Energy utilization and activity patterns of the vole arvicola terrestris amphibius (l)

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ENERGY UTILIZATION AND ACTIVITY PATTERNS OF THE VOLE ARVICOLA TERRESTRIS AMPHIBIUS (L.)

By

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PREFACE

This thesis is submitted for the degree of Doctor of Philosophy in the University of Durham. The research described was carried out in the Department of Zoology, Durham, during the period from October 1970 to September 1973 under the supervision of Dr. K. R. Ashby.

My thanks are due to the Natural Environment Research Council for the financial support of a Research Studentship and to Professor D. Barker of the Department of Zoology, Durham, for the provision of research facilities.

I should like to express my gratitude to Dr. K. R. Ashby for his helpful advice and support over the period of this research and to Dr. J. C. Coulson and Dr. P. R. Evans of the Department of Zoology, Durham, for their advice and encouragement. I am indebted to Dr. K. Bowler of the Department of Zoology, Durham, and to Dr. M. Gębczyński of the Mammals Research Institute, Bialowieża, for their advice on the use of the Kalabukhov-Skvortzov respirometer and to Mr. D. A. L. Wilson of the Department of Mathematics of the University of Aston in Birmingham for his advice on statistical method. Finally, I should like to thank all those friends and colleagues who have supported me by their advice and constant encouragement.

To the best of my knowledge the work described in this thesis is original except where reference has been made to the work of others. No part of this thesis has been previously submitted for any degree, diploma or other qualification at this or any other University.

M. A. Vincent.

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May 1974.

ABSTRACT

The energy assimilated by a small population of _Arvicola terrestris amphibius_ (L.) occupying a 380m stretch of stream in south Durham was calculated by quantifying the parameters of population respiration and tissue production and was subsequently related to the available food supply.

The changes in population density, size and age structure were monitored by frequent live-trapping over the entire calendar year and an assessment was made of the population structure and tissue production over consecutive periods of twenty days. The temperature and above-ground activity experience of representatives of the population were investigated implementing artificial burrow systems built into outdoor enclosures under simulated stream conditions. The pattern of day to day activity was monitored by recording thermographs which registered the temperature changes in vole nests caused by the intermittent presence of the animal's body heat. Nest chamber and soil surface temperatures were recorded concurrently. The patterns of vole activity were analysed and related to conditions of social inter-reaction and to variations in weather parameters. The oxygen consumption of representative members of the population was investigated at a range of experimental temperature during periods of both rest and activity by means of a closed-circuit respirometer. The population respiration demand was estimated over consecutive periods of 20 days with corrections included for the seasonal variation in population size and age structure, ambient temperature and the proportion and quality of above-ground activity. The available food supply was estimated by regular sampling of the vegetation within the feeding range in conjunction with an

investigation of the rate of plant decomposition. The feeding preferences of the population were examined and the energy flow between primary and secondary production deduced.

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SMALL MAMMAL ENERGETICS

INTRODUCTION 1: SMALL MAMMAL ENERGETICS

The role and importance of rodent populations as a component in the total energy flow through natural ecosystems has received increasing attention over the past decade. Golley (1960) described the energy budget of the vole Microtus as twice its Fasting Metabolic Rate, a model modified by Wiegert (1961) who included a correction for the effect of body size on the rate of metabolism. McNab (1963) considered the effect on rodent metabolism of the wide range of temperature encountered by wild populations and of their complex patterns of activity and behaviour. Contemporary ecological knowledge of these phenomena however could not satisfy the requirements of McNab's (1963) theoretical model and much subsequent research has been directed into the assessment of the influence of temperature, activity and behaviour upon rodent metabolism.

Macfadyen (1967) states that the purpose of investigation into the energy flows through ecosystems is "to compare the overall energy flow throughout whole populations in order to assess the relative importance of competing species within a trophic level, of successive levels in an ecosystem, and of one ecosystem with another".

The principal equations of energy transference by animal populations are those described by Petrusewicz and Macfadyen (1970) where:

1) Energy Assimilated = Energy Consumed as food - Energy rejected by the organism as faeces and urine.

2) Energy Assimilated = Energy employed in Production + Energy used in Respiration.

where Production is defined as energy accumulated by a population through growth and reproduction, and Respiration as that energy taken in as food which is converted into heat and dissipated in the life process: all parameters applying to a defined period of time.

In wild populations of rodents Equation 1 has been difficult to solve as it has not been found possible to measure the calorific content of food consumed nor to measure that of food consumed but later rejected as faeces and urine. In consequence the estimation of Assimilated Energy in the present study has been considered by the evaluation of the components in Equation 2. This equation has the added advantage of allowing consideration of those factors influencing the channelling of assimilated energy into Production and Respiration, a consideration not possible from any field assessment of the components in Equation 1 up to this time. Indeed this has largely eluded even laboratory estimations of this equation under carefully selected environmental conditions. However Equation 2 allows of no assessment of the efficiency of energy assimilation from initial consumption and only by the use of controlled laboratory techniques in solving Equation 1 have Drożdż (1968) and Drożdż et al. (1971) been able to demonstrate that not only does the efficiency of assimilation vary considerably between rodent species and food sources but that this efficiency may alter seasonally with the changing quality of the food.

Taken together Equations 1 and 2 can be expressed as Equation three:

3) Energy used for Production + Energy used for Respiration = Energy consumed x Efficiency of Assimilation.

Chew and Chew (1970) state that on an annual basis 14% of the energy used for respiration in the Kangaroo Rat <u>Dipodomys merriami</u> Mearns was used for active work and 86% was utilized in the body functions and in thermoregulation. Consequently an examination of rodent activity and its effect upon the rate of respiration is necessary before laboratory data on a wild species can be extrapolated to natural populations. In his review on the activity patterns of small mammals Crowcroft (1953) observed that the duration of the short-term feeding rhythm in small mammals is proportional to the size of the animal and Grodziński and Górecki (1967) quote a variety of authors to support a statement that herbivorous rodents are active for a greater proportion of the day than granivorous ones, those with a diet incorporating a mixture of the two food types occupying an intermediate position, and that the duration of daily activity in summer generally exceeds that in winter.

While it is unlikely that rodents under natural conditions reflect the figures of Janský (1959) that the metabolic rate during short term exercise can exceed the Basal Metabolic Rate by as much as seven times in the vole Clethrionomys glareolus, Górecki (in litt. in Grodziński and Górecki, 1967) has shown that under laboratory conditions C. glareolus regularly demonstrates a ratio of maximum to minimum respiration values of 2.1 during its daily, unstimulated activity cycle. It is therefore imperative that in an estimate of the energy used for respiration in Equation 3 that the duration and intensity of the animal's daily activity and resting phases be accurately quantified on both a short-term and seasonal basis.

The relationship between respiration rate and body-size in mammals is generally considered to be one represented by the expression:

$$Y = W^a$$

where Y represents the metabolic parameter, W = Bodyweight, 'a' = a power of the order of 0.75 (Petrusewicz and Macfadyen, 1970), although other authors have suggested values for 'a' ranging from 0.55 to 0.75 (Brody, 1945; Kleiber, 1961; Hansson and Grodziński, 1970). Grodziński and Gōrecki (1967) compared the respiration rates of rodents whose movements were restricted by small wire-mesh containers, Resting Metabolic Rate, and those whose free movement was permitted and which were allowed to engage in many of their natural daily activities, Average Daily Metabolic Rate. They found that the negative correlation of bodysize to respiration per unit weight of A.D.M.R. to be less significant than the corresponding correlation measured for R.M.R. and that the gradient of the regression line of A.D.M.R. was less steep. This may suggest that the energy expended in muscular activity may have an important function in reducing the energy required by small mammals for thermoregulation, especially at low environmental temperatures.

The effect of environmental temperature on respiration rate may be illustrated by the work of Gōrecki (1966) on the vole Clethrionomys glareolus Schreber and Gębczyński (1966) on the mouse Apodemus flavicollis Melchior which shows that the respiration rate of both species is approximately double at 5°C. what it is at 30°C. This increase may be less marked in winter (Gębczyński, 1966; Grodziński and Gōrecki, 1967) when in different rodent species the insulation afforded by the thicker winter pelage is increased by 5 - 13%. (Grodziński and Gorecki, 1967), and in certain American rodents the increase may be even greater (Hart, 1956).

The environmental temperature experienced by many rodents is much modified by the ameliorating influence of the underground burrow and nest chamber in which they pass by far the major proportion of their lives. Daniel (1964) determined the temperature of the upper part of the nest cavity of C. glareolus for a period during the breeding season in Czechoslovakia to vary little between 17 - 19°C which according to Kalabukhov (Kalabukhov, 1957; in Grodziński and Górecki, 1967) lies close to the preferred temperature of this vole of 18 - 23°C.

Not only is the poor temperature exchange between nest chamber and the exterior of value to the animal in reducing daily and seasonal variability in this parameter but the rodent itself can more actively influence the temperature it experiences by the manner in which it creates and utilizes the nest itself. Trojan (1969) discussing this activity with respect to the vole Microtus arvalis Pallas states,

> "When temperatures are low, the animals build their nests carefully and the energy saved in this way amounts to more than 30% of R.M.R. In the thermoneutral zone nests are built without due care and their insulating role is three times less. At temperatures of 25 - 30°C hole-nesting animals do not use their nests and very often destroy them."

In this way small rodents are able to retain the body heat they themselves are producing in an air barrier between their bodies and the cooler walls of the nest chamber, thereby raising the ambient temperature of their immediate environment and reducing the energy cost of body temperature regulation.

The temperature of the nest chamber is also affected by the numbers and biomass of animals remaining in the nest. This is so both when a number of animals sleep at a distance from one another in the same chamber by simply increasing the temperature of the chamber itself but, more especially, when several animals huddle together thereby experiencing on one or more sides the surface body temperature of their fellows, this acting in concert with the straightforward rise in nest chamber temperature mentioned previously. Ponugaeva (Ponugaeva, 1960 in Grodziński and Górecki, 1967) kept a variety of voles, mice and rats in groups of from 3 - 5 animals and recorded a decrease in R.M.R. of between 8 - 17% on animals kept singly. Trojan (1969) found that the huddling effect of 7 - 8 individuals of <u>Microtus arvalis</u> rendered the animal's maintenance costs almost independent of experimental temperatures, at least to temperatures as low as 5°C.

It is clear that an appreciation of the respiration costs of a rodent population requires investigation not only into the age structure of the population but also into the relative expense of periods of activity undergone at the temperature of the bank surface and also of the periods of lower activity and sleep taking place within the confines of an insulating nest which may be occupied by more than one individual. Some examination of these basic parameters is a pre-requisite for any possible extrapolation from laboratory data to wild populations.

Periods of active tissue growth in members of a population can also affect their respiration rate especially as Production/Assimilation efficiencies may change dramatically within a short space of time. Migula (1969) working on the vole Microtus arvalis found that the production of newborn young by the female indicated a production efficiency of 11.5%, and if the production of the placentae and membranes was included of 13.9%, this being increased during the period of lactation to 15.4%. Pearson (1962) notes that the rate of development of young voles changes during the period of lactation, being nearly twice as high during the second half as during the first, there being a sharp rise at about the twelfth day of postnatal life when the young begin to see and move around.

The energy assimilated by the female increases during pregnancy in the vole Clethrionomys glareolus by 24% and during lactation by 92% (Kaczmarski, 1966) even when lactation and subsequent pregnancy do not overlap, and even higher figures are reported by Migula (1969) for M. arvalis. This increase in assimilation is reflected by an increase in respiration for M. arvalis of 9.9% during pregnancy and of 20.4% during lactation (Trojan, 1969).

The cost of reproduction of several litters annually to the females of wild rodent populations represents a considerable increase in energy assimilation over their non-breeding state. Changing production efficiencies in adult and juvenile animals will also affect their energy consumption, while the reduction of juvenile thermoregulation costs effected by the high body temperature of the nursing mother and also, increasingly as they grow, of their siblings is a reality which cannot be ignored when wild populations are considered; this over and above the simple changes in biomass that result from growth and reproduction.

When these factors are considered the study of a wild rodent population will require investigation into the importance of the following parameters in order to produce a satisfactory estimate of the Energy required for Respiration and Production.

1. The Production of a wild population for a defined unit area over a defined interval of time.

2. An estimation of the Age, Weight and Sexual Status of that population during that interval of time.

3. The effect of 2. on individual and population Respiration rate.

4. The ambient temperatures experienced by the population during that interval of time and their effect on Respiration rate.

5. The effect of activity and rest on Respiration rate and their relationship to ambient temperature.

The purpose of the present work is to examine these parameters as they will affect a wild population of the water vole[*] *Arvicola terrestris amphibius* (L.) occupying the banks of a small, slowly-flowing, lowland stream in South Durham and, if possible, to assess the significance of its feeding upon its energy source, the marginal vegetation of those banks.

[*] Note on nomenclature: The names *Arvicola amphibius* and *Arvicola terrestris* were published simultaneously by Linnaeus (1758) with *A. terrestris* occurring above *A. amphibius* on the same page but Blasius (1857) considered the two conspecific and his revision directed the use of *Arvicola amphibius* citing *terrestris* as a synonym. In Britain *Arvicola amphibius* has been regarded as an endemic species by Miller (1912) and Barrett-Hamilton & Hinton (1914), distinguished from *A. terrestris* of the European mainland by its large size, orthodont incisors and narrow nasals. The northern Scottish variety characterised by its smaller size and totally black pelage was described by Miller 1910 as the subspecies *A. a. reta*, and a variety in Yorkshire characterised by more pro-odont incisors was described by Thomas 1928 as the subspecies *A. a. brigantium*.

The *Arvicola* of continental Europe have likewise become regarded by some authors as representing a number of different species and sub-species, the three principal types being *Arvicola terrestris* L. of Northern Europe, *A. sapidus* Miller of France and Iberia, and *A. scherman* Shaw of the Upper Rhine and the Alps.

Heim de Balsac and Guislain (1955) separated *A. sapidus* from *A. scherman* on the shape of the baculum while Matthey (1955, 1957) gave a chromosome count of 2n=40 for *A. sapidus* and 2n=36 for *A. terrestris*. Similarly Reichstein (1963) from investigations of the proportions of the cranium regarded *A. sapidus* as specifically distinct from *A. terrestris*, *amphibius* and *scherman* on the basis of the width of the nasals, and also in the difference in size between *A. sapidus* and the other forms where the two occur together in the same locality.

Brink (1967) considers the external differences between *A. sapidus* and *A. amphibius* to be very small and on the chromosome count of Matthey (1955, 1957) and on the size differences between these and the *A. terrestris*, *A. scherman* group, body weight 150-280 g. as against 80-205 g., tail length 98-144 m.m. against 56-104 m.m., and length of hind feet 29-39 m.m. against 23-31 m.m.,[*] separates them into the single species *Arvicola amphibius*. Brink (1967) includes *scherman* and *terrestris* together with *reta* and *brigantium* in a second species, *A. terrestris*.

Although there is some doubt as to the number of

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[*] Except where otherwise stated in the text details of size and weight are reported according to van den Brink (1967).

chromosomes of A. amphibius, Corbet et al. (1970) have demonstrated that A. amphibius cannot be separated from either the subspecies reta or brigantium nor from the forms terrestris or scherman on the large variety of skull parameters that he examined whereas A. sapidus clearly distinguished itself from all the above types and on these grounds was regarded as a separate species. If the remainder are conspecific then according to the current International Code of Zoological Nomenclature, 1961, the usage of the first reviser should be followed and not original line priority, giving A. amphibius precedence over A. terrestris.

However in every subsequent revision the name terrestris has been given whenever the types have been considered conspecific and as Corbet et al. (1970) point out an attempt at reversion to the original amphibius would only admit unnecessary confusion especially as many Continental workers refer to the animal as terrestris.

In the present study the use of terrestris as the specific name is acknowledged but amphibius is retained as the subspecific. This usage allows a means of distinguishing the usual English form both from the subspecific A. t. reta and A. t. brigantium, and from the European sub-species A. t. terrestris and A. t. scherman which, especially the latter, are not only considerably smaller but may also show a behavioural difference in their greater independence from water coupled with a preponderently subterranean mode of life. (Bernard and Bollaerts, 1960; Myllymäki, 1969). When considered in relation to food energetics these behavioural differences together with the markedly altered diet they necessitate, represent a divergence between the English and Continental forms which would not be sufficiently emphasised if they were to be regarded as taxonomically identical.

INTRODUCTION 2

THE GENUS <u>ARVICOLA</u>

INTRODUCTION 2: THE GENUS ARVICOLA

The genus Arvicola occurs widely in the Palaearctic north of the Himalayas. It is common throughout Europe and Siberia extending southwards through Asia Minor into Syria and Iran (Barrett-Hamilton and Hinton, 1911; Ellerman, 1940), and although principally a lowland animal its range nevertheless includes the moors of Scotland up to 2,000' and the Alps up to 4,000'. Economically it is of some importance in continental Europe where it has been known to cause damage to dykes in Holland (van Wijngaarden, 1954) and to become a serious threat to bulb nurseries and orchards (van Wijngaarden, 1954; Bernard and Bollaerts, 1960; Tahon, 1970; Meylan and Morel, 1970; Hamar et al., 1970a) where the habit of the subterranean form A. terrestris scherman of burrowing along a line of fruit trees feeding almost entirely on their roots has been known to destroy substantial areas of young plantations. In Russia Arvicola is the largest reservoir of Brucella tularensis (McCoy and Chapin) which may be transmitted to man as the acute infectious disease Tularaemia. Van Wijngaarden (1954) notes that in 1953 a case of this disease was diagnosed in Holland. Although the symptoms resemble bubonic plague, the fatality in man is less than 5%. The importance of Arvicola in Europe has prompted investigations on its habitat and feeding (van Wijngaarden, 1954; Kraft, 1960; Bernard and Bollaerts, 1960;

Panteleev, 1962; Holišová, 1965, 1970; Zedja and Zapletal, 1969; Tahon, 1969), on distribution and dispersal (Panteleev, 1962; Pelikán and Holišová, 1969, Hamar et al.,1970a; Morel and Meylan, 1970; Pelikán et al., 1971; Zejda, 1972), and on activity (van Wijngaarden, 1954; Nikolaev and Chertova, 1962).

In Britain the natural history of A. t. amphibius has been described by Barrett-Hamilton and Hinton (1911), Ryder (1962), Southern (1964) and Corbet (1966). Perry (1943) demonstrated the seasonal changes in reproductive state in a sample taken principally from Shropshire, Hertfordshire and Perthshire and calculated the change in litter size through the summer. Worrall (1964) and Stoddart (1968, 1970) assessed home range and seasonal dispersal in Hertfordshire and Aberdeenshire respectively, while the latter also investigated breeding, young survival and the structure of the scent-producing flank organ (Stoddart, 1968, 1971, 1972).

Impens et al. (1965) suggested that the voles became inactive for periods during the coldest spells of the winter and interpreted these as periods of hibernation, whereas this reduction in activity, especially in Northern Europe and Scandinavia where the winters may be severe, may be caused by a disinclination for activity on the surface. Myllymäki (1969) describes a change in the behaviour of the vole in southern Finland which in spring "forages above the ground, feeding on the green parts of plants, but otherwise living in their underground tunnel systems. In autumn a change to a wholly subterranean life habit takes place.'

In Britain Stoddart (1965) recorded abnormally low trap catches during winter and suggested that a partial change to a subterranean mode of life might afford the explanation but little is known in detail of the behavioural reactions of *A. t. amphibius* to the milder winters of southern Britain.

Although most authors have considered *Arvicola* to be active during both day and night the published work is largely contradictory. Van Wijngaarden (1954), Stoddart (1969b) and Lund (1970) describe a diurnal and crepuscular preference while Ashby et al. (1969) report a more even diel pattern with minima at midday and early evening and Duckett (unpubl.) found a markedly nocturnal preference, at least with regard to range exploration. Ashby (1972) in a review of activity patterns in small mammals points out the variability demonstrated by mice and voles under natural conditions and Duckett (unpubl.) considered *Arvicola* to change the intensity of its periods of activity in response to changes in photoperiod.

The work of Daniel (1964), who investigated the microclimate experienced by the vole *Clethrionomys glareolus* within its nest during the breeding season, does not appear to have stimulated similar study of burrow temperatures throughout the year. Soil temperature data is inapplicable in this respect as it takes no account of the effect of the blocking and unblocking of tunnel exits on ventilation, the insulating effect of the nest or, especially, the effect of the heat output of the occupying animal itself.

A detailed knowledge of the duration and timing of *Arvicola* activity, the quality and intensity of that activity, and the thermal experience of the vole both in and outside the nest is required from animals under fairly natural conditions for an investigation of how any parameter of metabolism responds to natural changes during each day and season. Although Drożdż et al. (1971) have assessed both Resting Metabolic Rate (R.M.R.) and Average Daily Metabolic Rate (A.D.M.R.) of *A. t. terrestris* under laboratory conditions the data necessary for relating these results to the wild condition are as yet unavailable.

The present study investigates these parameters and relates them to laboratory metabolism data and subsequently combines the results in an estimation of the energy flow of a wild population. The results are presented in the following order.

1. The diel and seasonal activity pattern of *A. t. amphibius*.
2. The variety and intensity of external activity.

3. The daily and seasonal temperature experience of <u>A. t. amphibius</u>.
4. A wild population; seasonal changes in the population and an estimate of annual production.
5. Respiratory cost for the parameters of size, temperature, activity and sexual state.
6. The vegetation within the feeding range; floristic composition and an estimate of primary production.
7. An analysis of the diet of the vole population; seasonal variation.
8. The Energy Flow of the vole population.

All the work in the present study was carried out in lowland County Durham between latitudes 54°37' - 54°46'N and longitudes 1°34' - 1°35' and between altitudes 60m (200') - 75m (250').

The local climate is one of modified cyclonic Western European Maritime, characterised by relatively mild winters and cool, cloudy summers, the basic parameters of mean temperature, rainfall and sunshine are set out in Table 1. The figures are taken from data presented by the Durham Observatory, Lat. 54°46'N., Long. 1°35'W., Altitude 102m (336') above Ordnance Datum.

TABLE 1.

MONTHLY WEATHER PARAMETERS FOR DURHAM CITY.

Monthly Averages	Mean Temperature		Rainfall		Sunshine hours
	°C	°F	m.m.	inches	
January	3.3	37.95	49.3	1.94	50.2
February	3.5	38.25	38.1	1.50	64.1
March	4.4	40.0	45.0	1.77	106.0
April	6.5	43.65	46.0	1.81	134.1
May	9.7	49.4	54.1	2.13	160.0
June	12.5	54.5	50.1	1.97	174.6
July	14.6	58.3	65.8	2.59	159.3
August	14.3	57.75	68.8	2.71	146.9
September	12.0	53.55	50.5	1.99	126.0
October	8.75	47.75	64.3	2.53	91.8
November	5.2	41.4	56.9	2.24	58.8
December	3.7	38.65	61.5	2.42	41.8
Year	8.2	46.7	650.2	25.60	1313.6

The drift Geology is one of glacial sands and clays over-lying the limestones, sandstones and carbonaceous shales of Carboniferous and Permian age. The pattern of local vegetation is almost entirely the result of historical land use; the low plains being largely given over to arable farming and pasture land and, where they remain, the woodlands are deciduous although some coniferous and mixed deciduous and coniferous planting has taken place.

