29.37	0.94	50.40	4.3

[1] L = leaves, S = stems, b = bulb, W = whole plant.

Appendix Table XII. Results of proximate and soluble carbohydrate (TNC) analysis of some major plant species for the spring season, May 1979, in the abandoned apple orchard.

	Percent of dry weight					
Species[1]	Protein	Ether extract	Crude fiber	Ash	N.F.E.	TNC
Setaria sp.	18.75	3.74	22.34	9.40	45.77	6.2
Poa pratense	16.88	3.05	24.37	6.46	49.24	7.4
Muhlenbergia schreberi	17.00	2.17	25.33	6.86	48.64	4.9
Rubus flagellaris (L)	19.75	1.47	13.04	5.29	60.45	6.3
Rubus flagellaris (S)	8.00	1.20	29.42	3.67	57.71	4.7
Allium vineale (L)	19.63	4.59	24.87	7.01	43.90	6.8
Miscellaneous forbs (L & S)	18.50	3.35	17.82	13.43	46.90	6.0
Parthenocissus quinquifolia (L)	16.50	1.84	10.15	5.12	66.39	3.6
Parthenocissus quinquifolia (S)	16.63	1.24	19.06	---	---	5.9
Lonicera japonica (L)	12.50	3.21	12.23	8.43	63.63	10.0
Lonicera japonica (S)	5.00	0.74	28.37	3.41	62.48	8.4
Allium vineale (b)	9.13	0.00	8.30	4.98	77.59	29.0
Apple fruit	7.38	11.04	27.54	1.43	52.61	6.8

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[1] L = leaves, S = stems, b = bulb, W = whole plant.

Appendix Table XIII. Production of preferred grasses, forbs, woody vines, and fruit of pine voles in the maintained and abandoned apple orchard. Summer, 1978.

	Maintained Orchard		Abandoned Orchard	
	Biomass (g/m^2)	Gross Energy ($kcal/m^2$)	Biomass (g/m^2)	Gross Energy ($kcal/m^2$)
Grasses	110.00	479.10	3.21	13.73
Forb leaves	13.00	54.24	7.07	33.79
Forb stems	6.88	28.61	3.44	13.98
Woody vine leaves	2.99	12.65	10.00	42.72
Woody vine stems	0.84	3.27	0.89	3.55
Bulbs	1.29	4.80	0.06	0.26
Fruit	0.20	0.93	0.17	0.82
Total	135.20	583.60	24.84	108.85

Appendix Table XIV. Production of preferred grasses, forbs, woody vines, and fruit of pine voles in the maintained and abandoned apple orchard. Fall, 1978.

	Maintained Orchard		Abandoned Orchard	
	Biomass (g/m^2)	Gross Energy ($kcal/m^2$)	Biomass (g/m^2)	Gross Energy ($kcal/m^2$)
Grasses	79.04	354.66	0.52	2.26
Forb leaves	6.86	30.53	0.72	3.14
Forb stems	9.66	42.72	0.72	2.93
Woody vine leaves	5.01	22.97	1.70	7.58
Woody vine stems	0.34	1.31	0.17	0.66
Fruit	29.98	128.66	35.06	149.12
Total	130.89	580.85	38.89	165.69

Appendix Table XV. Production of preferred grasses, forbs, woody vines, and fruit of pine voles in the maintained and abandoned apple orchard. Winter, 1979.

	Maintained Orchard		Abandoned Orchard	
	Biomass (g/m^2)	Gross Energy ($kcal/m^2$)	Biomass (g/m^2)	Gross Energy ($kcal/m^2$)
Grasses	6.76	29.35	0.06	0.30
Forb leaves	2.54	11.23	0.87	4.23
Forb stems	0.06	0.26	0.02	0.10
Woody vine leaves	0.20	0.94	1.40	6.20
Bulbs	0.52	2.18	2.82	11.37
Fruit	37.25	179.72	3.22	16.34
Total	47.33	223.68	8.39	38.54

Appendix Table XVI. Production of preferred grasses, forbs, woody vines, and fruit of pine voles in the maintained and abandoned apple orchards. Spring, 1979.

	Maintained Orchard		Abandoned Orchard	
	Biomass (g/m^2)	Gross Energy ($kcal/m^2$)	Biomass (g/m^2)	Gross Energy ($kcal/m^2$)
Grasses	48.71	218.03	2.66	12.00
Forbs	8.86	38.51	1.82	8.21
Woody vine leaves	0.12	0.55	13.54	61.04
Woody vine stems	0.04	0.19	0.24	0.97
Bulbs	0.24	0.98	0.50	2.02
Fruit	9.20	48.49	5.44	28.46
Total	67.17	306.75	24.20	112.70

Appendix Table XVII. Monthly changes in body weight (g) of adult and juvenile pine voles collected by snap trapping from the maintained apple orchard. The mean, standard error and number of observations are indicated.

Month		Adults			Juveniles	
		Male	Female	Gravid and lactating	Male	Female
May	$\overline{X}$	25.7	24.1	28.4	14.8	15.5
	SE	0.6	1.1	1.0	---	1.1
	n	11	3	7	1	2
July	$\overline{X}$	22.8		25.4	16.9	17.4
	SE	1.3		0.8	0.7	---
	n	8		7	4	1
September	$\overline{X}$	23.9		27.0	13.0	9.0
	SE	1.1		1.5	1.8	0.8
	n	10		6	5	3
November	$\overline{X}$	24.7	26.8	28.6	13.5	14.1
	SE	0.8	2.8	1.4	---	0.1
	n	13	3	6	1	2
January	$\overline{X}$	25.9	24.9	25.0	14.1	15.8
	SE	0.6	1.5	2.3	1.5	0.9
	n	17	4	3	6	9
March	$\overline{X}$	22.8	22.4	28.6	15.3	15.5
	SE	0.6	1.1	0.6	4.5	---
	n	18	11	4	2	1

Appendix Table XVIII. Monthly changes in body weight (g) of adult and juvenile pine voles collected by snap trapping from the abandoned apple orchard. The mean, standard error and number of observations are indicated.

		Adults			Juveniles	
Month		Male	Female	Gravid and lactating	Male	Female
May	$\overline{X}$	24.4	23.2	25.8		
	SE	0.7	4.8	0.6		
	n	17	2	6		
July	$\overline{X}$	23.5	21.7	21.4	15.6	13.1
	SE	1.2	0.6	0.5	1.5	2.8
	n	7	2	5	2	4
September	$\overline{X}$	22.6	26.6	28.6	16.0	11.7
	SE	0.9	---	4.6	2.2	3.7
	n	9	1	2	3	2
November	$\overline{X}$	24.3	23.3	28.6	16.8	18.4
	SE	1.1	1.1	2.2	---	0.7
	n	10	6	2	1	3
January	$\overline{X}$	24.7	26.3	28.4	16.4	15.0
	SE	0.9	1.4	---	1.0	1.4
	n	9	5	1	6	4
March	$\overline{X}$	22.8	25.0		17.1	18.6
	SE	0.6	0.9		0.2	0.7
	n	13	12		2	3

BIOENERGETICS AND NUTRITION OF THE PINE VOLE *(MICROTUS PINETORUM)* IN TWO VIRGINIA APPLE ORCHARDS

by

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(ABSTRACT)

Bioenergetic measurements were made on adult, lactating female, and growing juvenile pine voles. Adult pine voles showed a seasonal cycle in daily maintenance energy requirements. Winter was energetically the most expensive season. Requirements during the summer season were lowest of all seasons. There was no significant difference in the daily energy requirements between adult male or female voles except during the summer season. Nesting material was found to be an important insulatory asset which significantly depressed total daily energy requirements of adults. The period of lactation among female pine voles was energetically very demanding. The average lactating female and her litter required 47.5 percent more metabolizable energy than nonbreeding adult females of equivalent body weight. The net conversion of metabolized energy into tissue production during the period of lactation was extremely high among lactating female pine voles. Production efficiency was estimated to be 26.0 percent over 21 days of lactation. Production efficiency of lactating female pine voles was considerably higher than estimates derived for other vole species. Juvenile pine voles between the ages of 22-46 days had metabolizable energy requirements which were similar to those of an adult. Over

the 24 days of postnatal development, the average juvenile pine vole metabolized 282 kcal of energy of which 25.8 kcal was deposited as tissue. The overall efficiency of production in juvenile voles was 9.2 percent which was considerably higher than estimates derived for other species of voles.

A lignin analysis of stomach contents showed a distinct seasonal cycle in the digestibility of foods consumed by voles from the maintained and abandoned apple orchard. The highest digestibilities coincided with the maturation of the apple crop. The quantity of primary production available during the winter was lowest of all seasons. It was estimated that the amount of primary production available to pine voles during the winter season could support 994 nonreproducing adult voles per hectare in the maintained orchard and 147 nonreproducing adult voles per hectare in the abandoned apple orchard.