Some nutritional studies on the -wood mouse apodemus sylvaticus

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Henderson, D.G. (1970) *Some nutritional studies on the -wood mouse apodemus sylvaticus*, Durham theses, Durham University. Available at Durham E-Theses Online: http://etheses.dur.ac.uk/8923/

Some nutritional studies on the wood mouse
<u>Apodemus sylvaticus</u>

by

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Being a dissertation submitted in accordance
with the regulations for the degree of
Master of Science

University of Durham September 1970.

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1.0 INTRODUCTION: THE SIGNIFICANCE OF ENERGY AND METHODS OF MEASUREMENT OF ENERGY FLOW.

A study of the functioning of ecosystems is tantamount to a study of the flow of energy through them. All living systems depend upon a supply of energy ultimately from the sun. This energy is first stored by green plants, by the process of photosynthesis, but eventually leaves the earth as heat. Hence there is a unidirectional flow of energy through the biosphere with high-energy solar radiation continually converted to low-energy heat.

Such a degradation of energy follows the classical 2nd Law of Thermodynamics but organisms themselves halt this flow, albeit temporarily by storage of energy in the form of biomass. Strictly speaking, classical thermodynamics is relevant only to states of equilibrium where there is no energy flow and cannot be applied to the steady state system of the biosphere (Morowitz 1968).

Hairston, Smith and Slobodkin (1964) hypothesized that the content of the biosphere as a whole is limited by the amount of energy that can be utilized. They believe that only herbivores are not generally limited by food supply, but they ignored the possibilities of self-regulation of animal numbers.

It is with some facets of energy flow through herbivores that this study is concerned. In particular, daily maintainence costs, rates of energy flow and periodicity of egestion have been investigated. The determination of maintainence energy required by an animal or group of animals involves the construction of an energy budget in which the inflow and outflow of energy are measured. Provided that the animal maintains constant weight the amount of energy degraded during a given period is equal to the cost of keeping it alive.

There are numerous equations which may be used in constructing energy budgets, and their usage depends upon the particular facet of energy flow which is to be studied (Slobodkin, 1962). One of the most widely used equations is:-

(i) ASSIMILATION = RESPIRATION + NET PRODUCTION (YIELD).

In an animal maintaining constant weight, net production is equal to zero. Assimilation during a given period can then be measured indirectly by finding the rate of respiration (usually measured as oxygen consumed); assimilation thus measured over a twenty-four hour period enables the construction of a Daily Energy Budget (D.E.B.). A Daily Energy Budget can also be derived from the formula.

(ii) ASSIMILATION = INGESTION - (EGESTION + EXCRETION).

Determination of an energy budget by this formula usually uses the 'gravimetric' or 'balance' method. A known weight of food is supplied each day and faeces and urine are collected over twenty-four hour periods. At the end of each twenty-four hours the uneaten food is collected and weighed; this value, subtracted from the weight of food supplied gives the weight of food ingested. With knowledge of the calorific value of the food, the energy ingested may be calculated. Values obtained for the energy lost as egestion and excretion over the twenty-four hours are substracted from the energy content of the food ingested to give the total energy assimilated. Daily Energy Budgets calculated using this method are normally expressed in terms of calories assimilated per day as foodstuffs vary considerably in calorific value.

A daily energy budget calculated from oxygen consumption under conditions of temperature and living fairly close to those which the test animal would normally experience in thewild is termed the Average Daily Metabolic Rate (ADMR). Average Daily Metabolic Rates for a few animals were first calculated by Pearson (1947) and have since been evaluated for a variety of small mammals.

Energy budgets can also be calculated from the Basal Metabolic Rate (BMR), the value obtained when the test animal is inactive, fasting and in its thermoneutral zone. Temperature corrections must be applied to transform BMR to ADMR. Alternatively the Resting Metabolic Rate (RMR) may be measured at a series of temperatures: for this the animal is not fasted but its activity is restricted to a minimum. Corrections for activity enable ADMR to be calculated from RMR.

Grodzinski (1966a) found that calculations of daily energy budget from ADMR differed very little from those of McNab (1963) who used RMR and BMR. McNab (1965) was further able to correlate budgets calculated from food assimilated with those calculated from RMR, corrected for activity. More recently Drozdz (1967) found that budgets calculated from food assimilation gave higher values than those obtained from measurement of ADMR (14% higher for voles and 12% higher in the case of mice). Grodzinski and Gorecki (1967) argue that, under laboratory conditions, ADMR's based upon oxygen consumption are more reliable and give more continuous readings than those based on food assimilated, but they do not explain the discrepancy found by Drozdz. Possibly the animal is exposed to different stresses in the different situations.

The principal objective of this study was to calculate Daily Energy Budgets for Apodemus sylvaticus kept on different diets, by measurement of the food assimilated. The effect on the DEB of keeping mice in pairs rather than singly was also investigated. This topic has been studied briefly in the bank vole Clethrionomys glareolus by Meese (1969), who used food assimilation, and by Gebczynski (1969), who measured oxygen consumption. The lowering of individual daily budgets by keeping animals in groups (otherwise known as "social thermoregulation") has suddenly received considerable attention, as a result of attempts to make laboratory conditions as natural as possible. Trojan and Wojciechowska (1969) have shown that DEB's calculated for single animals and then summed to give population energy budgets probably overestimate actual costs of maintainence in the wild by up to 65%. Not only is energy saved by 'huddling' of several animals in the nest, but behavioural interactions may affect metabolic rates. This has not yet been studied.

2.0. PREVIOUS STUDIES ON APODEMUS AND OTHER SMALL MAMMALS

Apodemus sylvaticus L., the wood or long-tailed field mouse is a rodent belonging to the sub-family Muridae; it is widely distributed throughout the British Isles and is found in rather similar habitats to the bank vole Clethrionomys glareolus Schr., these two species are the dominant small mammals of British woodlands.

The general features of Apodemus sylvaticus are described in Southern (1964) and the genus as a whole in Walker et al (1964). The ecology of the wood mouse has been studied in detail by Ashby (1967) while Evans (1942) and Crawley (1965) paid particular attention to the movements and population dynamics of this species. Population and home range studies using various marking techniques have been undertaken by Kikkawa (1964), Fairley (1967) Eldridge (1968), Brown (1956b, 1966, 1969) and Watts (1970).