CHAPTER 1

THE DIEL AND SEASONAL ACTIVITY PATTERN OF *A. T. AMPHIBIUS.*

CHAPTER 1

THE DIEL AND SEASONAL ACTIVITY PATTERN OF A. T. AMPHIBIUS.

Introduction

The existence of a polycyclic pattern of activity characteristic of mammals less than 500 gms in bodyweight which is superimposed upon the more biologically universal solar rhythm of approximately 24 hours, was proposed as the less labile rhythm by Miller (1955), who described it as a hunger cycle. Although the effecting mechanism of this intra-diel pattern has not been demonstrated its relationship to energy metabolism and body temperature regulation appears in an examination of the frequency of activity periods in correlation to bodyweight. Crowcroft (1953) investigated the intra-diel patterns of British shrews. He reported that the Pygmy Shrew Sorex minutus L. with a bodyweight of 3-8 gms. showed a frequency of 15-20 activity periods/day compared with 10-15 periods/day for Sorex araneus L., bodyweight 4-16 gms, and 8-10 periods/day for the Water Shrew Neomys fodiens Pennant 10-23 gms. Mice of the genera Mus, Apodemus, Peromyscus and microtines of the genera Microtus, Clethrionomys and Dicrostonyx varying in bodyweight from 12-50 gms have been reported to display activity frequencies of between 8-15 periods/day (Davis, 1933; Crowcroft, 1953; Brown, 1956; Hansen, 1957; Saint Girons, 1960, 1961; Erkinaro, 1961; Grodziński, 1963).

The frequency of intra-diel activity periods is not dependent only on the parameter of size for Saint Girons (1960) concludes that Clethrionomys glareolus demonstrates an increased frequency of activity periods in winter, rising to 8-10 periods/day from the summer figure of 5-7 periods/day. Grodziński (1963) notes the effect of food quality on Apodemus agrarius Pallas where a bulky, low caloric diet considerably extends the duration of the individual feeding period in comparison with animals fed on a diet of high calorific value. In contrast Hansen (1957) who investigated the intra-diel activity pattern of the Varying Lemming Dicrostonyx groenlandicus rubricatus Traill under the light regimes of total darkness, of 9.5 hours of light, and of continuous light, found the frequency of activity to be 8.5, 8.65, and 9.1 cycles/day respectively which suggests a fairly stable seasonal intra-diel frequency. However it must be remembered that under experimental conditions, where food is provided in excess of immediate requirement, the factor of differential food availability and quality may cease to exert its natural significance. It must also be remembered that the plentiful supply of food available to woodland mammals in the autumn seed fall will not be of benefit to grazing species where more nutritious feeding would occur during the early summer when any effect caused by an increase in food value would be most pronounced. It seems probable that those factors which affect energy metabolism and body temperature regulation,notably body size, ambient temperatures, fur and nest insulation, degree of activity, and nutritional quality of food, all inter-react and counter-react to influence the intra-diel frequency of activity pattern. Of the larger rodents *Rattus* (275-520g.) has been calculated to possess an activity rhythm of 3-4hrs duration (Richter, 1927; Crowcroft, 1953). Lund (1970) reports bursts of activity every 3-4 hours for a population of *A. t. terrestris* (80-205 g) and Duckett (unpubl.) calculated a frequency of 4.9-6.4 activity periods/day for individuals of *A. t. amphibius* (150-280 g).

The correlation between bodyweight and the frequency of activity periods noted above does not appear to be extended to the total duration of activity for each 24 hour period. Crowcroft (1953) calculates the coefficient of Activity 'Q', that is hours of activity per day/hours of rest per day, as 0.7 for *Neomys*, 1.46 for *Sorex araneus* and 1.36 for *S. minutus*, this corresponds to 9.9, 14.2, and 13.8 hours of activity respectively while Grodziński and Górecki (1967) considered that the duration of activity reflected the feeding habits of the particular species among rodents of similar size. For example granivorous mice (*Apodemus flavicollis*, *A. sylvaticus* L., *Mus musculus* L.) being active from 3 - 5 hours/day in summer and up to 2 hours/day in winter, herbivorous voles (*Microtus arvalis*, *M. agrestis* L., *M. oeconomus* Pallas, *Pitymys subterraneus* de Sélys-Longchamps being active for the longest period of 5 - 7 hours/day, and polyphagous voles and mice (*Clethrionomys glareolus*, *C. rufocanus* Sundevall, *Apodemus agrarius*) forming an intermediate group with predominantly nocturnal activity of a total of 5 hours duration per 24 hours in summer and 2 - 4 hours in winter.

In contrast Hansen (1957) recorded activity durations of 7.5 hrs/day, 5.3 hrs/day and 4.5 hrs/day on the herbivorous Lemming Dicrostonyx for light regimes of winter, spring and summer respectively, and Hamar et al. (1970a) note an average diel duration of activity of 9 hrs 19 mins on individuals of the herbivorous and partially fossorial Pine vole Pitymys subterraneus (12.5-23.5g), recorded in the field.

It appears also that the duration of daily activity is a reflection on intensity of activity as well as on food quality. Fossorial rodents have a far lower metabolic rate than is normal for animals of their size (McNab, 1966; Górecki and Christov, 1969). This is regarded both as an adaptation for reducing body heat production in the naturally high burrow temperatures of some of these species and to the necessity of obtaining their entire oxygen supply by diffusion through the soil in burrows without direct openings to the external atmosphere. Górecki and Christov (1969) recorded from an investigation of the respiratory rate of the Lesser Mole Rat Spalax leucodon Nordm. in laboratory viveria that the animals (average bodyweight 178 g.) were active for 13.4 hours daily, while Hamar et al. (1970b) studying the same species in the field found a daily duration of activity of only 8 hrs 30 mins.

In *A. t. terrestris* Drożdż et al. (1971) recorded a duration of activity in the laboratory of 5.5 hours/day, whereas under field conditions Hamar et al. (1970a) recorded an average activity duration of 9 hours 36 minutes for the more fossorial *A. t. scherman*.

Consequently the diel duration of activity among rodents must be regarded as being influenced by the parameters of size, mode of life and of diet.

The position and relative duration of activity periods during the diel cycle has received considerable attention in the past. Among the Muridae the genera *Apodemus* and *Rattus*, and among the Cricetidae the genus *Peromyscus*, have been found to be generally more active during the night than during the day (Chitty and Shorten, 1946; Miller, 1955; Brown, 1956; Grodziński, 1963; Falls, 1968; Stebbins, 1971), while among the Microtinae activity tends to be more uniformly spaced throughout the 24 hours. In *Clethrionomys glareolus* Miller (1955) and Pearson (1962) recorded a slight maximum of activity during the day whereas Saint-Girons (1960, 1961) reported that *Clethrionomys* was very largely nocturnal, particularly with regard to the males. In the females the nocturnalism was less marked and a diurnal majority of activity was observed in the spring. Pearson (1962) likewise found females to be more diurnal than males in this species but found that this pattern was the reverse in *C. rufocanus*.

As a demonstration of the variability of intra-specific populations Stebbins (1972) found the principal activity peaks of C. gapperi Vigors to occur during the night at latitude 62°N in the North West Territories of Canada but during the day at 53°N in Alberta, the pattern being maintained throughout the year.

Seasonal variation was observed by Saint Girons (1960, 1961) and Grodziński (1963), the latter noted that C. glareolus became more diurnal in winter and less so or even nocturnal in summer, a conclusion similar to that of Erkinaro (1961) for Microtus agrestis.

Brown (1956) considered C. glareolus to be active primarily during the day throughout the year reciprocating with Apodemus sylvaticus which was active at night, and regarded the resultant timing of activity to be a response to competition between the two, a competition that would cease to exist in the laboratory condition and might exacerbate the differences between Brown's population and that of Saint Girons (1960, 1961) which was kept isolated from wild populations of both Clethrionomys and other species.

The genus Microtus has been considered to be closely related to Arvicola (Corbet, 1966) and shows a slight nocturnal preference in several species, M. agrestis (Davis, 1933; Brown, 1956), M. ochrogaster Wagner (Calhoun, 1945); M.californicus Peale (Hatfield, 1940), although Hamilton (1937) showed M. pennsylvanicus Ord to be largely diurnal.

The inter and intra specific variability recorded above is reflected in the genus Arvicola. Van Wijngaarden (1954) and Stoddart (1969b) recorded a marked maximum of activity during the day on the basis of trapping results although the latter actually recorded greater catches during the night but corrected proportionately for duration discrepancies between light and dark periods, and Lund (1970) using a photo-electric recording system on an enclosed population recorded a persistant seasonal diurnalism with a definite response to the timing of dawn and dusk. Ashby et al. (1969) observed a wild population throughout the diel period and recorded fluctuating levels of activity apparently independent of light intensity, whereas Duckett (unpubl.) although noting a slight nocturnalism in animals under laboratory conditions found that wild populations he investigated, using a technique based on the timing and frequency of the laying down of footprints, were confining 90% of all range exploration activity to the hours of darkness. He concluded that differences in the type of activity, that is activity close to the nest during the day and a more widely ranging activity during the night could account for this difference, or that the causative agent could be human disturbance during the hours of daylight.

It is clear from the published work on the Microtinae that this sub-family demonstrates a more uniformly displaced activity during the diel period than do the previously mentioned genera of the **Muridae**, however, it is also clear that there may be considerable variation both inter and intra specifically, that the metabolic patterns shown up in isolation may be influenced by competitive species in the wild and that there may be significant differences between the sexes and between the seasons of the year, which taken together suggest a considerable flexibility in the potential for activity in the species concerned. However it must be remembered that the techniques used in measuring this activity do themselves vary in great degree, a variability which may well exceed that of the species concerned, a possible source of some of the conflict in published work.

Review of Methods for Recording Mammal Activity.

Estimates of small mammal activity have been carried out both on wild populations and upon individuals of these populations isolated from their fellows either completely in the laboratory or partially in enclosures placed in the field situation. The latter alternatives, which bring with them a likely modifying influence of restricted range, a plentiful food supply and exclusion from the remainder of the population, have been necessitated by the difficulty of recording the activity of rodents in the wild. Brown (1956), van Wijngaarden (1954), Stoddart (1969b) and Harling (1971) have used trapping techniques requiring animal release and resetting of the traps at frequent intervals throughout the diel period but the disturbance to the animals' normal rhythms which must occur when this method is used allow only generalised conclusions. The method is also very time consuming.

Brown (1966) used a technique based on the timing of the appearance of rodent footprints on prepared surfaces in artificial burrows and Duckett (unpubl.) used a similar technique to record the activity of Arvicola, preparing a smooth mud surface at the river's edge at predetermined intervals and recording the time when the footprints were laid down. Such methods must be modified to suit the species under investigation; they have the advantage of reduced disturbance to the population but share the disadvantage of trapping techniques of being labour or time intensive.

Hamilton (1939) blocked the tunnels of a population of Brewer's Mole Parascalops breweri True in several places and recorded the timing of their reopening as periods of burrowing activity. Chitty and Shorten (1946) investigated the feeding periodicity of the rat Rattus norvegicus Berkenhout by a clockwork recorder timing the food losses from an attached grain container. These methods have the disadvantage of being applicable only to the type of activity they were designed to monitor; neither the above ground activity of the mole nor the extra-feeding activity of the rats being recorded.

Chitty and Shorten (1946) and Ashby et al. (1969) observed directly wild populations of rodents throughout the diel period using low level lighting during the night but this method is either labour intensive or necessarily short term and the effect on the animals of the artificial lighting is difficult to determine.

Radio-active labelling of burrowing animals has been used by Hamar et al. (1970a) on individuals of Arvicola and Pitymus released into the field situation, in conjunction with automatic recorders, a method which combines freedom of movement in the wild with sensitivity of record and the technique may be applied to any localised burrowing rodent.

The principal advantages of the methods devised to record the activity of wild populations is the large sample size and the natural condition of range, food supply, climate, light, and inter and intra-specific interaction. The disadvantages are usually those of human interference and of the insensitivity typical of the methods employed.

In investigations of rodents in the laboratory these advantages and disadvantages are reversed. A variety of automatic activity recorders have been used but limiting factors of equipment and time for analysing the record usually restrict the number of animals in the investigation.

Actographs, apparatus sensitive to all movements of the animal in a suspended cage, have been used by Davis (1933) and Saint Girons (1960, 1961). These give a record of the duration and to some extent of the intensity of activity and can be subjected to detailed analysis. Alternatively make-break circuits operated by animals passing over treadles or against wires as they move from nest box to feeding cage, the resultant contact being recorded on a rotating drum, have been widely used (Crowcroft, 1953; Miller, 1955; Hansen, 1957; Erkinaro, 1961; Pearson, 1962; Lund, 1970; Stebbins, 1971, 1972) implementing a variety of mechanical, electrical and photo electric contact makers. This technique records the time of entrance and exit from a nest box and reveals the timing and not the duration of the activity period.

Cleminson (unpubl.) used a photo-electric cell to monitor activity during the day time and supplemented this technique with the use of time-lapse photography illuminated by a deep red flash at 20 second intervals during the hours of darkness. This method provided not only activity periodicity data but could also be analysed qualitatively for the type of activity involved.

Apart from the small numbers of individuals involved the principal disadvantages of these laboratory techniques remain those of modification of activity caused by the greatly reduced range, the isolation of the animal from its conspecifics and competitors, and the unnatural climatic and light conditions. The last of these disadvantages can be reduced both by the creation in the laboratory of an experimental photoperiod corresponding to that of the external environment together with gradual changes of light intensity at the dawn-dusk interfaces, but more especially by the translocation of the laboratory experiment back into the field situation as an enclosure with the associated automatic recorders protected from weather and mechanical interference. Stebbins (1971, 1972) used this method to record activity patterns of *Peromyscus* and *Clethrionomys*, not only reproducing the natural light and weather conditions but also re-creating certain of the effects caused by interaction with the natural inter and intra specific populations in the area. Consequently modification of behaviour was largely restricted to confined range and a freely available food supply.

In the present study it was considered that the sensitivity of an automatic recording method was necessary for a detailed appraisal not only of time of activity period but more especially of duration and period intensity. Although the monitoring of wild voles in the natural condition would have been the best of the alternatives, difficulties of disturbing occupied nests with the likelihood of desertion during the insertion of the recording device together with the probability of short circuiting of electrical apparatus and its possible damage or loss during periods of river flooding rendered this impracticable and it was decided that the monitoring of the voles' activity should be carried out from an external enclosure.

Method

Daniel (1964) used a resistance platinum recording thermometer placed in the upper part of the nest cavity to record the temperature and humidity of the nest chamber of the vole Clethrionomys glareolus but made no mention of the modifying effect of the presence or absence of the voles themselves on these parameters, possibly because the heat output of an animal of less than 40g. bodyweight fell below the sensitivity of the apparatus employed. However it was considered that Arvicola of bodyweight 150-300 gms. should produce a rise in temperature in its nest chamber of sufficient magnitude and rapidity to create a trace which in its plateaux would accurately reflect periods of rest and in its depressions periods of activity. At the same time this trace would indicate the general level of nest chamber temperature over the annual period, and provide information regarding the influence on this temperature of the animals themselves and on the general thermodynamics of the burrow system as a heat retention mechanism.*

To investigate this hypothesis a prototype enclosure incorporating an artificial burrow system was established in April 1971. The enclsure was T-shaped, the head of the T measuring 3m. x 1½m.. x 1m., with the projection of dimensions 1m. x 1m. x 1m. built midway along one of the two longer sides. It was placed in a small stream in the Zoology Dept. Field Station in Houghall Wood, some 2km. south of the main University site. The stream had vertical banks approximately 60cm. in height into which was cut an embayment 1m. x 1m. x 0.6m. necessary to permit entry of the vertical projection of the T enclosure. The enclosure comprised a wooden frame supporting 1cm. wire mesh on all external faces.

The burrow system consisted of a nest chamber 25cm. x 10cm. x 10cm. constructed from two plywood endpieces each 10cm. x 10cm. set 25cm. apart with the body of the chamber comprising a 25cm. x 40cm. sheet of 0.5cm. mesh wire netting stapled to the endpieces without further frame support. Both endpieces were protected on the inner surface by a layer of 0.5cm. wire netting and into one of these endpieces was cut a centrally-placed circular opening 5cm. in diameter and into the other a circular opening of diameter 2cm. placed 1cm. from both bottom and side edges. A copper tube was inserted through this latter opening and extended

*Recently Flowerdew (1973) has described a similar method for recording the activity of small mammals in the field.

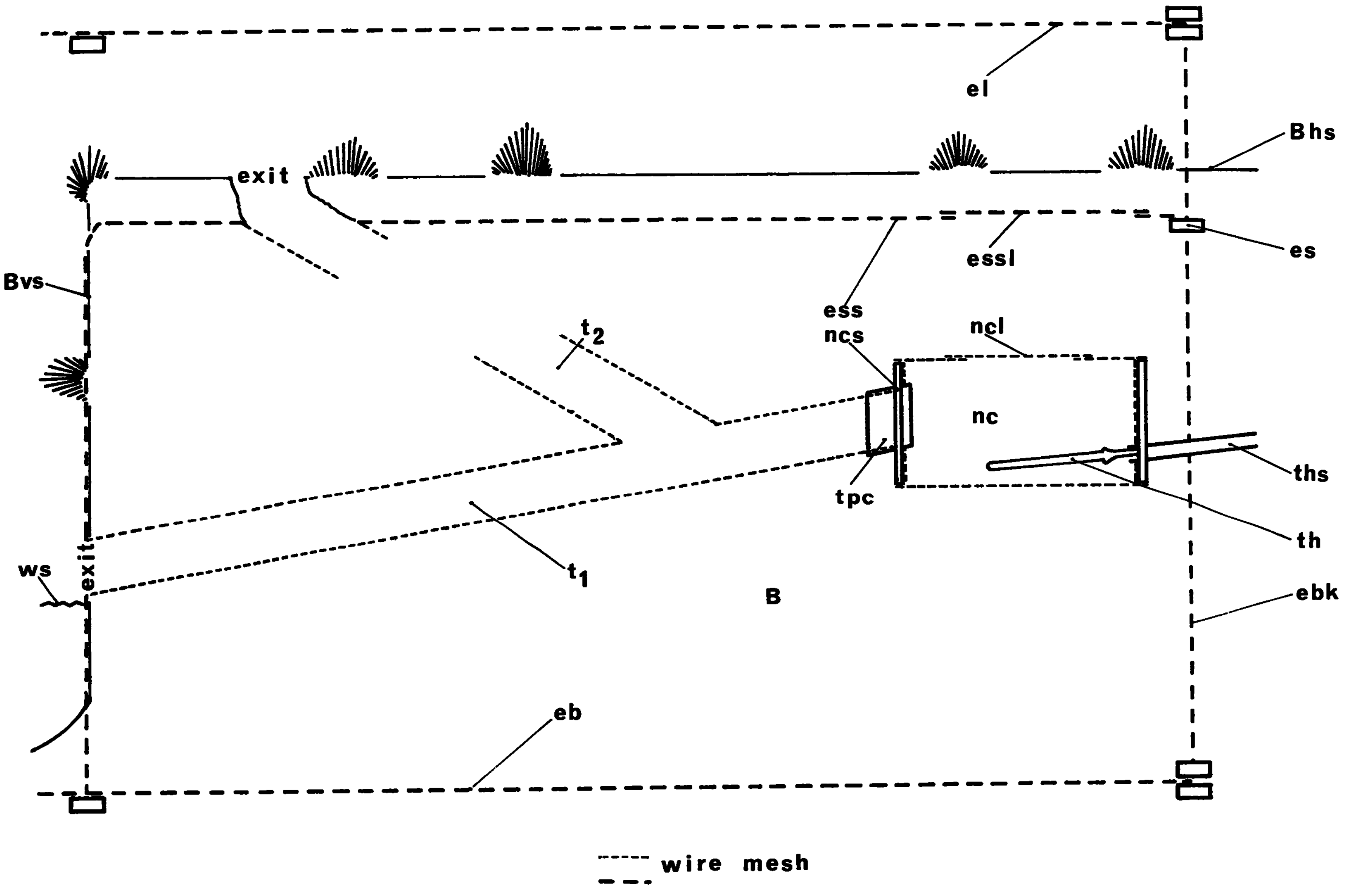
Diagram 1

The artificial burrow system.

The diagram shows a generalised burrow system of the type used to obtain the experimental results of Sections 1 and 3. Dimensions are given in the text.

Key

B	bank
Bhs	horizontal surface of the bank
Bvs	vertical surface of the bank
eb	basal floor of the enclosure
ebk	enclosure back
el	enclosure lid
es	wooden enclosure support
ess	enclosure sub-surface floor
essl	access door to the sub-surface floor
nc	nest chamber
ncl	access door to the nest chamber
ncs	nest chamber support
t1	main tunnel
t2	subsidiary tunnel
th	thermograph probe
ths	sheath for thermograph probe
tpc	tunnel perspex collar
ws	water surface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ths
th
ws
exit
t1
B
ebk
eb
wire mesh

outside the enclosure to allow for ready entry and exit of the temperature probe. A burrow of diameter 5cm. constructed entirely of 0.5cm. mesh wire netting and extending 60cm. in length was inserted into the larger endpiece opening. 10cm. from this insertion a second burrow of similar diameter led into the first so that the distal entrance of this second burrow lay some 12cm. below that of the first. A third burrow led off 10cm. behind the distal end of the second leading vertically upwards for 50cm.

A horizontal wooden strip was fixed across the entrance of the projection of the T enclosure, 60cm. above the enclosure floor and continued laterally round all four sides of this projection at this height. The burrow system was then suspended inside the T projection and the vertical face covered in $1cm^2$ mesh wire netting to the height of the wooden strip. The two forward projecting burrows were affixed into this wire netting with the mesh covering their entrances removed. The temperature probe of a Cambridge Instrument Recorder was inserted into the nest chamber so that the probe lay along one side of the lower floor of the chamber. The T enclosure projection was then filled to a height of 60cm. with the excavated earth, heavy clay beneath a light loam, so that the soil level rose flush with the adjacent sections of stream bank. This horizontal surface was then covered with wire netting except for the point of entry of the vertical burrow shaft. The 1m. x 1m. horizontal surface was then covered with the pieces of turf removed from the bank to a depth of 10cm.

When set in place the nest chamber lay at the back of the T projection 20cm. below the turf surface; the first burrow emerged 10cm. above the mean water level of the stream, the second at or just below the mean water level and the third emerged amidst the turves some 10cm. from the vertical bank edge. The base surface of the enclosure was below water level with mean water depth at 5-15cm. depending on location; mudbanks formed naturally at the edge of the vertical bank along the entire 3m. of the enclosure. A simplified burrow system is illustrated in Diagram 1 and in Plate 2 an enclosure system is shown in use.

A single male vole placed in the enclosure in spring 1971 immediately took residence in the nest chamber provided. It was fed on a diet of carrots, cabbage and grass, added in excess of requirements at weekly intervals when the record charts were also changed. By approaching the enclosure during a period of vole activity and thereby consequently frightening the vole into the nest chamber, it was possible to time the period at which this entrance into the chamber became discernable on the recording trace. This period proved to be in the order of 5 minutes. It may therefore be concluded that the recording apparatus was sensitive to periods of rest of five minutes or longer. An example of the recording trace is shown in Plate 3.

