Some aspects of energy balance in the bank vole clethrionomys glareolus

Meese, G.B.

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Some aspects of energy balance in the bank vole *Clethrionomys glareolus*

by

G. B. Meese, B.Sc.(Lond.)
M.A.F.F., Infestation Control Laboratory,
Worplesdon, Surrey.

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"struggle for existence is the struggle for free energy available for work."

Boltzmann (1886)

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1.0 INTRODUCTION TO ENERGY STUDIES

If we accept that the characteristics of any plant or animal are adaptations to existence within an environment then ecology covers more of the field of zoology than the third claimed for it by Elton (1927). Living organisms are part of the functional units of ecology, the ecosystems. Within any ecosystem two important processes can be distinguished (1) the cycling of material (2) the one way flow of energy. Energy is one of the dominant functions controlling living organisms and the obtaining of sufficient of this commodity enables normal activities to be undertaken.

Energy, unlike material, is continually lost from the system and although it can be stored even for thousands of years it will eventually be lost. Our ultimate source of energy is that emitted from the sun in the form of electromagnetic waves. This energy is utilised by plants with chlorophyll enabling them to make organic material, a store of energy. This material is then available as food to herbivores in an ecosystem. It is with the relations between plants and herbivores that I shall be concerned, in particular with the amount of energy taken in by an animal to supply its normal daily needs.

The energy which an animal takes in as food has to serve two main purposes: (1) to provide energy for the normal life processes (2) to provide energy for the increase of biomass i.e. production. We can summarise the fate of consumed energy as:

$$C = P + R + U + F$$

$$D = P + R + U$$

$$A = P + R$$

Where C is consumption, D is digestion, A is assimilation, P is production, R is respiration, U is excreta and F is faeces (Petruesewicz, 1967b).

There are various ways of studying energy flow in vertebrate populations and these have been described by Golley (1967). All work so far has been based on two assumptions: that a population can be delimited in space and time and that the energy flow of a population is the sum of the energy flow of the individuals measured separately. Direct measures of metabolism in the field have been developed by Lifson, Gordon and McClintock (1955) using radio-active body water and by a number of workers (Odum and Golley, 1963) who have measured the rate of excretion of radio-active zinc. Intake of food has been measured directly in domestic animals (Van Dyne and Meyer, 1964) by a variety of techniques including the use of a rumen fistula. By including indigestible or radio-active matter (Crossley, 1963) in the food it is possible to measure food consumption. However the most widely used method is the "balance" method whereby an animal, usually kept in the laboratory, is supplied with a known amount of food daily. Collection of faeces and urine and determination of their energy content allow the construction of an energy budget. This method (except for the collection of urine) has been used in the present work. The calculation of energy budgets requires that body weight remains constant or a suitable correction factor be applied.

Workers on small mammal energetics are faced with a formidable list of factors all of which affect metabolism. Kleiber et al (1956) described the effect of age on rat metabolism and Kaczmarski (1966) has shown that pregnancy and lactation increase daily energy requirements. Other factors affecting metabolism include the season (Gebczynski, 1966), temperature (Irving, 1964), geographical locality (Hayward, 1965), social behaviour (Brown, 1963) fat content (Connell, 1959), the state of excitement (Folk, 1964), acclimatisation (Gorecki, 1966), activity (Hawkins et al, 1960) and diet (Drozdz, 1968b). Especially important amongst these factors are breeding condition and temperature. As the majority of a small rodent's energy intake is used for heat production (Davis and Golley, 1963) then clearly any change in temperature may have an appreciable effect if the animal is below its thermo-neutral zone. The major difficulties arise when one attempts to relate energy studies in the laboratory where conditions can be controlled to the wild where conditions are constantly fluctuating.

2.0 PREVIOUS WORK ON BANK VOLES

The bank vole, Clethrionomys glareolus (Schreber, 1780), is a rodent belonging to the sub-family: Microtinae. Its general characteristics are well described in Southern (1964).

Evans (1942) studied the population dynamics, movements and distribution of the species. More recently a number of people have examined its daily activity cycle; Brown (1956a) found evidence for diurnal activity but Miller (1955) and Osterman (1956) found it to be active throughout the 24 hours with more nocturnal than diurnal activity in summer. The home range has been studied by Miller (1958) and Brown (1956b). The effect of Clethrionomys on forest regeneration has been described by Ashby (1959, 67), Tanton (1965) and most recently by Turcek (1967). Particularly relevant to the present work are the extensive studies around Durham itself by Crawley (1965) and Ashby (1967), both of whom have paid some attention to feeding. Most work on feeding in Britain has been restricted to identification of foods taken, e.g. Miller (1954) and Watts (1968).

Since the start of the IBP (International Biological Programme) combined with the "discovery" that energy is important to the functioning of ecosystems, small mammal studies concerned with food and energy flow have received a great boost. Most of the published work has been done in Poland where there is a working group of the IBP devoted to small mammals. Some of the most important studies have been made by Drozdz (1964, 66, 67, 68a, 68b) who has worked on Clethrionomys and on other small rodents, both in the laboratory and in the field. He has studied the natural foods throughout the year and shown by analysis of gut contents that the food taken varies. Drozdz also measured the digestibility and assimilation of natural foods and calculated daily energy budgets using animals kept in metabolic cages. Gorecki (1966, 68) has looked at acclimatisation of the bank vole to laboratory conditions and has worked on metabolic rate. This work is particularly important in showing that animals which have been kept in the laboratory for more than a few days are quite likely to have different energy requirements from the wild animal. Studies on the metabolic rate and energy budget have shown that winter and summer rates are somewhat different (as expected, since the winter pelage is thicker than the summer). Grodzinski and Gorecki (1967) have evaluated various possible measures of daily energy budgets (see Section 4.5) and Gorecki (1967) has determined the calorific value of the whole body of the bank vole at different times of the year.

Work has been done in America on the ecological counterparts of the bank vole. Reference will be made particularly to the studies of Pearson (1947, 50, 62), McNab (1963) and the excellent work of Golley (1960) on Microtus pennsylvanicus. Much information has also been obtained from the standard works on energetics of domestic animals (Brody, 1945; Kleiber, 1961; Blaxter, 1962).

Except for the studies of the effect of voles on regeneration of oaks very little has been published in Britain in recent years that is particularly novel. The Polish work however has given us some insight into the role played by small rodents in the ecosystem. The present work was done in part to investigate whether the findings in Poland were applicable in Britain since the whole aim of IBP is to produce results which have world-wide relevance. The effect of grouping on energy flow, energy intake in the wild and the energetics of weight change were also studied.

3.0 GENERAL METHODS

3.1 THE SITES AND MATERIAL

All the animals used in feeding experiments were caught at Castle Eden Dene, a nature reserve of natural and semi-natural woodland. The vertebrates of this reserve have been studied by Crawley (196[illegible]) and Ashby and Crawley (1967). The voles were caught during May-June, 1969 using Longworth traps (Chitty and Kempson, 1949) baited with rolled oats. The trapping area was an open stand of Corsican pine (Pinus nigra) with some hardwoods. Ground cover was mainly dog's mercury (Mercuralis perennis) and bracken (Pterdium aquilinum).

Animals used to determine energy intake in the wild were caught with break-back traps baited with rolled oats. The traps were set in Houghall Wood, Durham, an area of mixed woodland. The ecology of the bank vole on this site has been studied over a long period by Ashby (1967) who also describes the vegetation. The traps were set in the morning and then periodically inspected during the day.

Only adult animals were used in the feeding experiments but all classes were caught in the break-back traps.

3.2 THE FEEDING EXPERIMENTS

During the feeding and starvation experiments the animals were housed in metal mesh cages measuring 40 x 20 x 25 cm. The cages were kept in the laboratory at a temperature of about 20°C and the animals disturbed as little as possible. With their volume of 20 litres and floor area of 800 cm^2 the cages were considerably larger than those used by Drozdz (1968b) in his studies. This variation in cage size could well have an important effect on the vole energy requirements by providing a larger area for exploration. Except in two experiments animals were housed individually. Water was supplied and food offered in a petri dish on the cage floor. Each day before placing the cage in its metal tray the latter was lined with a sheet of paper. This made collection of faeces and uneaten food much easier. Cotton wool was provided as bedding as it was important to use material that the voles would not eat.

After capture, the animals were given the appropriate test diet for a preparatory period of 5 days before measurements were started to ensure that they were accustomed to the diet and also had their alimentary tract filled with it. Each experiment involved 6 animals for a minimum of 7-day experimental periods after the preparatory periods.

Four test diets were used; oats (Avena fatua), wheat (Triticum aestivum, acorns (Quercus robur) and bluebell corms Endymion non-scriptus). Three diets were of a concentrated nature with low fibre and water content while one was a bulky diet with high water content. After the introductory period the cages were cleaned and fresh nesting material provided. The animals were then weighed daily to the nearest 0.1 g.

The basis of this work was the determination of energy requirements by the "balance" method (see Section 1.0). Each day a known weight of experimental diet was given. The food was always in excess of requirements. (Digestion and assimilation in mammals is not affected by excess, as far as is known, unlike many invertebrates). On the following day uneaten food was collected and weighed. Faeces were also removed and weighed, and samples taken for analysis of water content, ash content and calorific value.

Two further experiments were completed (see Section 5.0) in which two animals of the same sex were placed together at the start of the experimental period in a cage new to both of them and with fresh nesting material.

3.3 ANALYSIS OF FOOD AND FAECES

All the types of food used in the experiments were subjected to a simple analysis to determine water content and the percentage of organic material present. Faeces were also analysed in the same way.

Samples of food were ground into a fine powder using a pestle and mortar. A number of samples, usually 5, were then dried to constant weight in a vacuum oven at 65°C, this temperature ensured no loss of fat. Before weighing, samples were allowed to cool in a dessicator. When constant weight was reached, usually after about 5 days, the water content was calculated (by differences). Samples were taken from the dried material, placed in "Vitreosil" crucibles and burnt in a muffle furnace at 500°C for about 3 hours. The crucibles and contents were cooled in a dessicator, weighed and the organic content determined.

3.4 DETERMINATION OF CALORIFIC VALUE

Calorific values were measured by bomb calorimetry. The heat produced by burning a weighed sample of material in oxygen, under pressure, is a measure of the energy content of that sample. Blaxter (1962) has stressed that results obtained with bomb calorimeters, although reproducible, refer only to the conditions under which they were measured and so every attempt must be made to keep conditions constant.

The bomb used was a Gallenkamp "Ballistic bomb calorimeter" and the method is largely that used by Connell, Odum and Kale (1960). The material was dried to constant weight in a vacuum oven at 65°C and then ground into a fine powder. Accurately weighed pellets of about 0.5 g were burnt in the bomb in oxygen at 25 atmospheres of pressure. The galvanometer reading, indicating the amount of heat released, was converted to a calorific value by comparison with a calibration graph, constructed by burning a range of weights of pure benzoic acid (calorific value 6.324 Kcal/g) on the calorimeter. Results obtained with this technique are not perhaps as accurate as those with the miniature bomb calorimeter (Phillipson, 1964), but other quantities in the energy budget can be estimated even less precisely, so any errors are unimportant.

As ash content was known for the food and faeces, all the heat releases could be converted to Kcal/g, dry ash-free weight.

4.0 RESULTS AND DISCUSSION OF FEEDING EXPERIMENTS

4.1 FOOD AND FAECAL ANALYSIS

Details of the analysis of different foodstuffs are shown in Table 1 and in the Appendix (Tables A-D). The tables in the Appendix show the organic matter and ash content expressed as percentages of the dry matter content; in Table 1 they are shown as percentages of the fresh weight. In all cases there are differences in the percentage composition from the composition determined by Golley (1959) and Drozdz (1968b). This is not surprising however as the material examined by different workers must surely differ on such counts as the period for which it has been stored. The locality from which the plants were taken must also make a difference. These differences also show however that it is wrong to base any energy calculations on calorific values determined under different conditions.

Results of the analysis of vole faeces are given in Table 2 and the Appendix (Tables, E, G, J and K). Contents are expressed in the same way as the food analyses. Again there were differences from published results and these may be compared in the following table:

TABLE 1

	% Dry matter	% Water	% Organic matter	% Ash	Calorific value
Oats	89.2	10.8	86.4	2.8	4.77
Wheat	90.1	9.9	87.8	2.3	4.32
Acorns	59.9	40.1	58.2	1.7	4.36
Bluebells	28.7	71.3	28.1	0.6	4.33

Mean values of food analyses. Organic matter and ash content expressed as percentage of dry matter. Calorific values in Kcal/g, ash-free dry weight.

TABLE 2

	% Dry matter	% Water	% Organic matter	% Ash	Calorific value
Oats single	74.0	26.0	60.7	13.3	4.95
Oats in pairs	53.5	46.5	46.0	7.5	5.02
Wheat	76.4	23.6	70.1	6.3	4.93
Acorns single	58.2	41.8	52.3	5.9	4.91
Acorns in pairs	61.9	38.1	56.8	5.1	4.62
Bluebell corms	72.0	28.0	69.2	6.8	6.23
<u>Oats fed</u>					
24 h.starvation	88.5	11.5	71.6	16.9	4.73
24 h.starvation + 24 h.	63.3	36.7	52.8	10.5	4.86
24 h. no water	85.6	14.4	74.7	10.9	4.81
24 h. no water + 24 h.	87.1	12.9	74.0	13.1	4.68
<u>Wheat fed</u>					
24 h. starvation	78.3	21.7	67.3	11.0	3.07
24 h. starvation+ 24 h.	73.4	26.6	67.2	6.2	4.38
24 h. no water	92.0	8.0	85.2	6.8	4.55
24 h. no water + 24 h.	62.3	37.7	56.1	6.2	4.56

Mean values of faecal analyses. Organic matter and ash content expressed as percentage of dry matter. Calorific values in Kcal/g, ash-free dry weight.

TABLE 3

Diet	Weight	Food	Faeces	Energy digested	% of ingested energy digested	Energy assimilated	% of ingested energy assimilated	Kcal/g/day
Oats (single)	19.8 (16.5-23.5)	15.96 (10.88-22.74)	1.12 (0.60-1.78)	14.84 (10.28-20.96)	92.99 (92.17-94.49)	14.39 (9.97-18.82)	90.16	0.73 (0.55-0.94)
Oats (double)	19.1 (14.9-22.1)	10.64 (8.43-13.55)	0.62 (0.42-0.84)	10.02 (8.00-12.82)	94.17 (92.51-95.11)	9.72 (7.77-12.44)	91.35	0.51 (0.42-0.60)
Wheat	19.5 (18.0-23.0)	13.98 (12.60-15.37)	1.79 (1.40-2.18)	12.19 (10.99-13.19)	87.20 (85.82-89.49	11.82 (10.66-12.79)	84.55	0.61 (0.52-0.65)
Acorns (single)	15.0 (12.3-19.1)	8.29 (5.67-13.41)	1.33 (0.39-3.11)	6.96 (5.03-10.30)	83.96 (76.81-93.12)	6.75 (5.12-9.99)	81.42	0.45 (0.27-0.59)
Acorns (double)	15.4 (12.5-18.4)	4.43 (2.02-5.89)	0.82 (0.26-1.46)	3.61 (1.65-5.19)	81.49 (75.28-95.23)	3.50 (1.60-5.03)	79.01	0.23 (0.10-0.36)
Bluebell corms	15.4 (12.8-18.0)	8.78 (7.36-9.16)	1.78 (0.87-2.53)	7.00 (6.49-7.55)	79.73 (72.17-88.18)	6.65 (6.17-7.17)	75.75	0.43 (0.39-0.69)
Beechmast[1]	22.7	13.25	0.95	12.30	92.86	11.79	88.98	0.462
Mixed[1]	23.1	15.18	1.85	13.33	87.78	12.90	84.98	0.446
Oats[1]	22.9	13.01	1.42	11.59	89.11	11.20	86.09	0.422
Greens[1]	22.4	12.75	2.88	9.87	77.41	9.23	72.39	0.401

Mean values obtained in feeding experiments, all values based on approximately 30 readings with a weight change of less than 1.0g/day. Range shown in brackets.

1. Values taken from Drozdz (1968b), the energy flow figures were corrected for weight change and effect of the nest.

TABLE 4

Diet	% of water	% of ash	% of organic matter	Calorific value in Kcal/g/ash-free dry weight
Oats	10.8	3.1	96.9	4.77
Oats (Golley)	-	-	-	4.24
Oats (Drozdz)	15.0	1.71	98.29	4.39
Oats faeces	26.0	18.0	82.0	4.95
Oats faeces(Drozdz)	-	6.85	93.15	5.32
Wheat	9.9	2.6	97.4	4.32
Wheat (Golley)	-	-	-	4.28
Acorns	40.1	2.9	97.1	4.36
Acorns (Drozdz)	14.21	2.5	97.5	4.16

4.2 CALCULATIONS

From the values obtained for water content, ash content and calorific value of foodstuffs, and from weights of food consumed and faeces produced, energy budgets were calculated for each animal on each day. From the equations given in Section 1.0 the total energy digested per day and the percentage digestion were calculated as also were the energy assimilated per day and the percentage assimilation. On the basis of these figures the energy flow through a vole in Kcal/g live weight/day was determined.

The weights of voles were then examined for any weight changes during the 24 h. period. In all cases where the change exceeded 1 g. these results were rejected for reasons discussed in Section 7.3. Using these remaining results mean values were calculated in each experiment for: live weight, energy consumed and assimilated, and energy flow. The mean values for percentage digestion and assimilation were also determined. The mean values are shown in Table 3.

4.3 DISCUSSION

The amount of food taken in by an animal depends upon a variety of factors, in particular the energy content and the presence of different materials in the food. High energy intake may be of little use if an animal has a high protein requirement and there is little available in the food.

No separate analyses of fat, protein, carbohydrate and fibre content of the 4 foodstuffs and faeces were made in this study, so some of the values given by Drozdz (1968b) have been used.

The energy consumed minus the energy in the faeces gives a value for energy digested. A number of workers have determined the percentage of food digested by small rodents: Hawkins and Jewell (1962) found that the common shrew (Sorex araneus) digested about 90-92.5% of the energy consumed. Drozdz (1968a, b), working with Clethrionomys, found that digestion varied between 77% and 94%. Kaczmarski (1966) also determined a value for Clethrionomys of 90% digestion. The percentage of digestion is controlled mostly by the fibre content of food and in ruminants digestion can fall as low as 30% (Blaxter, 1962). In all cases measured in the present study the calorific value of the faeces was higher than that of the food ingested. As calorific value is dependent mainly on the amount of fat present, the results indicate that the percentage of fat in the faeces is higher than in the food. On the diet of oats, for instance, the calorific value of the faeces exceeded that of the food even though the faeces had a lower percentage content of organic matter. Thus it would appear that Clethrionomys is able to digest rather little fat. As Table 2 shows, the calorific value of bluebell faeces was very high and the proportion of energy digested was much lower than on other diets, which means that the food probably contained a very high proportion of fat, or that the voles were able to digest even less fat from bluebells than from the other diets. In Drozdz's (1968b) study, the ether extract of oats was 7.36% whilst that of the faeces was 14.25%, and in all cases where the fat content of the faeces fell below that of the food (e.g. on the beechmast diet) the calorific value of the faeces was lower than the value for food.

It would appear from Drozdz's work that on certain diets Clethrionomys is capable of digesting some fat, but that on the diets used in this work very little fat was digested.

Energy losses in assimilation will depend on the quantity of urine produced and on its calorific value. These two factors are partly controlled by water content of the diet and the proportion of nitrogen compounds present. As Brody (1945) has shown, about 5% of energy assimilated is used in the functioning of the kidneys and so a change in urine production could have an appreciable effect on metabolism. Calorific value of urine is usually determined by Nijkamp's method (1965).

It was not possible in this work to measure urine production and an estimated value was used. Brody (1945) determined a 9% energy loss in cattle through urine and rumen gas and Blaxter (1962) found that the loss of digested energy in cattle rarely fell below 5%. Davis and Golley (1963) suggested that the energy loss in herbivores was in the region of 5% and Drozdz (1968a, b) found a range of values for the bank vole, depending on diet, varying between 3.18% and 5.82%. In this study estimated values of 3% loss of the assimilated energy in the case of oats, wheat and acorns and 5% loss for bluebells were used. These values gave a range of assimilation from 75.75% to 90.16% (Table 3). Assimilation was calculated also by Conover's (1966) formula and gave the following results shown alongside the percentages determined in this study.

TABLE 5

Diet	Values from present work	Conover's formula
Oats (single)	90.16	81.9
Oats (double)	91.35	80.88
Wheat	84.55	70.00
Acorns (single)	81.42	73.74
Acorns (double)	79.01	66.67
Bluebells	75.75	79.35
Beechmast[1]	88.98	81.25
Mixed[1]	84.98	66.76
Oats[1]	86.09	76.12
Greens[1]	72.39	55.17

(1 - Values taken from **Drozdz**, 1968b).

Conover's method is based on the ratio of the ash content of the food to that of the faeces produced. If the assumption that digestive processes act only on the organic content of food is correct then Conover's method would give the 'true' figure for assimilation. In all but one of the above values the calculated figure is lower, this would be explained in two ways; (1) energy loss in the urine is far greater than has been calculated (2) some of the inorganic material is being removed. The second explanation is the more likely for at particular periods the demand for inorganic matter must be high e.g. during rapid growth and pregnancy. Even during adult life there will be some need for inorganic matter. The result obtained for those animals fed on bluebells could be due however to an overestimate of energy loss in the urine.

Finally, energy flow measured as Kcal/g body weight was calculated. In spite of later criticism of this figure, results were expressed in this manner for comparison.

The most striking feature is the wide range of values for maintenance costs. Overall mean daily weight changes on oats, wheat, acorns and bluebells were 0.8g, 0.8g, 0.7g and 0.5g respectively. Allowing for differences in the weight of the animals in each experiment it means that in spite of a large range in energy flow on different diets there was little difference in weight change. Other published values for energy flow (quoted in Drozdz, 1968b) lie between 0.32-0.96 Kcal/g/day where similar techniques have been used. Results using respirometers and oxygen consumption techniques vary slightly. One is forced to conclude that an animal probably has to compromise between food and energy requirements. On bluebells for instance they probably obtain sufficient food (i.e. protein, fat, carbohydrate etc.) along with a lower energy intake than on oats. In the wild where a choice of food material is available this problem may not arise. It poses the problem of how the animal accommodates.

Does it "burn up" energy if too much is taken in? Probably on some diets they are unable to get sufficient energy because of the nature of the food and have to adapt their behaviour accordingly.

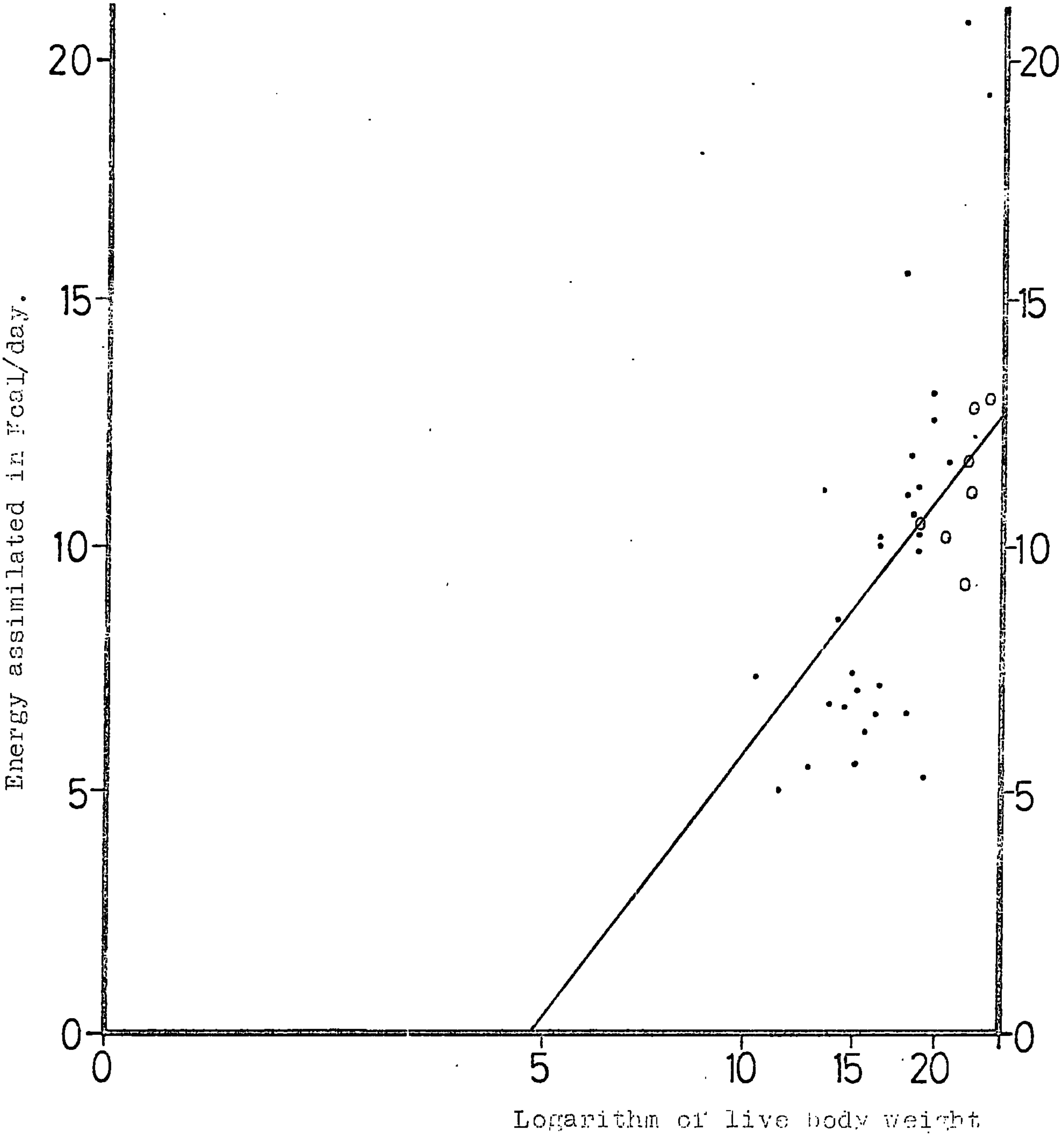
The obvious conclusion is that energy measurements on mammals in the laboratory may bear little relationship to energetics in the field.

4.4 ENERGY FLOW AS A FUNCTION OF BODY SIZE

That energy intake bears a relationship to body size is self evident; elephants eat far more food than do mice. Biologists have been looking for a long while for some way in which the energy flow of homeotherms of different weights may be compared. The problem is considered by Kleiber (1961, 65) who points out that as early as 1839 it was realised that metabolic rate was more closely correlated with surface area than with body size. Although a relationship of sorts existed there was little agreement on how to measure the surface area and it seemed that the law had to be continually modified to suit particular animals. It was then found that a linear correlation existed between the logarithm of metabolic rate and the logarithm of body size, meaning that rate was proportional to a body weight to a given power. A variety of values were suggested including some given to three places of decimals, implying a wonderful accuracy in energetics! The present accepted value is that of $\frac{3}{4}$ proposed by Kleiber, this is the value used in intraspecific comparisons. But, within a species such a relationship may not hold true or a simpler relationship may be valid. To test this in the present study the results of assimilation/day for voles living singly were plotted against the logarithm of body size (Figure 1). This gave a value for "r" of 0.835 for 32 degrees of freedom and $p < 0.001$. This may be compared with the results for the voles living in pairs (Figure 2), where the slope of the line is slightly less, showing the benefits obtained when they are grouped.

The results for the animals living in pairs were also plotted in two other ways: log assimilation/day against log body weight and body weight against assimilation/day. Both plots gave good correlations. The surprising result is that a good correlation can be shown no matter in which form the body weight or assimilation is expressed. Dealing with one species in which animals of similar weight are considered it would seem immaterial which axes are used in correlating energy assimilation and body weight.

Figure 1



Voles singly in cages.
= this work
= published results (Drozdz, 1968b)

4.5 WHAT HAS BEEN MEASURED?

As if the study of energy flow were not difficult enough a further complication has resulted from different people measuring different facets of metabolism. In this work an attempt has been made to measure:

1. The amount of energy needed (= assimilation) for an animal's normal activity over 24 h. This is called the Average Daily Metabolic Rate (ADMR).
2. The energy flow per gram body weight when weight change is less than a gram per day.

Much of the early work on metabolism used the Basal Metabolic Rate (BMR) as a measure. Benedict (1938) has indicated the requirements necessary before this can be evaluated i.e. the animal must be in the region of its thermoneutrality, be in a post-absorptive state and show no muscular activity. This condition is difficult to attain, even more difficult to measure and is of very doubtful value. The Resting Metabolic Rate (RMR) exceeds the BMR by the value of the Specific Dynamic Action (SDA) and is measured in quiet animals which have not been fasted. Many workers used this measure including Golley (1960) and Odum et al (1962). Yet another measure has been the Fasting Metabolic Rate (FMR) which has been used much in agriculture and is little different from the BMR.

McNab (1963) used values of RMR and BMR corrected for activity etc. to produce a Daily Energy Budget (DEB). This has been shown by Grodzinski and Gorecki (1967) to be little different from the ADMR. The ADMR was originally proposed by Pearson (1947, 48). It has the advantages of being easy to measure, is measured over 24 h instead of a short period and is probably the closest approximation to an animals real requirements.

5.0 EXPERIMENTS ON VOLES LIVING IN PAIRS

5.1 METHOD

The basic method is described in Section 3.2. One experiment involved 6 pairs of voles fed on oats, all the animals were males and 35 readings were obtained. The other experiment used 6 pairs of voles fed on acorns, all were males and 42 readings were obtained.

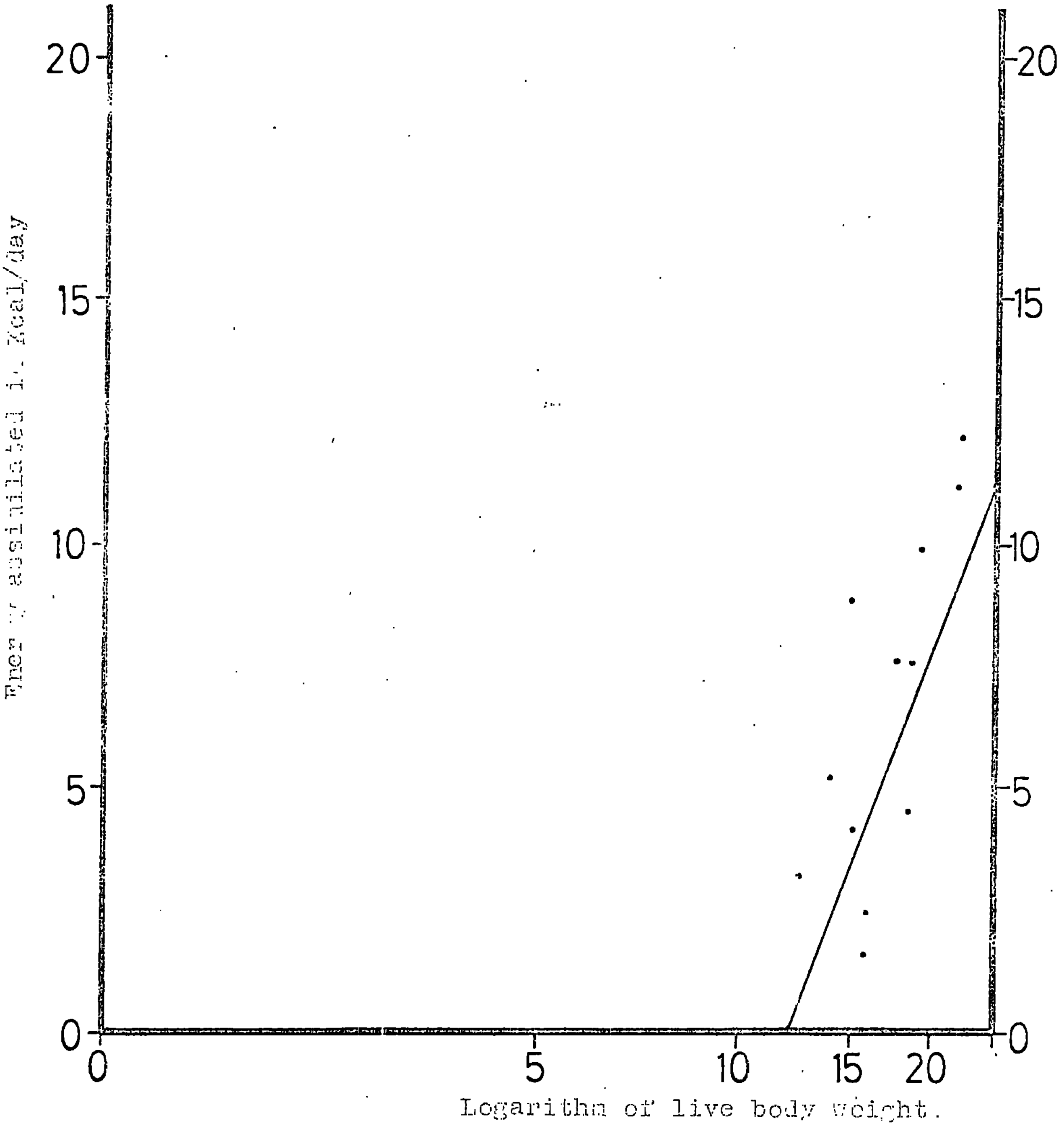
5.2 RESULTS

The normal procedure was used for calculating the energy budgets. Only the readings obtained when neither animal in a pair had changed its weight by more than a gram were used. Results were calculated and mean values determined for single animals not pairs i.e. intake and output per day were divided by two. In all cases the pairs were arranged so that animals of very similar weight were together. The final results are then expressed for a single animal but living in a pair. Faecal analyses are shown in Tables 3, F and H. The energy exchange results are summarised in Table 3. Energy losses in the urine were estimated as 3% of energy digested. The mean weight change for each animal per day was 0.7 g on both diets.

Figure 2 shows energy assimilated per day plotted against the logarithm of body weight. The correlation coefficient was determined as 0.743 for 12 degrees of freedom and p was equal to 0.01. The regression equation was calculated:

$$\text{Assimilation} = 36.806 \log \text{body weight} - 38.79$$

Figure 2



Voles living in pairs.

All values plotted are from this work.

5.3 DISCUSSION

When one considers the formidable list of factors which act upon metabolism it is obvious that experiments upon animals living singly will be difficult enough without considering what happens when two or more animals are placed together. Few workers have commented on this aspect and what results exist are conflicting.

Hawkins and Jewell (1962) in their studies on the metabolism of some small mammals did all their work on animals living individually except for harvest mice (Micromys minutus) where there were 3 animals together. In their results they found that their food intake was considerably less than that of other small mammals of equivalent size. This they explain by saying that the harvest mouse seems a placid animal when compared with shrews. Ponugaeva (1960) found that rodents kept in groups of 3-5 lowered their metabolic rate by 8-17%. Brown (1963) on the other hand, working with house mice (Mus musculus), found that those living at high densities used 13% more energy than when living at low densities. The additional expenditure was due to increased behavioural activity, grooming for instance was increased by 10.9%. Buckner (1964) also found that increased density affected metabolism and in his work shrews at 4 to the acre used 18-22% more oxygen than those living at 2 per acre. Gorecki (1968) discovered that bank voles in groups of 2-4 decreased their DER by 13% and makes the useful point that voles regularly huddle in groups in their nests. Does this mean that all energy calculations for the vole are over-estimates because in the wild their heat loss would be reduced by grouping? It would appear that when animals are kept in groups there is probably a conflict between the benefits to be obtained by huddling and the increased energy demand brought about by the need for greater social activity. In the present work after an initial period of aggression all the pairs settled down and by the time the experiments were started had had a period of at least five days together. Aggression was never seen again and the pairs showed huddling in the nest and so would appear to have derived a benefit.

The results summarised above may be compared with the findings of the present work described in the section following.

(a) The animals fed on oats, as can be seen from Table 2, produced faeces with a higher energy content than the faeces from oats-fed voles living singly. The faeces of the former were higher in energy content but only fractionally so. 5.02 instead of 4.95 Kcal/g. Added to this the animals living in pairs both digested and assimilated more of their ingested energy and so overall were more efficient feeders. The explanation for this is difficult and the only possible answer is that they were indulging in a greater amount of refection or that food passed through the gut more slowly.

Bank voles are known to do this (Ashby - pers.comm.) but little is known of the details. The energy flow calculated on the basis of energy/gram was lower in the grouped animals who were perhaps reducing their energy demand as a result of reduced heat losses. The energy intake, digestion and assimilation were all lower, further evidence for the benefits gained from huddling. The mean daily weight change was 0.7g compared with 0.8g for the voles living singly so that grouping clearly produced no greater tendency to gain or lose weight.

(b) The group of animals fed on acorns produced extremely surprising results. Their faeces differed little in composition from those produced by animals living singly although their calorific value was a little lower (4.62 instead of 4.91 Kcal/g). In view of the large composition change of the faeces produced by the group living on oats this is surprising and using the previous explanation we can only suppose that refection is not occurring with these faeces. The percentage of ingested energy which was digested or assimilated was lower than that from the single voles so in fact in this case the animals were less efficient. In spite of this the energy per gram live weight was drastically reduced from 0.45 to 0.23 Kcal/g. The animals used were very similar to those in the single experiments as far as weight was concerned and had an average weight change of

0.7g compared with 0.5g. It would appear that on a diet of acorns the voles were capable of obtaining their maintenance requirements from much smaller amounts of food. The calorific value of acorns was about the same as wheat and bluebells so this is no explanation. Drozdz (1968b) did find however that the coefficient of digestibility of acorns was lower than would be expected. A possible explanation is that voles cannot obtain sufficient energy from acorns for normal activity and so are forced to modify their behaviour and spend longer periods resting. In the wild this situation would not arise as acorns would probably be taken by the wood mouse and so the choice of acorns as an experimental diet was perhaps an unfortunate one.

Overall the two experiments have added little to what is known of the effect of grouping and quite clearly a lot of work could be done on this aspect. One obvious point is that the effect will depend very much on the habits of the particular animal e.g. whether much time is spent in the nest and whether this time is in the company of other animals. Drozdz (1968b) in his work allowed for a 20% reduction of maintenance costs by the provision of a nest so the reduction of heat losses by the presence of another animal must be considerable. This work has shown that for the vole at least this probably occurs and causes a 30% reduction in maintenance when fed on oats. It is interesting to note that if the two regression lines of Figures 1 and 2 are combined they illustrate that the benefit to be gained from grouping is proportionally greater for the smaller animals whose heat loss would also be larger.

6.0 ANALYSIS OF WHOLE ANIMALS

Most authors (Davis and Golley, 1963; Grodzinski and Gorecki, 1967) have compared energy flow in different animals on the basis of Kcal/g live weight. In view of the work of Gorecki (1967) who has shown that dry matter and organic content vary throughout the year this method of expressing results cannot be considered satisfactory. Furthermore if results are to be expressed on the basis of that part of the animal which is metabolically active then we must surely take into account the amount of fat which is present. Fat has been described by Benedict (1938) as "an energy demanding factor" varying with the age of the animal and the season. A number of people (King, 1961; Evans, 1969; Newton, 1969) have shown the fat content of birds to vary with season. Evans (pers.comm.) says that the fat content of <u>Microtus agrestis</u> shows no regular variation through the year. So far regular annual variation in fat content has not been shown for any small rodent. Armsby and Moulton (1925) and later Reid et al (1955) have studied the fat content of cattle and sheep showing it to be highly variable and inversely related to the water content. They also conclude that the proportions of protein, water and mineral matter all change with age; protein and ash content increasing and water content decreasing rapidly in the young animal.
The constancy of composition of the body is not attained

until very late in life.

6.1 METHODS

(a) Five animals were examined, 2 caught in the wild and 3 after captivity for four weeks. After removal of the stomachs and stomach contents the bodies were weighed, cut into small pieces and the water and ash content determined after the method described in Section 3.3.

(b) Fat extractions were done using a modification of the method used by Odum (1960). After removal of the stomachs and their contents the bodies were dried, weighed, ground in an electric mill and boiled in petroleum ether in a Soxhlet apparatus for 30 minutes. The filtrate was poured off and the boiling repeated with fresh ether. At the end of the boiling the residue was retained, dried and weighed.

Strictly speaking petroleum ether does not give a true figure for lipids as it dissolves out some waxes and oils. This is compensated for to some extent by lipids which ether cannot remove.

6.2 RESULTS AND DISCUSSION

The results are shown in the following table. There is obviously insufficient material to show any real differences. All weights are shown in grams.

TABLE 6

No. of animal	11	12	13	17	19
Wet weight	11.731	14.034	15.472	16.371	17.077
Dry weight	3.595	4.690	4.132	5.196	5.337
% dry matter	30.6	33.4	26.7	31.7	31.3
% water	69.4	66.6	73.3	68.3	68.7
Dry weight	3.559	4.690	4.096	5.186	5.294
Ash weight	0.560	0.666	0.653	0.861	0.933
% organic matter	84.3	85.8	84.1	83.4	82.4
% ash	15.7	14.2	15.9	16.6	17.6

Animals 11, 12, 13 were laboratory animals, 17 and 19 were caught in the wild.

The mean value for dry matter content was 30.7% with little difference between the wild and laboratory animals. The wild animals however had a slightly lower organic content, probably because the laboratory voles had deposited fat. In the field greater energy demands would be made on the animal in searching for food, temperature regulation and social behaviour. Gorecki (1967) found that water and ash content varied throughout the year, the values of the latter were lower than recorded in this work. Differences in diet would probably account for differences in body content.

The results of the fat analyses were variable but the 23 caught in the wild and 6 from captivity had mean fat values (as a percentage of dry matter) of 11.8% and 18.1%. The higher values for the captive animals were in agreement with their organic content values.

On the basis of these figures it can be seen that the weight of metabolically active tissue present can vary appreciably and might it not be more accurate if comparisons were made with energy flow expressed in relation to dry weight, ash-free and fat-free.

7.0 THE STARVATION EXPERIMENTS

A series of experiments were performed in an attempt to determine the energy cost, above normal maintenance requirements, of putting on weight. It was also hoped to determine the energy released by breakdown of body material.

7.1 METHODS

(a) In one experiment 6 voles were fed on oats and 6 on corn. After the normal acclimatisation period and introduction to the diet they were deprived of food for 24 h. though water was supplied. The faeces produced during this period were collected and analysed later in the normal way. The faeces produced during the following 24 h. were also collected and analysed. In all other respects the experimental procedure was the same as that used during the normal feeding experiments.

(b) One short experiment involved 5 animals fed on a diet of oats. These were starved over 18 h. and their weight taken at regular intervals during the period. The faeces were not collected in this experiment.

7.2 RESULTS

The results of the faecal analysis appear in Tables 2, N and P. The weight losses during the 24 h. starvation and the weight gains over the following 24 h. are shown in Table Q.

The results of the faecal analysis for the animals fed on oats show that during the 24 h. of starvation they produced a small amount of faeces usually weighing about 0.1g. These would have been produced from the food left in the gut when the experiment was started. The water content of these faeces was lower than the normal ones produced on the diet but the proportion of organic matter and ash did not vary, so it would appear that the animals had extracted more water from their faeces than was normal. This, combined with the slightly lower calorific value of the faeces, could suggest that they were being retained in the body for a longer period than was usual. During the following 24 h., the water content changed by about 25% to exceed the content of normal faeces, though again the ash and organic matter content barely altered. The calorific value was only 0.09 Kcal/g below that recorded for normal faeces but in every case in the subsequent 24 h. the percentage of energy digested increased to around 95% instead of the normal 91.35%. The animals did not take in more food than was usual but obviously utilised it a little more efficiently, this could have been due to the gut being empty before the food went in. Perhaps in some way this increased the percentage of food digested and assimilated. Fasting has been examined in many animal species (Kleiber, 1961) but this aspect of change in faeces has not been studied. The animal would seem to be able to make up for fasting by increased efficiency on the occasion when food is returned. It could however be due simply to the fact that under normal circumstances collecting the faeces gave one faeces resulting from food supplied on the previous day as well as food from the day in question. When an animal had been starved for 24 h. this would not apply, so the overall amount of faeces collected would be less than usual and give an impression of increased digestion and assimilation. In view of the weight changes following the restoring of food (see later) the most likely reaction would be reduced activity. Unfortunately during this work there was no way of recording activity or of measuring urine production.

The voles previously fed on wheat showed many changes similar to those fed on oats but differed in producing faeces, after starvation, of a much lower calorific content (3.07 instead of 4.93 Kcal/g). This, allied to their much lower organic content, could be due only to their assimilating some high energy-level component such as fat. The water content did not vary very much and the only major alteration was in the percentage of organic matter. By the end of the following 24 h. the components of the faeces were approaching normality but still differed sufficiently to have a calorific content of only 4.38 Kcal/g. This illustrates how little can be done without detailed analysis of the components of food and faeces e.g. protein, fibre and especially fat.

As in the experiment described above, in the 24 h. after food was restored the percentage digestion exceeded the normal figure by about 5%.

7.3 RESULTS OF THE SHORT FASTING EXPERIMENT

TABLE 7

Time in B.S.T.	Animal number and weight					Mean weight loss(grams.)
	1	5	10	14	16	
09.00	16.6	20.2	18.0	19.8	19.8	0.0
12.00	16.4	20.4	18.3	18.7	19.2	0.0
15.00	16.3	20.1	17.8	18.3	19.5	0.5
18.00	16.2	20.1	18.0	18.5	19.1	0.5
22.00	15.6	19.6	17.4	18.1	19.5	0.8
03.00	15.6	19.8	17.0	18.1	19.3	0.9

This fasting experiment lasting 18 h. was an attempt to find how long an animal could exist on the food left in the gut at the beginning of the experiment and the energy obtainable from glycogen in the liver. After this period the animal would lose weight at the expense of its own body tissue. If this point could be determined it would allow the calculation of the energy released by breakdown of body tissue in the first starvation experiments.

7.4 DISCUSSION

Drozdz (1968b) introduced a correction for changes in body weight during his experiments assuming them all to be the result of gain or loss of body tissue. This is an obviously erroneous assumption as a variety of factors e.g. an empty gut or full bladder could well be responsible. He accepted the values of King (1961) that a decrease in weight was due to the breakdown of fat, releasing 7 Kcal/g of energy. Weight increase involved energy above maintenance requirements at the rate of 14 Kcal/g, of this however only $\frac{2}{3}$ g was high energy fat, the rest being water, proteins and carbohydrates, so the cost was reduced to 9 Kcal/g. Keys and Brozeck (1953) suggested values of 6 Kcal/g. Blaxter (1962) shows that the nature of material which is deposited means that in cattle at least its calorific value could vary between 1.5 Kcal/g and 9.3Kcal/g depending on age and diet. Therefore any "gains in body weight cannot give any precise information about the gain of energy by the body." When the nature of the increase and decrease in body composition is not known and the variation due to other factors is ignored the direct application of these values becomes unacceptable.

Two approaches were used and calculations were based only on those animals whose weight change exceeded 1 g. The following refer to weight losses:-

1. The values obtained in the 15 h. fasting would suggest that weight is lost rapidly over about 9 hours. So we can assume that the animal is capable of living for about 9 hours on its gut contents and glycogen before breaking down its

fat reserves. Using the values obtained in the feeding experiments it was possible to calculate how much energy would be required to exist for the remaining 15 hours. This energy would then have to come from the weight loss minus 0.5 g which could be explained by other factors, e.g. an animal weighing 17.1 g would require 8.05 Kcal to live for 18 h., this was supplied by 2.4-0.5 g. Therefore the energy release was 3.96 Kcal/g. Using this method mean values of 3.93 and 3.12 Kcal/g were obtained for the animals fed on oats and wheat respectively.

2. The second approach started with the assumption that any animal would contain about 5% of its daily energy requirements in its gut (see Section 9.3). Thus the weight loss minus 0.5 g would be sufficient to supply an animal with 95% of its daily needs. Values of 6.09 and 4.57 Kcal/g were obtained for the oats and wheat.

The four different results obtained illustrate that the assigning of any value would be purely arbitrary and that the value probably depends to some extent on the diet on which the animal was feeding. There is in all probability a reduction in searching behaviour and if activity were reduced it would mean that the animals energy requirements for a day would also be reduced.

The weight gains were extremely difficult to explain and in nearly every case the energy actually assimilated was equal to the energy calculated to meet normal maintenance requirements. This can only mean that on the days following fasting maintenance requirements were lower than normal so that the energy actually taken in was sufficient for maintenance and the depositing of fresh body material. The only explanation again is that perhaps the activity cycle was altered so reducing the energy expenditure. Also on these days the percentage digestion and assimilation exceeded normal.

The weight changes shown during the normal feeding experiments were not used in these calculations as it was felt that far too many unknown factors were involved to make the results at all valid. On most occasions however when weight in excess of [illegible] g was put on the energy assimilation exceeded normal and vice-versa when weight was lost. These results were extremely variable.

In conclusion, the results obtained indicate that the breakdown of body material released in the region of 3-6 Kcal/g. No satisfactory figure could be obtained for the cost of putting on weight.

8.0 DEPRIVATION OF WATER

At the conclusion of the starvation experiments 6 voles fed on oats and 6 voles fed on wheat were deprived of water for 24 h. on two occasions. Food was supplied in a normal manner and the rest of the experimental procedure was normal.

The results obtained were difficult to analyse and, as this aspect of the voles biology has not previously been investigated, no comparative results exist. In all cases when water was removed the energy intake dropped drastically to a mean value of 3.95 Kcal/day in the case of oats fed and 3.05 Kcal/day in the case of wheat fed animals. This can be compared with a normal intake of 15.96 Kcal/day and 13.98 Kcal/day respectively. The faecal output was higher than would be expected due to faeces produced from food taken in on the previous day and this had the effect of giving an apparently lower percentage digestion and assimilation. In fact on some days the energy intake was less than the energy content of the faeces produced.

On the oats diet the reduction in energy content of the faeces compared with the normal faeces was accompanied by a drop in organic matter, where this was measured as a percentage of dry matter present. The same situation applied in the case of animals fed on wheat, but here the drop in calorific value went with a very small drop in organic content; 8.2% to 7.4% of dry matter. This would indicate that the lack of water was not lowering ~~even further~~ the voles ability to digest fat. ~~and could well be due to the higher fibre content of wheat as compared with oats.~~ Drozdz (1968a) has shown that the vole is characterised by a wide range of digestibility coefficients for different diets.

The removal of water for 24 h. resulted in a considerable weight loss, mean values of 2.5g for oats and 2.8g for wheat were recorded for each day. These results can be compared with the mean weight losses of 2.7g and 2.6g on oats and wheat during the 24 h. starvation experiments. So in spite of taking in over 3 Kcal/day the animals still lost weight in the same amounts as when their energy input had been nil. Presumably most of the weight loss in the animals deprived could be accounted for in water loss i.e. some dehydration and the lack of urine. Ideally one would require sufficient material to analyse body components at the end of the period without water. It does however illustrate the inaccuracy of assuming that all weight losses could be accounted for by the breakdown of body fat.

In the 24 h. following the lack of water the weight was quickly regained, in the case of oats a mean weight gain of 1.5g was found and 2.1g in the animals fed on wheat. In a further 24 h. the oats fed animals had made a mean gain of 2.1g and the wheat fed a gain of 2.5g. The animals fed on oats assimilated on average 11.70 Kcal/day and 12.53 Kcal/day in the 24 h. and 48 h. after the experiments. The animals fed on wheat likewise assimilated 10.47 Kcal/day and 9.04 Kcal/day. In both cases these values fall below the respective means under normal conditions which means that the animals were quite capable of putting on a considerable amount of weight (in the region of 10%) besides indulging in normal activity. This adds further to the evidence that it is very difficult when an animal loses weight to judge precisely what has been lost. Clearly water loss must play a considerable part.

9.0 THE ENERGETICS OF VOLES IN THE FIELD

Golley (1967) has been careful to point out that too much work on energetics has made far too many assumptions. Energy studies normally consist of taking a number of animals from a population and subjecting them to a series of tests whilst in a completely strange environment. The factors affecting metabolism are numerous (see Section 1.0). Findings are then extrapolated to the field and the population on the outcome of results from isolated individuals. Much of this present work was perforce of this nature but an attempt was made to determine energy intake in the field.

9.1 METHODS

(a) Animals were caught (Section 3.1) in break-back traps in Houghall Wood. They were slit open and the stomachs and their contents removed; the remainder was weighed. The stomach contents were scraped out onto a watch glass and weighed. They were then placed in an oven at 65°C and dried to constant weight. Some of the dried contents were selected and ashed in a muffle furnace. All the remaining dried samples were ground up in a pestle and mortar and their calorific content determined in the bomb calorimeter.

(b) A sample of 10 voles which had been in captivity for some time were killed at intervals during a 24 h. period. These had been on a diet of oats for 10 days and it was intended to determine from the calorific content of food in the gut the number of times they filled their gut in a day, knowing their energy requirements from previous experiments. The gut samples were treated in the same way as those recovered from animals killed in the wild.

9.2 RESULTS

(a) A total of 22 guts was analysed (Table 8) and of these 2 came from juveniles and were left out of the general calculations as their energy intake is far different from that of an adult. Using the results from the bomb calorimeter the energy content of each gut was calculated and also the calorific value of 1g. of the gut contents. A mean live weight for the twenty adults was calculated as 18.4g with a mean gut content of 1.82 Kcals. The calorific value was corrected to ash-free weight, the ash content being determined as 5.2%. The mean value for the energy content of the gut samples was 4.13 Kcal/g.

(b) The results of the laboratory animals analysed are shown in Table 9. They had a mean live weight of 15.4g and a mean value for stomach contents of 0.63 Kcal taking into account the ash content which was determined as 5.4% of the dry matter. Five complete guts were combusted in the bomb calorimeter and gave a mean value for energy content of 4.07 Kcal/g.

No attempts were made to analyse the gut contents which would have taken far too long. Food has been examined

TABLE 8

Animal	Sex	Live weight minus stomach and contents	Wet weight of stomach contents	Dry weight of stomach contents	% of dry matter	Dry ash-free weight of stomach contents	Calorific value of gut contents	Calorific value of 1g of gut contents	Comments	Date of capture
6	♂	18.1	0.993	0.445	44.81	0.422	1.66	3.96		21.5.69
15	♀	17.2								12.6.69
17	♀	16.7								12.6.69
18	♂	15.4								12.6.69
19	♂	17.2								12.6.69
25	♀	22.0	1.534	0.502	32.72	0.476	2.00	4.16		19.6.69
26	♂	22.3	0.807	0.228	28.25	0.216	0.89	4.04		20.6.69
27	♀	21.2	1.067	0.397	37.21	0.376	1.49	3.96		20.6.69
29	♂	17.0	2.239	1.062	47.43	1.007	4.81	4.54		25.6.69
30	♂	21.2	0.815	0.269	33.01	0.255	1.24	4.77		25.6.69
31	♀	21.9	1.076	0.402	37.36	0.381	1.83	4.82	Pregnant, with 4 embryos	25.6.69
32	♀	15.4	1.933	0.823	42.58	0.780	3.45	4.42		25.6.69
33	♀	28.0	1.821	0.354	19.44	0.336			Lactating	26.6.69
34	♀	9.9	1.404	0.672	47.86	0.637	3.65	5.45	Juvenile	26.6.69
35	♂	21.1	0.950	0.449	47.26	0.426	1.80	4.19		26.6.69

TABLE 8 (Contd.)

Animal	Sex	Live weight minus stomach and contents	Wet weight of stomach contents	Dry weight of stomach contents	% of dry matter	Dry ash-free weight of stomach contents	Calorific value of gut contents	Calorific value of 1g of gut contents	Comments	Date of capture
36	♀	24.3	0.470	0.133	28.30	0.126			Pregnant, with 4 embryos	26.6.69
37	♀	19.7	1.055	0.296	28.06	0.281	1.12	4.00	Lactating	26.6.69
38	♀	19.1	1.047	0.459	43.84	0.435	1.90	4.14		26.6.69
39	♂	18.3	0.826	0.325	39.35	0.308	1.14	3.67		27.6.69
40	♂	20.4	0.738	0.187	25.34	0.177	0.73	4.06		27.6.69
41	♀	18.2	1.154	0.248	21.49	0.235				27.6.69
42	♀	21.9	1.566	0.399	25.48	0.378	1.61	4.24	Lactating	27.6.69
43	♂	17.7	1.197	0.546	45.61	0.518	2.17	4.18		27.6.69
44	♀	17.2	1.268	0.338	37.51	0.320	1.47	4.60	Lactating	27.6.69
45	♂	16.9	0.803	0.223	27.77	0.211				28.6.69
46	♀	6.9	0.810	0.305	37.65	0.289	1.18	4.07	Juvenile	28.6.69
47	♀	17.8	1.202	0.450	37.44	0.427	1.85	3.92		28.6.69
48	♂	17.8	0.629	0.163	25.91	0.155	0.63	3.96		28.6.69
49	♀	17.8	1.561	0.428	27.42	0.406	1.67	4.07		28.6.69
50	♂	19.8	1.430	0.569	39.79	0.539	1.79	3.31		28.6.69

Analysis of animals killed in the wild. Organic matter expressed as percentage of dry matter. Calorific values of gut contents in Kcal, weights shown in grams.

by Miller (1954), Crawley (1965), Drozdz (1966), Ashby (1967) and Watts (1958). Watts claimed that bank voles were completely herbivorous, eating mainly the leaves of woody plants instead of herbs and finding, unlike Drozdz, little evidence for insect material. The animals used in this work had guts containing what appeared to be only green material the bulk of it in many cases being bracken. Other plant parts were obviously present and some animals complicated the situation by having eaten a considerable amount of oats (used as bait) before being captured.

9.3 DISCUSSION

The main purpose behind this work was to determine the number of times an animal filled its gut in the field and by knowing the mean energy value for gut contents determine the energy intake per day. This method was first used by Golley (1960) working on meadow voles. He caught the animals in the field and made the assumption that the average stomach content, in weight, was equal to half a full stomach, if one supposed that (a) animals were most likely to be captured during feeding trips and (b) the average animal would be caught in the middle of feeding. These suppositions seem quite valid when one is dealing with a fairly large sample as this should cover the whole range of animals from the beginning to the end of a feeding cycle. Using then the knowledge that voles filled their gut about 10 times a day it was possible to work out the food intake in the wild. Golley found a good correspondence between values in the field and laboratory. Schmid (1965) has used this technique with mourning doves and Storr (1963) used a modified method with wallabies.

In this work two further assumptions had to be made (a) although voles in captivity may not spend so much time in activity as do those in the wild they are still active and fill their gut for the same number of times and (b) they fill their gut in order to obtain the required amount of energy and not to derive some physical expression of a 'full gut.' The latter assumption may be very much in doubt but would lend itself fairly easily to examination using diets of the same calorific value but different bulk. If an animal were fed on a very concentrated diet would it feed less times per day or the same number of times taking in less weight? Activity patterns in small mammals are not easily modified and so perhaps the second course of action is the most likely. Blaxter (1962) admits that the theories for control of appetite are not entirely satisfactory. Brobeck (1957) has proposed a thermostatic theory where an animal eats in response to a fall in heat production. Kennedy (1961) and Hervey (1969) have proposed that eating occurs in response to a change in body fat. Milford (1960) working with sheep and Blaxter et al (1961) found that on low quality diets the animals did not eat enough to meet their energy requirements so that intake was not being regulated according to energy needs. Perhaps, however, it is wrong to use evidence from domestic animals, selected for such features as the ability to gain weight, and then apply it to animals in the wild. In view of the lack of evidence either way one is probably justified in accepting the view that they eat to fulfil energy requirements.

From Table 9 it should be possible to calculate how many times the voles filled their guts. The value for energy content of the gut samples at 4.07 Kcal per g is lower than that found for oats, 4.77 Kcal/g but also lower than that of the faeces, 4.95 Kcal/g. This would suggest that some high energy components are very quickly assimilated but that in all the animals examined assimilation was by no means complete. The ash value of the gut contents (5.4%) would also agree with this view, being higher than that of the food (2.1%) but much lower than the faeces (18%). So it was necessary to make a correction to the gut contents to allow for assimilation and the value of 90% was used. It was then possible to calculate the number of times the gut was filled assuming they were only half full when the animal was killed.

TABLE 9

Animal	Sex	Live weight minus stomach and contents	Wet weight of stomach contents	Dry weight of stomach contents	% of dry matter	Ash-free weight of stomach contents	% of organic matter	Time killed. Hours in B.S.T.	Calorific value of gut contents
II	♂	16.4	0.375	0.159	42.4	0.150	94.3	09.00	0.61
I	♂	15.4	0.658	0.039	5.9	0.037	94.9	11.00	0.15
III	♀	15.7	1.012	0.405	40.0	0.383	94.6	13.00	1.56
VI	♂	16.6	0.715	0.076	10.6	0.072	94.7	15.00	0.29
V	♂	16.6	0.475	0.103	21.7	0.097	94.1	17.00	0.39
VIII	♂	13.7	0.621	0.102	16.4	0.096	94.1	19.00	0.39
VII	♂	15.8	0.673	0.068	10.1	0.064	94.1	21.00	0.26
X	♂	16.8	1.077	0.260	24.1	0.246	94.6	23.00	1.00
IX	♂	12.6	1.453	0.299	20.6	0.283	94.6	07.00	1.15
XI	♂	14.0	0.876	0.127	14.5	0.120	94.5	10.00	0.49

Analysis of animals killed in captivity. Organic matter expressed as percentage of dry matter. Calorific values in Kcal, weights in grams.

1. Energy flow on a diet of oats is 0.73 Kcal/g/day energy requirements for a vole weighing 15.4g is 15.4 x 0.73 Kcal/day.
2. Full gut contents equal 0.63 x 0.9 x 2.0 Kcal.
3. Therefore the gut is filled $\frac{11.24}{1.14}$ times.
4. In captivity the vole fills its gut 10 times a day.

Quite a lot of work has been done on activity in voles which may be of help here. Miller (1955), Brown (1956a), Osterman (1956), Saint-Girons (1960, 61), Pearson (1962) and Kikkawa (1964) have all examined this problem in the field and laboratory. From Pearson's paper one obtains the value of 45% of the day spent in activity and Kikkawa points out that much of the day is spent out of the nest. Saint-Girons however has data showing that males fill the stomach about 11 times a day and females 9 times. So a value obtained in this work of 10 times a day would seem quite reasonable.

Using this value of 10 it was possible to work out the energy intake in the wild. The ash content of 5.2% gave a corrected mean energy value for stomach contents of 1.76 Kcal. By the same reasoning as before it was assumed that assimilation had not occurred and a figure of 80% was taken in view of the large amount of green material present. With a mean weight of 19.4g it meant that in the field the energy intake was:

$$\frac{1.76 \times 0.8 \times 20}{19.4} \text{ Kcal per g per day}$$

or 1.45 Kcal/g/day.

The value was twice that of the energy flow determined for the animals living in the laboratory and obviously indicates much greater energy expenditure in the wild. It must also be remembered that a number of the animals were pregnant or lactating and this would have greatly increased their energy requirements. Kaczmarski (1966) has shown that a pregnant bank vole will take in 24% more energy and a lactating one needs 92% more. On the whole the breeding season increases the demand by 58%. Taking just the males in Table 8 gave a fractionally lower value of 1.38 Kcal/g/day. The values obtained with juveniles are not sufficient to draw any worthwhile conclusions but would indicate a higher food intake per gram body weight than is found in the adults.

One final point worth mentioning is the wide range of water contents and of calorific value of 1 gram of the gut contents. Although there is some effect from the different stages of assimilation attained, they also reflect the different foods and different relative amounts present.

9.4 IMPACT ON WOODLAND PRODUCTIVITY

Drozdz (1967) found that the net productivity in beech woodland in Poland was of the order of 44,000 Kcal/m^2/year. Which, if true of Britain, would mean that the voles are taking a very small percentage of the year's production.

This illustrates that a measure of energy is not sufficient in evaluating the role and importance of any animal in the ecosystem. Of this total production only a small amount is available as food to the voles and, as Ashby (1967) has shown, the effect of small rodents on woodland regeneration is considerable because they eat tree seeds and seedlings. Turcek (1967) has found that the bank vole in Poland is capable of consuming 30% of a beech seedling crop in addition to eating the seeds. So although the amount of energy flowing through the vole population may be small, they play a highly important part in the woodland ecosystem by removal of a vital component. The practical influences of this seemingly unimportant animal must not be ignored.

10.0 CONCLUSIONS

The conclusions reached as a result of the present study will be found at the end of each section and in the summary, but it is worthwhile indicating the ways in which the work could have been improved.

The two major omissions in the work were a method of measuring activity, especially in view of the different energy flow on different diets, and greater analysis of food and faeces. Faecal analysis would have contributed much to the section on starvation and deprivation of water, in particular with regard to the ability to digest fat on various diets. Collection of the urine produced would also have been of interest. The starvation experiments would have been more meaningful if sufficient material had been available for analysis of whole body constituents at the end of a starvation period. Many more repeats are needed of the short fasting experiment and in view of the apparent change in percentage digestion and assimilation the speed of movement of food through the gut under different conditions should be determined. The use of Conover's formula where it is assumed that no inorganic matter is assimilated, by comparison with assimilation determined from faecal and urine energy loss, might allow the determination of inorganic needs. It was obvious that the effect of grouping depends very much on the species and size of animal. The time of year and the consequent variation in social behaviour must also play a part. Here again further analysis of faeces and activity is needed.

It has been stressed all along that there is probably little correlation between results obtained in the abnormal laboratory conditions and those pertaining to the field. Field techniques are obviously difficult to develop but it is on this branch of animal energetics that I feel much more work should be concentrated.

11.0 SUMMARY

1. Energy flow in the bank vole, *Clethrionomys glareolus*, was examined in the laboratory using the "balance method" of investigation.
2. Daily energy budgets were calculated on four different diets, oats, wheat, acorns and bluebell corms using calorific values determined with a bomb calorimeter.
3. Faeces produced accounted for an energy loss of 5.83-20.27% depending on the diet. Faeces were always of higher calorific value than the food on which the animal was maintained, therefore it would appear that with the diets examined the voles could digest little fat.
4. Energy flow, measured in Kcal/g live weight, was found to vary between 0.43-0.73 depending on the diet. As weight change was similar on all diets it is suggested that activity may vary.
5. A correlation was shown between body size and energy intake per day.
6. Voles living in pairs had lower values for energy flow. They showed a correlation between body size and energy intake per day. The relationship was different to that of the voles living singly.
7. Analysis of water, ash and fat content of the whole body confirmed that the percentage of metabolically active material shows variation.

8. Water loss was shown to play an important part in weight change. No suitable value could be given for the energy released by tissue breakdown or for the energy cost of depositing new material.
9. Voles in the field were found to have much greater values for energy flow: in the region of 1.4 Kcal/g/day.
10. The validity of energetic studies in the laboratory and their relationship to energetics in the field is questioned.

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APPENDIX

In the following section all weights given are in grams.

TABLE A

	A	B	C	D	E
Wet weight	5.576	4.896	5.130	5.843	6.837
Dry weight	4.969	4.418	4.545	5.210	6.063
% dry matter	89.1	90.2	88.6	89.2	88.7
% water	10.9	9.8	11.4	10.8	11.3
Dry weight	6.055	3.681	5.893	6.380	3.402
Ash weight	0.198	0.111	0.144	0.191	0.130
% organic matter	96.7	97.0	97.5	97.0	96.2
% ash	3.3	3.0	2.5	3.0	3.8

Analysis of oats.

TABLE B

	A	B	C	D	E
Wet weight	5.833	6.776	5.395	4.751	6.477
Dry weight	5.288	6.109	4.847	4.266	5.814
% dry matter	90.7	90.2	89.9	89.8	89.8
% water	9.3	9.8	10.1	10.2	10.2
Dry weight	5.007	5.769	4.685	5.028	5.828
Ash weight	0.124	0,143	0.134	0.135	0.149
% organic matter	97.5	97.5	97.1	97.3	97.4
% ash	2.5	2.5	2.9	2.7	2.6

Analysis of wheat.

TABLE C

	A	B	C	D	E
Wet weight	9.745	9.167	7.045	7.897	8.254
Dry weight	5.792	5.449	4.236	4.762	4.975
% dry matter	59.4	59.4	60.1	60.3	60.3
% water	40.6	40.6	39.9	39.7	39.7
Dry weight	5.446	4.790	6.508	4.316	4.331
Ash weight	0.155	0.135	0.225	0.120	0.123
% organic matter	97.2	97.2	95.5	97.2	97.2
% ash	2.8	2.8	3.5	2.8	2.8

Analysis of acorns.

TABLE D

	A	B	C	D	E
Wet weight	5.778	3.904	5.543	5.265	5.395
Dry weight	1.673	1.093	1.572	1.644	1.438
% dry matter	29.0	28.0	28.4	31.2	26.7
% water	71.0	72.0	71.6	68.8	73.3
Dry weight	1.149	1.577	1.600	1.724	1.562
Ash weight	0.026	0.030	0.038	0.034	0.030
% organic matter	97.7	98.1	97.6	98.0	98.1
% ash	2.3	1.9	2.4	2.0	1.9

Analysis of bluebell corms.

TABLE E

	A	B	C	D	E
Wet weight	0.613	0.385	0.241	0.200	0.315
Dry weight	0.457	0.288	0.174	0.148	0.234
% dry matter	74.6	74.8	72.2	74.0	74.3
% water	25.4	25.2	27.8	26.0	25.7
Dry weight	0.155	0.241	0.182	0.270	0.467
Ash weight	0.029	0.042	0.034	0.048	0.081
% organic matter	81.3	82.6	81.3	82.2	82.7
% ash	18.7	17.4	18.7	17.8	17.3

Analysis of faeces produced by voles living singly.
Fed on oats.

TABLE F

	A	B	C	D	E
Wet weight	0.614	0.665	0.619	0.441	
Dry weight	0.359	0.352	0.322	0.256	
% dry matter	58.4	52.9	52.0	58.0	
% water	41.6	47.1	48.0	42.0	
Dry weight	0.310	0.191	0.511	0.189	0.358
Ash weight	0.044	0.027	0.076	0.026	0.049
% organic matter	85.8	85.9	85.1	86.2	86.3
% ash	14.2	14.1	14.9	13.8	13.7

Analysis of faeces produced by voles living in pairs.
Fed on oats.

TABLE G

	A	B	C	D	E
Wet weight	0.562	0.782	0.488	0.556	0.550
Dry weight	0.344	0.487	0.292	0.302	0.292
% dry matter	61.2	62.3	59.8	54.3	53.1
% water	38.8	37.7	40.2	45.7	46.9
Dry weight	0.392	0.202	0.258	0.667	0.212
Ash weight	0.038	0.022	0.026	0.059	0.023
% organic matter	90.3	89.1	89.9	91.2	89.2
% ash	9.7	10.9	10.1	8.8	10.8

Analysis of faeces produced by voles living singly.
Fed on acorns.

TABLE H

	A	B	C	D	E
Wet weight	0.663	0.920	0.950	1.112	0.699
Dry weight	0.408	0.544	0.591	0.683	0.458
% dry matter	61.5	59.1	62.2	61.4	65.5
% water	33.5	40.9	37.8	38.6	34.5
Dry weight	0.681	0.456	0.587	0.406	
Ash weight	0.057	0.043	0.043	0.032	
% organic matter	91.6	90.6	92.7	92.1	
% ash	8.4	9.4	7.3	7.9	

Analysis of faeces produced by voles living in pairs.
Fed on acorns.

TABLE J

	A	B	C	D	E
Wet weight	0.791	0.513	0.255	0.187	
Dry weight	0.610	0.390	0.195	0.142	
% dry matter	77.1	76.0	76.5	75.9	
% water	22.9	24.0	23.5	24.1	
Dry weight	0.266	0.253	0.275	0.236	0.378
Ash weight	0.024	0.017	0.023	0.021	0.031
% organic matter	91.0	93.3	91.6	91.1	91.8
% ash	9.0	6.7	8.4	8.9	8.2

Analysis of faeces produced by voles living singly. Fed on wheat.

TABLE K

	A	B	C	D
Wet weight	0.598	0.579	0.532	1.042
Dry weight	0.437	0.430	0.364	0.753
% dry matter	73.1	74.3	68.4	72.3
% water	26.9	25.7	31.6	27.7
Dry weight	0.836	1.221	0.537	
Ash weight	0.076	0.105	0.056	
% organic matter	90.9	91.4	89.6	
% ash	9.1	8.6	10.4	

Analysis of faeces produced by voles living singly. Fed on bluebell corms.

TABLE L

	A	B	C	D	E	F	G	H
Wet weight	0.213	0.389	0.153	0.178	0.161	0.105	0.191	0.183
Dry weight	0.183	0.342	0.129	0.151	0.137	0.092	0.166	0.159
% dry matter	85.9	87.9	84.3	84.8	85.1	87.6	86.9	86.9
% water	14.1	12.1	15.7	15.2	14.9	12.4	13.1	13.1
Dry weight	0.255	0.340	0.342			0.419		
Ash weight	0.032	0.045	0.042			0.063		
% organic matter	87.5	86.8	86.7			85.0		
% ash	12.5	13.2	12.3			15.0		

Analysis of faeces produced by voles living singly. Fed on oats, columns A-E after 24 h. with no water. Columns F-H are the subsequent 24 h. on normal diet.

TABLE M

	A	B	C	D	E	F	G	H
Wet weight	0.161	0.358	0.213	0.335	0.324	0.275	0.234	0.489
Dry weight	0.150	0.325	0.196	0.205	0.209	0.170	0.150	0.292
% dry matter	93.2	90.8	92.0	61.2	64.5	6.18	64.1	59.7
% water	6.8	9.2	8.0	38.8	35.5	38.2	35.9	40.3
Dry weight	0.326	0.323		0.411	0.594			
Ash weight	0.026	0.022		0.040	0.060			
% organic matter	92.0	93.2		90.3	89.9			
% ash	8.0	6.8		9.7	10.1			

Analysis of faeces produced by voles living singly. Fed on wheat, columns A-C after 24 h. with no water. Columns D-H are the subsequent 24 h. on normal diet.

TABLE N

	A	B	C	D
Wet weight	0.110	0.122	0.330	0.324
Dry weight	0.088	0.106	0.211	0.203
% dry matter	90.0	86.9	63.9	62.7
% water	10.0	13.1	36.1	37.3
Dry weight	0.093	0.085	0.219	0.208
Ash weight	0.018	0.016	0.039	0.032
% organic matter	80.6	81.2	82.2	84.6
% ash	19.4	18.8	17.8	15.4

Analysis of faeces produced by voles living singly in starvation experiments where previously fed on oats.

TABLE P

	A	B	C	D
Wet weight	0.098	0.091	0.404	0.351
Dry weight	0.078	0.070	0.297	0.257
% dry matter	79.6	76.9	73.5	73.2
% water	20.4	23.1	26.5	26.8
Dry weight	0.086	0.072	0.300	0.260
Ash weight	0.012	0.003	0.026	0.021
% organic matter	86.0	85.8	91.3	91.9
% ash	14.0	14.2	8.7	8.1

Analysis of faeces produced by voles living singly in starvation experiments where previously fed on wheat.

TABLE Q

Diet			
Oats		Wheat	
Weight	Weight change	Weight	Weight change
18.5	- 2.8	17.5	- 3.3
18.4	- 3.5	17.4	- 2.9
15.3	- 3.0	16.0	- 4.3
16.4	- 1.9	23.3	- 3.0
15.5	- 3.3	23.1	- 3.0
20.7	- 2.2	17.4	- 2.7
20.4	- 3.1	20.4	- 1.9
20.7	- 2.8	19.9	- 2.8
18.3	- 2.6	20.3	- 2.9
18.3	- 1.8		
17.1	- 2.4	14.5	+ 1.5
		20.3	+ 2.8
15.7	+ 2.0	18.5	+ 1.4
18.5	+ 1.9	19.3	+ 1.0
14.5	+ 1.0		

Weight changes during starvation experiments.
Animals fed previously on oats and wheat.