Elton Ford and Baker (1931), Miller (1955) and Brown (1956a) have investigated circadian activity in Apodemus. They found it to be primarily a nocturnal species with the peak of its activity shortly after dusk.

The food taken by the wood mouse in Britain has been studied by Miller (1954). Crawley (1965) and Watts (1968). Parallel work has been undertaken in Europe on the yellow-necked field mouse Apodemus flavicollis Melchior in Poland by Gorecki and Gebczynska (1962) and Drozdz (1966, 1967) and in Czechoslavakia by Holisova (1967a, b). Both species are largely granivorous, taking a wide variety of seeds, but both supplement their diet with green food, invertebrates (especially insect larvae) and fungi; the relationship between the supply of certain tree seeds and winter breeding in the wood mouse is discussed by Smyth (1967), while Ashby (1959), Tanton (1965) and Turcek (1967) have investigated effects of both Apodemus and Clethrionomys on the regeneration of woodlands. This problem has also been reviewed by Mellanby (1968).

Most of the work on bioenergetics of Apodemus species has been on the yellow-necked field mouse. Particularly relevant to this study are the papers of Turcek (1956, 1957) and Drozdz (1968a, b), who determined digestibility and assimilation of various foodstuffs. Gebczynski (1966) evaluated the seasonal variation in the daily energy budget of *A. flavicollis* while Gorecki and Grodzinski (1966) calculated daily energy budgets for a variety of rodents. Also relevant to the present study are the works of Connell (1959) and Odum, Connell and Davenport (1962) on *Peromyscus polionotus*, the ecological replacement of *Apodemus* in North America, Mention will be made also of studies on the bioenergetics of some other small mammals, notably *Clethrionomys glareolus* (Meese 1969, Gorecki 1969), *Microtus arvalis* (Trojan and Wojciechowska 1969) and *Microtus pennsylvanicus* (Golley 1960).

Although studies of the energetics of animals in the laboratory can give a good idea of the relative efficiencies with which they are able to make use of certain diets, the relevance of such results to calculations of the energy requirements of wild populations need to be examined most carefully. Furthermore, Gorecki (1966) has shown that, in *Clethrionomys glareolus* animals bred in the laboratory differ from wild individuals in that they do not undergo such marked seasonal changes in body insulation.

3.0. MATERIALS AND METHODS

3.1. TRAP SITES AND METHOD OF TRAPPING

All animals usediin the experiments were caught along the wooded banks of the River Browney at Witton Gilbert, Co. Durham. The wooded areas consist largely of Oak (*Quercus robur*), Hawthorn (*Crataegus monogyna*) and Willow (*Salix* sp.) with ground cover deminated by Stinging Nettle (*Urtica dioica*) Bluebell (*Endymion non-scriptus*) and Garlic (*Allium ursineum*).

Mice were caught in Longworth traps (Chitty and Kempson 1949) baited with wheat. Traps were inspected every morning and evening.

3.2. CONDITIONS OF CAPTIVITY

Mice were housed in wire mesh cages, measuring 37x21x15 cm, in a room subject to normal daylight hours and a temperature of 20 ± 3°C. The size of cage used could have a considerable effect upon an animal's activity and hence upon its energy budget. Since the cages I used has a volume nearly eight times that of the metabolic cages used by Drozdz (1968a, b) caution is needed in comparing our results (neither my cages nor those of Drozdz incorporated an activity wheel).

Food was offered in plastic petri dish and water in a conventional dropping bottole. It was necessary to provide non-edible material for the mice to use for their nests. Initially cotton wool was supplied, but it was found difficult to separate the faeces from it; rolled tissue paper was given instead. Faeces and discarded food were collected in a metal tray beneath the cage; with this type of cage it was not possible to measure accurately the quantity of urine excreted and so no samples were collected.

Each newly-trapped mouse was given a five-day period of acclimatization during which it was able to adapt to a new diet. Five days is sufficient time for the digestive tract to be cleared of food which the animal had eaten before it was trapped. Three diets were used:Wheat (*Triticum aestuvum*), Oats (*Avena fatua*) and Monkey-nuts or Ground Nuts (*Arachis hypogaea*). All three diets are concentrated i.e. they have low fibre and water contents. Groundnuts have a particularly high fat content and oats a high carbohydrate content. Carrots (Daucus carota) was also tried as food but although mice were able to maintain constant weight on this diet they seldom survived more than three days before dying.

After the period of acclimatization each animal was weighed to the nearest 0.1 gm. and put in a clean cage with a fresh supply of bedding material. A measured amount of test food was given, always in excess of the animal's needs and water was given ad lib. It was discovered that Apodemus sylvaticus did not adjust to captivity very quickly. Hence, to minimize disturbance, faeces and uneaten food were collected every 48, and not every 24, hours. Each animal was weighed every 48 hours. If there was a change of 10% (about 2 gm.) or more in body weight during this period no faeces were collected (for reasons see Chapter I). Where there was a weight change of less than 10% the weight of uneaten food was recorded and the wet weight of faeces collected was determined.

3.3. ANALYSIS OF FOOD AND FAECES

Each sample of faeces collected was dried to constant weight in a vacuum oven at 60° C. This operation took up to five days but use of a higher temperature results in the loss of any volatile fats present, and hence alters the calorific value. The dry samples were then cooled in a desiccator and weighed accurately; samples were then crushed into pellets (about 0.5 gm) and reweighed and then burnt in oxygen in a Ballistic Bomb Calorimeter to determine their calorific value. The samples were pelleted in order to ensure controlled combustion of different materials. Gorecki (1965), using an Adiabatic Bomb

Calorimeter claimed satisfactory results without crushing samples into pellets. Blaxter (1962) has stressed that results obtained from calorimeters refer only to the conditions under which they were obtained and every effort was made to keep conditions as consistent as possible for each combustion. Each sample was ignited in 25 atmospheres pressure of oxygen and each dried sample exposed to air for a minimum time period. No correction factor was applied for the heat emitted by the cotton thread used to ignite the sample but a standard length (5 cm) was used each time. The heat emitted by each sample when burnt was recorded by a thermocouple attached to a galvanometer. This reading was converted to calories by comparison with a calibration graph constructed by burning a series of weights of pure benzoic acid (calorific value 6319 cals/gram). Thus the calorific value of each sample could be calculated per unit dry weight.

Results obtained were found to be reproducible to within 10%, but not as accurate as the readings obtained with miniature bomb calorimeters by Slobodkin and Richman (1960) and Phillipson (1964).

Variations in readings may have been caused by variations in oxygen pressure, sample size or room conditions.

4.0. ANALYSIS OF DIETS AND EXPERIMENTS ON SINGLE MICE

TABLE I

ANALYSIS OF DIETS

DIET	% DRY MATTER	% WATER	KCALS (GM DRY WT. ± S.D.
OATS	89.7	10.3	4.69 ± 0.20
WHEAT	89.6	10.4	4.41 ± 0.02
GROUNDNUTS	94.4	5.6	7.02 ± 0.12

These results are the mean values of the readings obtained for five samples of each food. For details see Tables A-C (Appendix)

The figures correspond fairly closely to those of Drozdz (1968b) for oats, and to those of Meese (1969) for both oats and wheat. However, time and conditions of storage could have a significant effect on water content and possibly calorific value of foods and so it is important to refer to analyses of the food actually used. There is very little published data on the analysis of groundnuts, and Nehring et al (1962) found that the high fat content gave rise to digestive disturbances amongst some larger herbivores.

No analysis of the foods into fats, proteins, carbohydrate fibre and ash fractions was attempted in this study.

TABLE II

ANALYSIS OF FAECES

DIET	% DRY MATTER	% WATER	KCALS/GM DRY WT ± S.D.
OATS	84.5	15.5	5.13 ± 0.28
WHEAT	84.1	15.9	4.97 ± 0.18
GROUNDNUTS	81.3	18.7	4.70 ± 0.30

4.1. CALCULATIONS

The weight of food ingested and that of faeces egested by each animal on each day was converted into a calorific value using the results shown in Tables I and II. Using these values, and equation (ii) given in Chapter I, calories digested per day and percentage digestion could be calculated. As no attempt was made to collect urine samples a correction factor was applied order to calculate food assimilated. In general, *Apodemus* species tend to lose less energy through urine than other small mammals and Drozdz (1968b) found a range of values from 0.73% to 2.67% of food digested depending on diet. In the present study, a correction factor of 1.5% was applied for those animals fed on oats and wheat and 1.25% for those fed on groundnuts. The value for oats and wheat is based on that obtained by Drozdz (1968b) *Apodemus agrarius*; the value for groundnuts is based on that obtained by the same author for *Apodemus flavicollis* fed on hazelnuts a similar protein-fatty food to groundnuts and having a comparable water content.

Application of the appropriate correction factor for energy loss through urine allowed calculation of calories assimilated and percentage assimilated by each animal on each day, and division of the calories assimilated by live body weight (in grams) gave a daily energy budget in terms of calories

TABLE III

CALCULATION OF DAILY ENERGY BUDGET

DIET	WT. Of Mouse ± S.D. (in Grams)	KCALS INGESTED ± S.D.	KCALS EGESTED ± S.D.	KCALS DIGESTED ± S.D.	% Digested	KCALS ASSIMILATED ± S.D.	% ASSIMILATED	KCALS ASSIMILATED (GM. Body WT./Day) ± S.D.
OATS	16-6 ± 2·8	10·7 ± 1-1	0·8 ± 0·2	9·9 ± 0·3	92·1	9·7 ± 0·3	90·8	0·59 ± 0·09
WHEAT	18-6 ± 4·4	12·6 ± 2·0	0·8 ± 0·2	11·8 ± 1·8	93.8	11.6 ± 1.8	92.5	0.62 ± 0.07
GROUNDNUTS	16.8 ± 4.5	14.0 ± 2.0	0.8 ± 0.1	13.2 ± 1.9	94.4	13.1 ± 1.9	93.2	0.78 ± 0.12

These are mean values, each based on approximately 40 readings.

assimilated per gram live body weight.

Calculations of energy budgets for single mice on the three test diets are set out in Table III.

4.2. DISCUSSION

A comparison between the analyses of food samples and faeces will show that there is more than a 5% increase in the water content of the faeces of mice fed on oats and wheat and that mice fed on groundnuts are able to compensate exactly for the low water content of their diet. Measurements of water content of faeces using the method of collection adopted in this study are subject to at least some measure of error in that the faeces are likely to become contaminated by urine and drops from the water container, so that water contents actually measured do not mean much.

In his study of the energetics of *Clethrionomys*, Meese (1969) has shown the water content of the faecal material to be more than double that of the food in animals fed oats and wheat. This difference in water content of faeces between *Apodemus* and *Clethrionomys* can be related to dietary differences in the wild. Watts (1958) has shown *Apodemus* to be principally granivorous whereas *Clethrionomys* is almost wholly herbivorous, and therefore usually takes food with a much higher water content.

The calorific value of the faeces of mice fed on oats and wheat is higher than that of their respective foods, and this difference is statistically significant ($p =< 0.05$). Drozdz (1968b) found similar values for *Apodemus agrarius* and showed that faeces of mice fed on oats had a fat content virtually double that of their food. Hence it seems likely that in the present study the increase in calorific value of faeces was due to mice failing to digest fat in the foods.

These results contrast with those for mice fed on groundnuts. Here there is a great drop in calorific value of the faeces and this parallels the results of Drozdz (1968b) for high-calorie foods given to *Apodemus agrarius* and *Apodemus flavicollis*; Drozdz found a 25-30% drop in the calorific value of faeces of these species when fed on high-calorie foods and in his analyses of faeces found that the fat content was sometimes less than 25% of that of the food. It seems reasonable to conclude that the low-calorie value of the faeces of mice fed on groundnuts in this study is due to their digesting a large proportion of the fat present in the nuts. The fact that mice fed on an ample supply of groundnuts did not gain in weight suggests that all the fat assimilated was used to provide energy for daily activity. The percentage of each food type digested (the 'coefficient of digestibility') is given in Table III. The digestibility of a given food depends to some extent on its fibre content: the high coefficients of digestibility found for the three foods used in this study reflect their low fibre content.

Table III shows Apodemus sylvaticus to be very efficient in assimilating all three foods supplied, and previous work on other small granivorous mammals suggests that most are highly efficient at assimilating suitable foods. Drozdz (1968b) found a 91.37% efficiency for Apodemus flavicollis fed on hazelnuts and an 89.0% efficiency for Apodemus agrarius fed on oats, while Davenport (1960) found that Peromyscus polionotus was able to assimilate up to 93.9% of some foods provided. That assimilation efficiency does depend to some extent on diet was shown by Golley (1960) in experiments on Microtus pennsylvanicus; when fed on alfalfa they were able to assimilate 89.8% of the dry weight of food ingested, while on a mixed diet of lettuce carrots and oats they were able to assimilate only 82.2%.

The daily energy budgets given for mice fed on each of the three test foods shows that those fed on oats and wheat were able to maintain weight on approximately the same energy intake but that mice fed on groundnuts utilized more food each day in spite of their ability to assimilate a higher percentage; this difference is statistically significant ($_p$ =<0.05). Possibly the mice fed on groundnuts were more active in order to use up the excess calories taken in; if one food fraction (e.g. protein or carbohydrate) is in short supply then this could dictate the minimum daily intake and could mean that mice had to take in a surplus of fat in order to obtain other essential food fractions. The daily energy budget then, is a combined effect of the coeffi-ent of digestibility of a particular food and the proportions of the necessary fractions of protein, carbohydrate, fat etc., that are present.

Calculations of daily energy budgets by the 'balance' method have been subject to some critiscism especially by Grodzinski and Gorecki (1967) who advocated measurement of oxygen consumed as a more reliable method but Odum Connell and Davenport (1962) reasoned that the 'balance' method gives more meaningful results due to the more 'natural' activity pattern exhibited by animals in larger cages. Odum Connell and Davenport (1962) calculated daily energy budgets for Peromyscus polionotus by both methods and in all cases the results of the 'balance' method gave higher values and smaller coefficients of variation between individuals.

4.3. RELATIONSHIP BETWEEN BODY SIZE AND ASSIMILATION

Kleiber (1965) proposed that metabolic rate and body size could be correlated if a suitable correction factor was applied to the latter. He proposed that body weight raised to the 3/4 power should be used to calculate 'metabolic body size' but this value is only applicable when metabolism is measured in terms of Basal Metabolic Rate. Grodzinski and Gorecki (1967) have shown that when Average Daily Metabolic Rate is measured, 'metabolic body size' is proportional to body weight raised to the 3/4 power.

In this study mean values for the Average Daily Metabolic Rate for each mouse were calculated and a positive correlation was found between 'metabolic body size' and ADMR ("r" = 0.70 for 11 degrees of freedom; $p = < 0.01$). Similar correlation using oxygen consumption to measure ADMR have been shown in Apodemus agrarius and Apodemus flavicollis (Grodzinski 1961).

5.0. EXPERIMENTS ON MICE LIVING IN PAIRS

5.1. METHOD

The experimental procedure was identical to that used on mice lviing singly. For this experiment mixed pairs of mice were fed on each of the three test diets anda single pair of females was fed on wheat. It was found impossible to keep pairs of male Apodemus sylvaticus together because of continued agression between them. During trial runs it was discovered that mice kept in pairs tended to lose some weight initially (up to 15% body weight) and then maintained weight at the lower level. Because of this, mice were paired and then left until both animals maintained a steady weight before any readings were taken.

5.2. RESULTS

Table IV gives the analysis of faeces of mice kept in pairs and Table V shows coefficients of digestibility and assimilation, plus daily energy budgets. The values given in Table V are for individual mice but living in a pair, The results were calculated by the methods described in the previous chapter and similar corrections for energy loss in urine were applied.

TABLE IV

ANALYSIS OF FAECES

PAIR	DIET	% DRY MATTER	% WATER	KCALS /GM DRY WT ± S.D.
MIXED	OATS	83.8	16.2	5.00 ± 0.24
MIXED	WHEAT	83.0	17.0	5.14 ± 0.20
MIXED	GROUNDNUTS	80.5	19,5	4.49 ± 0.16
FEMALES	WHEAT	82.2	17.8	5.01 ± 0.22

5.3. DISCUSSION

Table IV shows that mice in pairs egest faeces of a similar calorific value to those of mice kept singly: neither is there a significant difference in water content.

The daily energy budgets for mice kept in pairs showa that the energy intake per mouse is lower than that found in mice kept singly. This is reflected in the reduction of the energy budget as a whole and this reduction is statistically significant ($p = < 0.05$). There are no significant changes in assimilation efficiency in mice kept in pairs and so the reduction in the daily energy budget is due mainly to a decrease in the amount of food ingested.

TABLE V

CALCULATION OF DAILY ENERGY BUDGET

PAIR	DIET	WT OF MOUSE IN GRAMS ± S.D.	KCALS INGESTED ± S.D.	KCALS EGESTED ± S.D.	KCALS DIGESTED ± S.D.	% DIGESTED	KCALS ASSIMILATED ± S.D.	% ASSIMILATED	KCALS/GM/DAY ± S.D.
MIXED	OATS	17.6±1.2	10.5±0.1	0.8±0.1	9.7±0.9	92.4	9.6±0.9	91.4	0.54±0.05
MIXED	WHEAT	20.3±1.7	11.8±0.3	0.8±0.1	11.0±0.3	93.2	10.8±0.3	91.5	0.53±0.04
MIXED	GROUND-NUTS	20.4± 1.1	10.5±0.4	0.5±0.1	10.0±0.4	95.2	9.8±0.4	93.3	0.48±0.11
FEMALES	WHEAT	17.3±1.2	11.8±0.3	0.5±0.1	11.3±0.6	95.9	11.1±0.6	94.5	0.65±0.10

These are mean values, each based on approximately 20 readings

A decrease in energy intake is especially noticeable in mice fed on peanuts where mice consumed on 75% of the calories ingested per day by single mice. Mixed pairs of mice living on oats decreased their daily energy budget on average by 8.3%, those fed on wheat by 14.6% and those on groundnuts by 38.5%. Although it was clear that pairs of mice living on groundnuts did decrease their energy requirements compared with single mice, the magnitude of the reduction is to be questioned, as pairs of mice were not kept on groundnuts for as long a period as was desired.

The consequences of the 'group effect' or social thermoregulation upon the daily energy budgets of small mammals had been studied very little until fairly recently. Ponugaeva (1960) found that rodents kept in groups of 3-5 lowered their energy requirements by 8-17%, while Gorecki (1968) found a 13% decrease in the individual metabolism of bank voles kept in groups of 2-4. However, Gebczynski (1969) found that individual bank voles in groups of three had a lower metabolic rate than those kept in groups of five, and attributed the difference to increased activity among the larger group. Gebczynski (loc.cit) also investigated the effect of temperature upon thermoregulation and found that at 30° C bank voles did not exhibit social thermoregulation. Hence social thermoregulation is not simply dependant upon groups of animals being present but also the animals must be held at temperatures below their zone of thermoneutrality. That social thermoregulation does depend to some extent on group size was shown by Trojan and Wojciechowska (1968) in a study on Microtus arvalis; they found that at 20° C groups of two or three animals maintained constant oxygen consumption but in groups of six, gross oxygen consumption was reduce by 39.1%.

Ponugaeva (1960) found that in groups of male voles oxygen consumption increased by 17%; however these results are at variance with those of Meese (1969) who found a reduction in the energy budgets of male bank voles kept together. Perhaps the time of year that measurements are made influences the rate of activity, as aggressiveness change, according to season. In the present study, the single pair of female mice did not show the reduction in energy requirements seen in mixed pairs, and the former displayed much more activity during the daytime.

6.0. CHANGES IN CALORIFIC VALUE OF FAECES WITH TIME.

6.1. INTRODUCTION

The question of possible changes in the chemical composition of faeces with time was first raised by Newell (1965). He found that faeces of the marine molluscs *Hydrobia ulvae* and *Macoma balthica* increased in nitrogen but decreased in carbon content over a period of three days. Comparison between faecal pellets cultured for several days in the light and in the dark revealed no differences in their chemical composition. Newell concluded that the changes in composition with time were caused by growth of a population of non-photosynthetic microorganisms which synthesised protein at the expense of fats and carbohydrates initially present in the faeces.

The present experiment was designed to discover if the calorific value of the faeces of wood mice is also affected by the time they are left before collection.

6.2 METHOD

The experiment involved four animals, two of which were fed on oats and two on wheat. Animals were housed in conditions similar to those described in Chapter 3 and were given food and water in excess of requirements. Faeces from each mouse were collected after one, two, three five and seven days. The whole series of readings was done in duplicate. No faeces were collected from animals that had changed in body weight by more than 5% (1 gram) during a single day, or 10% (2 gram) over a period of two to seven days.

After collection, the faeces were dried immediately in a vacuum oven at 60° C for a period of five days. This method of drying allows quantitative retention of any volatile fats in the faeces, but the temperature is high enough to cause death of most microorganisms. Each sample, or a portion thereof, was pelleted, weighed accurately, and burnt in a ballistic bomb calorimeter to determine its calorific value (for details see Chapter 3).

6.3. RESULTS

TABLE VI

TIME PERIOD (DAYS)	OAT FAECES (KCALS/GM. DRY) WT. ± S.D.	WHEAT FAECES (KCALS/GM. DRY WT ± S.D.)
ONE	5.13 ± 0.02	4.96 ± 0.22
TWO	5.13 ± 0.28	4.96 ± 0.17
THREE	4.72 ± 0.10	4.46 ± 0.02
FIVE	4.38 ± 0.11	4.45 ± 0.10
SEVEN	4.62 ± 0.23	4.52 ± 0.02

Each value is the mean plus standard deviation of four readings. For details see Tables D-E (Appendix)

6.4. DISCUSSION

Table VI shows that the calorific value of faeces analysed did not vary significantly until the end of the second day. There was then a drop during the next 24 hours of 8% in the calorific value of wheat faeces and 11% in oat faeces. Thereafter the calorific value remained fairly constant over the next four days. The values obtained for wheat faeces for 24 and 48 hours periods are significantly greater at the 5% level than those from three to seven day periods. A similar result holds for oat faeces except that the difference between calorific values of faeces collected after two and five days respectively, though large, is not significant at the 5% level. The decrease in overall calorific value suggests that the materials of high calorific value in the faeces have been removed, perhaps by bacterial action. Zobell and Feltham (1942) have shown that bacteria are able to multiply more often than once per hour so that three days is enough time for a population to develop under suitable conditions.

This apparent change of calorific value of faeces with time could influence the calculation of daily energy budgets. Faecal material from different foods may be subject to different rates of decomposition and hence this could invalidate comparisons of energy budgets on different diets of faeces were collected after denaturation had started.

7.0. PERIODICITY OF FAECAL OUTPUT

7.1. INTRODUCTION

The purpose of this study was to investigate the periodicity of faecal output in Apodemus sylvaticus under laboratory conditions and to relate the results to the activity pattern recorded in previous studies, especially that of Miller (1955). The diet activity of wild wood mice in a natural twelve-hour photoperiod has been investigated by Elton Ford and Baker (1931) and Kalabukhov (1939), while Miller (1955) has looked at diet activity in captive mice under different lighting regimes.

7.2. METHOD

Faecal pellets were collected with a machine based on the design of Lewis and Rentmore (1963). A cage containing one wood mouse was suspended above the machine so that egested material dropped through the cage floor onto a moving roll of polythene. As the experiment relied on the collection of (if possible) all the faeces produced, no conventional bedding could be used. The mouse was given a small bottomless cardboard box into which it could retreat, and the box secured so that it could not be overturned. A particularly tame animal was chosen for the experiment so that any incidental disturbance would have a lesser effect upon its normal activity. The mouse was provided with food (wheat) and water in excess of its requirements.

The machine was switched on and the animal given one hour to settle down before any faecal material was collected. The time switch was set to revolve the polythene roll once every hour, and after 24 hours the cage was removed and the polythene roll wound back so that faecal material passed during each one-hour period could be collected. Since the average number of faecal pellets produced per hour was small, to minimize the effect of one or two pellets failing to be caught on the polythene roll samples were counted for four-hour periods.

DIEL RHYTHMS IN APODEMUS SYLVATICUS

FIG 1.

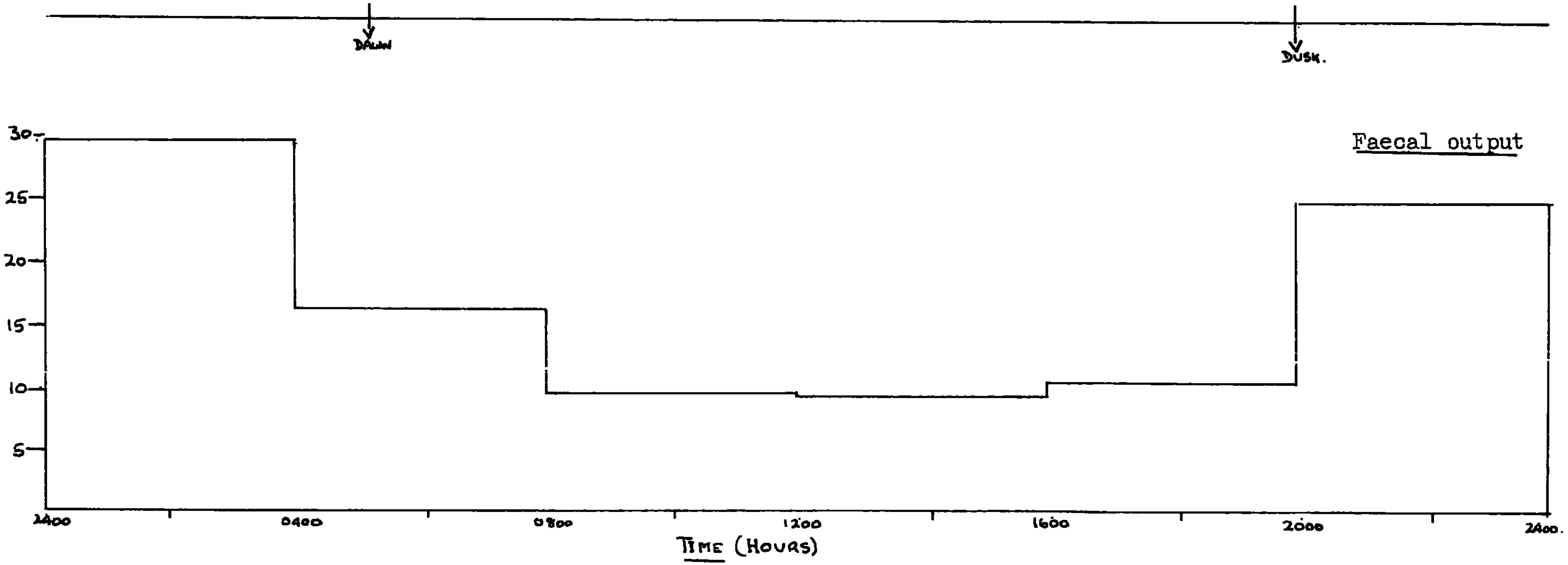
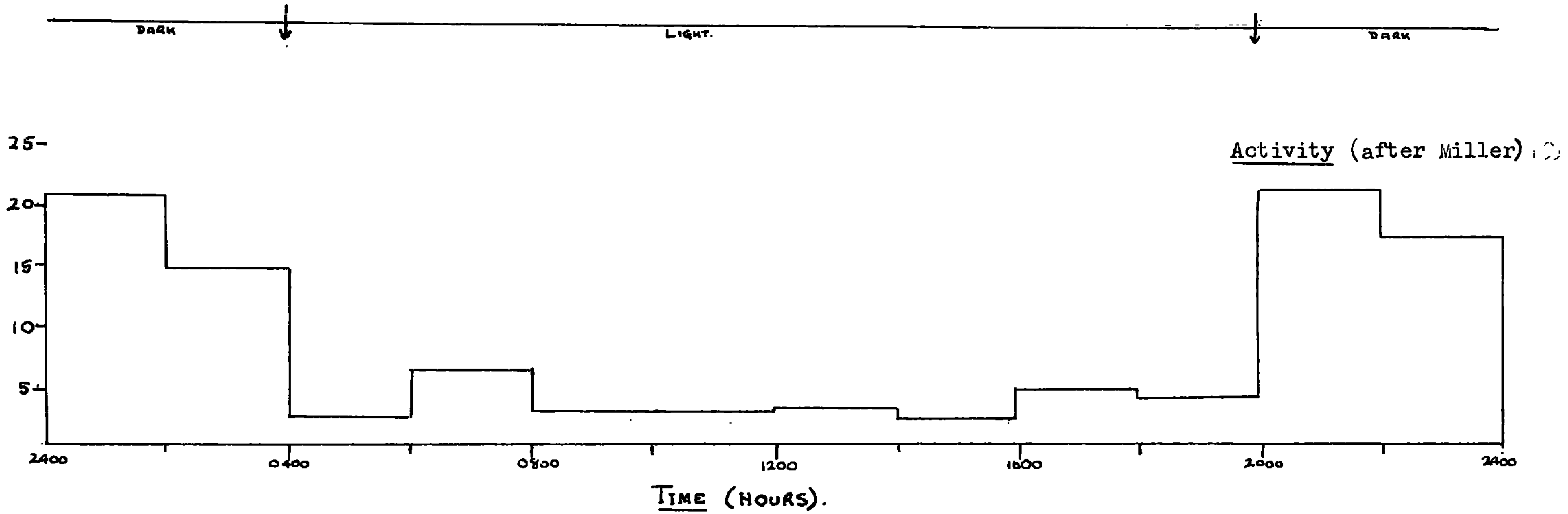


FIG 2.



After collection each four-hour sample was dried in a vacuum oven at 60° C for five days and then weighed accurately. The dry weight of each sample was expressed on a percentage of the total dry weight of faeces collected during each 24 hour period and the mean values plotted on a histogram.

7.3. RESULTS AND DISCUSSION

Figure I is a histogram of results averaged over five 24 hour periods and Figure 2 is a histogram of results adapted from Miller (1958) showing periodicity of diel activity in Apodemus sylvaticus subject to a 16 hour day. Miller's original results were expressed as percentage activity during each two hour period but in order to compare his results with those obtained in the present study, they are here expressed as percentage of total diel activity. A point of difference between the two studies is that Miller subjected mice to a 16 hour photoperiod with no periods of reduced light whereas in this study the test mouse was subject to a 15 hour photoperiod with periods of reduced light at dusk and dawn.

In this study, nearly two-thirds of the total faecal output during each 24 hours occurred during the eight hours after dusk. There was a marked drop in faecal production just before dawn; for the hours of daylight after 8 p.m. output remained fairly steady at approximately 9-11% of the total daily output during each four hour period.

Comparison between figures 1 and 2 will show that faecal output tends to be quite closely linked with degree of activity. Miller found a bimodal activity for mice subjected to a sixteen hour photoperiod but mice subjected to an eight hour photoperiod showed only a slight bimodality. Elton Ford and Baker (1931) found a striking bimodality in wood mice subjected to a natural twelve hour photoperiod; this they said could be explained if the mice had two peaks of feeding activity during the night, and the period of lowered activity could be due to the time taken to digest the first meal. In the present study no bimodality in faecal output was found although any existing bimodality could have been masked by the grouping of faecal material into four hour samples; if the results of Miller are grouped into corresponding four hour periods then the bimodality is lost.

Thus the choice of a four hour grouping of faecal material was perhaps an unfortunate one, but the results show that diel periods of activity can be linked to some extent with rate of faecal output.

8.0. THE RATE OF PASSAGE OF FOODSTUFFS THROUGH THE ALIMENTARY CANAL

8.1. INTRODUCTION

There have been numerous studies on the rates of passage of food through the digestive tracts of various animals. While most of the research has been on domestic animals (e.g. Castle 1956) some work has been on wild mammals e.g. that of Honigmann (1936) Pravdina (1960) and Kostelecka-Myrcha and Myrcha (1964).

The rate of passage of foodstuffs is usually measured either by introducing into the diet of the test animals a natural foodstuff that gives distinctively-coloured faeces or by feeding with dyed foods. The first mentioned method was first used by Weiske (1878) who fed geese with dandelion and then suddenly changed the diet to barley; he then noted the time taken for the barley to appear in the faecal pellets and the time taken for the last of the dandelion to be egested. This method has been criticized by Honigmann (1936) on the grounds that a change in diet may alter the rate of digestion. However such a method can certainly be used to demonstrate varying times of digestion using different diets. Honigmann (1936) used dyed foods to compare rates of digestion amongst a few animals and, more recently, Pravdina (1960) and Kostelecka-Myrcha and Myrcha (1964) used dyed foods to determine rate of passage of foods through the alimentary tracts of some small mammals.

This experiment was designed to determine rates of passage of two different foods through the alimentary canal of a wood mouse using Weiske's method.

8.2. METHOD

The method of collection of faeces was the same as that described for the determination of periodicity of faecal output (see Chapter 7), and the conditions of housing of the test animal were identical. The test animal was fed on oats for 24 hours and then the diet switched suddenly to carrot, the latter producing bright orange faeces after digestion. After a further 24 hours the polythene roll was wound back and the faeces passed during each hour were collected. The diet was changed at 8 p.m. - i.e. immediately before a peak of activity.

The difficulty in using this method come when one attempts to quantify results - i.e. it is difficult to ascertain the proportion of foodstuff present in the faeces. In this study, parameters used to estimate the constitution of faeces were those of colour and granularity. The time taken for the faeces of the new diet to appear was noted as were the times at which approximately 50%, and 90% of the faecal material was formed from the new diet.

8.3. RESULTS

TABLE VII

RATE OF PASSAGE OF OATS THROUGH THE ALIMENTARY TRACT

	% of new diet in faeces		
	Trace	50%	90%
TIME IN HOURS ± S.D.	2.0 ± 0.8	9.4 ± 1.0	29.0 ± 2.5

Each value is the mean of 5 experiments
For details see Table G (Appendix)

TABLE VIII

RATE OF PASSAGE OF CARROT THROUGH THE ALIMENTARY TRACT

	% of new diet in faeces		
	Trace	50%	90%
TIME IN HOURS ± S.D.	1.0 ± 0.0	3.6 ± 0.3	10.4 ± 1.2

Each value is the mean of five experiments .
For details see Table H (Appendix)

8.4. DISCUSSION

Tables VII and VIII show that the rate of passage of carrot through the alimentary tract of wood mice is considerably greater than the rate of passage of oats. This difference is significant at the 5% level. With both foods, the rate of passage of foods slowed down considerably after approximately 50% of the replaced food had been assimilated. The rate of passage of carrot was more rapid than expected and in all five experiments, carrot appeared in the faeces during the first hour of feeding. Kostelecka - Myrcha and Myrcha (1964) fed green food stained with basic fuchsin to four species of Microtine rodents and collected faeces every hour. They then estimated the proportion of dyed food in the faeces and constructed graphs based on those of Balch (1950) to show rates of passage of food through the alimentary tract. They subsequently calculated that 5% of green food took a mean time of only fourteen minutes to pass through the gut of the bank vole, and stained green food appeared after less than one hour in the faeces of all three species of Microtus examined.

Thus the passage of green food through the alimentary tract of small rodents so far examined is very rapid indeed. Pravdina (1960) concluded that principal foods take longer to pass through the gut than do atypical foods, and one might expect a longer assimilation time in herbivores than in granivores as the latter do not need to digest cellulose.

Kostelecka - Myrcha and Mrycha (1964) found that 90% of stained green food appeared in the faeces of the bank vole after a mean time of 9¼ hours but that the remaining 10% took virtually another eight hours to be egested. In the present study, the method used was not thought to be accurate enough to measure the time of egestion of the last fraction of carrot but traces were found in the faeces a minimum of 15 hours after the diet had been changed back to oats.

The rate of passage of seeds through the alimentary tract of the wood mouse was found to be comparable with that shown by Kostelecka - Myrcha and Myrcha (1964) for the bank vole except that the latter found some trace of stained wheat seeds in the faeces during the first hour of feeding.

The results of the present study seem to strengthen the conclusions that in small rodents generally, rate of passage of food through the gut is dependant largely on the nature of the food itself and not on the animal species (Kostelecka - Myrcha and Myrcha (1964).

9.0. GENERAL DISCUSSION

The results of each aspect of energy flow studied are discussed in the appropriate chapter. Opportunity is taken here to discuss the study as a whole and to suggest the lines along which further investigations would have been conducted.

The results of the studies on daily energy budgets would have been more meaningful if it had been possible to analyse food and faeces into their constituent fractions. In the context, fat content of food and faeces would have been of special interest, particularly analyis of the low-calorie faeces egested by mice fed on groundnuts. The fact that no urine samples were collected was not considered of great importance,; collection of urine generally involves the use of metabolic cages where thetest animal's opportunity for activity is greatly reduced. Perhaps the subsequent reduction in activity would affect the results to a greater extent than the failure to allow for energy losses through urine.

Resulsts of the experiments on pairs of animals showed that there was a decrease in energy flow per unit body weight when mice were kept in pairs but more results were needed to show that there is such a marked drop in the energy budgets of pairs of mice fed on groundnuts. Similarly, it would have been of interest to keep pairs of female mice together for a much longer period of time to show more convincingly that pairs of wood mice do not exhibit social thermoregulation to the degree seen in mixed pairs.

Wood mice showed a wide range of responses to being kept in pairs and the response was reflected mainly in the degree of activity. Some pairs were observed to settle down immediately and were often seen huddled together during the daytime, whereas other pairs were more aggressive towards each other. Such variations in response could have an important effect not only on activity (and hence on food intake) but also on opportunity for social thermoregulation (chiefly by huddling). The effect of this range of responses on calculations of energy budgets could have been lessened by use of a greater number of animals.

The results of leaving faecal material in the experimental cages for different periods of time did show that significant changes in calorific content can occur in faecal material left for more than two days. Clearly, these results, if generally applicable, could have an important effect on results of studies using the 'balance' method. Use of the machine described in Chapter 7, and a large number of samples could monitor hour-by-hour rates of calorific change, and measurements of change of low-calorie faeces egested by mice fed on groundnuts would have been of interest.

Periodicity of faecal output in wood mice shoed some parallel with periods of activity measured in previous studies; use of a much larger number of samples could show only significant hour-by-hour variations and could confirm or deny the existence of aparallel bimodality in faecal output.

Results of the study on the rate of passage of foods through the alimentary tract of the wood mouse are consistent with those of previous studies on small rodents but it would have been of value to compare rates of passage of food with efficiency of assimilation using a variety of foods.

Clearly there is great scope for work on small mammal enersetics, and the value of the machine designed by Lewis and Rentmore (1968) in studies involving various aspects of assimilation is unquestionable.

10.0. SUMMARY

1. Some facets of food assimilation in the wood mouse *Apodemus sylvaticus* were investigated by use of the 'gravimetric' or 'balance' method.
2. Coefficients of digestibility and assimilation, and daily energy budgets were calculated for mice fed on three diets - wheat, oats and groundnuts.
3. Calorific value of faeces was higher than that of the food in mice fed on oats or wheat but lower than that of the food in mice fed on groundnuts.
4. Mice kept singly were found to digest between 92.1% and 94.4% of the food ingested depending on diet.
5. Daily energy budgets were calculated for mice fed on each of the three diets and ranged between 0.59 and 0.78 Kcals (gram live body weight) day depending on diet. A correlation was found between 'metabolic body size' and calories assimilated per day.
6. Coefficients of digestibility of mice kept in pairs did not vary significantly from those of mice kept singly but reduction of food intake by mice kept in mixed pairs was reflected in a drop of between 8.3% and 38.5% in daily energy budget depending on diet. No reduction in energy budget was found in female mice kept in pairs.
7. Analysis of faecal material kept in experimental cages for different lengths of time showed that calorific values of the faeces remained steady for two days, but then there was a drop of 7.1% in the calorific value of oat faeces and 11.3% in the calorific value of wheat faeces.
8. Periodicity of faecal output over 24 hours was found to be broadly similar to activity rhythm shown in previous studies.
9. Rate of passage of carrot through the alimentary tract of wood mice was found to be between two and three times greater than the rate of passage of oats.

11.0. BIBLIOGRAPHY

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ACKNOWLEDGEMENTS

I would like to thank Dr. Peter Evans who supervised this work and read the final manuscript: my grateful thanks are also due to Mr. Frank Venmore for making the faecal sample collector.

APPENDIX

TABLE A

ANALYSIS OF OATS

SAMPLE	% DRY MATTER	% WATER	KCALS/GM DRY WT
A	81.5	12.5	4.82
B	91.1	8.9	4.92
C	89.2	10.8	4.35
D	91.3	8.7	4.60
E	89.4	10.6	4.77

TABLE B

ANALYSIS OF WHEAT

SAMPLE	% DRY MATTER	% WATER	KCALS/GM DRY WT
A	89.0	11.0	4.41
B	89.2	10.8	4.37
C	90.0	10.0	4.47
D	89.9	10.1	4.46
E	89.8	10.2	4.37

TABLE C

ANALYSIS OF GROUNDNUTS

SAMPLE	% DRY MATTER	% WATER	KCALS/GM DRY WT
A	94.9	5.1	7.35
B	93.6	6.4	7.01
C	94.2	5.8	6.72
D	94.5	5.5	7.05
E	95.0	5.0	6.95

TABLE D

ANALYSIS OF OATS FAECES LEFT FOR 1 to 7 DAYS

TIME (DAYS)	KCALS/GM DRY WEIGHT			
	A	B	C	D
1	5.16	5.04	5.14	5.19
2	5.16	5.50	4.99	4.86
3	4.72	4.84	4.80	4.52
5	4.76	4.99	4.90	4.82
7	4.70	4.40	4.51	4.85

TABLE E

ANALYSIS OF WHEAT FAECES LEFT FOR 1 to 7 DAYS

TIME (DAYS)	KCALS/GM DRY WEIGHT			
	A	B	C	D
1	5.19	4.74	5.05	4.86
2	5.04	4.80	5.18	4.92
3	4.44	4.39	4.52	4.48
5	4.34	4.39	4.50	4.55
7	4.54	4.49	4.43	4.60

TABLE F

PERIODICITY OF FAECAL OUTPUT

Sample No. / Time Period (hrs)	Dry Wt. expressed as % of Total dry Wt over 24 Hrs.				
	A	B	C	D	E
0000-0400	28.2	26.1	28.6	33.0	30.0
0400-0800	24.8	17.8	24.4	3.9	14.4
0800-1200	15.8	5.6	2.8	12.5	8.6
1200-1600	7.9	11.2	3.5	9.6	11.5
1600-2000	4.6	13.1	12.2	14.8	11.7
2000-2400	18.7	26.2	28.5	26.2	23.8

TABLE G

RATE OF PASSAGE OF OATS THROUGH ALIMENTARY TRACT

SAMPLE NO. / % OATS IN FAECES	TIME (HOURS)				
	A	B	C	D	E
TRACE	2	1	3	3	1
50%	9	9	11	10	8
90%	30	26	27	32	30

TABLE H

RATE OF PASSAGE OF CARROT THROUGH THE ALIMENTARY TRACT

SAMPLE NO. / % Carrot in faeces	TIME (HOURS)				
	A	B	C	D	E
TRACE	1	1	1	1	1
50%	4	4	3	4	4
90%	9	11	9	12	11