The method was used successfully from May to October

Plate 1

Arvicola terrestris amphibius

Plate 2

The experimental enclosure

The enclosure has two burrow systems, a door in the partition at water level may be opened to allow the voles access to both systems. An observation hide is shown in the background.

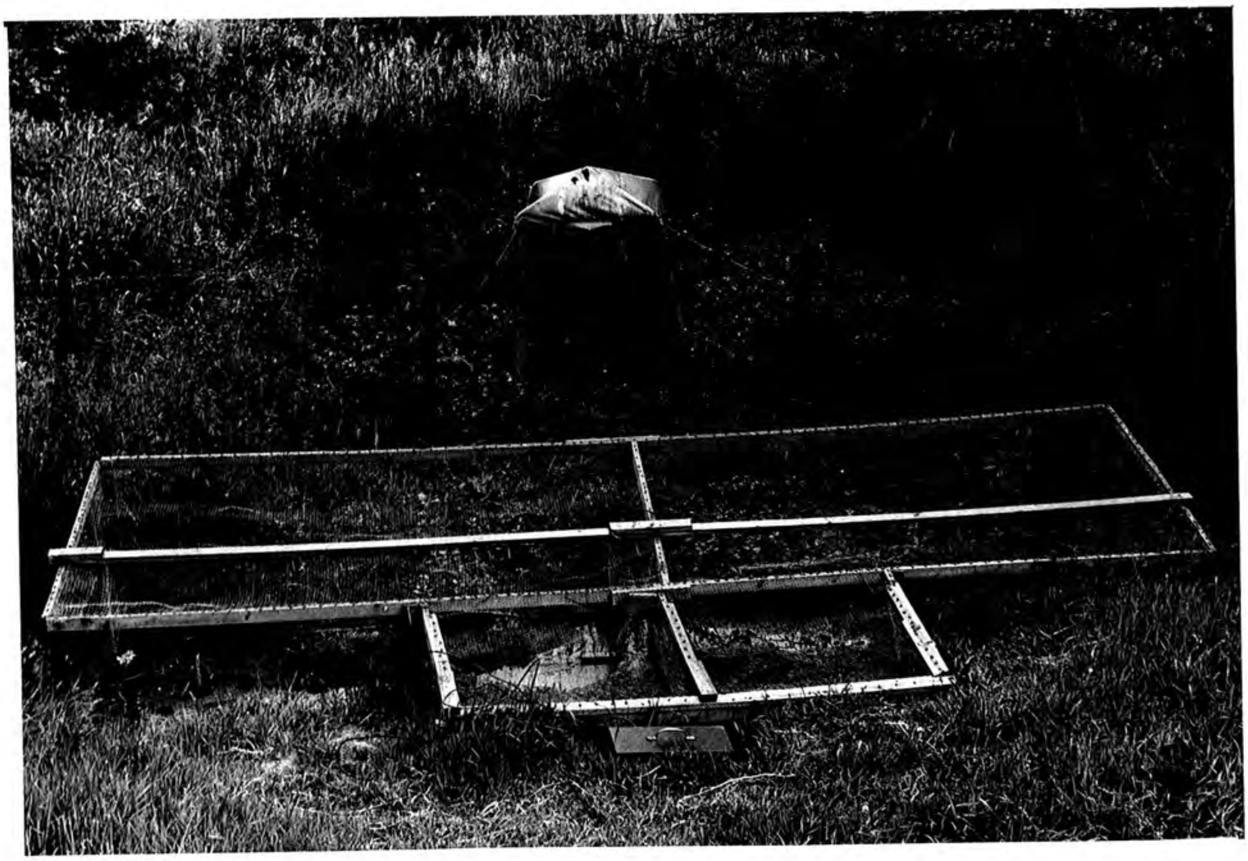
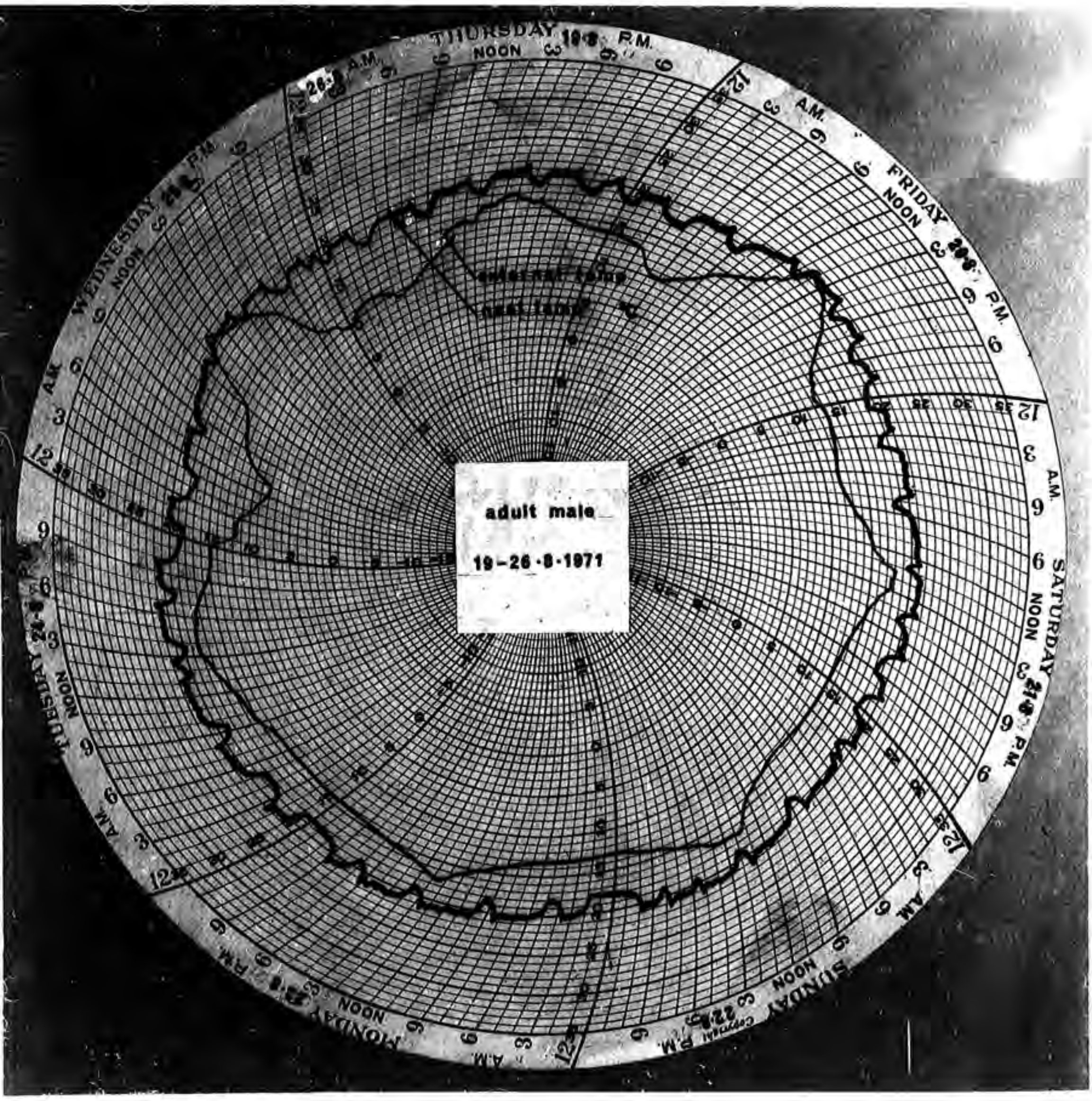


Plate 3.

The thermograph record.

The activity and temperature record is given by the thermograph trace for the period 19-26 August 1971. The periods of above-ground vole activity are seen as depressions in the nest temperature trace while periods of rest appear as intervening plateaux. The temperature difference between rest and activity periods is in the order of $1.5^{\circ} - 3^{\circ}$C. The trace for nest temperature is about 4 hours in arrears of that for surface temperature (external, at G.M.T.).


THURSDAY 19-8
FRIDAY 20-8
SATURDAY 21-8
SUNDAY 22-8
MONDAY 23-8
TUESDAY 24-8
WEDNESDAY 25-8
26-8
NOON
A.M.
P.M.
external temp
nest temp °C
adult male
19-26-8-1971

1971, when a second, larger, enclosure was constructed, external dimensions 4m. x $1\frac{1}{2}$m. x 1m. with a T projection of 2m. x 1m. x 1m. (Plate 2). This enclosure was partitioned transversely into two halves and a burrow system placed in each half. A Negretti-Zambra recording thermograph with a probe placed in each nest chamber was used to record the two temperature traces. This enclosure and burrow system was similar to the prototype except that the burrow systems were now limited to a rather larger nest chamber, 30cm. x 10cm. x 10cm. necessary to take the longer recording probes, and a single burrow 60cm. in length, the distal end inserting 10 cm. above mean water level. This simplification was suggested by the failure of the vole in the prototype enclosure to utilize the under water or vertical entrances on any occasion, these entrances eventually becoming blocked by earth fall and remaining unopened subsequently. A male and female vole introduced, one into each of the burrow systems in November 1971, accepted the nest chambers immediately.

In both enclosures food was inserted through the roof of the T projections which were constructed so that they could be opened and re-fastened. A removable roof was also found to be an advantage in the construction of the nest chambers themselves, particularly in easing the task of removing any vole that should die in the nest chamber prior to introducing a replacement.

Assessment of the Method

i.) The Burrow System

The value of the information derived from the system described above must depend upon how accurately this reflects the natural conditions under which the voles normally exist. With respect to the relevance of the temperature data obtained this relevance requires that the size, shape and siting of the burrow should approximate as closely as possible to the respective features in natural burrows made by the species. Published descriptions of the burrows of A. t. amphibius are largely in agreement with one another. Adams (in Barrett-Hamilton and Hinton, 1911-21) described the burrows as being of two principal types, simple retreats or more elaborate nesting and nursery burrows. In the simple retreat it is usual for the burrow to extend into the bank for approximately 30cm. before turning either to the left or right, sometimes both, parallel to the river, and opening into an enlarged chamber area. These burrows are said to be used as refuges for short periods when the voles are disturbed while feeding away from the nest. In contrast the permanent sleeping and nursery quarters themselves usually consist of a longer burrow running parallel to the bank for 2-3m. with usually more than one short exit burrow at right angles to it emerging near or below the water level. The nest chamber usually lies off the main burrow a short distance from one of these exit holes and is sometimes associated with an auxiliary chamber for storing food. The distance from nest to exit hole is in the order of 1m.

Ryder (1962) described a similar arrangement of fairly short access burrows, usually three in number, leading upwards from the entrances near the water's edge towards a nesting chamber which generally lies in association with a feeding chamber. She described the burrow systems as being in a state of seasonal change and noted that the creation of vertical shafts in the spring allowed the voles to feed higher up the banks without extending the distance between the feeding site and the refuge of the burrow.

The burrow galleries of *A. t. scherman* differ considerably from those described above. Bernard and Bollaerts (1960) excavated several of these galleries in Belgium where they occur considerable distances from water and recorded that the galleries may extend for 300m, lying at a depth of 5-10cms. A nest they examined located at a depth of 50cms, was 20cms in diameter and approximately spherical in shape giving a volume of some 4 litres. Hamar et al. (1970a) record the galleries and above ground tracks of *A. t. scherman* to be 34m. - 80m. in length for adults and 8m. - 10m. for juveniles running at a depth of 10-30cm. with the nest situated at a depth of 15 - 40cm.

The gallery systems of *A. t. scherman* are functionally different from those of *A. t. amphibius* in that they are largely feeding tunnels, excavated in the search for root material during the winter. The great length of these tunnels may also serve to allow for ample diffusion of an oxygen supply through the soil when the exit holes are blocked by the animals during the colder months (McNab, 1966). The short nesting burrows of *A. t. amphibius* in contrast are used principally for sleeping, the food being sought on the surface, there is furthermore no evidence to suggest that the blocking up of all burrow exits to the exterior is a feature of this vole.

In 1969 a pilot study was conducted at Durham University by M.R.Creasy (unpubl.) into the burrow systems of *A. t. amphibius* in the banks of the River Wear in Co. Durham. The (M.R.C.) author's findings agreed with those of Adams that the burrows were of both simple refuge and nesting/nursery types and his measurements of the latter showed that the burrows generally extend away from the water parallel to the rising surface of the bank at a depth of 20-30cms. for a distance of from 50 - 100 cms. Two such burrows may converge and open into the nest cavity which is some 20-25cms in length with the floor some 30-40 cms below the surface of the bank..

The prototype burrow system used in this study was essentially as described by Creasy but modified by the inclusion of a vertical shaft as described by Ryder. The volume of the nest chamber of between 2.5 and 3 litres was identical to that of Creasy and of the same order as that described by Bernard and Bollaerts (1960) for A. t. scherman. As neither the underwater nor surface exits were used by the voles in the prototype system it was considered reasonable to exclude them from the larger enclosure, this change caused little difference in temperature means between the two systems and is not thought to be a major source of error in the estimation of nest temperature.

ii.)Range

Estimations of the range of Arvicola vary in published work principally with the duration of the time over which the estimations are made, so that actual daily range lengths are not known with any accuracy and are in any case no doubt very variable. Over periods of several days Worrall (1964) estimated the mean range length on a small river in Hertfordshire to exceed 200m. in both male and female A. t. amphibius. Stoddart (1970) found mean range lengths of 112.5m. for males and 76.5m. for females in A. t. reta on a stream in Aberdeenshire, the difference between the sexes being significant. Pelikán and Holišová (1969) have demonstrated for A. t. terrestris in Czechoslovakia that small individuals moved 20m. on average between successive trapping periods while the heaviest individuals moved 71m. in the males and 47m. in the females.

The actual daily range length is probably smaller than these respective figures and may be influenced by the degree of lateral extension of range from the water's edge, but even supposing the distance regularly visited over 24 hours to be in the order of 75m. in males and 50m. in females this still represents a great increase over the enclosure condition especially as the latter effectively provides only one bank. The 2 - 4m. of enclosure bank must be compared with an effective 100 - 150m. of natural range, the proportion between the two being 1:25 and 1:75 assuming a lateral range of 1m. as suggested by Ryder (1962), a reduction which might well find itself reflected in reduced activity levels in the experimental condition. This could be expected to be least during the initial weeks after capture when the vole is acclimatized to its pre-capture intensity of activity and to increase with time as this acclimatization changes with that of the reduced range.

Secondly, although the naturally sited external enclosures will provide, locally at least, as many natural predators as would the wild condition the experimental stream does not carry a permanent resident population of <u>Arvicola</u>, although individuals do frequently extend their range from a downstream habitat and may provide some natural intra-specific reaction, with the result that this impoverishment in external stimulus may again tend to reduce experimental activity levels artificially. Some idea of the effect of this lack could be deduced by comparing the activity levels of the voles in adjacent burrow systems with those in the solitary enclosure and it was hoped that such a correction, if necessary, will become apparent in this way.

.iii). Nutrition

Information concerning the diet of the fluvial Arvicola suggests that their preferences are largely confined to the vegetative plant material but within these limits the composition of the food taken follows that of the dominant accessible vegetation within their normal range. In shallow lakes Holišová (1970) found A. t. terrestris to feed on Phragmites communis Trinius while ignoring the co-dominant littoral emergent species in association with it, Typha angustifolia L. and T. latifolia L.; 95% of total volume of ingested food was found to be vegetative plant material, 69% of which was composed of aerial tissues. Along a canal the same author (Holišová 1965) found that again nearly all the ingested food was aerial vegetative material, dominated in this instance by grasses forming about 50% of the total. In the later summer the fruits of Prunus growing locally became an important component, rising to 15% of the total food ingested during this season.

Ryder (1962) records A. t. amphibius as being very largely a grass feeder and this was also found to be the case in the present study (Section 7). Both Ryder (1962) and Stoddart (1968) record their partiality to apple and the present writer has noted that A. t. amphibius is an avid feeder on both apple and carrot, captive animals will also eat a wide variety of fruits and roots when these are offered. These observations demonstrate that although in the wild condition A. t. terrestris and A. t. amphibius may feed predominantly on reeds and grasses they would undoubtedly accept a large number of fruits and roots should these become available.

In the natural condition not only does the food supply change in bulk and species composition seasonally but changes in the quality of the food may become pronounced between the summer and winter seasons. Grodziński (1962, 1963) has shown that the activity pattern of *Apodemus agrarius*, *Microtus* sp. and *Clethrionomys* sp. changes when the food offered is bulky and of low calorie value from that observed when on a concentrated, high calorie diet.

In the experimental condition carrots, cabbage and grass were fed to the voles throughout the year. All these foods are bulky and of low calorie value. Drożdż et al. (1971) investigated the degree of assimilation by *A. t. terrestris* of several foodstuffs and found that carrot was far more efficiently assimilated than grass, (88% and 48% of dry weight respectively). But because of the slightly lower calorific value of carrot, (4.123 kcal/gm dry weight as opposed to 4.293 kcal/gm) and higher water content, (88.5% as against 80.0%) the calorific value of assimilated energy per gm. of fresh food is 0.42kcal for both carrot and grass. No figure is available for cabbage but the brassica Kohlrabi was found to have an even lower calorie value of assimilated energy per gram of fresh food at a figure of 0.22 kcal due both to a low calorific value, 3.669 kcals/gm dry weight, and very high water content, at

92%. Since cabbage is in any event the least eaten of the experimental foods it is considered that the difference between experimental and natural foods should not seriously affect the validity of the activity patterns in the spring and summer. However it is not known to what extent the reduced bulk and possible poorer quality of available foodstuffs in the natural condition might affect the activity pattern of the wild population in winter which would not be reflected in the experimental individuals. The writer has noted that the grazing activities of wild voles on bankside verges does in fact keep the grass cover free of decomposing material and these grasses retain a bright green appearance throughout winter. However it is not known to what extent this appearance is deceptive with regard to food quality, and the problem of reduced quantity may still be an important factor.

iv.) Validity of the Record

It has been noted that the sensitivity of the recording apparatus produced a discernible change in the thermograph trace when a vole had entered its burrow, after a period of approximately five minutes. It cannot be guaranteed that periods of rest or activity outside the nest of shorter duration than this would be noticed at all if they interrupted a longer period of activity or sleep respectively. In the case of short periods of rest this loss of accuracy, if it exists, would appear negligible unless these periods were frequent and observations of the enclosures suggests that such behaviour does not take place. Very short feeding periods however might be a source of error in total activity estimation in that a vole may consume several grams of food in even so short a time so that a number of such sorties might result in an underestimation of the total duration of feeding activity. Again however direct observation over many hours suggests that such short-term feeding behaviour is rare and it is considered that the delay in reaction time of the recorder does not result in serious discrepancies between recorded and actual duration of total activity.

With regard to the size of nest chamber and recording thermograph used it is clear that the sensitivity of the trace is directly proportional to the size of animal in the enclosure. At bodyweights smaller than 100 g. the trace would not have been considered reliable as the sharp plateaux and depressions which are characteristic of the trace of an adult animal have been found here to become smoothed out, however this is itself largely a reflection on the static size of the nest chamber which the voles have been found to fill partially with nesting material thereby reducing the rapidity of the temperature changes between the chamber and the exterior. It is considered that by the use of a small nest chamber an adequate trace could have been obtained with much smaller animals if this had been required. It is clear that the magnitude of the rise in temperature during occupation will reflect both the heat output of the individual and the volume of the chamber required to be heated.

Other factors affecting sensitivity, which demands at least a slight fall in nest chamber temperature on the vole's emergence from the burrow, will be the diameter and length of the burrow and the degree of the blocking of the exit from chamber to tunnel with nesting material. As long as these factors correspond to the natural condition the data on ambient temperature should remain valid, and only a fall in nest chamber temperature of 1.0°C is needed to provide a clear record of external activity and rest. It is believed that these requirements were maintained throughout the experiments.

The disturbance caused to the voles when food was given and the temperature charts changed would only rarely exceed ten minutes in duration and then become a factor only if these activities were carried out during a period of vole activity. The voles were also observed from a hide opposite the enclosures on over 30 occasions over the two years of records but again disturbance was minimal and observations made from this hide suggested that a vole frightened into its burrow by any disturbance will normally re-emerge within ten minutes of its cessation.

1 The Diel and Seasonal Activity Pattern of A. t. amphibius.

Results

1.1 The Diel Pattern of changes in Activity frequency.

The incidence of Arvicola activity outside the burrow system was transcribed from the thermograph record for successive periods of one hour duration. Each record estimated the proportion of external activity which had taken place during that hour, in tenths of one hour. The readings for each hour of the 24 hour diel period were then summated for each calendar month and divided by n, the number of vole days within that month, to give the proportion of each hour during which external activity occurs, p; the remaining proportion being occupied by rest within the burrow system. Frequency histograms were then drawn for the diel period for each month, the records of solitary and accompanied voles, of males and females, and successive years being taken together. The time scale always refers to Greenwich Mean Time commencing at midnight, 0.00 hrs.

Typically the variation in the proportion of activity over the diel period resulted in sequences of peaks and intervening depressions. In many instances these became marked enough to permit speculation that they resulted from synchronisation of activity by the voles over a number of days. However it is probably not valid to compare the levels of peaks with their adjacent depressions by the simple parametric or non-parametric tests for the comparing of two sample means, such as for example the Binomial test described by Bailey (1959), because the data may be regarded as being in a continuous time sequence. The data for activity at 9.00 hrs for example may not be regarded as independent of the data for this parameter at 6.00 hrs, indeed it is reasonable to assume that a period of activity occurring during one hour will exert a powerful influence on the duration of activity during the next hour. Statistical methods such as Time Series analysis and Spectral analysis have been developed to describe the random or patterned distribution of events in a continuous time sequence but these more sophisticated methods have not been employed in this section as they would examine the voles' behaviour individually rather than as pooled data, the latter being more important for the present purpose, and because the results obtained would not have been central to the theme of this thesis. Section 1.1 therefore confines its analysis to the portrayal of the hourly estimations of the proportion of activity (p) over the diel period for each of the twelve calendar months in Figures 1-12, and to a brief description of what are considered to be the salient features of each month's activity pattern with some additional comment on general seasonal trends.

The discussion of the activity histograms is presented in a sequence of four seasons. Three calendar months have been allocated to each season. Winter comprises the months of December, January and February (Figs. 1-3), Spring the months of March, April and May (Figs. 4-6), Summer those of June, July and August (Figs. 7-9), and Autumn those of September, October and November (Figs. 10-12). These seasons do not necessarily conform to any clear set of characteristics but have been arranged in this way for ease of presentation. In all subsequent sections of this thesis where the data are presented on a seasonal basis, each season has been allocated the months described above.

The photoperiod is shown in Figures 1-12 by the means of a continuous line representing darkness which ends at the midpoint of the range of the commencement of civil twilight at dawn and of the end of civil twilight at dusk. It has been considered here that the period of civil twilight constitutes part of the diel photoperiod and not part of the night as during this period there is still sufficient light to see the detailed features of the external surroundings clearly. However to allow comparison with other work the monthly range of sunrise and sunset are also shown in the figures. The source for the civil twilight and sunrise and sunset data was Whitaker's Almanack (1971).

1.1.1 Winter Season

In December (Fig.1) the proportion of activity between 19.00 and 8.00 was fairly stable ranging from $p = 0.22$ to 0.35. Between 8.00 and 19.00 the proportion of activity was more erratic with two fairly well defined peaks at 12.30 and 15.30 separated by depressions at 9.30, 13.30 and 18.30. The diel minimum of activity was at 9.30 where p = 0.12, and the diel maximum at 7.30 where p = 0.35. The mean proportion of activity for December was p = 0.250.

In January (Fig.2) the proportion of activity between 19.00 and 7.00 was fairly stable ranging from p = 0.18 to 0.27. Between 7.00 and 19.00 the proportion of activity was more erratic and rather higher than that previously with a diel maximum at 8.30 of p = 0.38. After 17.00 the proportion of activity declined sharply with a diel minimum at 18.30 of p = 0.13. The mean proportion of activity for January was p = 0.251.

In February (Fig.3) the proportion of activity throughout the diel period was fairly constant ranging from p = 0.19 to 0.34 with the exception of the period of 19.00 - 24.00 where a peak of p = 0.37 at 19.30 was followed by a depression of p = 0.20 at 20.30, a subsequent peak of p = 0.38 at 22.30 and a subsequent depression of p = 0.20 at 1.30 hrs. The general level of activity was more constant than in either December or January. The mean proportion of activity for February was p = 0.274.

The activity histograms of December and January demonstrated some degree of agreement in the location of their peaks and depressions. There were corresponding peaks at 7-9, 11-13, 15-16 and possibly 20-21 G.M.T. and corresponding depressions at 2-4, 9-11, 13-14, 18-19.

Figures 1 - 3

The distribution of Diel Activity in the Winter Season

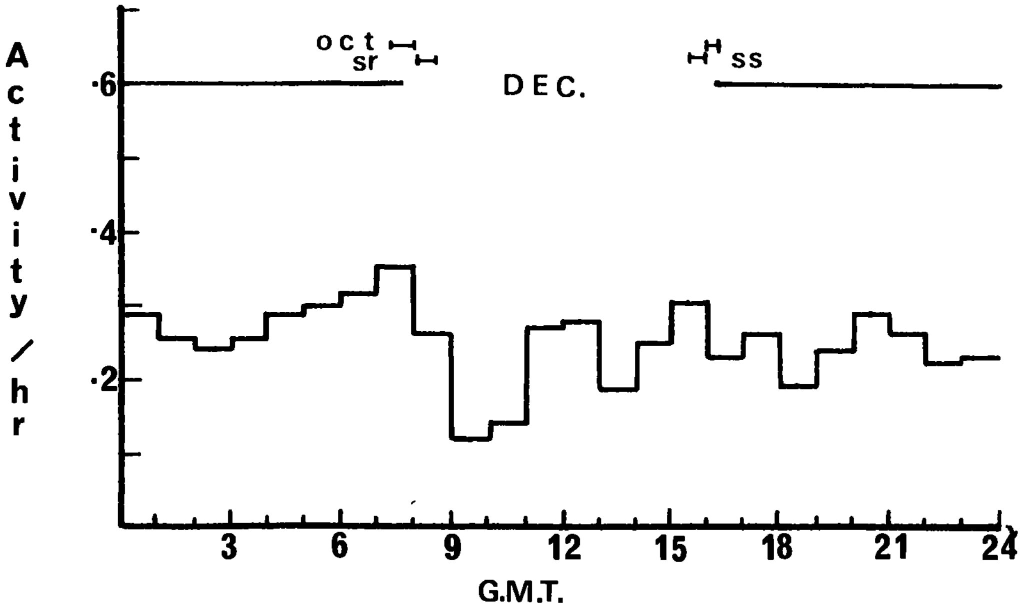
Figure 1	December	(n = 154; 6 voles)
Figure 2	January	(n = 131; 5 voles)
Figure 3	February	(n = 104; 5 voles)

Activity/hr = above-ground activity expressed as a proportion of the maximum possible (1.0) at hourly intervals commencing at midnight (0.00 hrs).

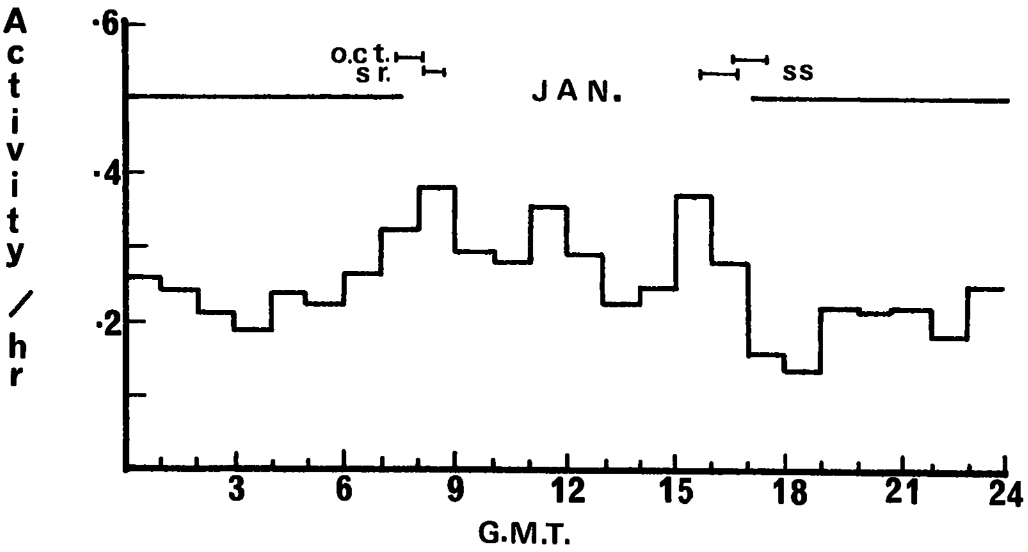
o.c.t. = the monthly range of the timing of the onset of civil twilight. The mean duration of night is signified by a continuous black line.

sr., ss. = the monthly range of the timing of sunrise and sunset.

Figs. 1-3


Activity / hr
·6
·4
·2
oct
sr
DEC.
ss
3
6
9
12
15
18
21
24
G.M.T.

1


Activity / hr
·6
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o.c t.
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J A N.
ss
3
6
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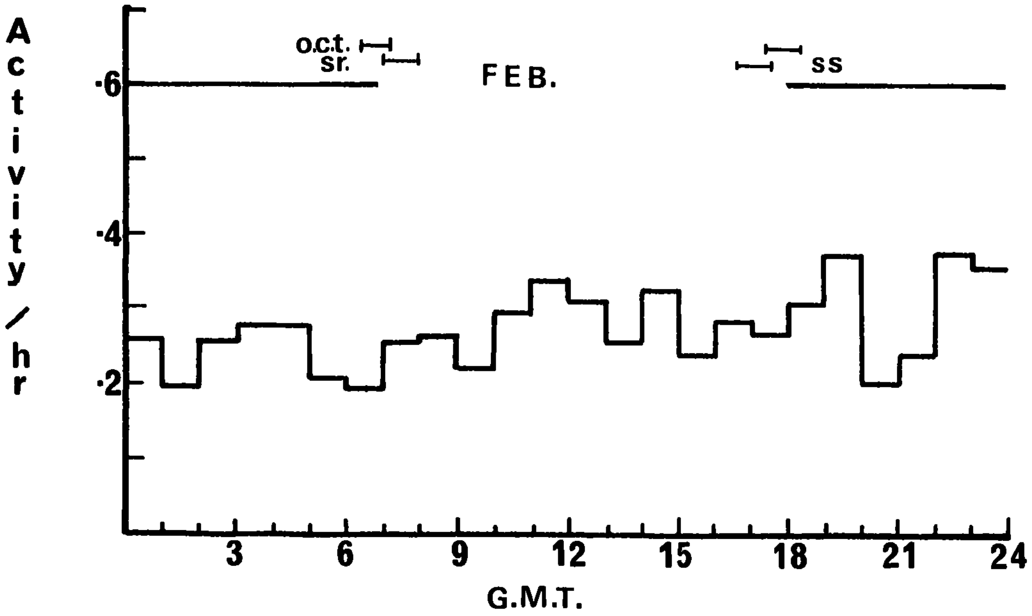
18
21
24
G.M.T.

2


Activity / hr
·6
·4
·2
o.c.t.
sr.
FEB.
ss
3
6
9
12
15
18
21
24
G.M.T.

3

This agreement did not continue into February where the former pattern largely disappeared.

The proportion of activity during the night was greater relative to that during the day in December than it was in January or February. This is discussed further in Section 1.4.

The mean proportion of activity was similar in December and January, p = 0.250 and 0.251 respectively, but showed a small increase in February to p = 0.274.

1.1.2 Spring Season

In March (Fig. 4) the proportion of activity between 22.00 and 9.00 was fairly stable ranging from p = 0.20 to 0.29. Between 9.00 and 22.00 the proportion of activity was more erratic. It rose rapidly from 9.00 to a diel maximum of p = 0.48 at 10.30 after which followed a gradual decline, interrupted by subsidiary peaks at 13.30 and 18.30, to a diel minimum of p = 0.10 at 21.30. The mean proportion of activity for March was p = 0.261.

In April (Fig. 5) the proportion of activity between 12.00 and 23.00 was fairly stable ranging from p = 0.21 to 0.30. Between 23.00 and 12.00 the proportion of activity was more erratic with fairly well defined peaks of activity at 0.30, 4.30 and at the diel maximum of p = 0.41 at 9.30. After 9.30 the proportion of activity fell rapidly to the diel minimum of p = 0.18 at 11.30. The mean proportion of

Figures 4 - 6

The distribution of Diel Activity in the Spring Season

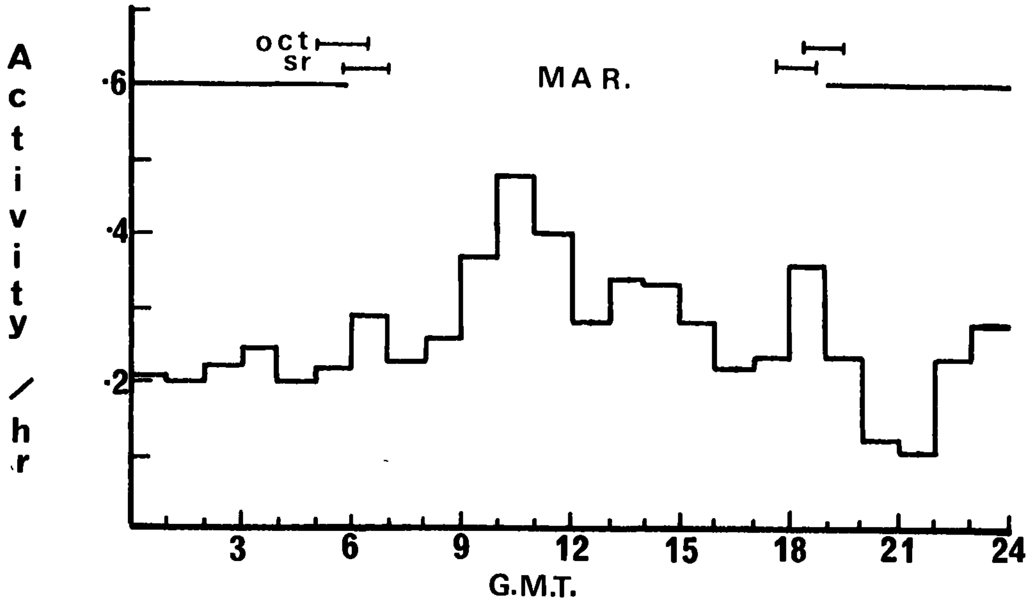
Figure 4	March	(n = 119; 4 voles)
Figure 5	April	(n = 79; 5 voles)
Figure 6	May	(n = 68; 6 voles)

Activity/hr = above-ground activity expressed as a proportion of the maximum possible (1.0) at hourly intervals commencing at midnight (0.00 hrs).

o.c.t. = the monthly range of the timing of the onset of civil twilight. The mean duration of night is signified by a continuous black line.

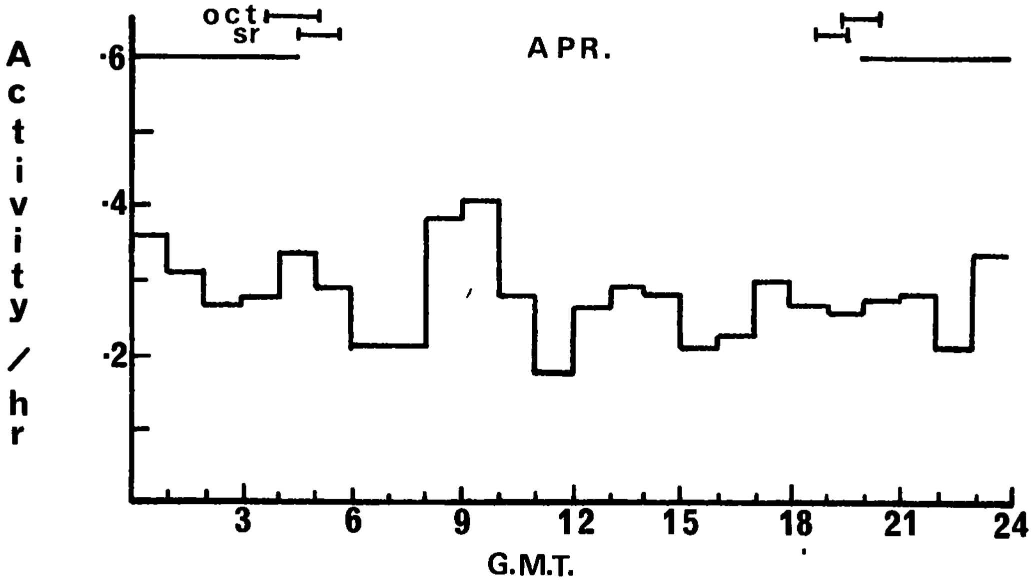
sr. = the monthly range of the timing of sunrise and sunset.

Figs. 4 - 6



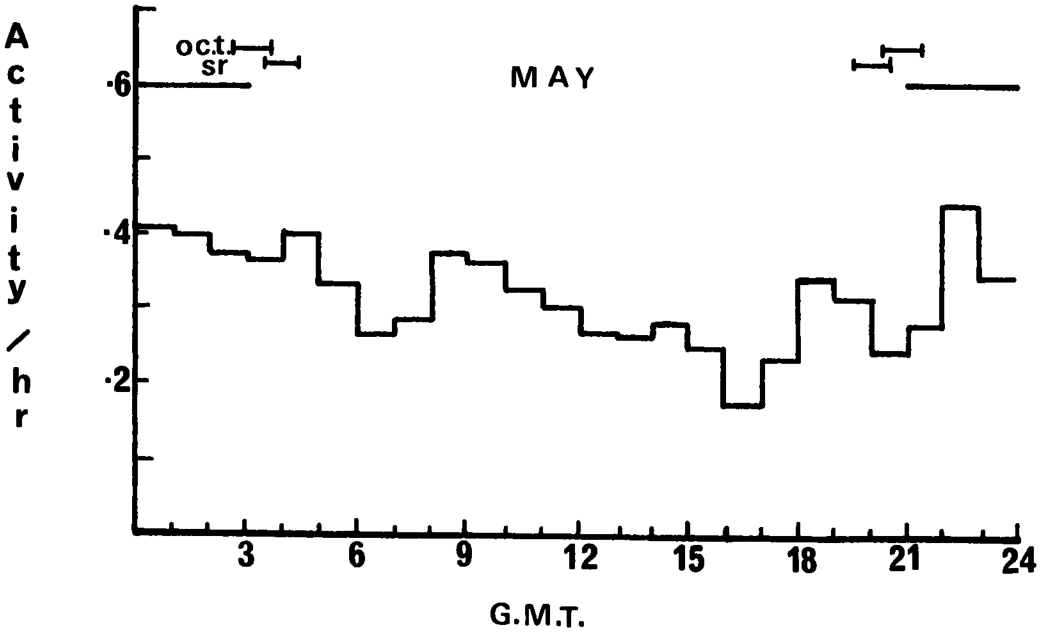
Activity/hr
·6
·4
·2
oct
sr
MAR.
3
6
9
12
15
18
21
24
G.M.T.

4



Activity/hr
·6
·4
·2
oct
sr
APR.
3
6
9
12
15
18
21
24
G.M.T.

5



Activity/hr
·6
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oct.
sr
MAY
3
6
9
12
15
18
21
24
G.M.T.

6

activity during April was $p = 0.279$.

In May (Fig. 6) the high proportion of activity at 0.30 hrs of $p = 0.41$ declined steadily through the day until 16.30 where a diel minimum of $p = 0.17$ was reached. After 17.00 the proportion of activity rose, albeit erratically, to the high night-time level. The diel maximum of $p = 0.44$ was attained at 22.30. The mean proportion of activity during May was $p = 0.319$.

The activity histograms of March and April showed some agreement in the location of their peaks but little in that of their depressions. There were corresponding peaks at 9-11, 13-15 and 23-24, but there was some shift in emphasis even here and the intervening depressions became somewhat displaced. The activity histogram of May is unlike that of either March or April although an intermediate condition may be discerned in the latter.

In March a fairly well defined increase in diurnal activity over the nocturnal level was noted, a condition which disappeared in April and showed a tendency to become reversed in May, where nocturnal levels of activity marginally exceeded those during the hours of daylight (see section 1.4).

Although the mean proportion of activity for March was lower than that of February, at 0.261 as compared with a February mean of 0.274, there was nevertheless a tendency for the means to increase with season to $p = 0.279$ in April and 0.319 in May.

1.1.3 Summer Season

In June (Fig. 7) the high proportion of activity at 3.30 of $p = 0.54$, the diel maximum, declined through two fairly well defined sequences of peaks and depressions with peaks at 7.30 and 12.30, to a diel minimum at 16.30 of $p = 0.15$. This was followed by a steady rise to a level of $p = 0.34$ at 19.30 which remained stable until 24.00 after which a second steady rise occurred until the maximum was reached at 3.30. The mean proportion of activity during June was $p = 0.316$.

In July (Fig. 8) the high proportion of activity at 1.30 of $p = 0.62$, the diel maximum, declined through one fairly well defined sequence of peak and depression, the peak at 6.30, to a diel minimum of $p = 0.25$ at 9.30. After 10.00 the proportion of activity remained stable with only minor fluctuations until 23.00 when it rose steeply to a level of $p = 0.60$ at 23.30 and then marginally further to the maximum at 1.30. The mean proportion of activity during July was $p = 0.380$.

In August (Fig. 9) the high proportion of activity at 1.30 of 0.61, the diel maximum, declined through two well defined sequences of peaks and depressions, with the peaks at 5.30 and 9.30, to the diel minimum of $p = 0.12$ at 13.30. This was followed by a steady increase in activity, interrupted by an ill defined peak at 15.30, until 20.30 at

Figures 7 - 9

The distribution of Diel Activity in the Summer Season

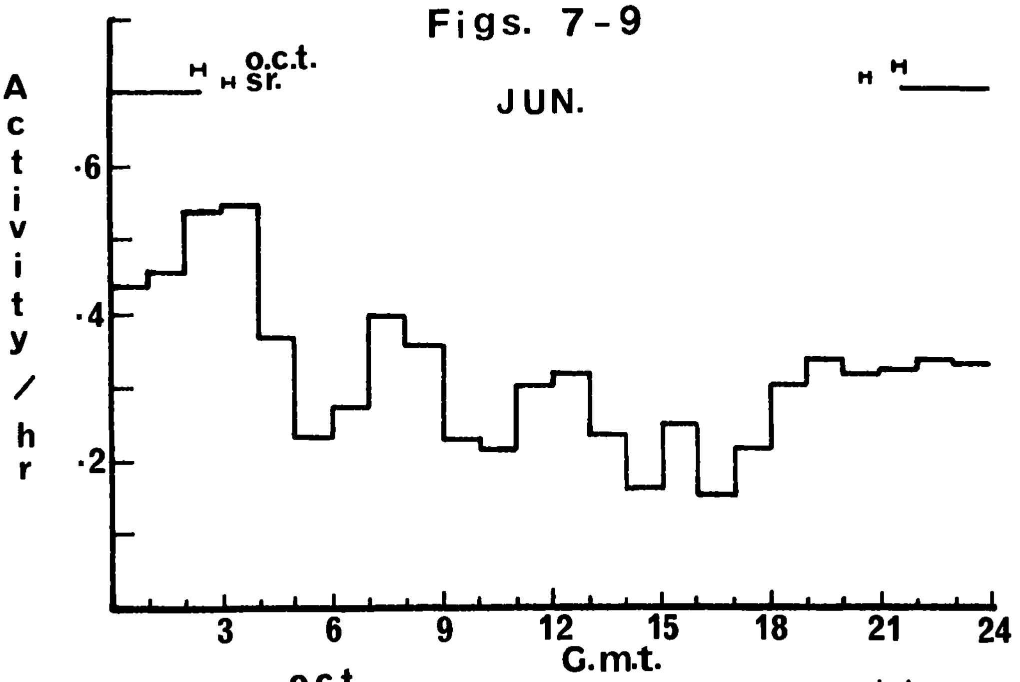
Figure 7	June	(n = 57; 5 voles)
Figure 8	July	(n = 72; 4 voles)
Figure 9	August	(n = 47; 4 voles)

Activity/hr - above-ground activity expressed as a proportion of the maximum possible (1.0) at hourly intervals commencing at midnight (0.00 hrs).

o.c.t. - the monthly range of the timing of the onset of civil twilight. The mean duration of night is signified by a continuous black line.

sr. - the monthly range of the timing of sunrise and sunset.

Figs. 7-9


o.c.t.
sr.
JUN.
Activity / hr
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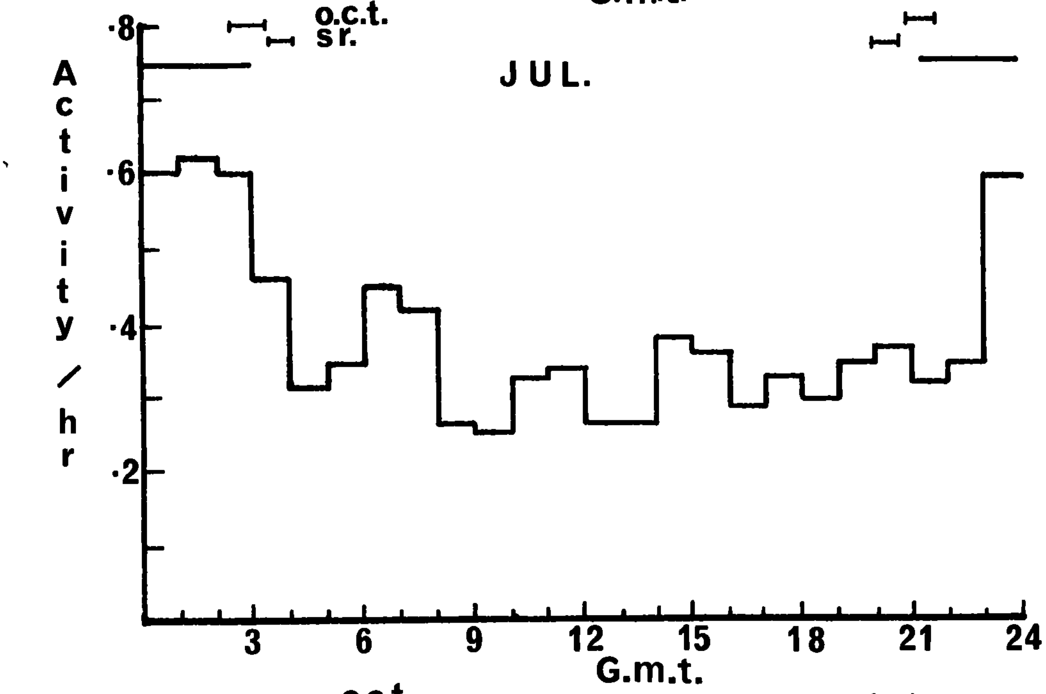
12
15
18
21
24
G.m.t.

7


o.c.t.
sr.
JUL.
Activity / hr
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12
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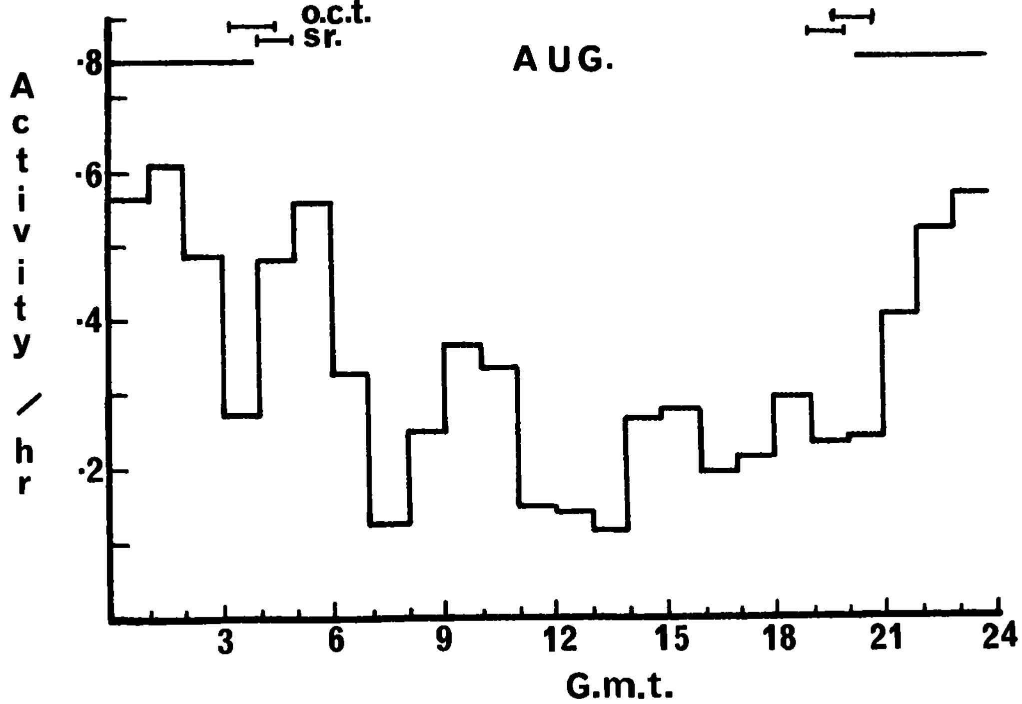
21
24
G.m.t.

8


o.c.t.
sr.
AUG.
Activity / hr
·8
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15
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21
24
G.m.t.

9

a level of $p = 0.24$ whereupon the rise showed a sharp increase until the maximum was reached at 1.30. The mean proportion of activity during August was $p = 0.331$.

The activity histograms of June, July and August showed good agreement in the location of their peaks and depressions. There were corresponding peaks at 1-3, 7-8, 11-12 and possibly 15-16 G.M.T., and corresponding depressions at 4-6, 9-10, 13-14 in June and July, which before 14.00 appear approximately one hour earlier in August. The three months showed a development of the trend suggested by the May histogram of a steady though interrupted decline from high activity levels during the night and early morning to a minimum at noon or early afternoon. This was followed by a subsequent rise in the early afternoon or evening to the maximum level, a rise interrupted by sequences of peaks and depressions which were rather less pronounced than in the morning.

A clear preference for nocturnal activity can be seen to have developed (see Section 1.4).

The mean proportion of activity was similar in June to that of May, $p = 0.316$ as compared with 0.319, the marginal reduction being reversed in the annual maximum of 0.380 in July. August however showed a decline in the proportion of activity to $p = 0.331$.

1.1.4 Autumn Season

In September (Fig. 10) the high proportion of activity at 1.30 of $p = 0.50$, the diel maximum, declined through two fairly well defined sequences of peaks and depressions, with peaks at 5.30 and 9.30, to a diel minimum of $p = 0.09$ at 13.30. This was followed by a steady rise in activity interrupted by only minor fluctuations until 19.30 at a level of $p = 0.20$ whereupon the rise increased more rapidly until the maximum was reached at 1.30. The mean proportion of activity during September was $p = 0.2475$.

In October (Fig.11) the proportion of activity was fairly stable with the most clearly defined sequence of peak and depression having its peak at 6.30 where the proportion of activity is at the diel maximum of $p = 0.34$, the diel minimum of $p = 0.14$ occurring at 21.30. The mean proportion of activity during October was $p = 0.216$.

In November (Fig. 12) the mean proportion of activity for the month of $p = 0.252$ was the result of repeated sequences of fairly well defined peaks and depressions, with peaks at 2.30, 7.30, 11.30, 17.30 and 20.30. The diel maximum of activity was at 7.30 with $p = 0.34$ and the minimum of activity at 14.30 with $p = 0.16$. The sequences of peaks and depressions were regularly spaced and were similar in magnitude.

The activity histograms of October and November showed good agreement in the location of their peaks and depressions. There were corresponding peaks at 6–8, 11–12, 15–17 G.M.T.

Figures 10 - 12

The distribution of Diel Activity in the Autumn Season

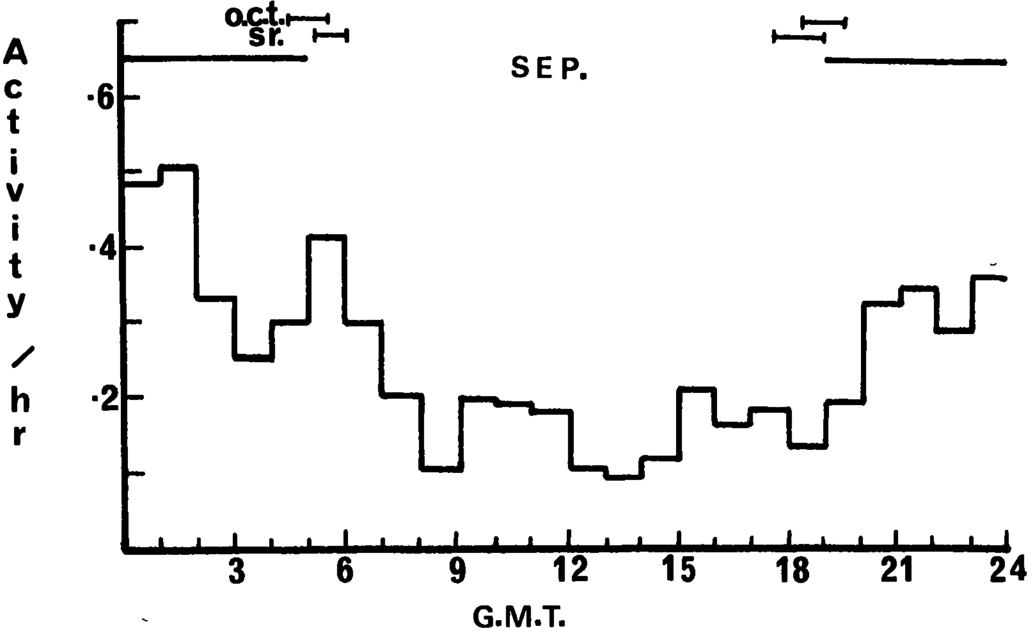
Figure 10	September	(n = 56; 3 voles)
Figure 11	October	(n = 93; 3 voles)
Figure 12	November	(n = 106; 6 voles)

Activity/hr = above-ground activity expressed as a proportion of the maximum possible (1.0) at hourly intervals commencing at midnight (0.00 hrs).

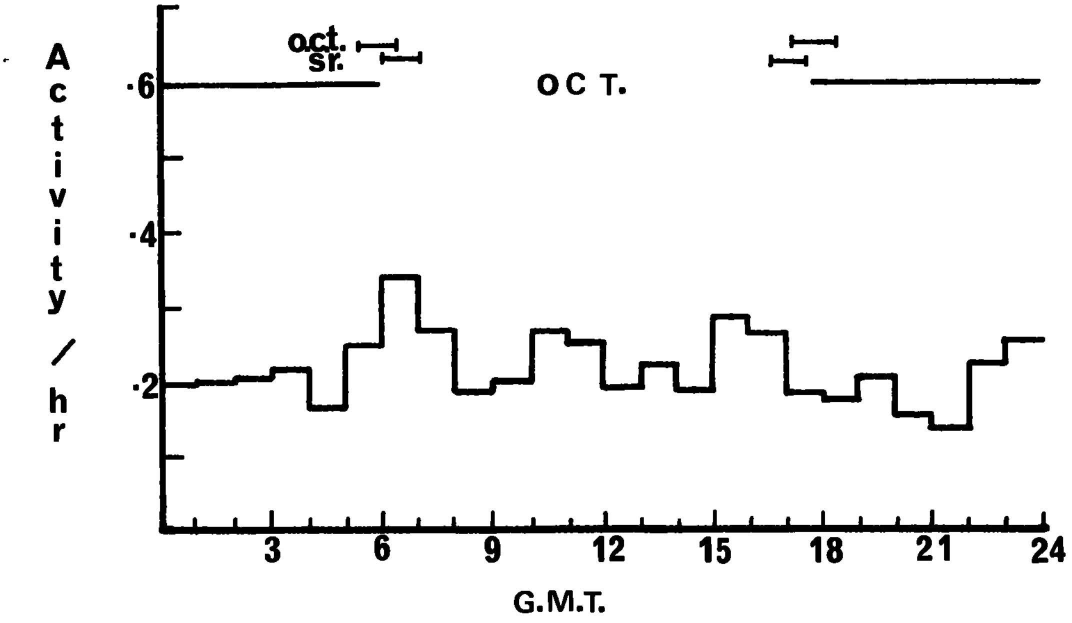
o.c.t. = the monthly range of the timing of the onset of civil twilight. The mean duration of night is signified by a continuous black line.

sr. = the monthly range of the timing of sunrise and sunset.

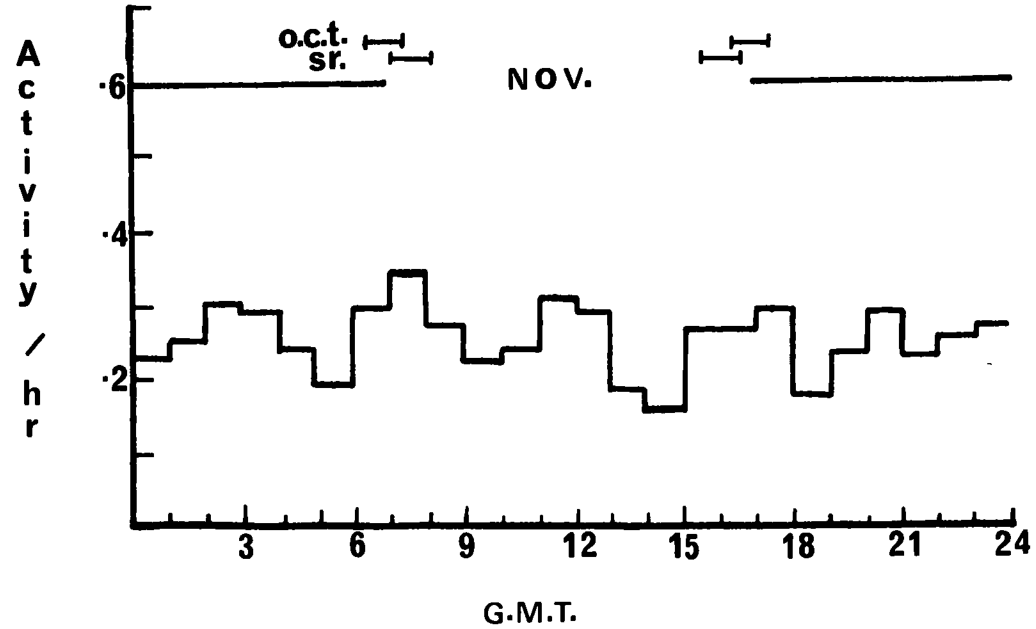
Figs. 10-12



10



11



12

and corresponding depressions at 4-6, 9-10, 14-15. The September histogram showed some similarity in peak location but before 12.00 the sequences occur approximately 1 hour earlier.

The September histogram resembled more closely that of August, with peaks at 0-2, 5-6, 9-11, 15-16 and depressions at 3-4, 7-9, 12-13, and in its characteristic of high night activity levels falling to an early afternoon minimum it resembled the summer season histograms as a whole. October and November however demonstrated the more even diel levels of activity that characterized the histograms of the winter season.

The mean proportion of activity declined from the August level of 0.331 to 0.2475 in September and fell further to 0.216 in October but rose in November to 0.252. This level was held with little variation until February.

Summary to Sections 1.1.1-4

In general shape the monthly histograms appear to fall almost equally into one of two categories. With minor variations the months October through until April were without strong diel trend, their variability being confined to the location of peak and depression sequences. An exception to this occurred in the histogram for March where a diurnal activity preference was clearly discernible. The second category involves the months of May to September where an increasingly strong diel trend developed with maxima of activity occurring during the night and early morning and the minima during the early afternoon.

There is also some evidence for considering that the mean level of activity increased from a December level of 0.25 with minor fluctuations until a maximum of 0.38 was reached in July. Subsequently the level declined, but more sharply, reaching an annual minimum of 0.216 in October. The October level may have been unusually low however as the remaining months from September until April show a narrow range from 0.2475-0.279.

The locations of the peaks and depressions indicated closer accord between adjacent months than non-adjacent months.

1.1.5. The Light-Dark Interface.

Lund (1970) reported that A. t. terrestris showed a definite response to dawn and dusk, a response which might be important in the day to day synchronisation of the vole intra-diel activity pattern. If the voles were responding strongly to dawn and dusk this response could be expected to show through the inevitable variation occurring in the timing of activity periods both between voles and from season to season.

The present data were examined for such a response. Three categories of response to the light-dark interface are possible; a response indicating a decline in activity at the interface (-1); no response at the interface (0);

and a response indicating an increase in activity at the interface (+1).

The monthly histograms in figures 1-12 were examined for a response in a total of five tests. The mean timing of sunrise was examined in each monthly histogram and a visual assessmont made as to whether the activity level in the data noticeably declined within $\frac{1}{2}$ hr of that period (-1), stayed the same (0), or whether it noticeably increased (+1). These were valued judgments and the size of the decline or increase required to substantiate a negative or positive response varied relatively with the general level of variation through the day for that month.

The twelve monthly samples were separated into -1, 0, +1 categories. The same assessment was carried out at the mean period of sunset, at the mean period of the beginning of civil twilight in the morning, and also at the mean period of the end of civil twilight in the evening. One further test for response was carried out. It is clear that the mean position of sunrise, sunset and that of the onset of civil twilight will change by several hours throughout the year. If the timing of activity periods were to remain the same through the year then a point which moves at monthly intervals across these positions is bound to record a response as the activity period changes to a rest period later in the day or vice versa. It was decided therefore to compare the four tests described above with a fifth point which remained entirely within the regime of daylight but which altered from month to month at a similar rate to dawn and dusk. The fifth test therefore involved a daylight control point which fluctuated from 14.00 in January, to 9.00 in June, to 14.00 in December, a fluctuation similar to that of dawn and dusk.

The results for the 5 tests were totalled for the twelve histograms and are as follows:

	Dawn			Dusk			Control		
	-1	0	+1	-1	0	+1	-1	0	+1
Mean Onset C.T.	2	9	1	2	7	3	4	7	1
Mean Sunrise/set	6	6	0	2	10	0			

Only one of the four trials, that of mean sunrise, demonstrated a response stronger than the control and even here the total number of responses, positive and negative, failed to exceed the no-response total. These data do not demonstrate that dawn and dusk produced a clear response in Arvicola activity.

Discussion on Section 1.1

Any natural variability from day to day, among individuals, between sexes, the accompanied and unaccompanied condition, and particularly between years, will combine to smooth out any clear sequences of synchronized activity when these data are taken together as in figures 1-12. Clearly-defined sequences of peaks and depressions ranged from a total over the 24 hour period of two in February to four in August. It is unlikely to be coincidental that the better defined sequences occurred in June, August and September when the sample size was smallest. In consequence of this natural variability, activity histograms of this kind cannot be expected to give accurate information on the frequency of the intra-diel activity pattern which must therefore be analysed from other data.

The apparent trend in total activity levels of winter minima and summer maxima should also be analysed in greater detail.

The apparent changes in vole preference for diurnal and nocturnal activity which may be a reason for the contradictory results of other workers (van Wijngaarden, 1954; Ashby et al., 1969; Stoddart, 1969b; Lund, 1970) should also be investigated further particularly as such preferences may result in the active or passive selectivity of external environmental temperature, the avoidance of cold nights in winter and hot days in summer.

An attempt to analyse these three possible factors is made in subsequent sections.

1.2 Seasonal Variation in the Duration of Diel Activity.

Figure 13 shows the mean duration of activity outside the burrow system in hours of activity per day, for each month of the year. It may be seen that a duration of activity of approximately 6 hours/day was fairly constant for a period from September to March, with the months of October and February showing the greater deviation from this figure. From April to June there was a clear increase in the duration of activity to a level of 7.6 hours/day, followed by a sharp increase to the annual maximum in July of 9.1 hrs/day. Subsequently there followed a fairly sharp decrease to 7.9 hrs in August, a decrease which was continued to the winter level of approximately 6 hrs/day from September onwards. An attempt was made to determine the statistical significance of these changes.

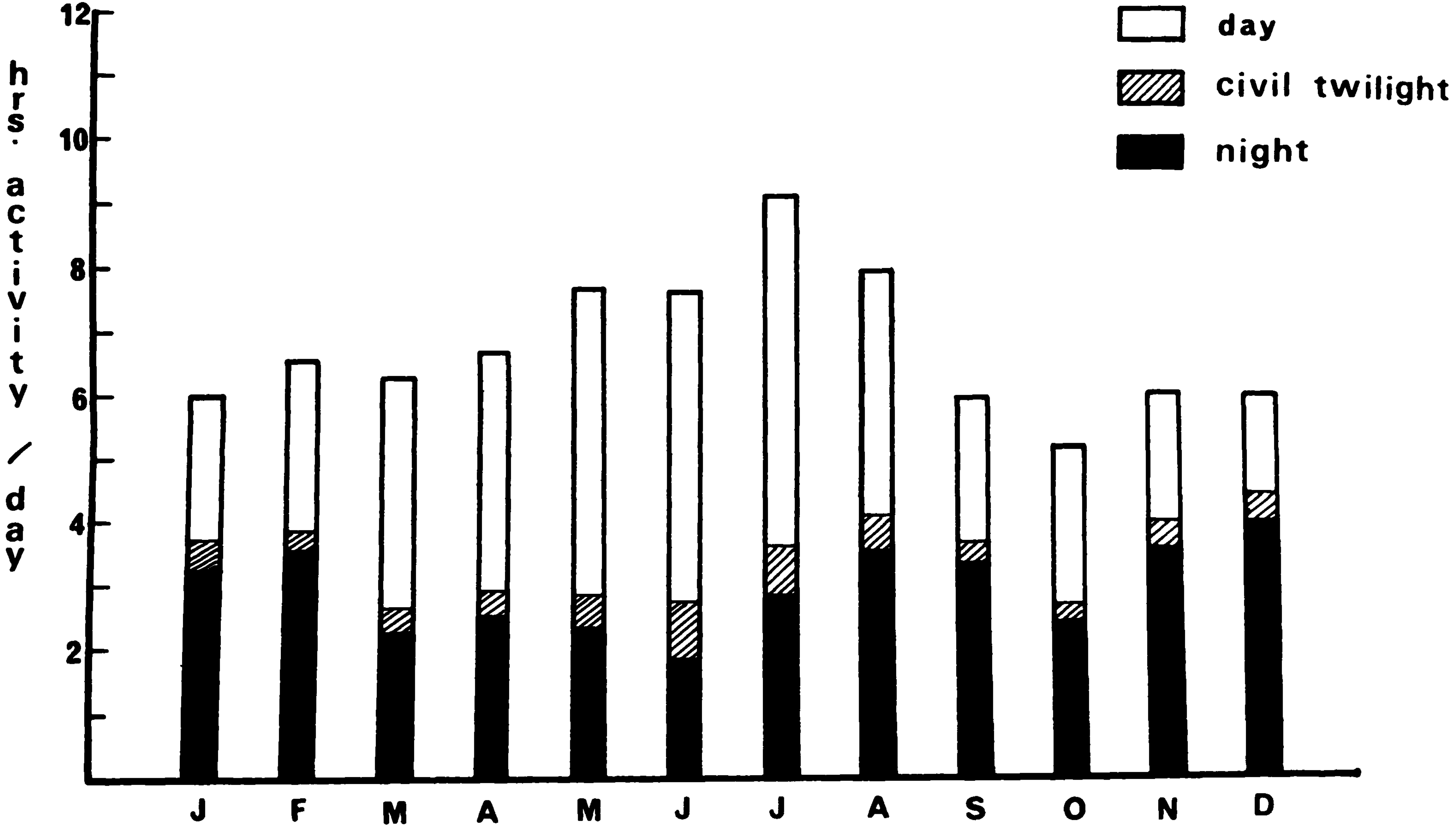
The frequency distributions of the daily duration of activity of individual voles over the monthly period usually produced a positively skewed curve, a departure from normality exacerbated when the data of all individuals for a calendar month are taken together, this either increased the skew or on several occasions created a bimodal distribution. Because of the loss of normality in the sample distribution curves much of the data in this and subsequent sections which use the same distributions have been analysed by a non-parametric statistic, in these cases the writer follows Siegel (1956) in the choice of the statistic employed.

In analysing the data for the duration of diel activity it was decided to compare the entire distributions of the monthly samples by the Kolmogorov-Smirnov two-sample Test. The test may be used to determine any kind of difference in two distributions under examination, either in central tendency, in dispersion, or skewness, in this case the two-tailed form of the test is employed. It may also be used to determine whether the values of one sample are stochastically larger than the values of the second sample, in this case the one-

Figure 13

Changes in the duration of Diel Activity with time of year

Diel activity is expressed as the mean duration of above-ground activity in hours of activity per day for each month of the year. The total daily duration of activity has been subdivided into that activity taking place during the day, during the period of civil twilight, and during the night. The mean monthly positions for the onset of civil twilight and for those of sunrise and sunset were used in the calculation of the duration of activity taking place during the period of civil twilight.


hrs. activity / day
12
10
8
6
4
2
J
F
M
A
M
J
J
A
S
O
N
D
day
civil twilight
night

tailed form of the test is employed (Siegel, 1956).

In the analysis of the monthly changes in the duration of diel activity it is the differences in the location of central tendency rather than the shape of the sample distribution curve which is of most interest and where this can be predicted it is the one-tailed form of the test that is the more valuable.

As the median of a sample is a better reflection of the location of central tendency of the frequency distribution curve than the arithmetic mean the median figures in hours of activity per day were found for the twelve monthly samples and these together with their 95% confidence limits (Campbell, 1967; Snedecor and Cochran, 1971) are shown in Table 2. It was considered that where the median figure of one month lay outside and below the 95% confidence limits of another then it was valid to predict that the values of the latter were stochastically larger, and a one-tailed test employed. Where the median fell within the 95% confidence limits of the second median the two-tailed form of the test was used in its place. Occasionally both tests have been employed.

The arithmetic means of monthly diel activity, the values of which were utilized in the compilation of Fig.13 are also presented in Table 2. The influence of the positive skew typical of the sample distributions is demonstrated in the arithmetic mean being numerically greater than the corresponding monthly median, although the months of August and October are exceptions.

Table 2.

The Mean Duration of External Activity

Month	Mean	Median	95% Limits	n
Jan	6.02	5.3	4.8-6.1	131
Feb	6.57	5.8	5.4-6.4	104
Mar	6.26	5.4	4.6-6.4	119
Apr	6.69	6.4	5.5-7.3	79
May	7.66	7.45	6.8-8.1	68
Jun	7.59	7.5	7.1-8.1	57
Jul	9.11	8.8	8.6-9.2	72
Aug	7.94	8.3	7.3-8.7	47
Sep	5.95	5.95	5.4-6.4	56
Oct	5.18	5.3	4.7-5.5	93
Nov	6.03	5.3	5.1-5.7	106
Dec	6.00	5.5	5.1-5.9	154

Table 2 continued.

Comparison 1 < 2	2-tailed $\frac{D}{\sqrt{n1+n2/n1n2}}$	1-tailed chi^2 2.d.f.	p	result
Jan≤Feb	0.857	2.9	0.05	n.s.
Fob=Mar	1.281		0.05	n.s.
Feb Mar		6.6	0.05	*
Mar Apr		15.1	0.001	***
Apr May		10.0	0.01	**
May≤Jun	0.535	1.1	0.05	n.s.
May Jul		24.6	0.001	**
Jun Jul		15.1	0.001	***
Jun Aug		2.8	0.05	n.s.
Aug Jul		7.9	0.05	*
Sep Aug		26.5	0.001	***
Oct Sep		6.4	0.05	*
Nov Sep		3.3	0.05	n.s.
Oct≤Nov	1.218	5.9	0.05	n.s.
Oct=Feb	1.657		0.01	**
Nov=Dec	0.601		0.05	n.s.
Dec=Jan	0.900		0.05	n.s.

The results in Table 2 demonstrate that the conclusion in Section 1.1 that the diel activity frequency distributions consisted of a stable winter sequence and a higher and changing summer sequence was substantially correct. The two-tailed test revealed no significant consecutive differences in the sample distributions from October until March suggesting that no long-term trend is taking place over the winter months. When however the two winter extremes of October and February were compared then a result of 1.657, $P < 0.01$, was obtained which demonstrates that differences between months could be significant even within the relatively stable winter condition. Where they have been examined the one-tailed tests have likewise failed to produce a significant result except in the case where February was predicted to exceed March where $\chi^2 = 6.6$, 2 d.f., $P < 0.05$, giving a significant result at the 5% level. Since such a trend would be a reversal of that found subsequently for late spring and early summer some doubt must be placed on its validity as a general conclusion.

From March until July however the one-tailed test revealed a trend of increasing diel activity, interrupted only by the non-significant result of May $<$June, $\chi^2 = 1.14$, 2.d.f., $P > 0.05$. After July this trend was reversed and diel activity decreased with significant results until October. The hypothesis that November $<$ September however gave $\chi^2 = 3.30$, 2.d.f., $P > 0.05$, a non-significant result, suggesting that the trend ended with September, October not being representative of the usual winter level of activity.

Consequently although fluctuations in the fairly stable winter level of activity did exist it may be concluded that there was no general trend in diel activity duration from September until March. From April onwards a gradual and, with the exception of May (June, significant increase occurred until a peak was reached in July, after which followed a decline in activity until September.

1.3. Population Variation in the Duration of Diel Activity.

In analysing the seasonal variation in the duration of daily activity the data for voles differing in sex, in the accompanied and unaccompanied condition, and from consecutive years, were taken together, so that variation due to seasonal changes could be observed to override these other factors. However the frequency distributions of diel activity of groups and individuals may be tested against one another by comparing each of two distributions with the median of the two distributions when combined by (1) the Median Test, and by (2) the Fisher Exact Probability Test (Siegel 1956). The Median test may be used when the combined sample sizes, $n_1 + n_2$ exceed 40, and for combined sample sizes between 20 and 40 when all cells of the 2 x 2 contingency table exceed 5. The Fisher Test may be used when the sample size, $n_1 + n_2$, is less than 20, and for sample sizes between 20 and 40 when any cell of the 2 x 2 contingency table is less than 5.

1.3.1 Differences between sexes

Three tests on potential sex differences were carried out on those monthly data that allowed a comparison between two voles of each sex. This required taking the data for two years together, one vole of each sex being represented in each year. The same individuals were used in all of the tests.

The null hypothesis, Ho, that there is no difference between the sexes in the duration of diel activity is tested against the alternative hypothesis, H_1, that a difference exists. The Median Test is used on each occasion, $n_1 + n_2 > 40$, no prediction as to direction is made in H_1, the test is therefore two-tailed. In the following tables + and - refer to the number of days where the duration of activity exceeds and falls below the median of the combined distributions respectively. M and F refer to male and female voles respectively.

Month	Combined Median							
	M+	F+	M-	F-	n_1+n_2	chi^2 df=1	P	Result
Nov.	13	11	7	17	48	2.14	>0.05	n.s.
Dec.	25	26	26	26	103	0.01	>0.05	n.s.
Jan.	20	28	26	23	97	0.85	>0.05	n.s.

In no case is Ho rejected and it is therefore concluded that these data did not demonstrate any difference in the duration of daily activity between the sexes.

1.3.2 Differences between the Accompanied and Solitary condition.

The frequency distributions for the duration of daily activity of unaccompanied voles for two years were taken together and compared with the combined data for accompanied voles. Three tests for potential differences were carried out. In November and December two unaccompanied voles, one male, one female were compared with four accompanied voles, two male, two female. In October two unaccompanied voles were compared with two accompanied voles, in each case there was one vole of each sex. Ho that there is no difference between the two conditions is tested against H_1 that a difference exists. The Median Test is used on each occasion, $n_1+n_2>40$, no prediction as to direction is made in H_1 the test is therefore two-tailed. S and A refer to solitary and accompanied voles respectively.

Month	Combined Median							
	S+	A+	S-	A-	n_1+n_2	chi^{2}df=1	P	Result
Nov.	20	29	33	17	99	5.34	<0.05	*
Dec.	20	55	28	48	151	1.36	>0.05	n.s.
Oct.	22	23	38	8	91	10.06	<0.01	***

Two of the three tests rejected Ho at the 5% level or better, in the months of November and October therefore there was a significant difference in the duration of daily activity between solitary and accompanied voles. In the case of December however Ho was accepted, there was no difference in the duration of daily activity between solitary and accompanied voles in this month. Subsequently the data for the three months were taken together and re-tested, Ho and H_1 as previously.

S+	A+	S-	A-	n_1+n_2	$chi^2 df=1$	P
62	108	98	73	341	14.04	<0.001

The null hypothesis, Ho, is rejected at the 0.1% level. It is therefore concluded that a significant difference existed in the duration of daily activity between voles kept isolated from their fellows and those living in close contact with another vole. The direction of this difference proved to be that accompanied voles were active for a longer period each day on average than were isolated voles.

1.3.3. Differences between years.

The frequency distributions for the duration of daily activity of voles for three months during the winter of 1971-2 were compared with those of 1972-3. In the first instance the data for all individuals in the respective years were used in the comparison. The data for each sex were then taken separately and the duration of daily activity for voles of the same sex for the three months of 1971-2 were compared with those of 1972-3. In these latter comparisons the values of accompanied individuals only were included as in 1971 and again in 1972 only one solitary vole was present, a male and a female respectively. Although the conclusion of section 1.3.1 that there was no difference between the sexes in the duration of daily activity allows the inclusion of these data in the overall comparison the result of Section 1.3.2 that solitary individuals were less active than accompanied ones would indicate a bias if the data for solitary voles were included in either 1971-2 or 1972-3 but not both. The data for solitary voles are tested against each other in two further comparisons. All the voles in 1971-2 are of similar age to those of 1972-3. Ho that there is no difference between years is tested against H1 that a difference exists. In all but two comparisons the Median Test is used, in the two remaining cases $N_1 + N_2 = 20 - 40$ with at least one cell containing less than 5, and here the Fisher Test is employed. No prediction as to direction is made in H_1, the test is therefore two-tailed. 71 - 2 and 72-3 refer to the data of the winters 1971-2 and 1972-3 respectively.

Month Comb'd data	Vole Nos.	Combined Median 71-2$^+$	72-3$^+$	71-2$^-$	72-3$^-$	$n_1 + n_2$	ch^{2}df=1	p
Nov.	6	21	3	1	23	48	30.3	<0.001
Dec.	6	46	5	3	49	103	70.2	<0.001
Jan.	6	41	7	6	43	97	49.1	<0.001
Acc. males:								
Nov.	2	9	1	1	9	20	Fisher	<0.01
Dec.	2	22	3	3	23	51	26.8	<0.001
Jan.	2	21	3	2	20	46	25.2	<0.001
Acc. females:								
Nov.	2	11	3	0	14	28	Fisher	<0.01
Dec.	2	24	2	0	26	52	40.7	<0.001
Jan.	2	22	3	2	22	49	28.0	<0.001
Solitary:								
Nov.	2	21	7	8	19	55	9.6	<0.01
Dec.	2	19	5	6	17	47	11.2	<0.001

In every case Ho is rejected at the 1% level or higher; the figures for the duration of daily activity for the winter months 1971-2 were consistently and significantly greater than those of 1972-3. The reasons for this are by no means clear. Although December 1971 was markedly milder than December 1972 neither November 1971 nor January 1972 had higher temperatures than their respective months a year later. It might be that one of the pair of accompanied voles from Nov. 1971- Jan.1972 which were the same voles in each of the three tests, was a particularly active animal and its activity encouraged its enclosure partner to increase its own. It should be remembered however that the isolated vole during this period also exceeded its companion a year later.

A drawback of this comparison is the low number of voles involved. A maximum of six individuals have been compared in the combined distribution tests, but only two in the remainder of the tests. In these latter the test is at least as much one of variability between voles as of variability between years. However it is remarkable even so that the data for the duration of daily activity during the 1971-72 winter always exceeded that of 1972-3 and at very high levels of significance.

It may therefore be concluded that the voles tested differed significantly in their activity from year to year, but it is not demonstrated whether this was due to yearly or individual variability.

Summary to Sections 1.3.1-3

1. No difference could be found in the duration of diel activity of males and females.

2. The mean duration of diel activity of accompanied voles was significantly greater than that of solitary voles.

3. There was a significant difference in the duration of diel activity between consecutive years but it was not demonstrated whether this difference reflected variability between years or between individuals.

Discussion on Section 1.3.

A disadvantage of the results reported in Section 1.3 is the low number of individual voles involved. Two male voles are compared with two females for three months in section 1.3.1, two solitary voles with a maximum of four accompanied voles in Section 1.3.2, and a maximum of three individuals for 1971-2 with three for 1972-3 in Section 1.3.3. One advantage of the comparisons in Sections 1.3.1 and 1.3.2 however is that the records are those from combined data of consecutive years which allows a greater confidence of general conclusion than would otherwise be possible.

1.4 The Effect of Light and Dark on Diel Activity.

Figure 13, besides showing the mean numbers of hours of external activity per day for each month of the year compiled from the entire data, also indicates the proportion of that activity taking place during the hours of darkness and of daylight respectively. The light-dark interface here is drawn at the mean monthly time of occurrence of the onset of civil twilight. However to enable comparison with other research that for an interface at the mean time of occurrence during the month of sunrise and sunset is also calculated. It can be see from Fig.13 that more than 50% of the activity took place during the night in September and from November until February, the remainder of the year displaying a majority of activity during the day. The corresponding result: for a sunrise/sunset interface is that there was a night-time majority of activity from August until February and a day-time majority for the remainder of the year. These results are set out in Table 3.

In Table 3 the mean duration of daily activity is calculated in hrs/day for each month, where n is the total number of vole days present per month.

Under the heading "Onset of Civil Twilight" the mean daily activity in hrs/day for each month is separated into the mean duration of activity taking place firstly during the hours of darkness and secondly those of daylight, assuming that daylight commences at the onset of civil twilight in the morning and continues until the end of civil twilight in the evening. The proportion of the activity taking place during the hours of darkness and of daylight are then expressed as a percentage of the total daily activity. Under the heading "Sunrise/Set" the proportion of the activity taking place during the hours of darkness and daylight are exoressed as a percentage of the total daily activity assuming that daylight commences at sunrise and continues until sunset. The mean monthly positions of the onset and end of civil twilight and of sunrise and sunset are used in the calculations.

Table 3. The Day and Night-time Proportions of Above-ground Activity.

		Onset of Civil Twilight					Sunrise/set	
Month	n	hrs/ day	hrs-dark	hrs-light	% dark	% light	% dark	% light
Jan.	131	6.02	3.23	2.79	53.7	46.3	61.7	38.3
Feb.	104	6.57	3.55	3.02	54.0	46.0	58.8	41.2
Mar.	119	6.26	2.27	3.99	36.3	63.7	42.2	57.8
Apr.	79	6.69	2.50	4.19	37.4	62.6	43.2	56.8
May	68	7.66	2.33	5.33	30.4	69.6	37.1	62.9
Jun.	57	7.59	1.84	5.75	24.2	75.8	35.8	64.2
Jul.	72	9.11	2.82	6.29	31.0	69.0	39.1	60.9
Aug.	47	7.94	3.54	4.40	44.6	55.4	50.9	49.1
Sep.	56	5.95	3.36	2.59	56.5	43.5	62.1	37.9
Oct.	93	5.18	2.39	2.79	46.1	53.9	52.2	47.8
Nov.	106	6.03	3.54	2.49	58.7	41.3	65.6	34.4
Dec.	154	6.00	3.97	2.03	66.2	33.8	73.5	26.5
Total	1086	6.75	2.94	3.81	43.6	56.4	51.9	48.1

Consequently it may be seen that for five months of the year only did a majority percentage of the diel activity take place during the night. Since the photoperiod exceeds 12 hours for seven months of the year when civil twilight is included these data suggest that the voles appear to have timed their activity without specific preference for either daylight or darkness. To test this hypothesis the duration of activity recorded for the light and dark periods of each diel total were divided by the respective duration means of daylight and darkness. In this way the proportion, p, of each hour during which the vole was active may be calculated for the light and dark periods separately.

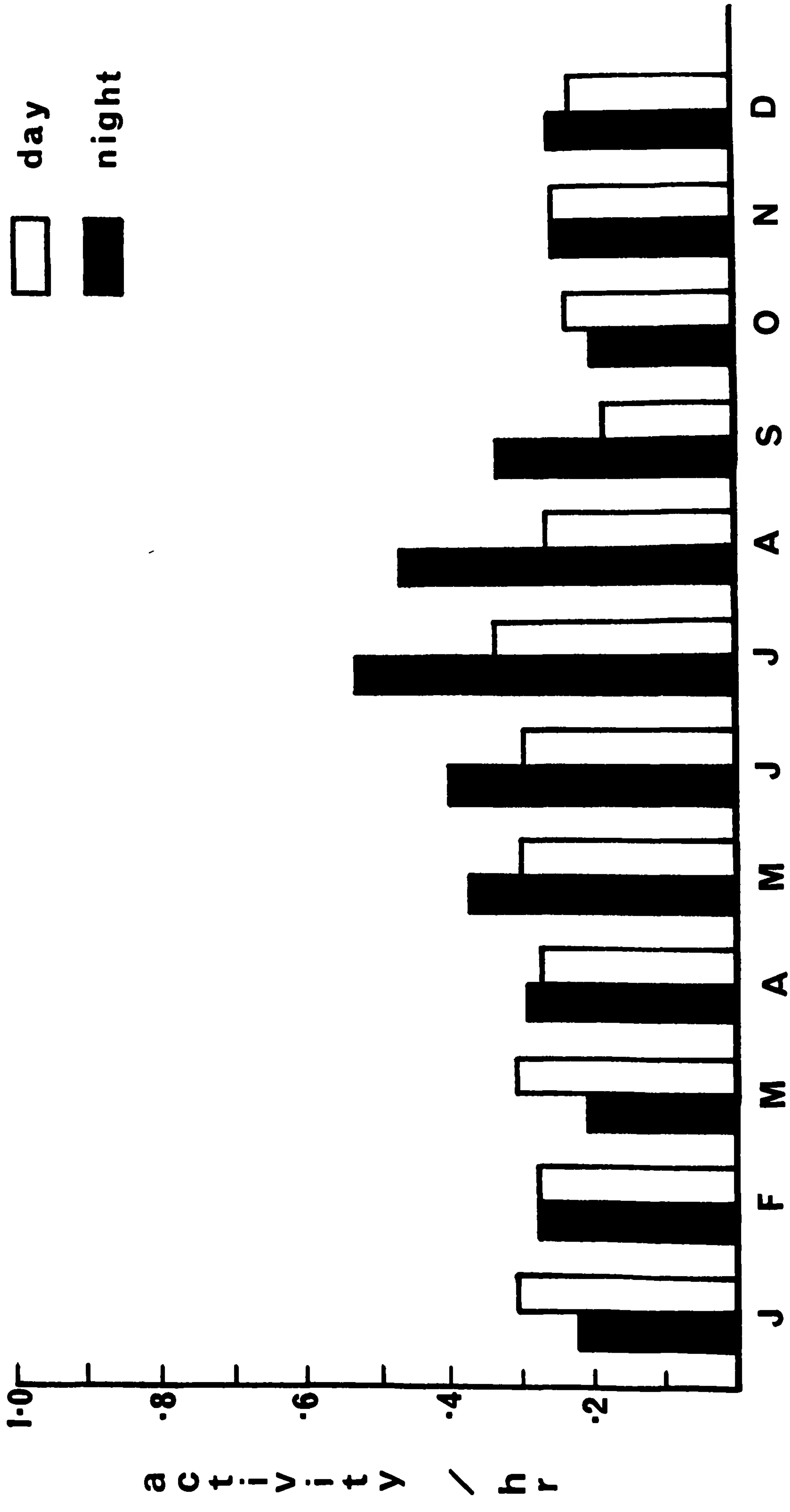
Figure 14 shows the proportion of each hour of light and darkness during which the voles were active for each month of the year. It may be seen that in the months of November, December, February and April there was little, if any, difference in the proportion of activity per hour of light or darkness. In January and March, however, and to a lesser extent also in October, the proportion of daily activity taking place per hour of daylight exceeded that taking place per hour of darkness to a noticeable degree. This excess of daylight activity over night-time activity amounted to an increase of 19.3% in October, 38.4% in January and 50.0% in March. It may be concluded in broad terms therefore that during the period from October until April the proportion of activity taking place per hour of daylight was similar to that taking place per hour of darkness but that when a marked preference was displayed it was a preference for daylight activity.

During the period May until September however the proportion of activity taking place per hour of darkness

Figure 14

Changes in the proportion of Diel Activity taking place during the day and night with time of year.

Activity/ hr = above-ground activity expressed as a proportion of the maximum possible (1.0) during 1) the night and 2) the day. In the calculation the period of civil twilight has been incorporated as part of the day. The mean monthly positions for the onset of civil twilight have been used in the calculation.


day
night
activity / hr
1·0
·8
·6
·4
·2
J
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exceeded that taking place per hour of daylight. This excess of night-time activity over daylight activity amounted to an increase of 24.7% in May, 34.7% in June, 57.3% in July, 76.0% in August and 81.6% in September. The differences were both consistent in direction and marked in degree.

The results shown in Figure 14 therefore indicate two annual groupings of activity preference between the hours of daylight and darkness. From October until April the voles showed either no preference at all or a preference for activity taking place during the day. From May until September the voles showed a continued and, from July until September, substantial, preference for night-time activity. These two preference groupings are in partial opposition to the trends of winter decrease and summer increase of photoperiod and may indicate that the voles attempted to compensate for the short day length in winter by increasing the relative proportion of hourly activity during the day, and for the short summer nights by increasing the relative proportion of hourly activity during the night. However the effect of this should not be exaggerated, the percentage of activity taking place during the night in June was 24.2%, a figure not greatly different from the night-time proportion of the 24 hours of 19.2%. There can be no question however that the summer nocturnal preference at least was a result of an alteration of the timing of activity. This was clearly shown in Figures 6-10 by the concentration of activity during the night and early morning at the expense of that during the early afternoon. This preference was not simply a result of the shifting lines of dawn and dusk moving over stable periods of rest and activity although this too may have been a factor.

Discussion on Section 1.4

It is somewhat surprising that it was the summer nocturnal preference which was held most continuously while the winter diurnal tendency which could be expected to have been adopted to avoid the severe night-time temperatures was intermittent, and since it occurred in October, January and March and not in November, December and February, apparently not temperature dependent. The reason for the summer nocturnal preference is not clear. It was not strong enough greatly to influence what was, in fact, a pronounced summer diurnalism yet the activity minima occurred during the early afternoon, as demonstrated in Section 1.1, suggesting a possible avoidance of the highest summer temperatures, an avoidance that might become more pronounced in the enclosures, where the voles tended to keep the bank vegetation close-cropped, than in the wild where considerable shade is afforded by the thick streamside vegetation. It is by no means certain however that the voles have a need to avoid the afternoon because of the excessive heat. The modest effect of the nocturnal preference on the summer diurnalism would not seem to allow much protection from diurnal predators,, and under the experimental conditions there was no question of sustained human interference.

A possible explanation may be that the voles are obliged by their food requirements to maintain a regular feeding cycle of activity regardless of season and that the observed preferences are the maxima allowable in the face of continuous metabolic energy demands. The question of whether these seasonal preferences affect temperature experience is discussed in Section 3.

1.5 Variation of Diel Activity with Weather Conditions

The more profound weather effects were observed to have an indisputable influence on vole activity at least with regard to the usual cycle of external activity and nest chamber quiescence. For example the influence of a deep cyclonic depression bringing a sustained period of heavy rain may result in a rise in stream level to a point where the lower Arvicola galleries and nest chambers become flooded and the voles forced either into the upper galleries or onto higher ground in the open. A less frequent phenomenon, but nevertheless one occurring several times during an average year, is a rise in water level sufficient to overflow the normal bank limits.

This resulted in the voles taking shelter in shallow depressions in the sides of whatever part of the bank remained above the water level until the flood subsided. The freezing over of the habitat stream necessitates a change in some aspects of normal vole behaviour also. In these circumstances the voles are no longer able to take refuge from a predator by diving into the stream as the surface ice prevents this and instead they must run to the burrow for safety. Under freezing conditions it has been observed that a clear reduction in above-ground activity takes place in marked contrast to the reaction to flooding where the voles are forced above ground possibly for days at a time.

These two examples represent extreme changes in vole behaviour in response to adverse weather conditions that combined might occur less than twenty times during an average year. As such they are less a response to weather than to a changed environment and may force a behavioural response upon the voles which is quite different to their response to the more usual weather systems.

The day-to-day activity of a vole fluctuates within approximately two hours of its median throughout any specific month, and while the fluctuation may be much less than this range, except in extreme weather circumstances as exampled above, it is rarely greater. Nevertheless this two hour fluctuation may represent a precise response to temperature, windstrength, rainfall or sunshine and a selection of the data were examined with regard to these possibilities.

Where the daily activity records for an individual vole are available for twenty or more days during any particular month the duration of each day's activity was correlated with the appropriate figure for temperature, rainfall, windstrength, sunshine and cloudiness from data presented by the Durham Observatory, a meteorological station approximately 2 km from the enclosure areas. No data for changes in pressure were available and the effect of these was not tested. It was not considered possible to assume that the correlation scores were from a bivariate normal distribution, in consequence the non-parametric Spearman's Rank Correlation was employed as a test of association. During some months one or more variables tended towards a constant, for example in winter the majority of a month may be continuously overcast, or in summer rain may fall on only two or three occasions during a particularly dry month. On such occasions it was not possible to test for an association with vole activity.

In the following tests for association rs represents the correlation coefficient, and t the test for significance with n-2 degrees of freedom. Where two or more ranks were equal a correction for ties was applied in the calculation of rs after the method suggested by Siegel (1956). The individual voles are described by sex and by their unaccompanied (S) or accompanied (A) condition. The sample size n refers to the number of days in the correlation.

1.5.1 Winter Period

Correlation between the Duration of Daily Activity and Weather Factors. January 1972. Mean temperature 3.05°C.

		Temperature				Rainfall			
Vole	n	rs	t	p	result	rs	t	p	result
♂ S	31	0.630	4.363	<0.001	***	-0.033	0.18	>0.05	n.s.
♂ A	25	0.415	2.188	<0.05	*	0.229	1.13	>0.05	n.s.
♀ A	25	0.533	3.018	<0.01	**	-0.001	0.00	>0.05	n.s.

		Sunshine				Cloudiness			
		rs	t	p	result	rs	t	p	result
♂ S	31	-0.378	2.195	<0.05	*	0.290	1.634	>0.05	n.s.
♂ A	25	-0.440	2.349	<0.05	*	0.501	2.774	<0.05	*
♀ A	25	-0.277	1.384	>0.05	n.s.	0.318	1.608	>0.05	n.s.

		Windstrength			
		rs	t	p	result
♂ S	31	0.302	1.706	>0.05	n.s.
♂ A	25	0.096	0.458	>0.05	n.s.
♀ A	25	-0.08	0.381	>0.05	n.s.

December 1972. Mean Temperature 4.4°C.

		Temperature			
Vole	n	rs	t	p	result
♀ S	23	0.465	2.407	<0.05	*
♂ A	27	0.460	2.590	<0.05	*
♀ A	28	0.166	0.856	>0.05	n.s.

January 1973. Mean Temperature 2.9°C. Temperature

Vole	n	rs	t	p	result
♂ A	20	0.416	1.938	> 0.05	n.s.
♀ A	20	0.626	3.406	< 0.01	**

The data for January 1972 are correlated with all the weather variables under consideration, those for December 1972 and January 1973 with temperature only. The results clearly indicate that the duration of daily activity was not independent of weather. It would appear that rainfall and windstrength were not important day-to-day factors in determining activity fluctuations, the correlations were found to vary in direction and none proved significant. Activity showed a positive correlation with temperature however which proved to be significant in six of the eight cases examined at the 5% level or above and it may be concluded therefore that as temperature fell so too did the duration of daily vole activity. The correlation with sunshine produced three negative correlations two of which proved to be significant at the 5% level, while the association with cloud cover produced three positive correlations one of which proved significant at the 5% level, the remaining two falling below the levels of significance. These data suggest evidence that as the duration of sunshine decreased and cloudiness increased, so the daily duration of vole activity became extended.

In winter warm, cloudy weather which follows in the wake of depressions moving in from the Atlantic is a frequent occurrence, as is cold, sunny weather associated with the air of anticyclones positioned over Continental Europe. It is possible therefore that where these two weather types dominate the weather experienced during a winter month a positive correlation of the duration of activity with temperature will also result in a positive correlation with cloudiness and a negative correlation with sunshine.

It is considered from these data that in winter the voles were more active during periods of mild cyclonic weather than during spells of cold anticyclonic weather. Weather conditions sometimes encountered during winter which would upset this general trend would be the warm, dry, sunny weather brought by air currents from the Azores region and the cold, damp, cloudy weather from the Arctic Ocean, these systems are however less frequent in normal years than the two already mentioned. It may well be that the significant association was with temperature, the correlations with sunshine and cloudiness being corollaries of those cyclonic systems which most usually bring higher temperatures in winter.

1.5.2. Summer Period

Correlation between the Duration of Daily Activity and Weather Factors.

May 1972, Mean Temperature 9.65°C.

June 1972, Mean Temperature 11.25°C.

July 1972, Mean Temperature 14.3°C.

			Temperature				Rainfall			
Month	Vole	n	rs	t	P	result	rs	t	p	result
May	♀ S	25	0.307	1.547	>0.05	n.s.	0.146	0.708	>0.05	n.s.
Jun	♀ S	27	0.336	1.784	>0.05	n.s.	-0.160	0.810	>0.05	n.s.
Jul	♀ A	31	0.304	1.718	>0.05	n.s.				
Jul	♂ S	25	0.146	0.707	>0.05	n.s.				

			Sunshine				Cloudiness			
Month	Vole	n	rs	t	P	result	rs	t	P	result
May	♀ S	25	0.094	0.454	>0.05	n.s.	-0.194	0.947	>0.05	n.s.
Jun	♀ S	27	-0.241	1.243	>0.05	n.s.	-0.098	0.492	>0.05	n.s.
Jul	♀ A	31	-0.099	0.536	>0.05	n.s.	0.029	0.156	>0.05	n.s.
Jul	♂ A	25	-0.028	0.134	>0.05	n.s.	0.015	0.072	>0.05	n.s.

			Windstrength			
Month	Vole	n	rs	t	P	result
May	♀ S	25	0.367	1.892	>0.05	n.s.
Jun	♀ S	27	-0.033	0.165	>0.05	n.s.
Jul	♀ A	31	-0.256	1.426	>0.05	n.s.
Jul	♂ S	25	-0.299	1.503	>0.05	n.s.

Although the temperature correlations show the strongest association and the least variability none of the four tested proved to be significant. Of the remaining correlations none of the variables showed a consistent direction of association and no test proved significant. If there was any association between temperature and the duration of activity remaining it had weakened considerably from its winter level. It is possible that if a genuine aversion to sunshine did exist as suggested in 1.5.1 then the summer weather condition of increasing temperature with increasing sunshine would have tended to weaken the temperature-activity association. However whether or not this was an underlying feature it is concluded from these data that weather had little discernible effect on diel activity duration during the late spring and summer.

1.5.3. Autumn Period

Correlation between the Duration of Daily Activity and Weather Factors.

October 1972. Mean temperature 9.65°C.

		Temperature				Windstrength			
Vole	n	rs	t	P	result	rs	t	P	result
♀ S	31	0.471	2.875	<0.01	**	0.344	1.970	>0.05	n.s.
♂ A	22	0.004	0.018	>0.05	n.s.	-0.312	1.470	>0.05	n.s.

		Sunshine				Cloudiness			
Vole	n	rs	t	P	result	rs	t	P	result
♀ S	31	-0.015	0.080	>0.05	n.s.	0.142	0.773	0.05	>n.s.
♂ A	22	-0.130	0.586	>0.05	n.s.	0.237	1.091	0.05	>n.s.

The only significant result in the autumn correlations is a positive correlation with temperature in one of the two voles which proved significant at the 1% level. The temperature correlation for the other vole is non-significant however as are all the other results. It is not clear here whether the significant result was a demonstration of the reassertion of the winter association or whether it was a result of chance. Apart from this result weather did not appear to be affecting diel activity in these data.

1.5.4 The Effect of Severe Cold on the Duration of Daily Activity.

The sensitive non-parametric Mann-Whitney U Test was employed to examine the hypothesis that the voles were less active during the six coldest days of each month than during the six warmest, and whether such an examination could provide greater insight into the alteration of the duration of daily activity during the winter season in particular. The data for individual voles is taken together such that each is equally represented both with the other individuals and between each side of the comparison. This grouping procedure will increase the relevance of the general conclusion of the result, any individual variability serving to make the test a conservative one. Therefore any significant results may be depended upon to be significant at least at the level demonstrated if not at a higher level. The null hypothesis Ho that there is no difference in the duration of diel activity of the six coldest and the six warmest days is tested against the alternative hypothesis H_1 that the voles are less active in cold weather. There is a prediction as to direction in H_1, the test is therefore one-tailed. In the following comparisons the notation R_1 refers to the sum of the ranks of the six coldest days and the statistic U is calculated from

$$U^1 = n_1 n_2 + \frac{n_1(n_1 + 1)}{2} - R_1$$

where n_1 and n_2 refer to the sample number of coldest and warmest days respectively, and thence from

$$U = n_1 n_2 - U^1$$

whichever of U or U^1 is the smaller (Siegel, 1956).

Comparison of the Duration of Daily Activity between the six Coldest and six Warmest Days.

January 1972, Mean Temp. 3.05°C. 3 voles, $n_1 = 18$, $n_2 = 18$
$R_1 = 202$, $U = 31$, $P = <0.001$, ***

December 1972 Mean Temp. 4.4°C. 2 voles, $n_1 = 12$, $n_2 = 12$
$R_1 = 153.5$, $U = 68.5$, $P = >0.05$, n.s.

January 1973, Mean Temp. 2.9°C, 2 voles, $n_1 = 12$, $n_2 = 12$
$R_1 = 96.5$, $U = 18.5$, $P = <0.001$, ***

July 1972, Mean Temp. 14.3°C, 2 voles, $n_1 = 12$, $n_2 = 12$
$R_1 = 133$, $U = 55$, $P = >0.05$, n.s.

October 1972, Mean Temp. 9.65°C, 2 voles, $n_1 = 12$, $n_2 = 12$
$R_1 = 127$, $U = 49$, $P = >0.05$, n.s.

It may be seen from these comparisons that not only were the significant results confined to the winter but to the coldest part of the winter. The January 1972 and 1973 tests are significant at the 0.1% level, these months had a mean temperature of 3.05°C. or less of which the coldest six days in each case were largely made up of occasions when the mean temperature failed to exceed 0°C. December 1972 however, adjacent in time to the January 1973 result and based on the same individual voles, did not give a significant result. This month was one of fairly even temperature without periods of exceptional cold and there was little difference in magnitude between the temperature of the six coldest and six warmest days, the mean monthly temperature at 4.4°C. being higher than either of the January figures.

No significant result was obtained from July or October. There is no evidence here that the colder days of these months produced a response of limitation of activity in the voles studied.

Summary to Section 1.5

There is little doubt that in the coldest months of winter the reduction of temperature was associated with a reduction in the duration of daily activity. There is some evidence that the duration of sunshine was negatively correlated with the duration of daily activity and that the degree of cloudiness was positively correlated with it. However these correlations with sunshine and cloudiness may have reflected the winter weather pattern of mild, cloudy depressions and cold, sunny anticyclones indicating an association of sunshine and cloudiness with temperature rather than with activity. In summer when the correlation between the duration of daily activity and temperature disappeared so also did the correlations of sunshine and cloudiness with activity. No correlation was found between the duration of daily activity and either rainfall or wind-strength at any time of the year.

In late spring and summer no correlation with any weather variable was observed. It is possible that if a genuine aversion to sunshine did exist then the summer weather condition of increasing temperature with increasing duration of sunshine would have reduced the association between activity and temperature.

In autumn one significant and one non-significant temperature correlation was obtained while no other correlation proved significant.

There is some evidence to suggest that it was principally during severe weather, that is where the mean daily temperature failed to exceed 0°C. that temperature became most limiting on the duration of activity.

Discussion on Section 1.5

The possible vole aversion to sunlight is suggested on very slender evidence, especially when the variable exerts an influence for only part of the 24 hours and in winter, when the association was significant, for only a small part. Yet such an aversion would not only explain the loss of a significant summer temperature association but might also account for the early afternoon minimum of activity during the summer months, the early afternoon being a time of day when the sunlight would be at its strongest. However there remains the alternative explanation for the loss of a summer temperature association that the temperature minima were not low enough to require a response reducing the duration of activity.

Although the principal conclusions of this section must be that no clear response to changing weather was observed for the majority of the year no suggestion is made that the voles were unresponsive to immediate changes in weather in any way whatsoever. The writer has observed voles in the enclosure carrying out normal activity during light rain while on another occasion a vole reacted sharply at the commencement of a heavy shower by running immediately to its burrow to re-emerge very shortly after the shower had ceased. Its duration of diel activity is unlikely however to have been affected by this rapid change in weather.

The effect of snowfall on vole activity was doubtful as the former occurred in conjunction with low winter temperatures when activity could be expected to be unusually low in any case. However it should be noted that the lowest levels of activity recorded, in this case several instances of less than one hour of vole activity per day, occurred after periods of moderate snowfall. There was little evidence to suggest that the voles attempted to create feeding burrows beneath the snow cover although since this lasted for spells of only two or three days there may have been insufficient time for this to take place. The snow cover during the research period was never deeper than 5-8 cm, deeper snow cover might have resulted in a different behavioural response.

1.6 Correlation of Diel Activity with Photoperiod and Temperature.

In an attempt to discover whether there was a clear correlation between the duration of daily activity and either photoperiod or temperature the median figures for the duration of daily activity for each of the twelve months were ranked and compared with the corresponding ranks of (a) Photoperiod and (b) Temperature by the non-parametric Kendall Rank Correlation (Siegel 1956).

In the following correlations the notation S is equal to Σd in a ranking sequence where one axis, y, of the correlation having been placed in natural order, rank $1,2 - - n$, the ranks of its comparison, x_1, $x_2 - x_n$, are examined and the total number of those ranks to the right of x which fall below it in magnitude are deducted from the total of those which exceed it, so that the number of ranks $> x_1$ - no. of ranks $< x_1 = d_1$. The statistic r, the Kendall Rank Correlation Coefficient, $= \frac{S}{\frac{1}{2}N\,(N-1)}$, and the test of significance z is found when $N > 10$ by the transformation

$$z = \frac{r}{\sqrt{\frac{2(2N+5)}{9N(N-1)}}}$$

when N = the number of paired samples. When two or more ranks are equal a correction for ties is applied in the calculation of r. (Siegel, 1956).

a) Correlation between the duration of diel activity and Photoperiod.

$N = 12$, $S = 46$, $r = 0.713$, $z = 3.230$ and $P < 0.01$, **

The correlation is significant at the 1% level; it may be concluded therefore that a positive correlation existed between the duration of diel activity and photoperiod.

b) Correlation between the duration of diel activity and daily mean temperature.

$N = 12$, $S = 44$, $r = 0.682$, $z = 3.089$, $P < 0.01$, **.

The correlation is significant at the 1% level; it may be concluded therefore that a positive correlation existed between the duration of diel activity and temperature.

During the year the periods of maximum and minimum temperature and photoperiod do not co-incide, the temperature maximum and minimum occurring at least one month after those of photoperiod. It was considered that it might be possible to ascertain which of these two factors was the more important in the determination of the increase in the duration of daily activity during the summer by partialling out the effect of each variable by means of the Kendall Partial Rank Correlation. The coefficient rxy.z is determined from the formula $rxy.z = \frac{rxy-rzy.rxz}{\sqrt{(1-rzy^2)(1-rxz^2)}}$ where the coefficients rxy, rzy, rxz are the Kendall rank correlation coefficients between each of the three sets of ranks. The coefficient rxy is that between photoperiod and activity, rzy between temperature and activity, and rxz between photoperiod and temperature which is presented below.

[*] c) Correlation between Photoperiod and Temperature.

$N = 12$, $S = 44$, $r = 0.667$, $z = 3.018$, $P < 0.01$, **

The correlation is significant at the 1% level.

Therefore rxy = 0.713, rzy = 0.682, rxz = 0.667.

The influence of temperature, z, may be partialled out by the Kendall partial rank correlation.

rxy.z = 0.474. This compared with the original coefficient of 0.713, the reduction in association is considerable, -0.239, it is not possible therefore to conclude from this result that the correlation between light and activity was independent of temperature.

By a re-assignment of notation the influence of photoperiod (photoperiod is now z, as temperature becomes x, rxy = 0.682, rzy = 0.713, rzx = 0.667) may be partialled out.

rxy.z = 0.396. This compares with the original coefficient of 0.682, again the reduction in association is considerable, -0.286, it may not be concluded from this result that the correlation between temperature and activity was independent of photoperiod. Unfortunately the sampling distribution of the Kendall partial rank correlation is not as yet known and therefore no tests of the significance of an observed rxy.z are possible. (Siegel, 1956).

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[*] The discrepancy between the values of r for (b) and (c) where S and N are identical is a result of the correction for tied ranks in (b).

It is concluded that these data show strong positive correlations between photoperiod and the duration of activity, and between temperature and the duration of activity but do not demonstrate which of photoperiod or temperature had the greater modifying influence. Moreover it does not seem improbable that since the two are in such close association throughout the year that they may have acted in concert in the timing of the increase of duration of diel activity during the late spring and summer months.

1.7 The Daily Periodicity of Activity.

1.7.1 Comparison between Months .

It was noted in Section 1.1 that the grouping of data from several individuals would obscure the frequency of the intra-diel activity cycle unless the voles' activity happened to demonstrate perfect synchrony of timing. Therefore in order to evaluate the number and duration of daily activity periods the record of each vole-day had to be assessed individually. The results could then be evaluated on a monthly basis. The method employed was to transcribe the thermograph chart record onto consecutive parallel lines, each line representing 24 hours, as a series of bars and spaces, each bar representing a period of activity and each space a period of rest. Each line consisted of equally-spaced, hourly divisions beginning and ending at midnight. The method has been employed by Saint Girons (1960, 1961) and an illustration is shown in Figure 15.

Unfortunately periods of activity were not entirely discrete and were sometimes interrupted by a brief return to the burrow system. This results in a short break in the activity bars and raises the question as to whether the record represents two activity periods or one, interrupted, activity period. It was decided that an arbitrary figure of the duration of rest had to be fixed so that if the interruption lasted for less than this figure the activity sequence could be accepted as a single period, and if it exceeded it as two periods. The length of interruption decided upon was one hour. This time interval was accepted bearing in mind the average length of a rest period during those records when no short-term interruption occurred, which was in the order of three hours. It was considered that the adoption of the limit of short-term interruption of one hour was one sufficiently distant from this to avoid major error. Although therefore a standard is set which allows comparison between the data presented here, the results of other workers may not be comparable.

The number of activity periods taking place during each twenty-four hours was recorded. Where an activity period lay partially within one day with the remainder of the activity period in the next, half the activity period was included in the total of each day. The sample frequency distribution of the number of activity periods per day during any month approximated closely to a normal distribution. The Standard Error of the daily mean for each month was found by the formula: Standard Error $= \frac{\sigma}{\sqrt{n}}$, where σ is the sample standard deviation and n the number of vole days for the sample month. The mean number of daily activity periods for each month can then be compared by the parametric t test where $t = \frac{\bar{x}_1 - \bar{x}_2}{\sqrt{(S.E_1)^2 + (S.E_2)^2}}$, where $\bar{x}$ are the sample means, with $n_1 + n_2 - 2$ degrees of freedom. Table 4 shows the mean frequency of intra-diel activity periods for each month of the year together with a number of monthly comparisons of these means. In Table 4 the mean number of activity periods/24 hrs is referred to as Diel Periodicity.

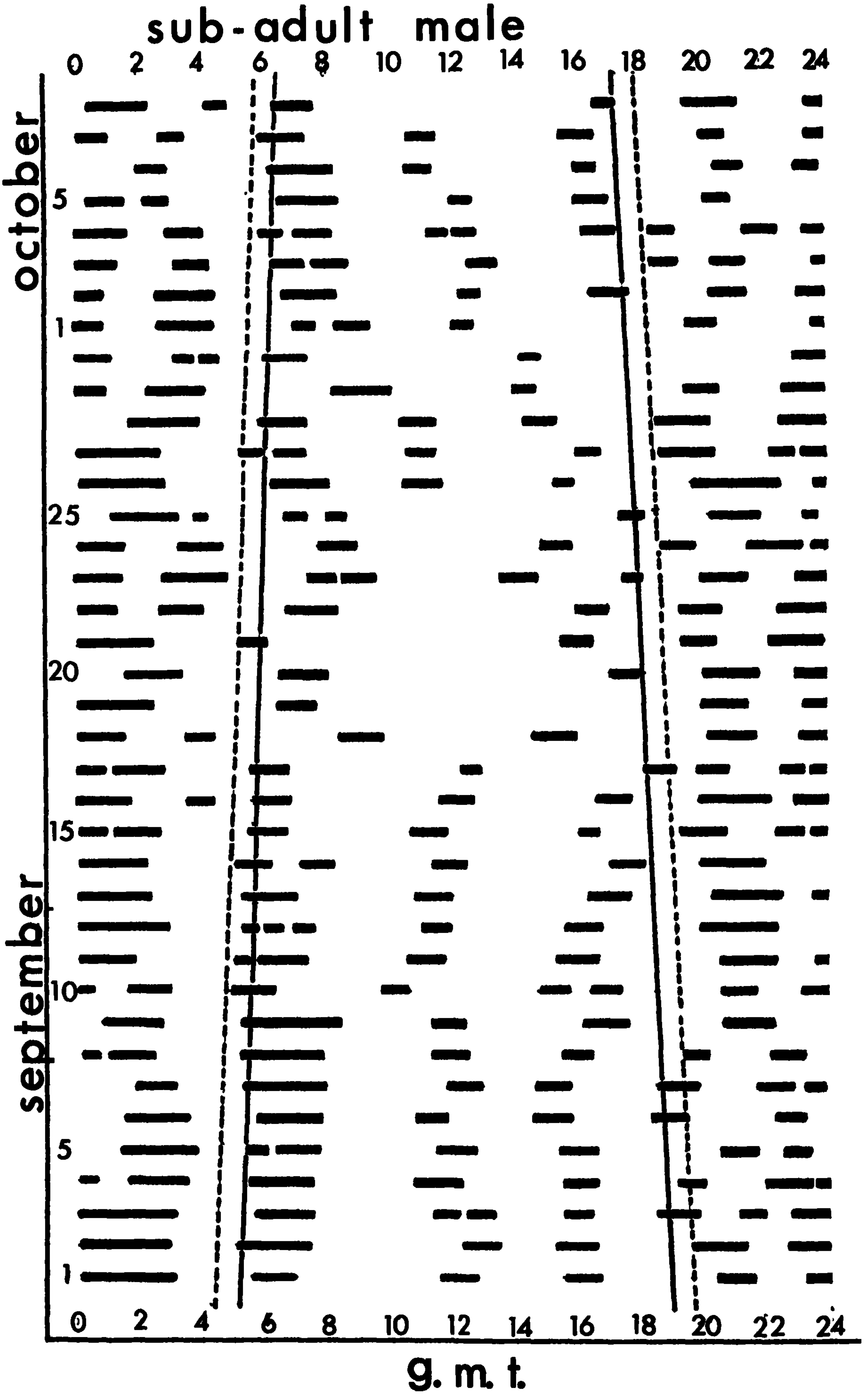
Table 4 Monthly Means of the Intra-Diel Frequency of Activity Periods.

Month	n	Diel Periodicity Mean	S.E.	Comparison a <	b	t	p	result
Jan	87	5.49	0.122	Jan	Feb	1.131	> 0.05	n.s.
				Jan	Mar	2.232	< 0.05	*
Feb	82	5.67	0.102	Feb	Mar	1.170	> 0.05	n.s.
				Feb	Apr	3.077	< 0.01	**
Mar	119	5.83	0.091	Mar	Apr	2.243	< 0.05	*
Apr	81	6.21	0.143	May	Apr	0.322	> 0.05	n.s.
May	68	6.15	0.120	Jun	May	1.188	> 0.05	n.s.
Jun	66	5.96	0.106	Jul	Jun	0.379	> 0.05	n.s.
Jul	72	5.90	0.118	Aug	Jul	1.158	> 0.05	n.s.
				Jul	Apr	1.674	> 0.05	n.s.
Aug	47	5.69	0.138	Aug	Apr	2.620	< 0.01	**
				Sep	Aug	2.058	< 0.05	*
Sep	54	5.30	0.130	Sep	Oct	0.264	> 0.05	n.s.
Oct	78	5.35	0.138	Oct	Nov	0.321	> 0.05	n.s.
Nov	67	5.42	0.169	Nov	Dec	2.499	< 0.05	*
Dec	125	5.90	0.091	Jan	Dec	2.692	< 0.01	**
				Feb	Dec	1.683	> 0.05	n.s.
Annual total								
	12	5.74 ± 0.091						

Figure 15

The Synchronisation of the intra-diel activity periods: an example of the data sheets.

The timing of the periods of above-ground activity for a sub-adult male vole have been shown as continuous data from 1.9.71 to 8.10.71. The periods of above-ground activity are drawn as dark bars separated by spaces representing periods of rest. The number of activity periods taking place per day may be counted for each of the 38 days shown assuming that an activity period which commences on one day and continues into the next is counted as ½ period for each of the two days. The positions of sunrise and sunset are shown by the near-vertical, continuous lines and those for the onset of civil twilight by the near-vertical, broken lines.


sub-adult male
0 2 4 6 8 10 12 14 16 18 20 22 24
october
5
1
25
20
15
september
10
5
1
0 2 4 6 8 10 12 14 16 18 20 22 24
g. m. t.

The data are not readily interpretable biologically. There appears to have been a steady and rapid increase in activity period frequency from a level of 5.49/day in January to an annual maximum of 6.21/day in April. The increase is significant between January and March at the 5% level and between February and April at the 1% level. After April a steady decrease in frequency occurred through the summer until an annual minimum was reached in September. The decrease is significant between April and August at the 1% level and between August and September at the 5% level. After December the frequency fell to the January level, the decrease significant at the 1% level, before it increased once more to the spring maximum. The annual daily mean of activity periods was 5.74 and the annual range only 5.3-6.21 representing an average cycle length varying between 3.9-4.5 hours.

Although these data demonstrated real differences in the mean number of activity periods/24 hours the differences were fairly small in magnitude and it is not clear that they represented an easily understandable biological trend. The peaks of April and December did not correspond to either maxima or minima of the duration of diel activity, indeed they represented a period when the latter was relatively stable. The high figures of April and May however did represent a period when the voles were entering breeding condition, were growing rapidly and in consequence could be expected to have been undergoing a maximum of hormone secretion and relative physiological excitement. This explanation however does not apply to the December peak which lying as it does within two Standard Errors of the annual mean may have been a result of chance variation.

There is little evidence to suggest from these data that the increase in the duration of daily activity during the summer months concluded in Section 1.2 was a result of increasing the diel frequency of the activity periods. The August frequency figure of 5.69 was below that of the annual mean of 5.74 yet the activity duration figure for this month was the second highest in the year. It must be admitted however that all the monthly means, with this single exception, from April until August, which were regarded as representing a period of summer increase in activity duration in 1.2, exceeded the annual mean of activity period frequency. Table 5 sets out the average duration of activity and rest of each cycle of activity and rest, the figures are derived by dividing the monthly mean duration of daily activity by the respective mean number of activity periods/24 hours.

Table 5. Composition of the Activity Cycle.

Month	hrs. Activity/ Cycle.	hrs. Rest/ Cycle.	Duration of Diel Activity. Hrs.	I_1 Hrs.	I_2 Hrs.
Jan	1.10	3.28	6.02	6.35	6.46
Feb	1.16	3.07	6.57	6.69	6.67
Mar	1.07	3.04	6.26	6.17	6.86
Apr	1.08	2.79	6.69	6.23	7.30
May	1.25	2.66	7.66	7.21	7.23
Jun	1.27	2.75	7.59	7.33	7.01
Jul	1.54	2.52	9.11	8.89	6.94
Aug	1.40	2.82	7.94	8.08	6.69
Sep	1.12	3.41	5.95	6.46	6.23
Oct	0.97	3.52	5.18	5.60	6.29
Nov	1.11	3.32	6.03	6.40	6.37
Dec	1.02	3.05	6.00	5.88	6.94
Annual Mean	1.17	3.02	6.75		

It may be seen from Table 5 that the changes in the number of activity periods/24 hours from month to month indicated in Table 4 had little influence on the duration of daily activity. If this had been the case then the monthly figures for each period of activity could be expected to have been very similar. That this was not so may be seen by a comparison of the figures for July and December. The increase in the mean duration of daily activity between December and July was 52% whereas the increase in the duration of activity per activity cycle was 50%, the figures are almost identical. In this instance the increase in diel activity in July was accomplished by an extension of the active proportion of each intra-diel cycle and a reduction of that of rest. Unfortunately this did not apply equally to a comparison between the two extremes in activity period frequency April and September. Here the increase in the mean duration of daily activity of April over September was 12% while the average duration of activity per activity cycle was only 96% of the September figure. However the increase in the number of daily activity periods was 17% and in this example the resultant increase in the duration of daily activity was effected rather more by changes in activity period frequency than by changes in the duration of activity in each intra-diel cycle.

The Wilcoxon Matched - Pairs Signed Ranks Rest was employed to determine whether the daily frequency of activity periods or whether the proportion of activity within each activity cycle was the more important regulator of the duration of daily activity over the year as a whole. In the application of this test two hypothetical approximations of the duration of daily activity were calculated for each month and compared with that figure which has actually been found in Section 1.2. For the first approximation each month's figures are calculated on the hypothesis that the duration of daily activity was a result of the varying proportion of activity within each of a seasonally stable number of intra-diel activity cycles. In the calculation of this an index, I_1 is deduced by dividing the yearly mean of the duration of diel activity (6.75 hrs) by the yearly mean duration of activity per activity cycle (1.17 hrs). $I_1 = 6.75/1.17 = 5.77$. I_1 is then multiplied by the mean duration of activity/cycle for each month.

In the second series of approximations for the duration of daily activity each month's figures are calculated on the hypothesis that the duration of daily activity was a result solely of the varying frequency of intra-diel activity periods, the duration of activity in each intra-diel cycle remaining effectively constant. In the calculation the index I_2 is deduced by dividing the yearly mean of the duration of diel activity (6.75 hrs) by the yearly mean frequency of intra-diel activity periods. (5.75). $I_2 = 6.75/5.74 = 1.176$. I_2 is then multiplied by each month's mean frequency of intra-diel activity periods. These two hypothetical approximations together with the monthly figures for the duration of daily activity are presented in Table 5. The difference is then found between each monthly approximation and the appropriate figure for the duration of diel/activity and the two differences deducted from each other to give the statistic d which is then assigned either a + or - value depending on whether the approximation calculated from I_1 or I_2 respectively is nearest to the actual value for the duration of daily activity. The d statistics, $d_1 \ldots\ldots d_{12}$ are then ranked in magnitude and given the same sign as the appropriate d, the smallest difference receiving the rank ± 1. The ranks of whichever sign appears less frequently are then summed to give the statistic T. The null hypothesis Ho that the sum of positive ranks = the sum of negative ranks is tested against the alternative hypothesis H_1 that the sum of positive ranks $\neq$ the sum of negative ranks. No prediction as to direction is made in H_1, the test is therefore two-tailed.

In the present test where $n = 12$, + refers to the approximation of the changing duration of activity/cycle and - to the approximation of the frequency of activity cycles/day.

$N = 12$, $+ = 8$, $- = 4$, $T = 12$, for $N \leq 25$, $P = < 0.05$, *

The test produces a significant result at the 5% level. It may be concluded from these data that the voles significantly altered the daily duration of their activity more by having increased the duration of activity in each intra-diel activity cycle than by having increased the number of activity cycles per day.

1.7.2 The Effect upon Activity Cycle Frequency of the Solitary and Accompanied Conditions.

It has been concluded in Section 1.3.2 that there was a significant difference in the duration of diel activity of voles kept under solitary and accompanied conditions. In view of this the conditions were also compared as to the frequency of intra-diel activity periods. Table 6 shows the mean and standard error of each of these conditions for each month. The condition means for each month are compared by the parametric t test with $n_1 + n_2 - 2$ degrees of freedom. In the notation where the Solitary monthly mean $>$ the Accompanied mean a + is signified and where the Solitary mean $<$ Accompanied mean a -.

Table 6 Activity Cycle Frequency, a comparison between the Solitary and Accompanied condition.

Frequency of Activity Cycles/Day

	Solitary			Accompanied						
Month	n	Mean	S.E.	n	Mean	S.E.	t	p	result	sign
Jan	28	5.29	0.25	59	5.58	0.13	1.029	>0.05	n.s.	-
Feb	14	6.14	0.23	68	5.57	0.11	2.236	<0.05	*	+
Mar	31	5.81	0.13	88	5.83	0.11	0.117	>0.05	n.s.	-
Apr	25	6.56	0.16	56	6.06	0.19	2.013	<0.05	*	+
May	37	6.54	0.13	31	5.68	0.15	4.333	<0.001	***	+
Jun	27	5.59	0.13	39	6.22	0.15	3.174	<0.01	**	-
Jul	46	5.79	0.15	26	6.10	0.19	1.281	>0.05	n.s.	-
Aug	40	5.68	0.14	7	5.75	0.38	0.173	>0.05	n.s.	-
Sep	54	5.30	0.13	0	-	-	-	-		
Oct	59	5.20	0.17	19	5.79	0.20	2.248	<0.05	*	-
Nov	57	5.24	0.17	10	6.45	0.52	2.212	<0.05	*	-
Dec	51	5.55	0.15	74	6.14	0.11	3.172	<0.01	**	-
Year	12	5.724	0.143	11	5.925	0.091	1.186	>0.05	n.s.	-

Of the eleven comparisons tested seven proved significant at the 5% level or higher. However four of these indicated an accompanied mean which exceeded the solitary mean and three indicated the reverse. The annual daily mean unweighted for sample size was greater in accompanied than in solitary individuals, but the difference is not significant ($t= 1.186$, $P > 0.05$, 21 d.f,) It cannot be concluded from these data that the solitary and accompanied conditions influenced the frequency of intra-diel activity periods. The data examined in Section 1.7 refers to the major intra-diel cycles of activity and rest. Nevertheless as observed earlier these major cycles of activity may be interrupted by one or more short periods of from 10-60 minutes duration when the voles returned to the nest. It is not known whether these interruptions demonstrated a subsidiary rhythm of activity and rest or whether the activity was simply continued inside the nest chamber as nest building, feeding or grooming. It was noted however that the incidence of these interruptions varied with individuals, in particular one female, an elderly vole of approximately eighteen months of age, demonstrated this behaviour far more than was usual while some voles showed little or no sign of it. No general conclusions are made concerning this behaviour.

Summary to Section 1.7

The frequency of intra-diel activity cycles was fairly stable throughout the year ranging from 5.3 to 6.21, representing a mean cycle duration which varied between 3.9-4.5 hours. The annual mean of 5.74 ± 0.091 represents a mean cycle duration of 4.18 hours.

The frequency increased in magnitude from a low point of 5.49 in January to an annual maximum of 6.21 in April. It remained high in May, 6.15, but subsequently showed a steady decline until the annual minimum was reached in September. A secondary and isolated peak occurred in December. It is suggested that the spring frequency maximum may have resulted from the excited physiological condition during this season but no conclusion is made concerning that in December.

The duration of activity in each intra-diel cycle showed a range from 0.97 hours in October to 1.54 hours in July, whereas the duration of rest in each cycle ranged from 2.52 hours in July to 3.52 hours in October. The annual means were 1.17 and 3.02 hours respectively.

It is concluded that the increase in duration of activity in each cycle was more important than the increase of cycle frequency in effecting the regulation of the monthly means of the duration of daily activity.

The annual mean frequency of activity periods was marginally greater in accompanied than in solitary individuals but the difference is not significant.

1.8. The Synchronisation of Intra-Diel Activity Cycles

1.8.1 Day to Day Synchrony

It was considered possible that an important facet of vole activity might be that the timing of the period of activity on day 1 might influence the subsequent timing of activity periods on day 2. This could be demonstrated if it could be shown that the timing of periods of activity on adjacent days was more closely synchronised than on days separated by a longer time interval. In the construction of a hypothesis to test such a possible difference in synchrony the data sheets of Section 1.7 were inspected for a repeated period of activity that could be discerned to occur at a similar time during the day for at least 25 days.

The hypothesis that the timing of the onset of a vole's period of activity showed a stronger synchrony with that of the period of activity occurring at a similar time on the following day than with that five days afterwards was tested initially by the Sign Test and subsequently by the more sensitive Wilcoxon Matched-Pairs Signed Ranks Test (Siegel, 1956).

A period of activity occurring at the same location during the 24 hours was examined over approximately 30 days. The differences between the onset of that period of activity on day 0 with that of day 1, and also that of day 5, were calculated in tenths of one hour. Where the difference in time between the onset of activity of days 0 and 1 was less than the difference between days 0 and 5 ($t0-t1 < t0-t5$) the result was assigned a + value, where however the difference in time between days 0 and 1 was greater than the difference between days 0 and 5 ($t0-t1 > t0-t5$) a - value was assigned. Similarly the second result of the sample is whether $t1-t2$ $<$ or $>$ $t1-t6$. This was repeated on consecutive days until the sample approached 25.

Five tests were conducted, the maximum possible for the data where such long-term sequences of strong activity cycle synchrony were unusual, asynchronous activity being the more common phenomenon. The results firstly for the Sign Test and secondly for the Wilcoxon Matched-Pairs Test are given below. H_0 that there is no difference in synchrony between t0 and t1, and between t0 and t5 is tested against H_1 that t0 and t1 will show greater synchrony than t0 and t5. A prediction is made as to direction, the test is therefore one-tailed. In the notation x = the number of minus values.

Test to compare Synchrony of Activity between days 0 and 1 with days 0 and 5.

		Sign Test				Wilcoxon Matched-Pairs Test		
Date	Vole	n	x	P	result	T	P	result
Aug-Sep	♂S	25	12	>0.05	n.s.	140	>0.05	n.s.
Oct-Nov	♂S	25	13	>0.05	n.s.	163.5	>0.05	n.s.
Jul-Aug	♂S	25	5	<0.01	**	40.5	<0.005	**
Nov-Dec	♀S	22	5	<0.01	**	28.0	<0.005	**
Nov-Dec	♀A	25	11	>0.05	n.s.	130.5	>0.05	n.s.

Two of the five results are significant at the 1% level or higher while the remainder show no difference between days + 1 and + 5 whatosever. If the data is taken together the normal approximation of the Sign Test may be calculated

$$Z \doteq \frac{(x \pm 0.5) - \frac{1}{2}N}{\frac{1}{2}\sqrt{N}}$$

$N = 122$, x 46, $Z = 2.6255$, one-tailed $P = 0.0043$, **

Although there was clearly considerable variation the summed result allows the rejection of Ho at the 1% level. It is concluded therefore that voles achieved closer Synchrony to day 0 in the timing of their activity periods on day 1 than on day 5.

However it may be noted that four of the five tests involved solitary voles although in the data as a whole the proportion of data for accompanied voles exceeded that for solitary individuals. The possibility exists therefore that the degree of day-to-day synchronisation of activity periods was reduced when voles received the stimulus of an accompanying animal.

1.8.2 Long-term Synchrony

The 2 x 2 Contingency test was employed to ascertain whether solitary voles were more likely to demonstrate synchrony in the timing of a particular activity period than were accompanied voles. Samples of 20 days duration were inspected as to whether or not any discrete activity period could be observed to be repeated at approximately the same time each day in more than 50% of the sample days. If this were so then the sample was counted as "Synchronous" and if not as "Asynchronous". The results for the samples of solitary and accompanied voles are set out below, they have also been separated as to sex.

	Solitary			Accompanied			Absolute Total
	♂	♀	Total	♂	♀	Total	
Synchronous	12	9	21	3	7	10	31
Asynchronous	2	3	5	6	9	15	20

Ho that there is no difference in the ratio of synchronous and asynchronous results in solitary and accompanied voles is tested against H_1 that a difference in this ratio exists.

chi^2 1.d.f.
$\chi^2 = 7.259$, P= < 0.01, **

Ho is rejected at the 1% level. Clearly solitary voles showed a much greater synchrony in the timing of their activity periods than did accompanied voles.

The data may also be examined by the chi^2 test to ascertain whether or not the solitary voles, the accompanied voles, or the data as a whole, show significant differences in the likelihood of whether the voles show synchronous or asynchronous timing of their periods of activity. Ho is that synchronous activity = asynchronous activity.

Comparison	N	Chi^2 1.d.f.	P	result
Solitary	26	9.846	< 0.01	**
Accompanied	25	1.000	> 0.05	n.s.
Total data	51	2.372	> 0.05	n.s.

The results demonstrate that although the accompanied voles showed a greater number of asynchronous than synchronous samples the difference was not significant. For solitary voles however the number of synchronous samples exceeded that of asynchronous samples, the difference being significant at the 1% level. The entire data showed no significant difference.

It is therefore concluded that solitary voles were more likely to show synchronisation in the timing of their activity periods than were accompanied voles. It seems probable therefore that voles in a wild population may not demonstrate activity period synchrony to a marked degree, and that the synchrony of solitary voles was a result of the lack of social stimulus.

The data may also be examined for sexual differences in synchronous and asynchronous behaviour. Three tests were carried out. The sexes of solitary and accompanied voles were compared separately by the Fisher Exact Probability Test and subsequently the data were taken together and compared by the 2 x 2 Contingency Test. In each case Ho that there is no difference between males and females in the ratio of synchronous and asynchronous activity is tested against H_1 that a difference exists.

Comparison	Chi^2 d.f.=1	P	result
Solitary	FISHER	>0.05	n.s.
Accompanied	FISHER	>0.05	n.s.
Total	0.090	>0.05	n.s.

In each case Ho is accepted. It is concluded that in these data there was no difference between males and females in the ratio of synchronous and asynchronous timing of activity periods.

Summary to Section 1.8

The timing of activity periods showed closer synchronisation between consecutive days than between days at least four days apart. A strong influence in the timing of an activity period lay in the timing of that period on the previous day.

Voles which are accompanied by another vole in an adjacent burrow system showed significantly less synchronisation of activity periods than did isolated voles. As defined in this section solitary voles showed a significantly greater proportion of synchronous than non-synchronous timing of their activity periods.

There was no difference between males and females in the ratio of synchronous and non-synchronous timing of their activity periods.

Discussion on Section 1.

The monthly range of the mean frequency of daily activity cycles of 5.3 - 6.21 with an annual mean of 5.74 ± 0.09, corresponding to a mean cycle length of 4.18 hours, accords well with the expected value for a microtine of 150-300 g. bodyweight. Richter (1927) and Crowcroft (1953) suggested a cycle duration of 3-4 hours for Rattus and Lund (1970) recorded bursts of activity in Arvicola every 3-4 hours also. The present result that there was little seasonal change in the frequency of the intra-diel pattern with a maximum in spring and a minimum in autumn agrees with the conclusion of Hansen (1957) for Dicrostonyx that the number of activity periods is seasonally stable but contrasts with that of Saint Girons (1960, 1961) for Clethrionomys glareolus where the frequency increased from a summer minimum of 5 cycles/day to a maximum of 8-10 cycles/day in winter. It has already been stated that there is a difficulty of interpretation of discrete activity periods in the present work but this would not account for a disagreement of this kind.

It was concluded that it was largely a change in the duration of activity in each intra-diel activity cycle which effected the seasonal change in total diel activity. The range in the duration of diel activity from a winter level of 6 hours to a July maximum of 9.1 hours is in agreement with the conclusions of Grodziński and Górecki (1967) and Stebbins (1971, 1972) that total activity levels in small rodents tend to be higher in summer than in winter, but in contrast Saint Girons (1960, 1961) for *Clethrionomys* found a maximum of activity to occur in February. The annual mean of 6.75 hrs/day in the present work comes within the estimated duration of 5-7 hours suggested by Grodziński and Górecki (1967) as being characteristic of the more purely herbivorous voles. The figure of 6.75 is fairly close to that of 5.5 hrs/day found by Drożdż et al. (1971) for *A. t. terrestris* in the laboratory but rather less than the 9 hrs 36 minutes found by Hamar et al. (1970a) for *A. t. scherman* in the field situation.

In the present work a distinction is drawn in the assessment of nocturnal and diurnal activity between the effect of changing photoperiod and of changing light preference. Activity levels were similar throughout the 24 hours from October until April and occasionally displayed a diurnal preference relative to day length. Nevertheless the reduced photoperiod necessitated that the majority of activity took place during the hours of darkness from November until February. From May until September a marked nocturnal preference was demonstrated relative to day length.

Nevertheless the extended photoperiod necessitated that the majority of activity took place during the hours of daylight with the exception of September where there was a slight nocturnalism. In March, April and October there was a slight diurnal majority of activity.

These results are in agreement with the majority of the published work on microtine rodents. A fairly even diel level of activity has been found by Miller (1955), Saint Girons (1961) and Pearson (1962). Saint Girons (1960, 1961) found that Clethrionomys showed a maximum of diurnal activity in spring and early summer and a minimum in autumn and winter, the voles demonstrating a nocturnal majority of activity throughout the year in males and for all but during the spring in females. Grodziński (1963) reported a summer nocturnalism in Clethrionomys, a conclusion similar to that of Erkinaro (1961) for Microtus arvalis. Lund (1970) found Arvicola to show a majority of activity to take place during the day throughout the year which became particularly pronounced from November until May, a result in partial contradiction to the present work where the slight diurnal preference of the winter was outweighed by the reduction in photoperiod.

Saint Girons (1960, 1961) with reference to Clethrionomys and Lund (1970) with reference to Arvicola suggest that the light/dark interface is important in the timing of diel activity. There is no evidence in the present work to support this view.

The weather preferences of _Arvicola_ suggested here of increased activity during mild, cloudy weather and a dislike of cold, cloudless weather, in winter, are similar to those of Nickolaev and Chertova (1962) although these authors also found a positive correlation with windstrength that was not repeated in the present study. