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ENERGY REQUIREMENTS FOR GROWTH IN *MICROTUS OCHROGASTER*

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ABSTRACT

The purpose of this work was twofold: *i*) to determine whether or not neonatal voles (*Microtus ochrogaster*) require more assimilated (A) energy than can be attributed to their smaller body size or to tissue production and *ii*) to determine the amount of energy required by individually maintained neonatal voles and compare it with the amount of energy used by the same neonates when maintained with littermates or female with litter. This was done to quantitate energy saving under a variety of family conditions.

Oxygen consumption and carbon dioxide production were measured to establish the energy produced by aerobic catabolism (R), caloric value of tissue added during growth was measured to determine production (P), $A = R + P$.

Metabolic rate (R) measurements were established on the adult colony of voles. The average from these measurements was projected, on the basis of $W^{0.75}$, to the juvenile body size. This was done to establish the increased energy (R) demand due solely to smaller body size. The neonatal energy (R) demands were compared to the adult, or body size, baseline. The remarkably higher energy (R) demand of the neonates above that which could be accounted for by smaller body size was attributed to lack of insulation and higher BMR requirements found during the growth period.

Tissue production was considered separately. An index of efficiency, the P/R ratio, was used. For individually maintained neonates the P/R was only 1.30%, indicating that the cost of heat production is extremely high when compared to the energy cost of tissue deposition.

Energy requirements (R) of the neonatal voles were then measured under a variety of family conditions. The larger the family group, the greater the energy savings was found to be. A savings of 90% over that required by individuals was found in the largest group used, a female with four babies. This is attributed to effectively establishing a smaller surface to volume ratio (less heat is lost) as well as to the insulative properties of the female.

The tissue production efficiency (P/R ratio) increased from 1.30% in neonates maintained alone to 3.42% when in an average group of 3 littermates, and to 4.02% when with female and 3 littermates.

The energy saving mechanism of family grouping may well allow for rapid rodent population turnover. Without huddling the energy cost of rapid reproduction would be too high to be feasible. The gradient between high energy demands of unprotected juveniles and lower energy demands of neonates when the female is present may also point to a mechanism involved in population stabilization. When there is high competition for available food supply the female would be obliged to leave the litter "uninsulated" for long periods of time. This would increase their energy demands and decrease their chances of survival. With food in abundant supply the female can spend longer periods of time with her offspring and increase their survival potential.

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INTRODUCTION

Determination of whether or not neonatal rodents require more energy[1] on a unit weight basis than adults is one goal of this work. If there is indeed a higher energy demand in neonates than adults, what are the causes? Another major question is whether or not there is a natural mechanism that effectively reduces the cost of growth. The vole, *Microtus ochrogaster*, was used as a representative rodent to examine some of these ideas.

An understanding of the energy required for growth is important in defining energy flow through populations and through ecosystems as well as in understanding growth processes. For better understanding of system functions, it is necessary to know not only the broad pattern of energy utilization, but also how energy is partitioned and how this partitioning can change with varying conditions. Because of the difficulty in determining the actual energy required for growth, especially in small wild mammals, the traditional approach has been to use lactation demands as growth costs. While this may be a legitimate way to handle the broad energy use pattern, it cannot describe the partitioning of individual growth needs or maintenance versus growth requirements in the young.

The next question is how much energy does the family group conserve over what is required of individuals maintained separately. The significance of answering this question lies in understanding adaptation to the environment and a possible method used for achievement of population stabilization.

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[1] Types of energy will be defined and discussed in the Literature Review.

To answer these questions for a microtine rodent:

(*i*) Measurements were taken of total energy spent by individuals for growth. This was considered to be a sum of the expended energy measured as heat production (R) plus the energy deposited as tissue (P).

(*ii*) The energy expressed as R was broken down into maintenance energy and the extra energy expended during growth.

(*iii*) Energy (R) required for mother with litter as would occur under natural conditions was measured.

(*iv*) Amount of energy saved by the family group (R_{group}) over what would be used by a sum of individuals (R_{sum}) was viewed as an energy saving adaptive technique.

Microtus ochrogaster was chosen as an experimental animal for several reasons. Primarily because of its presence on the IBP Grassland Biome sites, it may be used as a representative of the small mammal population in modeling the energy flow through the grasslands. Two other reasons are the voles relatively short life cycle and its ability to reproduce in the laboratory.

REVIEW OF LITERATURE

Measurement of Energy Used By an Animal

Types of Energy.

The amount of energy used by an animal can be separated into two components: *i*) energy available for anabolism, that is, energy that can be used for tissue production, and *ii*) energy for catabolism or the energy used for heat production of an animal (Kleiber, 1961).

Energy that has been used in the anabolic process can be determined by measuring the caloric content of deposited tissue in a bomb calorimeter (Brody, 1945) and reported in terms of kilocalories (P).

Energy for catabolism has been traditionally determined in three ways.

i) The first is by determining the assimilated energy (A) in an animal maintaining constant weight. That is, determination of the energy (Kcal) in food eaten over a 24-hour period (C_e), subtracting the kcal in feces (F_e) and urine and gas (U_e+G_e) and ending up with the value available for heat production (A_e). $A_e = C_e - F_e - (U_e+G_e)$ if the animal maintains a constant weight the energy assimilated (A) is assumed to be equal to energy required for heat production (Brody, 1945; Phillipson, 1966; and Petrusewicz and Macfadyen, 1970).

ii) The second method is direct calorimetry where heat produced by an animal is absorbed and measured in a closed chamber. Heat production is assumed to equal assimilation where the animal's weight remains constant (Brody, 1945).

iii) Indirect calorimetry, the third method, measures energy consumption uptake (Brody, 1945). As early as 1780, Lavoisier and LaPlace determined that the major portion of animal heat production

comes from oxygen combustion with organic compounds (Kleiber, 1961). This measurement yields the heat production by respiratory oxygen and so is termed R. If there is no weight gained or lost, A = R. If there is weight gain, then R = A - P or conversely A = R + P (Davis and Golley, 1963 and McNeill, 1970). The amount of heat produced (or energy used) by consumption of one liter of oxygen depends on the substrate being burned or the ratio of CO_2 produced to O_2 consumed. This ratio (CO_2/O_2) is called the respiratory quotient (RQ). For an RQ of 0.7, 4.686 kcal of heat are produced/one liter of O_2 consumed; for an RQ of 1.0, 5.047 kcal of heat are produced/liter of oxygen (Hawk, et al., 1954).

Metabolic Rate Measurements.

Heat production (R) can be measured in terms of metabolic rate, which is kcal/unit weight of animal/unit time. Metabolic rate has traditionally been measured for several conditions as covered below.

Basal Metabolic Rate (BMR) is defined as resting heat production in a thermoneutral environment with the animal in a post-absorptive state (Brody, 1945; Goldstone, 1966; and McNab and Morrison, 1963). BMR is useful as a baseline for measuring energy increments, i.e., energy required for thermoregulation or activity (McNab, 1963). However, it is very difficult to measure in wild animals. Most sources providing values for BMR in wild animals probably give fasting metabolic rate (Kleiber, 1961).

Fasting Metabolic Rate (FMR) has been defined as the measurement taken in the post-absorptive state, i.e., 12 hours since the last feeding for rats (Kleiber, 1961). FMR has been used as a minimal figure for metabolism in some ecosystem analyses (Golley, 1960 and

Trojan, 1969). Wiegart (1961) uses FMR and defines it further to be a fasting animal measured at the temperature of thermoneutrality with minimal activity. This is useful in wild animals since activity can scarcely be limited to zero.

Resting Metabolic Rate (RMR) is greater than the BMR by the specific dynamic action of food being digested and by thermoregulation costs of temperatures outside the thermoneutral zone (Gorecki, 1968). RMR has been used for studies where a variety of natural conditions are to be simulated (Gorecki, 1966; Hansson and Grodzinski, 1970; Trojan, 1968; and Trojan and Wojciechowska, 1967). It may be taken as a one-two hour measurement when the animals are quiet or as the minimal period in a 24-hour measurement (Pearson, 1947).

Average Daily Metabolic Rate (ADMR) is a series of measurements (or continuous measurement) taken over a 24-hour period. The conditions are usually varied according to natural conditions being simulated by the investigator. This measurement was used as early as 1947 (Pearson) for determining the diurnal cycle, maximum and minimum periods of daily metabolic rate, and the average daily metabolic rate of a series of small rodents. This measurement is especially constructive for diurnal models of animal behavior (Morrison, 1948 and Gorecki, 1966). The main advantage is the ability to measure animals in conditions closely simulating the normal environment (Grodzinski, 1961). This is the most widely used method in small rodent energetics (Trojan, 1968; Chew, Lindburg and Hayden, 1965; Hansson and Grodzinski, 1970; Gorecki, 1966 and 1968; Drozdz, Gorecki and Sawicka-Kapusta, 1972; and Drozdz, Gorecki, Grodzinski and Pelikan, 1971).

Energy Required for Growth

The importance of determining the energy requirements for growth has significance to two types of students. Because growth rate is so rapid and efficient in the post-natal period it has been of interest to stock breeders and experimental biologists (Brody, 1945 and Blaxter, 1962). Ecologists studying the bioenergetics of ecosystems and energy flow through population are also interested in the rate and efficiency of transformation of energy into tissue by animals (Drozdz, Gorecki and Sawicka-Kapusta, 1972; Davis and Golley, 1963; Phillipson, 1966; Petrusewica and Macfadyen, 1970; and Odum, Connell and Davenport, 1962). Almost half of the net production in some species of voles is known to take place during fetal development and lactation (Sawicka-Kapusta, 1970).

Measurement of assimilated energy required for growth must be divided into two parts: *i*) anabolism or the caloric value of tissue deposited during growth (P) and *ii*) catabolism or the caloric value as determined by O_2 consumption, consumed per unit body weight of a juvenile (R_j). Catabolism must be further broken down to determine the amount of energy consumed per unit body weight above what would be used for an adult of the same body size. This separates the maintenance requirement from the additional energy required during growth. To do this the relationship between adult metabolic rate and body weight must also be determined (R_a).

The combination of $P + R_j$ equals total assimilated energy required during the growth period (Davis and Golley, 1963). The additional assimilated energy required for growth (above adult maintenance requirements) may be considered as growth energy, $P + (R_j - R_a)$.

Apparently, these components have never been separated in studies dealing with small mammals or birds (Ricklefs, 1968).

Another way to view the same data shows net production efficiency, P/R or P/A, for the growing animal (Drozdz, Gorecki and Sawicka-Kapusta, 1972 and Davis and Golley, 1963). That is, the amount of tissue added for either energy of heat produced (R) or the energy assimilated (A).

A relationship between the adult body weight and energy required per unit body weight in the adult of a species must be determined before the increment of energy used for growth in the young can be established. Historically the metabolic rate (or energy used for heat production) was believed to be determined by the relationship between weight and surface area of an animal in this manner: $M = \underline{a}W^{2/3}$, where M equals the total kilocalories, W equals weight in kg, and $\underline{a}$ is a constant which is species specific (Kleiber, 1961). However, a study of homeotherms ranging from mice to cattle indicate that the metabolic rate per unit surface area is greater in larger animals. Linear correlation shows $W^{3/4}$ to be more accurate for a between-species relationship (Hart, 1971; Hemmingsen, 1960; and Kleiber, 1961). Swan (1970) explains this as being due to a combination of the surface to volume ratio plus the change in animal composition with size. The smaller animal has a greater proportion of high energy organs, such as brain and liver. Goldstone (1967) and Brody (1945) similarly suggested the metabolic rate is related to active tissue mass (as contrasted to supportive tissue).

The energy use-body weight relationship within species varies widely from the $W^{3/4}$ rule (Kleiber, 1961). Adults, therefore, must be

measured under a given set of conditions to give the relationship under those conditions.

Perhaps a more appropriate way to deal with the energy-body weight relationship is to put it in terms of metabolic rate instead of energy used by the entire animal. That is, calculate the energy used in terms of unit body weight.

$$M = aW^{b} \qquad \text{becomes} \qquad M/W = aW^{(b-1)}$$

Now the between species relationship is $M/W = aW^{-0.25}$ (Prosser and Brown, 1961). Hansson and Grodzinski (1970) show how a and (b-1) vary in $M/W = aW^{(b-1)}$ not only within species, but also with temperature and period of measurement. Drozdz, et al. (1971) show how a and (b-1) vary with numbers in a group and with nesting conditions. Therefore, rigid conditions must be maintained during the course of an experiment. There are no data available for adult *Microtus ochrogaster* but studies have been done on related species. Table 1 lists average values for ADMR and RMR at 20°C, for two species of *Microtus* and Table 2 lists the relationship between body weight and metabolic rate for several species of microtines, ADMR or RMR = $aW^{(b-1)}$.

ADMR measurements of R can also be used to find the energy consumed as food (C_e). When R = A, as it does when the animal is in weight balance, then C_e x (% digestibility - % energy lost in urine and gas) = A = R or C_e = R(% digestibility - % energy lost in urine and gas (Petrusewicz and Macfadyen, 1968).

Digestibility has been measured in small rodents under a variety of circumstances. *Microtus arvalis* on an *ad lib* diet of oats, carrots, and beets showed a digestibility of 88.4% between the ages of 20 and

Table 1. ADMR and RMR at 20°C for two species of *Microtus*.

Species	Ave. Wt. (g)	ADMR (kcal/kgxhr)	RMR (kcal/kgxhr)	Investigator
Microtus arvalis	18	32		Drozdz, Gorecki and Sawicka-Kapusta, 1972
Microtus arvalis	19	27		Trojan, 1968
Microtus pennsylvanicus	31.2	15.8	11.2	Pearson, 1947
Microtus pennsylvanicus	29	27		Johnson and Groepper, 1970

Table 2. Exponential equations for ADMR and RMR for some microtine species.

Species	Ave. Wt. (g)	$aW^{(b-1)}$ for ADMR	$aW^{(b-1)}$ for RMR	Investigator
Arvolica terristis	90	$122.3W^{-0.57}$	$93.44W^{-0.44}$	Drozdz, Gorecki, Grodzinski and Pelikan, 1971
Clethrionomys glareolus	21	$9.6W^{-0.34}$		Grodzinski, 1961
Arvolica agaricus	21	$8.3W^{-0.34}$		Grodzinski, 1961
Arvolica flavicollis	29	$8.9W^{-0.34}$		Grodzinski, 1961
Microtus agrestis	33	$9.2W^{-0.34}$		Grodzinski, 1961
Clethrionomys glareolus	22	$9.2W^{-0.47}$		Gorecki, 1968
Microtus agrestis	31	$93.6W^{-0.53}$		Hansson and Grodzinski, 1970

70 days (Drozdz, Gorecki, and Sawicka-Kapusta, 1972). *Microtus pennsylvanicus* showed digestibility values of 79.6% for immature voles and 72% for adult males on diets of Purina rat chow (Johnson and Groepper, 1970). Myrcha, et al. (1969) show the digestion coefficient to be 81.4% in pregnant and lactating *Mus musculus* when fed on a Polish commercial mouse food. Digestibility varies widely with diet as shown by Drozdz (1966). *Microtus arvalus* had digestibility values on different feeds ranging from 73.9% to 93.5%. The digestibility coefficient in *Clethrionomys glareolus* on varied diets ranged from 74.0% to 89.8% (Drozdz, 1966). This rather large range of values indicates that the digestibility must be determined on each colony of animals for the given experimental diet.

The percent of energy consumed (C_e) that is lost in urine has been measured for one species of microtines. *Clethronomys glareolus* lost from 3 to 4% of the C_e in its urine while on a concentrated compound diet (Drozdz, 1966).

Energy cost of growth has been studied in several ways. One approach has been to determine the energy cost of lactation. This has been studied by both respiration and assimilation methods. White mice assimilated an average 17.64 kcal/litter x day above demands of a nonpregnant, nonlactating female of the same body weight as the mother. This was determined over a 26-day lactation period (Myrcha, Ryszkowski and Walkowa, 1969). Studies on *Microtus arvalis* show an increase in metabolic rate (RMR) of 1.76 kcal/kgxhr from the nonpregnant mother to the last day of full lactation (Trojan and Wojiechowska, 1967). Kaczmarski (1966) shows the same trend from *Clethrionomys glareolus* using assimilation measurements. A litter of four required 289 kcal from growth to weaning.

These studies have the advantage of showing the amount of energy the mother consumes to raise a litter. The disadvantage is that it is impossible to separate the energy required for the mother to produce the milk and the energy needed by the offspring. Also, this method does not separate the energy deposited (P) from the respiration energy (R). These studies do not cover the growth period after weaning.

Another approach to defining the energy required for growth has been to determine the cost of production of new tissue. There are several standard ways of finding out this efficiency of tissue production. Two methods commonly used in wild animals are to determine the ratio P/R and to determine the ratio P/A (Davis and Golley, 1963). This ratio has been reported in several studies on microtines. Between 20 and 50 days of age *Microtus arvalis* assimilated 339 kcal energy (A) and deposited 16.1 kcal tissue (P) so the P/A = 4.75% (Drozdz, Gorecki and Sawicka-Kapusta, 1972). The P/R ratio of *Microtus arvalis* was determined to be 6.98% (Trojan and Wojciechowska, 1965). Again this method is good for following the broad pattern of energy used by populations, but cannot give the actual energy used by the young for growth.

A third approach has been to measure energy deposited in tissues (P) during growth. This has been measured in species of animals similar to *Microtus ochrogaster*. *Microtus arvalis* was found to deposit 5.68 kcal of energy between 20 and 30 days of age, 5.46 kcal of energy between 30 and 40 days, and 4.98 kcal in the period between 40 and 50 days (Drozdz, Gorecki, Sawicka, and Sawicka-Kapusta, 1972). White mice deposited 18 kcal in the first 21 days (Myrcha and Walkowa, 1968). This energy deposit does not have a linear

relationship with body weight gain because young animals contain a higher percentage of water than adults (Sawicka-Kapusta, 1972 and Myrcha and Walkowa, 1968). The amount of energy deposited in tissue must be actually measured and not determined from body weight gain. This method is an important step in determining the actual energy cost of growth.

A fourth approach has been to measure the actual metabolic rate (R) for certain species of young over certain times during the growth period. Brody (1945) reports a general relationship of $M = aW^{0.6}$ across species for growing animals (where he reported as factor of $aW^{0.7}$ for adults). Individual species have also been measured. ADMR of *Microtus arvalis* has been studied for a period from 20-50 days of age. The 20-day old group used 25.8 kcal/kgxhr, at 30 days the value was 22.2 kcal/kg/hr, at 40 days, 22.3 kcal/kgxhr, and at 50 days, 21.5 kcal/kg/hr were used. These results show a definite decrease in energy used with age/unit body weight (Drozdz, Gorecki and Sawicka-Kapusta, 1972). Dawes (1968) showed the same pattern with lambs kept in a thermalneutral environment. This is the second step in determining growth requirements, however, the decrease in energy/unit body weight is still hard to separate into maintenance requirements and growth changes with age.

There are many difficulties in measuring the energy required for growth in *Microtus ochrogaster*. The period of measurement required has often been questioned. Timiris (1972) claimed that newborn animals are acyclic so any period measured would be representative. On the other hand, Drozdz, et al. (1972), in a growth experiment on *Microtus arvalis*, found that ADMR (R) measurements gave values lower than

assimilation data (A) when determined for only one day. They concluded that one day measurements were too short. This would seem to be easily remedied by adding the tissue energy deposited (P) since A = R + P (Phillipson, 1966).

Another difficulty in measuring metabolic rate in animals as small as newborn *Microtus* (3 gr) is caused by their inability to thermoregulate. This is in part due to the large surface/volume ratio. (Timiris, 1972). The newborn rat, when exposed to temperatures below 30°C initially increases its heat production, but the core temperature still drops and because of this drop, the energy consumed also falls. This presumably is because of the slowing of chemical reactions (Dawes, 1968). This apparent change causes metabolic rate measurements to be erratic.

An additional problem that arises in studying neonates is whether to compare the infant metabolism to the ADMR of the adult or the RMR of the adult. The inactive neonate may actually be more comparable to the resting adult than to the daily average of the active adult.

Energy Conserved by Family Groupings.

The way animals conserve energy and the amount of energy saved has significance in an animal's ecological adaptation to the environment. Watt (1973) noted that the most important adaptations made by an animal are those that stabilize the population through regulation of reproduction, growth, and survival. The "family grouping" which results in energy conservation qualifies easily as an important adaptive factor in the life history of *Microtus*. If population pressure should increase and food supply decrease, the mother must leave the litter for increasingly longer periods. The energy demands

of the young increase while the mother is hunting food, and their survivability chances decrease (Sealander, 1952). Thus, this forms an example of the feedback control system involved in maintaining homeostasis in populations (Watt, 1973), which can play a vital role in assessing total systems function.

The fact that huddling adults conserve energy is well-documented. Food consumption/g body weight is lower for five mice/cage than for two mice/cage and lower for two mice/cage than with one mouse/cage. This held true over a temperature range of -4°C to +26°C (Prychodko, 1958). Drozdz, et al. (1971), showed that *Microtus arvalis*, when kept in a group of 3, saved 4% of the amount of energy used when the animals were maintained singly. Gorecki (1968) reported that *Clethrionomys glareolus* reduced energy costs by 13.9% when two voles are placed together.

The only data showing small, immature animals saving energy in a group comes from Great Tit nestlings. These data show a decrease in food consumed/g as the brood size increased from 3 to 13 (Royama, 1966).

EXPERIMENTAL DESIGN AND METHODS

Experimental Design

This experiment was constructed to determine energy requirements of *Microtus ochrogaster* for growth from a broad spectrum of approaches:

(*i*) The R energy required by the family group similar to what would occur in nature (mother with litter) was measured.

(*ii*) The energy required by a growing individual, for heat production (R_j) was determined.

(*iii*) The energy deposited by a growing individual as tissue (P) (or P/WT) was measured.

(*iv*) The net energy required by a neonate, Ag = P/WT + R_j was calculated.

(*v*) The energy of immature animals was separated into maintenance and growth energies; respiration of growth (R_g) = $R_j - R_a$. The juvenile respiration (R_j) is greater than the adult respiration (R_a) would be for the same body weight. The juvenile and adult will be considered to have the same body weight-maintenance energy relationship ($aW^{(b-1)}$). This necessitates determining a body weight-energy relationship for the adult colony.

(*vi*) The energy conserved by family groups was determined. This can be calculated by subtracting the energy used by the family group from a sum of individual energy requirements. $E_{(saved)} = R_a + (R_j)_n - R_{fb}$ where n equals the number of neonates in litter and R_{fb} is the R of the family group.

To accomplish these goals, metabolic rates (R) were determined on the following groups:

(*i*) ADMR and RMR values were determined on 68 adults, 34 males 34 females.

(*ii*) RMR was measured on 97 neonates between a 0 and 50 days of age.

Because of difficulty removing neonatal voles from the mothers nipples, there are fewer measurements in the very young:

Age	Number of Tests
0- 5	8
6-10	12
11-15	9
16-20	12
21-25	12
26-30	12
31-50	30

(*iii*) Fifty-five metabolic rate measurements were made on family groups (females and neonates).

(*iv*) Metabolic rate was tested on 11 liters of neonates huddled).

Energy deposited in tissues (P) was calculated from growing animals from 8 litters. An average of three neonates from each litter were killed between 1 and 60 days of age. Their total 60 day kilocalories was determined to give the amount of energy deposited during the growth period.

Digestibility and ADMR were measured simultaneously on a group of representative animals:

two weanlings, 18-25 days

two immature voles, 32-39 days

two immature voles, 39-46 days

two immature voles, 45-52 days

three voles, 60 days or older

two old adults

Methods

Conditions.

All animals were laboratory bred and maintained on a schedule of 12 hours of light and 12 hours of dark. They were kept at 22°C in glass cages with sawdust, water, and *ad lib* alfalfa pellets. Reproductively active animals were kept as family groups. This increased the reproduction rate and the "babysitting" phenomenon made it possible to separate babies from their mothers. For the ADMR measurements the animals or groups of animals were placed in 4 qt. pressure cookers fitted with plexiglas lids. The animals were given *ad lib* feed and water plus floor covering of sawdust. A 12:12 photoperiod and 20°C temperature were maintained during the experiment. Observation of behavior during the test period indicated no change from normal cage behavior.

Animals in the ADMR-digestibility study had the same conditions except they had a wire platform and no sawdust.

Determination of Metabolic Rate.

ADMR and RMR were determined by using a flow-through indirect calorimeter and automatic data collection system. (See diagram of metabolic suite, Fig. 1.) Explanation of the metabolic suite follows.

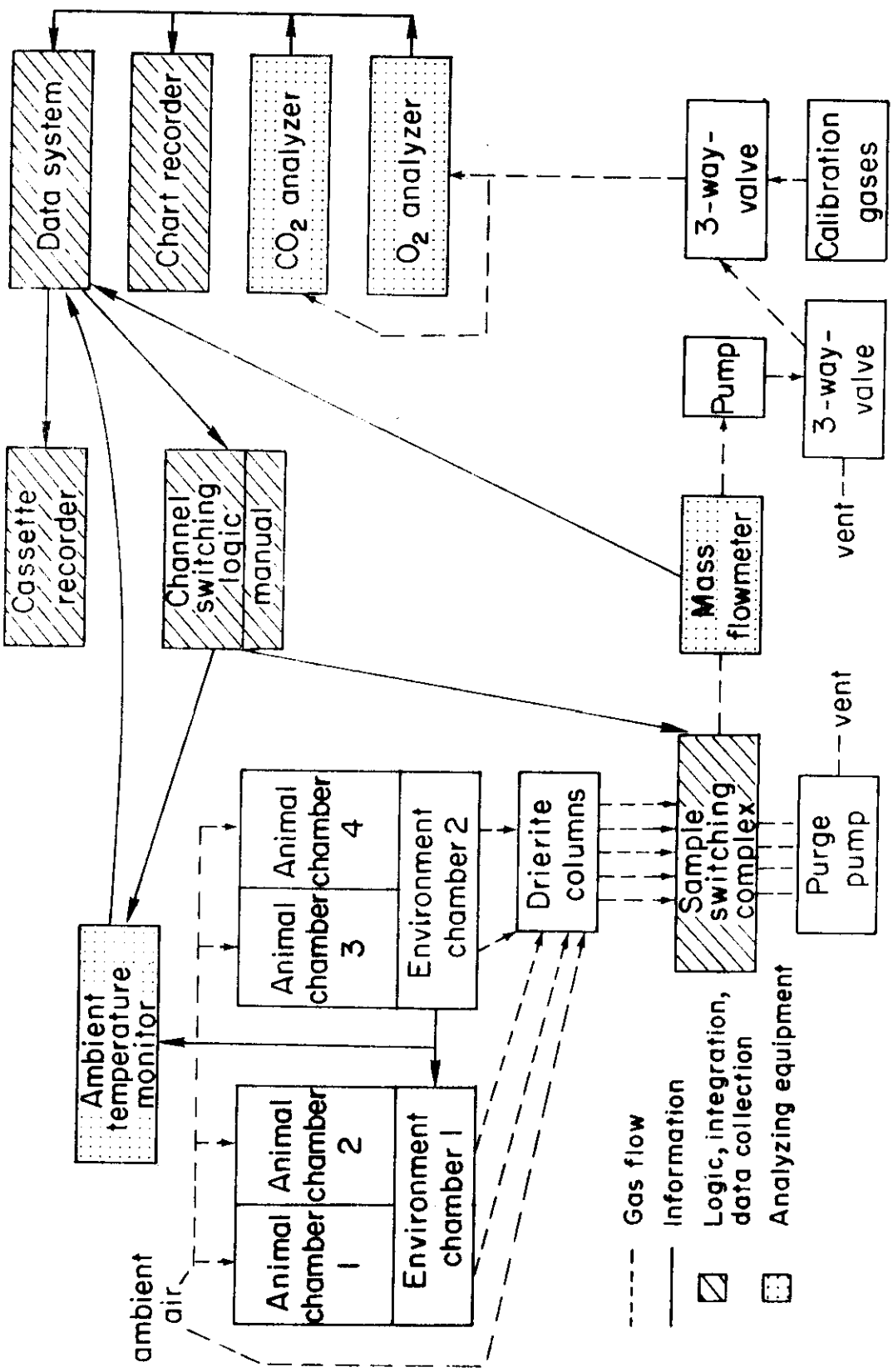


Fig. 1. Metabolic suite.

i) Two animal chambers (4 qt. pressure cookers with plexiglas lids) were placed in each of the two Environmental Chambers (Forma Scientific refrigerated incubators, Model 3710), giving a total of four animal chambers. The Environmental Chambers control light cycle and temperature.

ii) Air from the outside was drawn through (by negative pressure) the chambers and the % of O_2 and CO_2 entering the chambers was monitored.

iii) A sample switching complex (Beckman Automatic Stream Selector) allowed the animal chambers as well as the ambient air supply to be monitored for 5 minute periods in succession. Each animal was measured every 10 to 25 minutes depending on the number of other experiments being run simultaneously. The gas coming from the animal chambers was dried with drierite columns.

iv) Values monitored were: O_2 going into and coming out of the animal chamber (Beckman F3 O_2 Analyzer), % CO_2 going into and coming out of the animal chamber (Beckman 315A Infrared Analyzer); the flow rate (Matheson Gas Mass Flowmeter), and chamber temperature (Yellow Springs Instruments Telethermometer).

v) The O_2 and CO_2 percent were recorded continuously on a strip chart recorder (Bristol Model 2PH).

vi) Oxygen, CO_2, flowrate, temperature were integrated to obtain one reading for each five minute period by the automatic data system (Data Acquisition System developed at NREL). The data system also records chamber number, date, and time of day for every measurement. These data were recorded on a magnetic cassette recorder. Barometric pressure was measured separately.

vii) The data on the cassette is transfered to a magnetic tape and from there, automatically punched on data cards.

viii) These raw data were then converted by the Control Data Corporation Computer program METAB2 (see Appendix I), to provide following values:

$$\Delta O_2 = \%\ O_2 \text{ into chamber} - \%\ O_2 \text{ out of chamber}$$

$$\Delta CO_2 = \%\ CO_2 \text{ out of chamber} - \%\ CO_2 \text{ into chamber}$$

O_2 consumption (O_2 1/kgxhr) =

$$\frac{\Delta O_2\% \times (\text{BPmmhg}/760\text{mmHg})(273/273 + T_a, °C)\ \text{Flow in 1/min} \times 60\ \text{min/hr}}{\text{Animal weight in kg}}$$

CO_2 production (CO_2 1/kgxhr) =

$$\frac{\Delta CO_2\% \times (\text{BPmmHg}/760\text{mmHg})(273/273 + T_a, °C)\ \text{Flow in 1/min} \times 60\ \text{min/hr}}{\text{Animal weight in kg}}$$

$RQ = CO_2$ produced/O_2 consumed

Kcal = RQ factor x O_2 1/kgxhr

(RQ factor = $3.816 + 1.229RQ + .0015RQ^2$)

T_a = Ambient temperature

BP = Barometric pressure

Each of these calculations was made for every 5 minute period and then averaged over 2 and 24 hour averages. The relationships of ADMR = $aW^{(b-1)}$ and RMR = $aW^{(b-1)}$ were made with the CDC Stat program STAT38R for Stepwise Regression. From this it was possible to determine significance values for slope equalities and also the goodness of fit.

ix) Calibration of the CO_2 and O_2 analyzers was done routinely with five mixtures of O_2, CO_2, and N_2. Zero conditions and span gases were checked at the beginning and end of each experiment.

The entire flow through system was initially calibrated by burning an alcohol lamp and comparing theoretical CO_2 produced and O_2 consumed with measured values from the system (see Appendix VII).

Determination of Tissue Production.

The animals used for measuring whole body energy (P) were weighed, then killed and frozen until the experiment was concluded. The samples were ground in a Waring blender and lyophillized on the Virtis Manifold Freeze Dryer, Model 10-155. Dry weight was determined and the energy value of body energy per unit dry weight was determined on the Parr Adiabatic Calorimeter.

The ADMR-digestibility studies were performed as in the ADMR studies, but the animals were maintained on a wire platform instead of in sawdust. Daily collections of feces and orts were made over a one week period. Wet and dry weight measurements were made on the feed and feces and the samples were measured for energy content in the bomb calorimeter.

RESULTS

Metabolic Rate Measurements (R)

Adult Average Daily Metabolic Rate (ADMR).

The average daily metabolic rates (ADMR) were determined on the adult colony of microtines to determine the relationship between weight in kg (W) and metabolic rate in kcal/kgxhr (M/W). This was done to establish a baseline equation for metabolic rate determined by the method of oxygen consumption on adults (R_a). M/W is represented by R

Data from the combined colony of males and females (AMAF, n = 59) with weights ranging from 0.038 to 0.075 kg, gave an exponential relationship

$$R_{amaf} = 0.0785W^{-1.748}.$$

The exponential relationship for the females (AF) of the colony (n = 34) is

$$R_{af} = 0.148W^{-1.598}.$$

Colony males (AM) exhibited the following relationship:

$$R_{am} = 0.031W^{-1.991}.$$

Adult Resting Metabolic Rate (RMR).

A 2 hour period of minimum activity was also separated from the ADMR. This was done on the assumption that the adult inactive period of metabolism may actually be a better baseline for comparison with the inactive neonate. This RMR for the adult colony (MAMMAF) is

$$R_{mammaf} = 0.030W^{-1.987}.$$

Minimum periods for the females were so erratic that they will not be considered separately. The exponential expression for the minimum period of adult males (MAM) is

$$R_{mam} = 0.011W^{-2.306}.$$

Because of the high negative slope (b-1) values found in the adult colony, the average values for the RMR of the entire adult colony were used to project a curve according to the metabolic body size, $W^{0.75}$, relationship. The rationale for this is covered in the discussion section under Comparison of Data With Theoretical Values. RMR is used because a resting adult is assumed to be more comparable to the inactive neonate. The following steps were taken to obtain the adult baseline equation (R_a):

Average M/W = 13.55 kcal/kgxhr

Average W = 0.048 kg

$W^{0.75} = 0.1027$

Total kcal/hr = (13.55 kcal/kgxhr x 0.048 kg) = 0.652 kcal/hr

$$M = \frac{0.652 \text{ kcal/hr}}{0.1027} = 6.35W^{0.75}$$

$$M/W = R_a = 6.35W^{-0.25}$$

(see Fig. 2)

Baby Metabolic Rate Measurements.

Metabolic rate measurements were made on neonatal voles weighing from 0.003 to 0.030 kg. Because of the necessity of returning suckling voles to their mothers to insure continued survival, the measurement period was limited to 2 hours. When a relationship between weight and

Fig. 2. Comparison of energy relationships measured and calculated in this study.

P/WT (rate of energy deposited as tissue) = $1.66 - 32.47W$

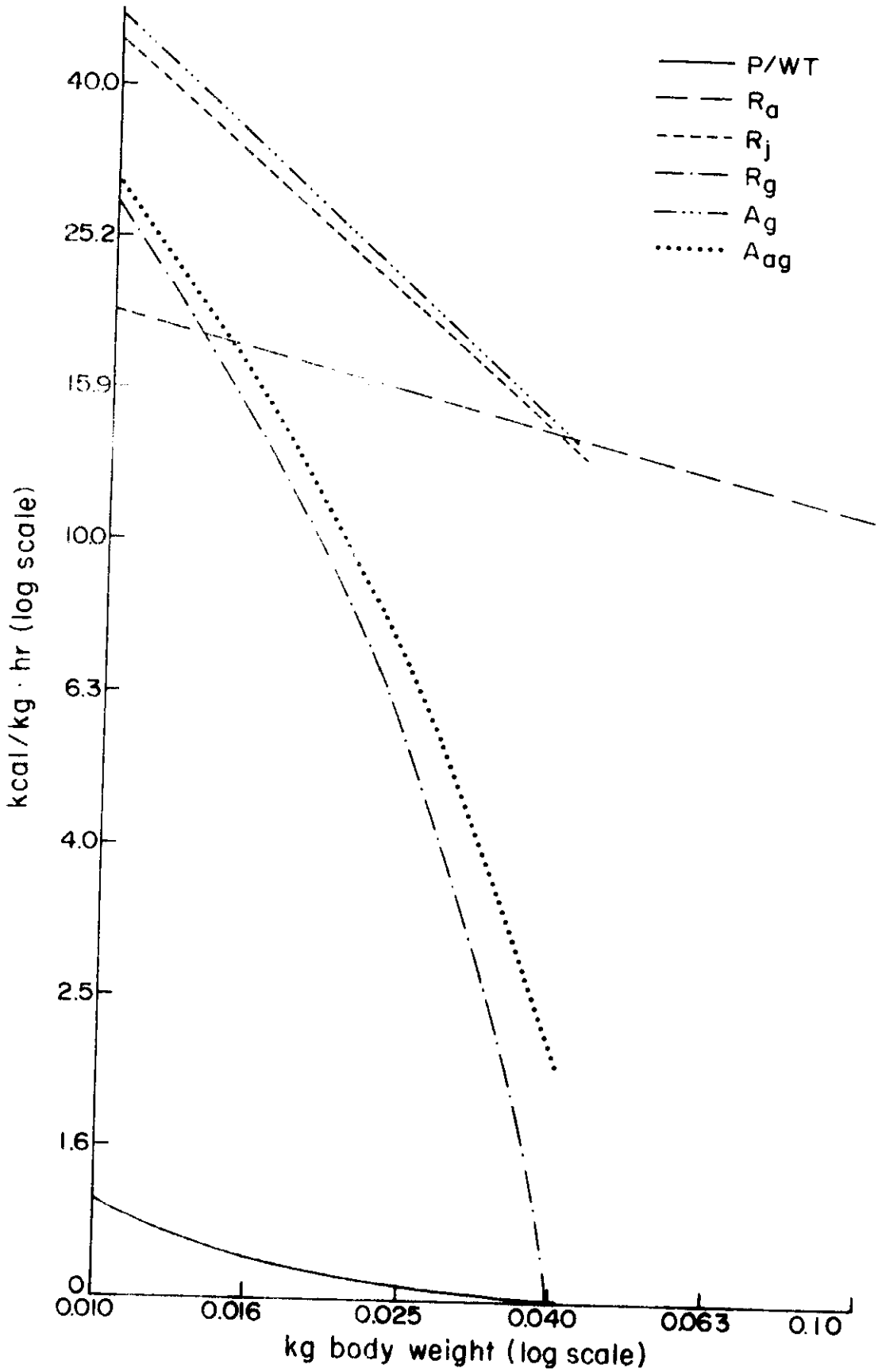
R_a (adult or "body size baseline" energy) = $6.35W^{-0.25}$

R_j (neonatal R energy) = $0.809W^{-0.889}$

R_g (R energy required during growth above adult "body size" energy) = $0.809W^{-0.889} - 6.35W^{-0.25}$

A_g (assimilated energy during growth) = $1.66 - 32.47W + 0.809W^{-0.889}$

A_{ag} (assimilated energy required during growth above that attributed to smaller body size) = $1.66 - 32.47W + 0.809W^{-0.889} - 6.35W^{-0.25}$


P/WT
R_a
R_j
R_g
A_g
A_{ag}
40.0
25.2
15.9
10.0
6.3
4.0
2.5
1.6
0
kcal/kg · hr (log scale)
0.010
0.016
0.025
0.040
0.063
0.10
kg body weight (log scale)

metabolic rate was established for the entire neonatal group, the data proved to be extremely erratic (R^2 = .24). With thorough examination of data from each individual throughout their experimental periods, the period in which they begin to thermoregulate becomes quite apparent[2] and can be determined for each individual (this point occurs around 11 days of age). When the data from the prethermoregulation period is discarded, the weight-metabolic rate relationship becomes much less variable (R^2 = .59), with an equation (n = 49) of

$$R_j = 0.809W^{-0.889}$$

R_j is the respiratory energy requirement of neonatal voles over 11 days.

Metabolic Rates of Females With Litters and Litters Separately.

ADMR values were determined on family groupings in an effort to delineate energy costs which might occur in nature.

Female voles with their litters (FB), ignoring the period where neonates are not able to thermoregulate, exhibited the following weight to metabolic rate relationship (n = 41):

$$R_{fb} = 1.20W^{-1.054}.$$

R_{fb} is the respiratory energy of female voles with their litters.

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[2]The values for M/W before the point of thermoregulation are extremely low. This presumably is caused by the vole losing a great deal of heat to the environment because of its large surface:volume ratio and its lack of insulation. The loss of heat is greater than can be compensated for by increasing metabolic rate, the body temperature drops and chemical reactions slow down.

Table 3. Logarithmic equations relating M/W (kcal/kgxhr) with W (kg) for groups reported in this work. M/W is represented by R.

Group	n	$R = aW^{(b-1)}$	R^2
Adult males and females (ADMR)	59	$R_{amaf} = 0.0785W^{-1.748}$	.56
Adult females (ADMR)	34	$R_{af} = 0.01482W^{-1.598}$	.50
Adult males (ADMR)	25	$R_{am} = 0.0313W^{-1.991}$	.63
Adult males and females (RMR)	59	$R_{mammaf} = 0.0302W^{-1.987}$	.48
Adult males (RMR)	25	$R_{mam} = 0.0111W^{-2.306}$	.62
Neonates over 11 days old	49	$R_{j} = 0.809W^{-0.889}$	.59
Females with litters	41	$R_{fb} = 1.20W^{-1.054}$	.35
Grouped littermates	10	$R_{gb} = 6.026W^{-0.465}$	.77
All animals AMAF + J	108	$R_{amaf+j} = 1.67W^{-0.716}$	.61

Litters of baby voles without the mother (GB) were also tested for metabolic rates. The relationship for 10 groups containing two or three littermates per group is

$$R_{gb} = 6.026W^{-0.465}.$$

R_{gb} is the respiratory energy for litters of neonatal voles.

Metabolic Rates of Adults and Neonatal Voles Taken as One Group (AMAF + J).

Finally, the adults and babies were pooled to establish an overall relationship:

$$R_{amaf+j} = 1.67W^{-0.716}.$$

The above data are tabulated in Table 3 and the raw data are listed in Appendix II.

Production Measurements

The energy stored during the growth period as tissue (production, P) was calculated in three steps.

i) A regression equation for body weight (kg) versus age was determined. The best fit (R^2 = .85) was given by a linear equation, W = 0.0031 + 0.0073Age (in days). This was converted to age in hours, W = 0.0031 + 0.0000304Age (hr). The rate of weight-gain/hr was determined (dW/dt) and equaled 0.0000304 kg/hr.

ii) The second step was to determine the relationship between production/unit body weight (kcal/kg) and body weight. The best fit (R^2 = .82) to these data was a polynomial equation of the form $y = a + bx + cx^2$.

$$P/W = 1007.92 + 548.56W - 535760.0W^2.$$

The average energy deposited as tissue between 0.003 and 0.030 kg (birth and approximate adult weight) is 13.26 kcal total (or 4.909 kcal/kg).

iii) The third step was to convert the equation in *ii* to a rate so it can be added to the equations for R, which are in the units of kcal/kgxhr and kg. This was done by taking the first derivative of the equation P/W with respect to time:

$$d(P/W)/dt = bdW/dt + 2cdW/dt$$

By substituting from steps *i* and *ii* the equation becomes:

$$P/WT = 1.662 - 32.467W.$$

The raw data used for these calculations are listed in Appendix III.

Determination of Additional Respiration Energy[3] During Growth (R_g), Assimilated Energy During Growth (A_g), and Assimilated Energy of Juveniles Above What Would be Expected From the Smaller Body Size (A_{ag})

Calculations were made to determine the *i*) differences between projected adult values (R_a) and neonatal values (R_j), termed additional respiration during growth, R_g, *ii*) individual assimilated energy used during growth (A_g) which is a sum of the total respiratory energy of juveniles and the energy deposited as tissue, and *iii*) additional assimilated energy required for the individual during growth above

[3]The term respiration energy is used for ease of discussion of energy measured by oxygen consumption.

projected assimilated energy requirements for an adult of the same size (A_{ag}).

Determination of R_g, Additional Respiratory Energy Demands During Growth.

$R_g = R_j - R_a$. R_g is an indication of additional energy used by an immature vole above what would be expected from the smaller body size.

$$R_g = 0.809W^{-0.889} - 6.35W^{-0.25}$$

(see Fig. 2)

Determination of Assimilated Energy During Growth (A_g).

The assimilated energy versus body weight of individual energy needs during growth if maintained individually (A_g) was determined by adding the juvenile heat production demands and the tissue production demands, $A_g = R_j + P/WT$.

$$A_g = 1.66 - 32.47W + 0.809W^{-0.889}$$

(see Fig. 2)

Additional Assimilated Energy Required for Growth (A_{ag}).

A_{ag} represents the assimilated energy demands of a juvenile above the amount that could be explained on the basis of a smaller body size. A_{ag} is calculated by adding the additional R demands of the neonates to tissue production energy. $A_{ag} = R_g + P/WT$.

$$A_{ag} = 1.66 + 32.47W + 0.809W^{-0.889} - 6.35W^{-0.25}.$$

(see Fig. 2)

Production Efficiency of Individually Maintained Neonates.

An integrated P/R ratio can also be determined for the production efficiency if animals had to be maintained individually. That is, P/R

shows the ratio of energy deposited as tissue to the total energy used as heat production during a given period.[4] Integrating the equations between birth weight (0.003) and approximate mature weight (0.030) gives

$$\frac{\int_{0.003}^{0.030} P/WT}{\int_{0.003}^{0.030} R_j} = 0.0130 \text{ or } 1.30\%$$

Respired Energy Saved by Family Grouping

The amount of energy saved by family grouping or huddling as opposed to what would be expended if the individuals were maintained separately was estimated: *i*) respired energy (R_{sum}) in kcal/hr of the individual family members was determined and summed to give a family total; *ii*) respired energy (R) in kcal/hr of the huddled family group was measured; and *iii*) the energy saved by grouping was calculated from $R_{sum} - R_{group}$.

The data was analyzed in several sections: *i*) all data including litters sizes one through four and neonatal voles before they began to

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[4]The literature dealing with production efficiencies uses several different denominators in production efficiency determinations. Metabolizable energy *above* maintenance may be used (ME^C), P/ME^C. This is not comparable to the P/R ratio. The production efficiencies would range from 30-60% in ruminents using the P/ME^C ratio. If the denominator is total digestable energy (DE) for ruminants the value becomes 6% (Reid, 1970). The P/DE is closer to P/R although DE = R + P + U and so, although more comparable to the P/R, it cannot be directly compared.

Brody (1945) reports growth efficiency for rats in terms of P/ME where ME is *total* metabolizable energy (ME = R + P) for rats and finds values of 0.6% to 13.6%. Converted to P/R, this data yields 0.62 to 15.6% efficiency--values vary comparable to the vole data.

thermoregulate were analyzed together; and *ii*) the data were then broken down into subgroups, data before the babies begin to thermoregulate were discarded and the remaining data were analyzed together and for different litter sizes.

For the set of all data (n = 74):

The sum of the energy used by family members = 1.953 kcal/hr

When in a group the same family used = 1.424 kcal/hr

Showing an energy savings = .529 kcal/hr

or 27% of what would be needed by the individuals. The means of the two groups were significantly different ($p < .001$).

When the family groups containing nonthermoregulating neonates were ignored, the values (n = 62) become:

The sum of the energy used by family members = 2.061 kcal/hr

The energy used by the group = 1.424 kcal/hr

The savings = .637 kcal/hr

or 28% of the amount needed to maintain individuals.

The family groups were then broken down into litter sizes. For female with one offspring:

The sum of the energy used by individuals = 1.247 kcal/hr

The amount of energy used when grouped = 1.282 kcal/hr

And there was no energy saved - .035 kcal/hr

For family groups with two in a litter:

The sum of energy used by family members = 1.896 kcal/hr

The group used = 1.405 kcal/hr

The energy savings = .491 kcal/hr

or 25.9% of what the animals need separately.

For family groups with three in a litter:

The sum of energy used by family members	= 2.350 kcal/hr
Grouped	= 1.923 kcal/hr
The energy savings	= .427 kcal/hr

or 18.2% of energy used individually.

For families with 4 in a litter:

The sum of energy used by family members	= 2.785 kcal/hr
Grouped	= 1.465 kcal/hr
The energy saved by huddling	= 1.320 kcal/hr

or 49.4% of what the animals need individually.

During the collection of data for this experiment some of the family groups (n = 20) were tested together and as individuals during the same day. These data are listed in Table 4 under "Measured Data." In another group (n = 54) only part of the data was collected during the 1 day period and other values were calculated from experiments on other days. These data are listed in Table 4 as "Calculated Data." The numbers reported above pool the measured and calculated data and are reported as "Total Data" in Table 4.

The discrepancy noticed in litter size one of the pooled sample (with a negative energy savings) is probably an artifact, since the measured values actually do show an energy savings. The data from litter size one was projected from data collected for all litter sizes containing predominantly two and three babies/litter. The relationship between energy costs to maintain individual neonates, individual babies maintained in groups and individual babies maintained in a litter with the female present was calculated and is plotted in Fig. 3. This shows M (total R energy/hr for an individual baby vole) against

Table 4. Data showing difference between total respired energy/hour in kcal/hr used by sums of individuals in family (R_{sum}) and family groups (R_{group}). Three data sets are shown: measured, calculated, and a pooling of measured and calculated called total.

Group	n	$\bar{x}$	s	Signif. Between Sum and Group	% Saved Over Sums	% Saved Over Groups
			Measured Data			
All Groups						
R_{sum}	20	1.756	.530			
R_{group}	20	1.421	.479			
Difference	20	.335	.447	7.005	19.1%	23.6%
Thermoregulating						
R_{sum}	17	1.899	.434			
R_{group}	17	1.494	.491			
Difference	17	.405	.406	7.025	21.3%	27.1%
One in Litter						
R_{sum}	2	1.256	.054			
R_{group}	2	1.078	.396			
Difference	2	.178	.462	ns	14.2%	16.5%
Two in Litter						
R_{sum}	15	1.950	.462			
R_{group}	15	1.553	.484			
Difference	15	.397	.406	7.050	20.4%	25.6%
			Calculated Data			
All Groups						
R_{sum}	54	2.025	.527			
R_{group}	54	1.480	.626			
Difference	54	.545	.715	7.001	26.9%	36.8%

Table 4. (Continued)

Group	n	$\bar{x}$	s	Signif. Between Sum and Group	% Saved Over Sums	% Saved Over Groups
Thermoregulating						
R_{sum}	45	2.056	.535			
R_{group}	45	1.741	.763			
Difference	45	.315	.735	7.050	15.3%	18.1%
One in Litter						
R_{sum}	7	1.126	.136			
R_{group}	7	1.370	.186			
Difference	7	-.254	.274	ns		
Two in Litter						
R_{sum}	13	1.773	.209			
R_{group}	13	1.207	.595			
Difference	13	.466	.633	7.005	26.3%	38.6%
Three in Litter						
R_{sum}	18	2.255	.297			
R_{group}	18	1.836	.812			
Difference	18	.419	.760	7.050	18.6%	22.9%
Four in Litter						
R_{sum}	7	2.779	.083			
R_{group}	7	1.417	.213			
Difference	7	1.362	.186	7.001	49.0%	96.1%
Total Data						
All Groups						
R_{sum}	74	1.953	.538			
R_{group}	74	1.424	.594			
Difference	74	.529	.656	7.001	27.1%	37.1%

Table 4. (Continued)

Group	n	$\bar{x}$	s	Signif. Between Sum and Group	% Saved Over Sums	% Saved Over Groups
Thermoregulating						
R_{sum}	62	2.061	.513			
R_{group}	62	1.472	.604			
Difference	62	.637	.549	7.001	28.6%	43.3%
One in Litter						
R_{sum}	11	1.247	.096			
R_{group}	11	1.282	.231			
Difference	11	-.035	.285	ns		
Two in Litter						
R_{sum}	27	1.896	.337			
R_{group}	27	1.405	.558			
Difference	27	.491	.533	7.001	25.9%	35.0%
Three in Litter						
R_{sum}	16	2.350	.122			
R_{group}	16	1.923	.821			
Difference	16	.427	.782	7.10	18.2%	22.2%
Four in Litter						
R_{sum}	7	2.785	.075			
R_{group}	7	1.465	.174			
Difference	7	1.320	.186	7.001	47.4%	90.1%

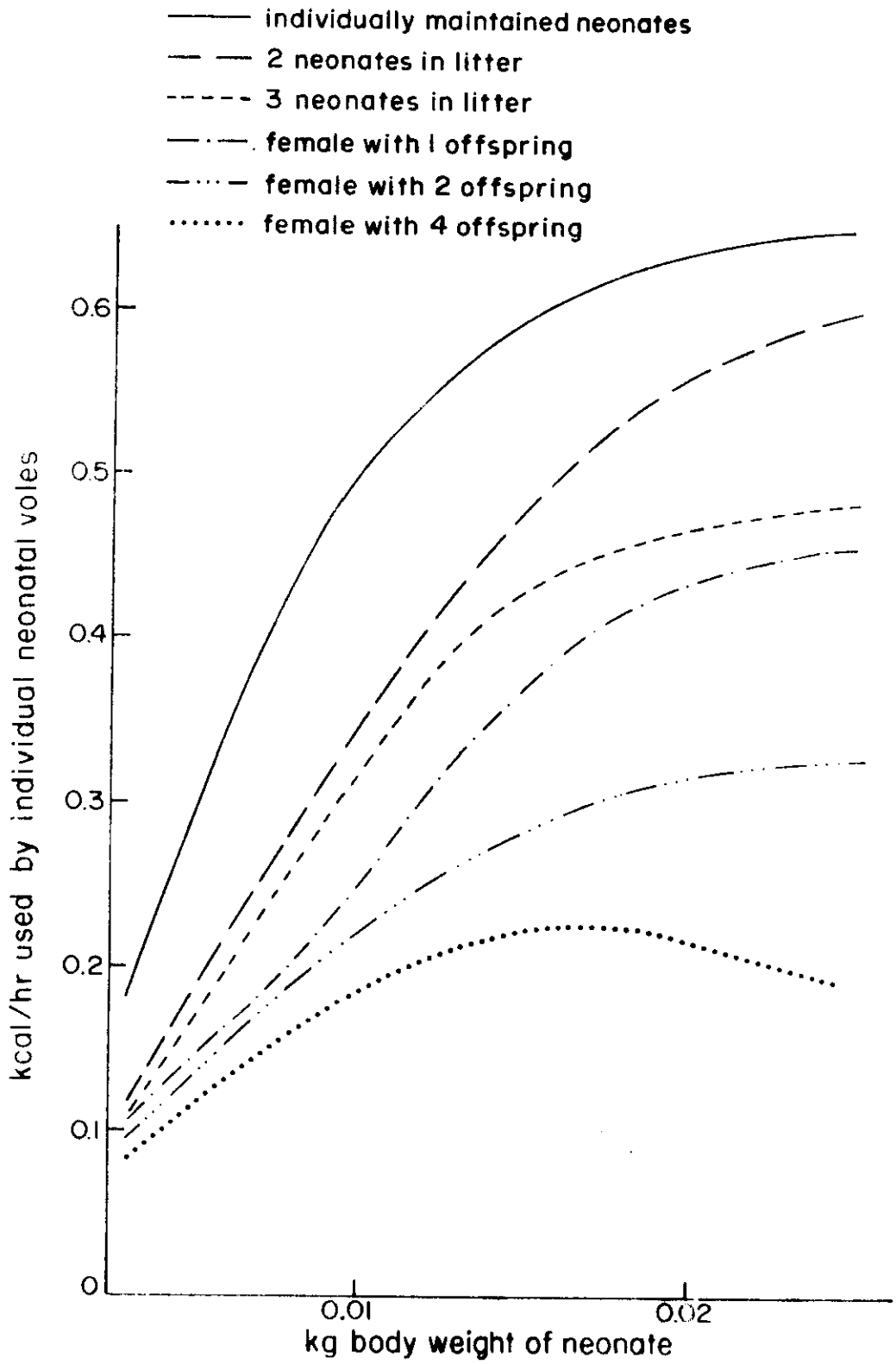

Fig. 3. Kcal/hr (R) used by individual neonatal vole in different family groupings.

individual baby weights (W) for individuals; litters of two and three; and females with one, two, or three offspring. These lines were calculated from the regression equations in Table 3. From this plot it is obvious that individual babies use the most energy (up to the approximate adult weight). Grouped babies use less energy/individual and the babies huddled with litter mates and mother use the least energy/individual.

P/R Ratio As an Index of Increased Production Efficiency With Family Groups.

Integrated P/R ratios show the increase in production efficiencies within family groups as opposed to the individual efficiency of 1.30%: for grouped babies, two to three in a litter between the weights of 0.009 and 0.036 kg.[5]

$$\frac{\int_{0.009}^{0.036} P/WR}{\int_{0.009}^{0.036} R_{gb}} = 3.42\%$$

Production efficiency for females with litters is[6]:

$$\frac{\int_{0.003}^{0.030} P/WT}{\int_{0.53}^{0.080} R_{fb}} = 4.06\%$$

---

[5]The values come from 0.003 x 3 voles = 0.009; 0.036 was used to keep the integration interval at 0.027.

[6]0.53 was chosen for female weight of 0.050 and baby weight of 0.003.

Determination of Digestible Energy With Simultaneous Measurement of Respired Energy.

Changes in digestible energy with age and weight were compared with simultaneously measured changes in respired energy with age and weight. This was done to determine digestibility values of the experimental colony under given experimental conditions and feed as well as to validate the method of measurement used for this paper. The percent of digestibility of the experimental voles on an *ad lib* diet of rabbit chow showed no significant change with age. The mean percent digestibility was 53.58 ± 8.65%. Equations pertinent to comparing results from the two methods follow:

Digested energy (kcal/kgxhr) = 52.290 - 0.653 Age $(R^2 = .56)$

Log digested energy = 2.945 - 0.9773 log Age $(R^2 = .65)$

Digested energy (kcal/kgxhr) = 54.527 - 859.84W $(R^2 = .58)$

Log digested energy = -0.3948 - 1.1774 logW $(R^2 = .72)$

Respired energy (kcal/kgxhr) = 43.47 - .491 Age $(R^2 = .36)$

Log respired energy = 2.488 - 0.726 log Age $(R^2 = .42)$

Respired energy (kcal/kgxhr) = 55.14 - 971.350W $(R^2 = .59)$

Log respired energy = -0.4347 - 1.1795 logW $(R^2 = .67)$

Slopes of the equations relating respired energy versus age and digested energy versus age were compared and found to be equal for both linear and logarithmic equations. The same similarity was found between the regression equations relating respiratory energy versus W and digested energy versus age. This shows that the two separate methods of determining ADMR are yielding the same form of equations.

Appendix V gives the linear and logarithmic equations as well as the R^2 values for all relationships in this study.

DISCUSSION

The exponential regression relationships derived in this thesis are valuable when taken in context of their true meaning, that is, in pointing out the existence of valid relationships, but should not be taken as an exact quantitation. Some of the discussion of partitioning of energy during growth that follows will be based on projections from the regressions and the values are good estimates of what happens and are not exact measurements.

Metabolic Rate Relationships (R) and Their Implications

Comparison of Data With Theoretical Values.

Data collected in this experiment compare favorably with projected values offered by Kleiber (1961). Average values from ADMR at 20°C for all males and females (AMAF) were used for one comparison. Conversion was made to BMR at 30°C. The average adult weight for AMAF was 0.0492 kg and ADMR at 20°C was 16.32 kcal/day. Converted to 30°C, ADMR becomes 10.2 kcal/day (factor for this conversion was derived from Gorecki, 1968). Converted to BMR at 30°C to compare with Kleiber's projected value, the BMR is 7.85 (factor for this conversion is derived from Gorecki, 1966). The BMR value projected by Kleiber for 0.049 kg is 8.4 kcal/day.

The Brody (1945) factor for maintenance energy, ME = 2 x FMR or $ME = 140W^{0.75}$ was compared to data from the RMR of the adult colony:

Average RMR (kcal/kgxhr) = 13.55 (M/W)

Average kg = 0.0481 (W)

$$M = \frac{13.55 \text{kcal/kgxhr} \times 24 \text{ hr/day} \times 0.0481 \text{ kg}}{0.0481^{0.75}} = 152.61 \text{ kcal/kg}^{0.75}/24 \text{ hrs}$$

which compares favorably with the standard value of 140 kcal/$kg^{0.75}$/ 24 hrs at 30°C.

The close comparison with traditionally projected values for metabolic rate at a given weight allows us to assume that the projection of data for the adult baseline along the interspecific body size-metabolic weight relationship, $W^{0.75}$ is valid. The equation derived in the results from such a projection should be a good indication of change in metabolic rate due to an animals smaller body size:

$$R_a = 6.35W^{-0.25}.$$

The Meaning of Reported Values For b-1 in the Equation $M/W = aW^{(b-1)}$.

The exponential equations relating the respiratory energy (R) with body weight, $M/W = aW^{(b-1)}$, for adult groups, have slope values (b-1) of less than -1.0. Conversion of these values to M versus W, ($M = aW^b$) shows b to be a negative number. In other words, the larger animal is producing less heat energy than the small animals. This was not expected from discussions found in the literature.

The apparent discrepancy may be due to the narrow weight range of data and actually be an artifact, or it may point to an interesting relationship between size and metabolic efficiency in this colony of voles maintained at 20°C. In Fig. 4, the exponential equations relating M and W for babies and adults are plotted as M (total kcal/hr) used by individual against body weights of progressively larger animals. As expected, the immature voles produce more R energy totally as they increase the body size. However, an intersection of neonatal and adult curves is reached where the animals actually use

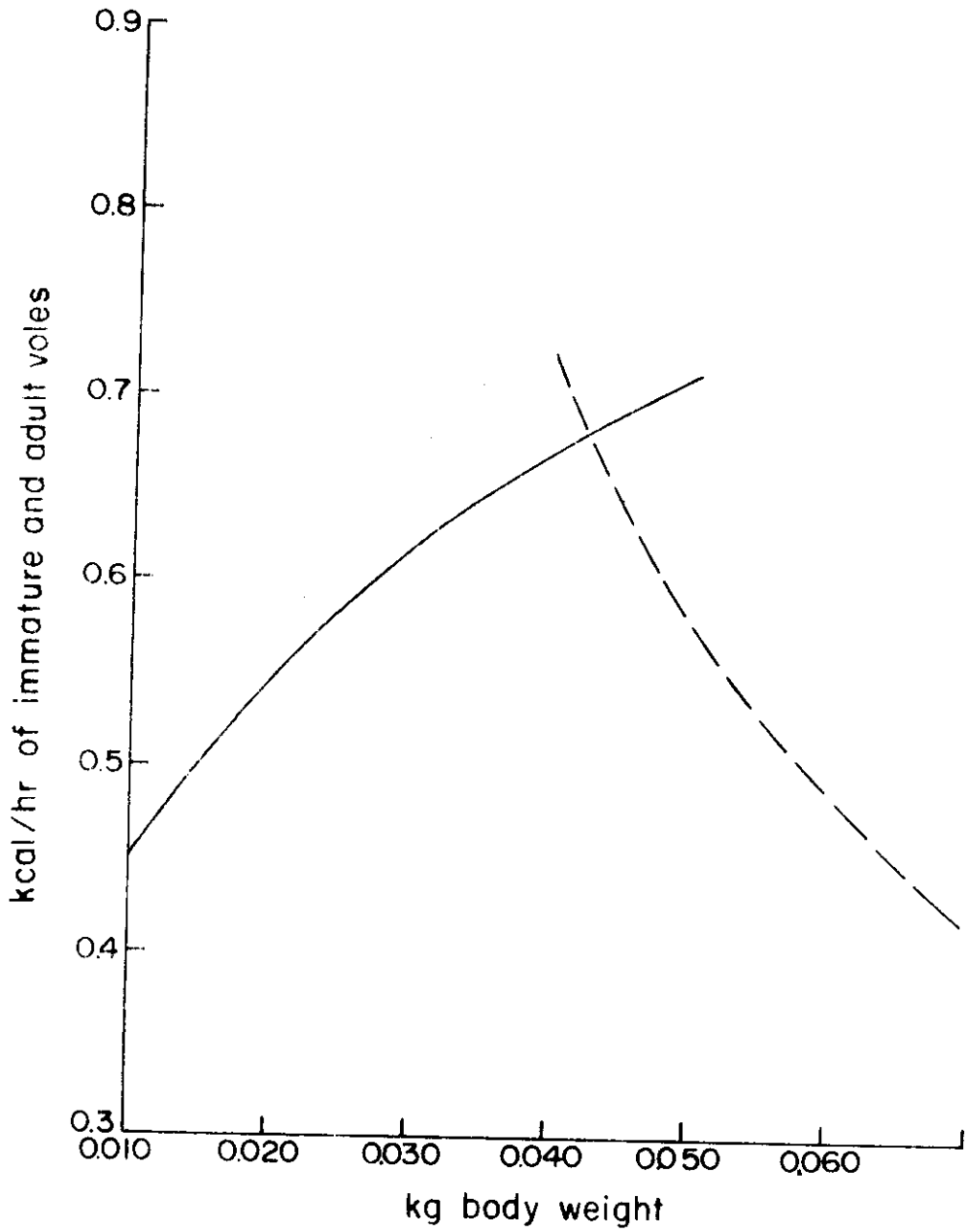

Fig. 4. Total metabolic requirements of neonatal (——) voles and adult (---) voles in kcal/hr. (Calculated by Rjxw and Raxw).

the most R energy. That is, the amount of R energy produced for the total animal is highest at a weight that would be considered average adult weight, 0.042 kg. (Remember the R measurement does not include energy deposited as tissue.) Animals over this weight seem to require less total energy as the body size increases. Is it possible that, over the small weight range represented by this colony of voles, a slight increase in weight actually decreases the surface:volume ratio, and thus, heat production required for thermoregulation at 20°C, so that the slightly larger vole actually needs less total energy for heat production? This experiment would seem to point to this size advantage.

Another possible explanation for the drop in total energy with increased size comes from work relating metabolic rate and age in humans (Kleiber, 1961). Total respiratory energy used per person dropped from 1700 kcal/day at 17 years to 1400 kcal/day at 62 years of age, with weight remaining relatively constant. This is evidently caused by a general slowing of the basal metabolic rate with age. It appears that it may be possible that this phenomenon (decreased metabolic rate with age) is also occurring here and that it shows up in the M/W to W relationship because there are proportionately more older, heavier adults. (Age was not recorded in the "mature" colony because they were all born within one year of each other--a significant age difference in mature voles.)

Energy Deposited as Tissue (P)

The importance of determining the P measurement lies in quantitating *i*) the amount of energy deposited as tissue, *ii*) the rate of

energy deposition as a factor in the total amount of assimilated energy (respired energy + deposited energy) during growth, and *iii*) production efficiencies--both as individual demands if neonates were maintained separately and efficiencies in the litter and in the female with litter. This third part will be covered more extensively in the discussion of energy savings by family groups.

However, the drop in energy use of the adult vole colony (over the weight range measured) was 38% as compared to a 17% drop over the entire adult time span in humans. The aging explanation could probably not account for such a rapid decrease.

A last possible explanation is that the heavier voles are actually fatter voles. Other researchers (Dr. Don Johnson, Colorado State University, personal communication) have experienced that fat animals self-impose a fast, even though they have ample food available, while in the semi-stressful environment of metabolic chamber. The lowest data observed (4.18 kcal/kgxhr) for the heaviest animal (0.070 kg) seems to confirm this observation.

$$M = \frac{4.18 \text{ kcal/kgxhr} \times 24 \text{ hrs/day} \times 0.070 \text{ kg}}{0.136 \text{kg}^{0.75}} = 51.63 \text{ kcal/kg}^{0.75}/24 \text{ hrs}$$

as compared with 70 kcal/$kg^{0.75}$/24 hrs as expected for fasting metabolism.

It is because of the variability imposed by all these possible factors that the adult baseline slope projected from actual data was neglected in favor or projecting average values along the well-established interspecific $W^{0.75}$ relationship.

The Amount of Energy Deposited as Tissue (P).

Production (P) per unit body weight (W) is given by the equation

$$P/W = 1007.92 + 548.56W - 535760.0W^2$$

where P/W is kcal of energy deposited as tissue per unit body weight in kg. This equation gives an average value of 13.26 kcal tissue deposited between 0.003 and 0.030 body weight (see Fig. 2) for each vole. This is comparable to production values found for *Microtus arvalis* (Sawicka-Kapusta, 1970).

Rate of Energy Deposition.

The rate of production is given by P/WT = 1.66 - 32.47W where P/WT is in kcal/kgxhr. This equation can be used to relate the amount of energy deposited as tissue (P/WT) to R energy for heat production. P/WT is also used to give an equation for assimilated energy, $A_g = P/WT + R_j$, and for additional assimilated energy, $A_{ag} = P/WT + R_g$.

A_g represents the amount of assimilated energy needed to maintain individual growing voles. A_{ag} represents the amount of additional assimilated energy above what would be expected from body size alone. From Fig. 2 it can be seen that only a small portion of the assimilated energy is actually used for tissue production in these individually maintained animals.

P/R Ratio as an Indication of Production Efficiency.

Integration of the P/R ratio between 0.003 and 0.030 kg body weight provides a measure of the amount of energy going into production of tissue as related to the amount needed for maintenance-thermoregulation (R). The P/R ratio is a good index of the relative

production inefficiency of growth in a neonate when maintained individually.

$$\frac{\int_{0.003}^{0.030} P/WT}{\int_{0.003}^{0.030} R_j} = .0130 \text{ or } 1.30\%$$

This low efficiency, 1.30%, reflects the high cost of maintenance or thermoregulation costs of small and immature mammals when maintained alone.

Differences in Metabolic Rates Between Neonatal Voles and Adult Voles

The Difference in Metabolic Rate Per Unit Weight Between Neonates (R_j) and Adults Projected to the Immature Body Size (R_g).

This equation is applicable between 0.003 and 0.040 kg body weight since neonatal and adult curves intersect at 0.040 kg. The phenomenon of higher metabolic rates/unit weight that occurs in the growing vole above that projected for adults of the same size has several possible explanations.

i) Insulation ability increases with age due to increased pellage. The heat production needed to compensate solely for lack of insulation is high at birth and decreases with age until the vole has adult pellage. Of course, weight increases with age up to maturity so the finding of decreased metabolic rate per unit weight would be expected to decline with increased weight as well as increased age.

ii) The ratio between highly metabolic tissues (such as brain, liver, and heart) and supportive tissues with a lower metabolic rate

(such as bone and inactive muscle) is much higher in the newborn decreasing with age. The high proportion of highly metabolic tissue in neonates would cause a higher BMR. The BMR declines with age and of course with increased weight during growth. This relationship follows the energy pattern seen here.

iii) One explanation for the decreased metabolic rate with age deals with the drop in thermoneutral temperature as voles mature. This is intimately tied with insulation, which has already been discussed, and with the surface:volume ratio. As the surface:volume ratio decreases with increased body size the amount of R energy required for heat production (thermoregulation) decreases. However, this factor is accounted for in the projected adult baseline relationship seen in Fig. 2. In fact, this is probably the major factor causing the drop in M/W with increased body size (W) that characterizes adult metabolism. Projection of metabolic rate from adult size to juvenile body weight provides visualization of the change due to change in size and surface:volume ratio. Therefore, although size is involved in elevating the juvenile energy requirements, it will not be considered a factor in elevating the maintenance cost over projected adult levels. And the factors considered to account for the difference in juvenile metabolic rate (R_j) and projected adult metabolic rate (R_a) are assumed to be due to decreased insulation and increased BMR in the neonates as compared to adults.

Neonatal voles contain more water (78%) than adults (60%). This implies that the tissue in young voles is even more metabolically active than would be visualized by the wet weight relationships reported here.

Assimilated Energy During Growth (A_g and A_{ag}).

The respired energy, of course, does not show the total energy demand. Determining the assimilated energy is the next step. Tissue production (P/WT) must be added to R_j. The equation derived from summing R_j and P/WT is A_g (in kcal/kgxhr):

$$A_g = 1.66 - 32.47W + 0.809W^{-0.889}.$$

This equation represents the total assimilation demands of the growing animal.

When adult assimilation (assuming R = A in adults) demands are separated from the total assimilation demands of juveniles, the changes with weight that occur in maturing voles above that caused solely by maintenance demands at a given body size can be evaluated (A_{ag}, additional assimilation energy required during growth).

$$A_{ag} = 1.66 - 32.47W + 0.809W^{-0.889} - 6.35W^{-0.25}.$$

The value A_{ag} represents the additive factors of lack of insulation, high BMR, and tissue production costs and emphasizes that factors other than simple body size are adding to the high energy cost in growing animals. Even the tissue production (see Fig. 2, P/WT = 1.66 - 32.67W) is a relatively small portion of this additional energy demand. The additional energy cost is assumed to be due primarily to lack of insulation and the higher BMR demands of the neonate.

Values for R_g, A_g, and A_{ag} discussed in the previous sections are of interest in showing the high potential developmental costs of growing animals and how the actual tissue energy deposit is a

relatively small amount of the total energy demands of the individually maintained microtine even when "adult body size" requirements have been eliminated.

Energy Saved by Family Grouping

Larger Family Grouping Conserves More Energy.

Reduction of the R energy used by the individual in different family groups was measured and is tabulated in Table 4. The most efficient family group was the female with the largest litter (four offspring), saving as much as 47% of the energy required to maintain the animals separately.

Figure 4 gives plots of the amount of energy required to maintain an individual vole (between weights of 0.003 and 0.024 kg) under varying family groupings. It is obvious that the larger the biomass of the family group, the greater the energy saved. That is, the individual baby uses less energy with more littermates and the least energy with female and three littermates. This is not always true of huddled adults (Drozdz, 1971 and Gorecki, 1968) where an optimum for energy savings may be two or three animals and may depend upon the sex of animals involved, owing to social behavior.

Areas of Juvenile Energy Use Where Conservation Occurs.

The cause for high metabolic demands of neonates kept individually has been discussed above and can be summarized in four parts: *i*) high surface:volume ratio causing high heat loss; *ii*) lack of insulation; *iii*) higher BMR because of higher ratio of metabolically active tissues in the young; and *iv*) tissue production (these are illustrated in Fig. 2).

Energy savings would not occur in *iii* and *iv* for production and body composition remain the same in this experiment. Therefore, the areas where energy savings occur must be from *i*, decrease in surface: volume ratio and *ii*, in increased insulation.

Effective decreased surface:volume ratio by huddling and thus decreased heat loss is undoubtedly one major mechanism in energy saving here as it has been shown to be in grouped adults.

The striking energy savings which occurs in the neonate when the female is present may have a great deal to do with her insulative effects on the babies. This conclusion is drawn from data discussed in the previous section where the juvenile is shown to demand a great deal of energy above what would be expected from small surface:volume ratio (projected adult R values). The only fraction of the energy demand that remains to be reduced is the demand due to insulation.

The energy savings attributable to each of the two factors cannot be separated further from data collected in this experiment.

Increase in Production Efficiency in Family Groups.

The increase in efficiency of growth or tissue production to the individual in family situation is illustrated by the following integrated P/R ratios:

Individual $\int_{0.003}^{0.030} \frac{P/WT}{R_j} = .0130$ or 1.30%

Grouped babies $\int_{0.009}^{0.036} \frac{P/WT}{R_{gb}} = 3.42\%$

$$\text{Female with litter} \qquad \frac{\int_{0.003}^{0.030} P/WT}{\int_{0.053}^{0.080} R_{fb}} = 4.06\%$$

These ratios show a three-fold increase in efficiency in tissue production as related to heat production from the individual to the family group.

Implications of Energy Savings by Family Group.

Implications of the energy savings can be divided into two categories: *i*) the advantage of lower cost of reproduction which enables rapid population turnover and *ii*) the possible population stabilization effects.

If small mammals were to be maintained themselves as entities during the neonatal period, as occurs in large mammals, the energy cost to the individual and the population would be exorbitant--up to 100% increase over family requirements (Table 4). The rapid population turnover which exists in rodent populations would be too expensive in terms of energy cost to the population. Huddling of the family, which perhaps has adaptive significance, helps make possible the rodent life cycle as we know it.

The energy savings in family groups as opposed to the high cost of maintenance for individuals, or even for litters without females, may have relevant implications in population stabilization. In an area densely populated with a given species (or animals eating a given food source) a female would be obliged to leave the litter for longer and longer periods of time in search of food. The offspring, as a result of being left comparatively "uninsulated,"

would require more and more energy for maintenance, i.e., need for more food. This would make an every increasingly energy expensive situation and lessen the chances for survival of the offspring (in addition to being left unprotected). Decreased survival rate would occur with an increased population. On the other hand, a low population density would allow the mother to spend more time with offspring, which in turn would decrease their energy demands and increase survival rates. This would seem to be an effective mechanism for aiding population stabilization.

Simultaneous Digestibility and Respiration Studies

A small study determining digestibility values was performed simultaneously with the growth study and served two purposes: *i*) to allow for conversion of assimilated (and respired energy) measurements to consumption energy (C_e) and *ii*) to compare the method of determining assimilated energy by measurement of respiration + production energy ($A_e = R + P$) with the more traditional food consumption method, ($A_e = C_e - F_e - U_e - G_e$).

Determination of Digestibility.

For a complete picture of energy use it is necessary to be able to convert assimilated energy (as discussed in the previous section) to consumed energy or C_e. $C_e = (R+P)/[1 - (\%\ \text{digestibility} - \%\ \text{energy lost in urine and gas})]$.

Urine and gas losses have been estimated at 4%. Percent digestibility was calculated to be 53.58 ± 8.65% in the age range between weanlings and adults with no age change. In the adult colony (AMAF), average ADMR (R) was 16.32 kcal/kgxhr for an average weight of 0.0492 kg. These values convert to a total average adult R value/day

of 19.19 kcal/day. The P of the adult colony is assumed to be equal to 0, since adults maintained constant weight. These values can then be substituted into the equation for C_e.

$$C_e = (19.19 \text{ kcal/day})/(1 - (0.54F_e/C_e) - 0.04(\%U_e+G_e)) = 45.69$$

kcal/day, or 0.929 kcal/grxday which is within the expected range for wild rodents as discussed by Drozdz (1968).

Comparison of Two Methods of Determining A.

Comparison of assimilated energy as calculated by the food consumption-fecal energy method and by the measurement of heat production by oxygen consumption method showed the two methods to be comparable when averaged over the adults in the group.

R is calculated from the O_2 consumption method and is assumed equal to A in these adults.

$$R = 19.55 \text{ kcal/kgxhr.}$$

A is calculated from the food consumption method

$$A = 36.02C_e - 17.10F_e - (0.04 \times 36.12)U+G_e = 16.51 \text{ kcal/kgxhr.}$$

The discrepancy here indicates that either the percent of energy in urine and gas is overestimated or the experimental animals were in a negative energy balance during the experiment. The standard deviations of this data, however, are large enough (see Appendix IV) to account for this 10% discrepancy.

A better indicator of the fact that the O_2 consumption method (R) is comparable to the food consumption method is the relationships between M/W and W as well as Age as measuring by respired and by

digested energy derived over the age range. The slopes of the equation are equal statistically with only a difference in intercept which would be expected to account for gas and urine energy loss.

SUMMARY

There is a higher metabolic rate per unit body weight, as measured by the O_2 consumption method, in neonatal voles than would be expected solely from the neonates smaller body size based on adult values. The additional energy expended as heat production may be attributed to the poorer insulative ability of immature voles as well as a high BMR in neonatal voles due to a large ratio of highly metabolic tissues to tissues with a low metabolic demand.

The P/R ratio of individually maintained voles is extremely low. This indicates the energy going into tissue production (P) is very low compared to the amount of energy expended in heat production (R).

The strategy of family grouping effectively and significantly reduces energy demands for heat production (R) in the neonatal voles. The production efficiency, as indicated by the P/R ratio, shows a threefold increase for neonatal voles maintained in family groups over individuals maintained separately.

The energy savings made by family grouping may have its importance in allowing a rapid turnover in the rodent population as well as acting as a population stabilization mechanism.

The method of determining energy use as used in this experiment, i.e., O_2 consumption as a measure of R plus tissue production (P) to yield A, assimilated energy, is comparable to the food consumption method of determining A. The average values for A found between the two methods actually show less variation than the data within each method. The changes in assimilated energy (by R + P) and digestible energy (by $C_e-F_e-U_e-G_e$) show statistically the same quantitative change

with age and weight. That is, the slopes of the two relationships are statistically the same.

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APPENDIX I

PROGRAM

```
      PROGRAM METAB2 (TAPE1,TAPE2,TAPE3,TAPE4,TAPE5,TAPE6,OUTPUT)
      COMMON SS(3,90,4),LC(4),STO(20),TM(5,3),SD(5)
C     READ IN REGRESSIONS
      READ(5,100) O2A,O2B,O2C,CO2A,CO2B,CO2C
  100 FORMAT (F6.3,F6.4,F5.3,F6.5,F6.5,F7.6)
C     READ IN ANIMAL WEIGHTS
      READ(5,200) BWT0,EWT0,BWT1,EWT1,BWT2,EWT2,BWT3,EWT3
  200 FORMAT(8F6.0)
      J0=J1=J2=J3=1
      LC(1)=LC(2)=LC(3)=LC(4)=0
      SC=-1.
      DO 18 I=1,4
      TM(I,1)=-1.
      SD(I)=-1.
      DO 18 J=2,3
      TM(I,J)=0.
      DO 18 K=1,90
      SS(1,K,I)=0.
      SS(J,K,I)=0.
   18 CONTINUE
      I=0
   20 CONTINUE
      I=I+1
      READ(5,300) FNO,CMBN,DATE,TIME,O2,CO2,TEMPA,TEMPB,FLOW,BP
  300 FORMAT(F4.0,3XF1.0,4(1X,F3.0),8X,3(1X,F3.0),16XF5.1)
      IF(EOF(5)) 25,22
   22 CONTINUE
      BP = 636.0
      IF(CMBN.EQ.4.) GO TO 20
      IF (CMBN.EQ.7.)CMBN=3
      IF (CMBN.EQ.5.)CMBN=1
      IF (CMBN.EQ.6.)CMBN=2
      T=TIME*2./60.
      N=CMBN+1
      IF(TM(N,1).GE.0.) GO TO 23
      SD(N)=DATE
      TM(N,1)=T
      TM(N,3)=T
      IF(SC.NE. -1.) GO TO 20
      SC=N
      ST=T
      GO TO 20
   23 IF(T.LT.TM(N,1)) GO TO 24
      TM(N,2)=TM(N,2)+(T-TM(N,1))
      TM(N,1)=T
      GO TO 20
   24 TM(N,2)=TM(N,2)+T+(24.-TM(N,1))
      TM(N,1)=T
      GO TO 20
   25 CONTINUE
      I=0
      TM(1,1)=TM(1,3)
      TM(2,1)=TM(2,3)
      TM(3,1)=TM(3,3)
      TM(4,1)=TM(4,3)
```

APPENDIX I (Continued)

```
      TM(1,3)=(EWT0-BWT0)/TM(1,2)
      TM(2,3)=(EWT1-BWT1)/TM(2,2)
      TM(3,3)=(EWT2-BWT2)/TM(3,2)
      TM(4,3)=(EWT3-BWT3)/TM(4,2)
      TM(1,2)=BWT0
      TM(2,2)=BWT1
      TM(3,2)=BWT2
      TM(4,2)=BWT3
      REWIND 5
   27 I=I+1
      READ(5,300) FNO,CMBN,DATE,TIME,O2,CO2,TEMPA,TEMPB,FLOW
      IF(EOF(5)) 30,29
   29 CONTINUE
      IF (CMBN.EQ.7.)CMBN=3
      IF (CMBN.EQ.6.)CMBN=2
      IF (CMBN.EQ.5.)CMBN=1
      IF(I.LT.3) GO TO 27
      IF(CMBN.LT.4.) GO TO 5
      CO2AM=CO2
      O2AM=O2
      GO TO 27
    5 CONTINUE
      N=CMBN+1
C     CORRECT FOR WT. LOSS OR GAIN
      CORWT=TM(N,2)-TM(N,3)
      CALL CALCS(O2,CO2,TEMPA,FLOW,BP,CORWT,O2A,O2B,O2C,CO2A,CO2B,
     /CO2C,TIME,O2AM,CO2AM,RQ,CKAL)
      STO(1)=CMBN
      STO(2)=DATE
      STO(3)=TIME
      STO(4)=FLOW
      STO(5)=TEMPB
      STO(6)=TEMPA
      STO(7)=CO2
      STO(8)=O2
      STO(9)=RQ
      STO(10)=CKAL
      CALL AVE(SC,ST,N)
   10 CONTINUE
      STO(4)=TEMPA
      STO(6)=FLOW
      LC(N)=LC(N)+1
      IF(LC(N).EQ.1) WRITE(N,400)
  400 FORMAT(1H15X*CHAMBER NUMBER*6X*DATE*6X*TIME*5X*TEMPAM*5X*TEMPBY*
     /5X*FLOW*5X 24HCO2L/KG/HR      O2L/KG/HR   7X*RQ*5X*KCAL/KG/HR*)
      WRITE(N,500)FNO,(STO(J),J=1,10)
      GO TO 27
   30 CONTINUE
  500 FORMAT(1H F4.0,6XF3.0,10X,F7.0,5XF5.2,6XF5.2,4XF6.2,6XF4.2,7X
     / F5.2,8X,F5.2,7X,F5.3,7X,F5.2)
      DO 40 I=1,4
      IF(TM(I,1).EQ.0.) GO TO 40
      II=1
      IN=78
      CALL SPLAT(I ,IN,II)
```

APPENDIX I (Continued)

```
      II=85
      IN=90
      CALL SPLAT(I ,IN,II)
      REWIND I
   35 CONTINUE
      READ(I,600)(STO(J),J=1,13)
  600 FORMAT(13A10)
      WRITE(6,600) (STO(J),J=1,13)
      IF(EOF(I),EQ.0.) GO TO 35
   40 CONTINUE
      CALL EXIT
      END
```

APPENDIX I (Continued)

```
      SUBROUTINE AVE (SC,ST,N)
      COMMON SS(3,90,4),LC(4),STO(20),TM(5,3),SD(5)
      IH=SC
      IF(STO(2).NE.SD(IH).A.STO(3).GT.TM(IH,1)) GO TO 4
      GO TO 5
    4 CONTINUE
      II=1
      IN=84
      CALL SPLAT(IH,IN,II)
      SD(IH)=STO(2)
    5 CONTINUE
    2 CONTINUE
      SH=STO(3)+.0005
      IH=SH/2.+1.
      IF(LC(N).GT.0) GO TO 6
      ICH=1
      ISH=IH
    6 IF(IH.EQ.ISH) GO TO 7
      ICH=ICH+1
      ISH=IH
    7 CONTINUE
      K=79
      L=85
      J=(ICH-1)*6+1
      DO 10 I=5,10
      SS(1,J,N)=SS(1,J,N)+STO(I)
      SS(2,J,N)=SS(2,J,N)+STO(I)**2
      SS(3,J,N)=SS(3,J,N)+1
      IF(MOD(J,6).EQ.0) SS(3,J,N)=STO(3)
      J=J+1
    8 CONTINUE
      SS(1,K,N)=SS(1,K,N)+STO(I)
      SS(2,K,N)=SS(2,K,N)+STO(I)**2
      SS(3,K,N)=SS(3,K,N)+1
      K=K+1
      SS(1,L,N)=SS(1,L,N)+STO(I)
      SS(2,L,N)=SS(2,L,N)+STO(I)**2
      SS(3,L,N)=SS(3,L,N)+1
      L=L+1
   10 CONTINUE
      SS(3,84,N)=STO(3)
      SS(3,90,N)=STO(3)
      RETURN
      END
```

APPENDIX I (Continued)

```
      SUBROUTINE CALCS(O2,CO2,TEMPA,FLOW,BP,CORWT,O2A,O2B,O2C,CO2A,CO2B,
     / CO2C,TIME,O2AM,CO2AM,RQ,CKAL)
  100 FORMAT (1H ,11 F 10.5)
      TEMPA=-23.984+.13904*TEMPA-.000067*TEMPA**2
      CALCULATE PERCENT
      ACO2PC=CO2A+CO2B*CO2AM+CO2C*CO2AM**2
      AO2PC=O2A+O2B*O2AM+O2C*O2AM**2
      CALCULATE CHANGED O2 AND CO2 PERCENT
      EO2PC=O2A+O2B*O2 +O2C*O2 **2
      ECO2PC=CO2A+CO2B*CO2+CO2C*CO2**2
      CALCULATE DELTA PERCENT,RQ
      DTO2=(AO2PC-EO2PC)*.01
      DTCO2=(ECO2PC-ACO2PC)*.01
      RQ=CO2=O2=0.
      IF(DTO2.EQ.0.) GO TO 5
      RQ=DTCO2/DTO2
    5 CONTINUE
      TIME=TIME*2./60.
      FLOW=(63.695+5.1572*FLOW)/1000.
      IF(CORWT.LE.0.) GO TO 10
      CO2=(DTCO2*(BP/760.)*(273./(TEMPA+273.))*FLOW*60.)/CORWT
      O2=(DTO2*(BP/760.)*(273./(TEMPA+273.))*FLOW*60.)/CORWT
   10 CONTINUE
      REGRQ=3.8163+1.229*RQ+.0015*RQ**2
      CKAL=O2*REGRQ
      RETURN
      END

      SUBROUTINE SPLAT(IH,IN,II)
      COMMON SS(3,90,4),LC(4),STO(20),TM(5,3)
   20 CONTINUE
      N=IH
      IF(TM(N,1).EQ.0.) GO TO 26
      DO 25 I=II,IN,6
      TN=SS(3,I,N)
      DO 24 J=1,6
      K=I+(J-1)
      IF(TN.LT.2.)GO TO 23
      SS(2,K,N)=(SS(2,K,N)-SS(1,K,N)**2/TN)/(TN-1)
      SS(1,K,N)=SS(1,K,N)/TN
      GO TO 24
   23 SS(2,K,N)=0.
   24 CONTINUE
      IF(I .EQ.1) NAM=6H2 HOUR
      IF(I .GE.79) NAM=6H24 HR.
      IF(I .GE.85) NAM=5HTOTAL
      SST=SS(3,K,N)
      SS(3,K,N)=SS(3,I,N)
      IF(TN.EQ.0.) GO TO 25
      WRITE(N,100) NAM, SST,((SS(M,L,N),L=I,K),M=1,3)
  100 FORMAT(1H0*STATISTICS FOR *,A6,* PERIOD ENDING AT *F5.2, 8X*TEMPBY
     /*5X*TEMPAM*5X*CO2L/KG/HR*2X*O2L/KG/HR*6X*RQ*6X*KCAL/KG/HR*/1H 30X
     /*MEAN*15X6F12.3/1H 30X*VAR.*15X6F12.3/1H 30X*NUM.*15X6F12.3)
   25 CONTINUE
   26 CONTINUE
      K=N
      LC(N)=0
      IF(IN.EQ.84) IN=90
      DO 30 I=1,3
      DO 30 J=1,IN
   30 SS(I,J,K)=0.
      RETURN
      END
```

APPENDIX II

Data list for kcal/kgxhr vs. kg (R).

Group Code	Body Wt. (kg)	Kcal/kgxhr	Group Code	Body Wt. (kg)	Kcal/kgxhr
AM (Adult males, ADMR)	.042	23.17	AF (ADMR)	.048	16.18
	.046	20.25		.049	15.88
	.042	26.24		.047	13.75
	.059	11.46		.049	18.20
	.070	4.18		.048	16.52
	.044	13.90		.047	21.20
	.042	14.08		.045	18.20
	.043	15.22		.039	30.60
	.043	15.19		.075	11.50
	.056	12.73		.062	8.68
	.057	12.10		.062	7.26
	.049	11.09		.060	8.92
	.046	17.05		.060	11.64
	.048	12.35			
	.044	11.74	MAM (Adult males, RMR)	.056	11.56
	.055	16.11		.060	7.49
	.047	15.49		.060	9.67
	.044	13.62		.060	10.21
	.039	31.54		.044	17.57
	.040	26.67		.040	19.27
	.039	24.45		.039	20.53
	.047	20.57		.040	21.90
	.060	12.05		.040	29.51
	.062	10.49		.047	12.29
				.055	11.08
AF (Adult females, ADMR)	.050	10.66		.048	10.29
	.057	12.82		.046	12.16
	.057	11.42		.049	7.59
	.048	21.80		.057	9.94
	.049	12.38		.043	11.18
	.044	12.47		.043	11.69
	.043	14.43		.043	11.02
	.045	15.71		.044	9.67
	.044	13.91		.070	3.08
	.053	14.89		.059	8.22
	.051	16.21		.042	26.24
	.053	15.67		.046	18.36
	.046	18.93		.042	19.28
	.052	16.90		.046	8.63
	.044	23.26		.044	15.45
	.056	17.26			
	.047	20.69	MAF (Adult females RMR)	.061	10.93
	.042	20.06		.045	14.70
	.048	16.92		.047	18.15

APPENDIX II (Continued)

Group Code	Body Wt. (kg)	Kcal/kgxhr	Group Code	Body Wt. (kg)	Kcal/kgxhr
	.048	15.49		.049	14.60
	.048	19.26		.049	14.67
				.048	12.36
MAF	.049	13.42			
	.048	12.90	GB	.045	25.77
	.048	13.34	(Litters)	.028	24.97
	.048	17.06		.031	28.65
	.046	15.18		.066	17.85
	.044	11.19		.065	24.24
	.053	12.84		.077	19.58
	.044	11.21		.083	19.18
	.051	13.76		.074	22.67
	.053	11.88		.023	43.49
	.044	11.20		.020	37.70
	.045	13.97			
	.043	12.37			
	.044	10.67			
	.049	9.20			
	.048	18.15			
	.044	20.98			
	.044	19.84			
	.043	12.65			
	.046	13.22			
	.050	8.00			
	.057	9.26			
FB	.056	15.39			
(Females	.066	20.50			
with	.107	20.57			
litters)	.094	17.89			
	.090	20.90			
	.090	19.45			
	.095	9.34			
	.075	20.54			
	.074	20.97			
	.066	23.63			
	.066	34.12			
	.061	18.28			
	.071	19.53			
	.068	21.60			
	.078	14.64			
	.072	16.95			
	.072	10.57			
	.076	17.16			
	.077	20.30			
	.066	41.83			
	.047	35.17			
	.097	12.40			

APPENDIX II (Continued)

Group Code	Body Wt. (kg)	Kcal/kgxhr (ADMR)	Age	Group Code	Body Wt. (kg)	Kcal/kgxhr (ADMR)	Age
Babies	.011	23.81	11	Babies	.025	18.89	30
	.011	47.70	11		.011	50.90	15
	.006	11.20	7		.012	46.70	13
	.005	32.30	6		.022	20.78	29
	.009	33.13	11		.027	12.56	40
	.003	19.57	1		.030	11.66	40
	.005	29.50	3		.026	16.84	14
	.010	66.61	8		.017	20.16	18
	.008	83.56	8		.019	15.03	19
	.004	92.53	2		.026	13.43	19
	.005	106.08	3		.019	22.64	20
	.005	34.16	4		.025	18.29	16
	.005	17.05	5		.031	15.16	21
	.005	16.00	5		.023	18.15	25
	.005	24.20	8		.026	19.71	22
	.007	27.15	8		.026	16.98	26
	.005	33.41	5		.024	17.41	29
	.007	15.33	7		.031	17.35	28
	.008	35.63	9		.023	24.44	25
	.010	23.96	10		.029	25.99	30
	.026	25.99	32		.025	16.50	26
	.026	27.85	32		.022	28.58	33
	.027	16.03	32				
	.025	29.64	32				
	.025	25.37	32				
	.031	21.63	32				
	.030	18.18	32				
	.007	99.80	15				
	.010	47.20	19				
	.012	43.20	21				
	.012	55.16	22				
	.008	76.43	14				
	.015	20.15	20				
	.015	20.17	20				
	.018	14.85	23				
	.022	28.60	27				
	.008	60.33	12				
	.023	22.13	27				
	.008	58.90	12				
	.025	25.40	28				
	.026	29.63	28				
	.031	31.83	33				
	.031	30.64	34				
	.009	82.56	8				
	.019	26.80	19				
	.031	31.45	42				
	.032	20.32	42				
	.019	37.10	30				

APPENDIX III

Body tissue production--raw data.

Animals	Age (days)	Body Wt. (kg)	Dry Wt. (kg)	Water (%)	Dry Wt. (kcal/g)	Ave.	Total (kcal)	Ave.	Kcal/kg
0115-0143	14	.011	.0036	67%	5.177		18.792		
					5.214		18.926		
					5.240		19.021	18.913	1.719
0115-0143	19	.017	.0054	68%	5.129		27.901		
					5.021		27.314	27.607	1.624
0115-0143	31	.024	.0084	65%	5.571		46.796		
					5.571		46.796	46.796	1.950
0115-0143	1	.003	.0066	78%	4.896		3.23	3.23	1.077
0115-0143	11	.010	.0031	69%	4.342		13.46		
					4.526		14.03		
					4.413		13.68	13.72	1.372
0121	4	.005	.0013	74%	5.880		7.640		
					5.888		7.650	7.645	1.529
0121	26	.027	.0094	65%	5.619		53.099		
					5.470		51.691		
					5.552		52.466	52.418	1.941
0121	16	.015	.0048	68%	5.184		24.883		
					6.574		31.555		
					5.112		24.537	26.991	1.799

APPENDIX III (Continued)

Animals	Age (days)	Body Wt. (kg)	Dry Wt. (kg)	Water (%)	Dry Wt. (kcal/g)	Ave.	Total (kcal)	Ave.	Kcal/kg
0121	60	.044	.0176	60%	5.744 5.797		101.094 102.027	101.527	2.307
2000-2002	1	.003	.007	78%	5.912		3.901	3.900	1.300
2000-2002	62	.045	.0180	60%	6.209 6.304		111.762 113.472	112.617	2.503
2000-2002	1	.003							
2001-2023	4	.005	.0013	74%	5.832		7.581	7.581	1.516
2001-2023	15	.013	.0048	68%	5.562 5.560		26.692 26.692	26.692	2.053
2001-2023	29	.026	.0091	65%	5.817 5.666		52.934 51.560	52.247	2.010
2001-2023	60	.048	.0192	60%	6.145 6.153		117.984 118.137	118.060	2.460
2001-2023	60	.037	.0148	60%	6.208 6.315		91.878 93.462	92.670	2.505
0114-0025	1	.003	.0007	78%	5.093		3.360	3.360	1.120
0114-0025	19	.014	.0045	68%	5.886 6.031 5.778		26.369 27.018 25.885	26.424	1.887

APPENDIX III (Continued)

Animals	Age (days)	Body Wt. (kg)	Dry Wt. (kg)	Water (%)	Dry Wt. (kcal/g)	Ave.	Total (kcal)	Ave.	Kcal/kg
0115-0143	1	.003	.0007	78%	4.822		3.182	3.182	1.061
1003-1004	0	.0025	.0005	79%	4.830		2.535	2.535	1.014
1003-1004	22	.023	.0080	65%	5.677 5.762		45.699 46.384	46.041	2.002
1003-1004	52	.031	.0124	60%	5.762 5.662		71.448 70.221	70.834	2.285
1005	65	.045	.0180	60%	5.863 5.725		105.534 103.050	104.292	2.318

APPENDIX IV

Data from simultaneous ADMR--digestion studies.

Animal	Age (days)	Food			Digested Energy			Assimilated Energy		Respiration Energy		% Dig.	% Ass.
		Wt. (kg)	Kcal/kgxhr	Kcal/wk	Kcal/kgxhr	Kcal/wk	Kcal/kgxhr	Kcal/wk	Kcal/kgxhr	Kcal/wk	Kcal/kgxhr	Kcal/wk		
0143-3	18-25	.0265	63.63	272.59	22.42	96.10	41.20	176.49	38.64	165.57	26.16	156.01	64.74	57.56
0143-4	18-25	.018	80.82	244.59	25.44	76.94	55.37	167.75	36.79	157.63	50.79	112.64	68.5	46.09
1003	30-37	.030	49.89	251.44	21.55	108.61	28.34	142.83	26.33	132.71	16.32	173.20	56.78	37.37
0023-3	32-39	.023	49.86	192.69	26.45	102.20	23.41	90.49	21.41	82.77	22.31	87.57	46.96	45.44
0023-4	32-39	.029	48.23	234.99	27.61	134.55	20.62	100.44	18.69	91.04	26.89	132.43	42.76	56.35
0114-3	39-46	.040	31.82	213.84	16.86	113.27	14.97	100.57	13.68	91.95	14.31	101.30	47.03	47.37
0114-4	39-46	.040	32.87	220.89	18.45	124.02	14.42	96.87	13.10	88.03	18.39	111.38	43.83	50.42
1003-3	45-52	.031	41.50	216.19	15.22	79.29	26.28	136.90	24.64	128.27	25.03	129.78	63.33	60.03
1003-4	45-52	.033	38.57	213.84	19.32	107.15	19.25	106.69	17.70	98.13	31.51	79.93	49.89	68.88
0215-3	60+	.0405	42.13	286.69	16.45	111.97	25.67	174.72	24.00	163.24	14.13	96.09	60.94	33.81
0215-4	60+	.0455	29.20	223.24	16.13	123.34	13.07	99.90	11.90	90.95	13.94	106.51	44.74	47.71
0011	60+	.054	24.35	220.90	11.39	103.37	12.95	117.53	11.98	108.68			53.20	
0014	60+	.052	28.25	246.70	13.05	114.04	15.19	132.66	14.55	112.78			53.77	
Means	43.46	.0356±	43.16±	233.74±			23.90±	126.44±			23.62±	117.07±	53.58	50.09
Std. Dev.	±14.15	.0001	15.77	26.04			12.36	31.14			10.83	28.78	±8.65	±10.12

APPENDIX V

Parameters and equations.

Parameter X	Parameter Y	Linear Equation	R^2	Exponential Equation	R^2
Age (days)	Food consumption	kcal/kgxhr = 84.397 - .949Age	.72	log kcal/kgxhr = 2.928 - .816log Age	.77
Wt (kg)	Food consumption	kcal/kgxhr = 88.252 - 1266.027kg	.78	log kcal/kgxhr = 0.147 - .997log kg	.89
Age (days)	Food consumption	total kcal/wk = 240.666 - 159Age	.01	log kcal/2k = 2.456 - .055log Age	.03
Wt (kg)	Food consumption	--No Equation--			
Age (days)	Digested energy	kcal/kgxhr = 52.29 - 653Age	.56	log kcal/kgxhr = 2.945 - .977log Age	.65
Wt (kg)	Digested energy	kcal/kgxhr = 54.527 - 859.840kg	.58	log kcal/kgxhr = -.395 = 1.177log kg	.72
Age (days)	Digested energy	total kcal/wk = 150.753 - .559Age	.06	log total kcal/wk = 2.439 - .216log Age	.06
Wt (kg)	Digested energy	total kcal/wk = 150.830 - 684.782kg	.11	log total kcal/wk = 1.828 - .178log kg	.14
Age (days)	Digestibility	% = 61.685 - .187Age	.09	log % = 1.983 - .16log Age	.14
Wt (kg)	Digestibility	% = 63.317 - 273.503kg	.12	log % = 1.459 - .180log kg	.13
Age (days)	Respired energy	kcal/kgxhr = 43.470 - .491Age	.36	log kcal/kgxhr = 2.488 - .726log Age	.42
Wt (kg)	Respired energy	kcal/kgxhr = 55.140 - 971.350kg	.59	log kcal/kgxhr = -.435 - 1.180log kg	.67
Age (days)	Respired energy	total kcal/wk = 160.044 - 1.062Age	.24	log total kcal/wk = 2.561 - .318log Age	.23
Wt (kg)	Respired energy	total kcal/wk = 149.961 - 859.467kg	.07	log total kcal/wk = 1.814 - .162log kg	.04

APPENDIX VI

Definitions of abbreviations.

A or A_e	Assimilated energy.
A_{ag}	Additional assimilated energy required during growth above the energy that would be expended by an adult vole projected to juvenile weight. $A_{ag} = R_g + P/WT$.
A_g	Total assimilated energy required by immature voles. $A_{ag} = R_j + P/WT$.
ADMR	Average daily metabolic rate as a representation of R.
AF	Adult females in the vole colony.
AM	Adult males in the vole colony.
AMAF	Combined adult males and adult females.
BMR	Basal metabolic rate.
C_e	Total energy consumed as food.
FB	Females tested with litters.
FMR	Fasting metabolic rate.
GB	Grouped babies--litters measured together.
Kg	Kilograms.
Kcal	Kilocalories or 1000 calories.
M	Total animal metabolic rate (kcal/hr).
M/W	Metabolic rate per unit body weight (kcal/kgxhr).
MAM	Minimum period of metabolic rate (RMR) from adult males in the colony.
MAMMAF	Minimum period of metabolic rate (RMR) for all adults in the colony of voles.
P	Production or tissue deposition.
P/R	Ratio of production energy/respiration energy.
P/W	Production per unit weight, kcal/kg.
P/WT	Rate of production per unit body weight, kcal/kgxhr.

APPENDIX VI (Continued)

R	Energy from aerobic metabolism as determined by measuring oxygen consumption. Considered to be equal to heat production and termed respiration energy.
R_a	R of the adult colony, energy or metabolic rate as a function of body weight.
R_g	The amount of R energy used by juveniles during growth above what would be expected for a smaller body size. $R_g = R_j - R_a$.
R_j	R of the juvenile colony, total amount of R energy as a function of body weight.
R_{gb}	R of litters tested together.
R_{fb}	R of females tested with litters.
RMR	Resting metabolic rate.
W	Body weight in kilograms.

APPENDIX VII

Calibration of metabolic suite with alcohol lamp.

Theoretical Calculations

Alcohol consumed = 3.36 g

$C_2H_5OH + 3O_2 \rightarrow 2CO_2 + 3H_2O$

(46g) (96g) (88g) (511g)

i) CO_2 produced = $\frac{3.36g\ ETOH + 88g\ CO_2}{46g\ ETOH}$

$= 6.428g\ CO_2$

22.4L = 1 mole = 44g CO_2

1L = 1.96g

$\frac{6.428g\ CO_2}{1.96g\ CO_2/L} = 3.28L\ CO_2$

ii) O_2 consumed = $\frac{3.36g\ ETOH + 96g\ O_2}{46g\ ETOH}$

$= 7.012g\ O_2$

22.4L = 1 mole = 32g O_2

1L = 1.428g

$\frac{7.012g\ O_2}{1.428g/L} = 4.910L\ O_2$

$RQ = \frac{3.28}{4.91} = .668$

Actual Experimental Calculations

2.258L/min x 75 min = 180.862L gas

180.48L x 0.0175% ΔCO_2 = 3.158L CO_2

180.48L x 0.027% ΔO_2 = 4.862L O_2

RQ = .650; CO_2 - 96.3% and O_2 - 99.0% (calculated/theoretical)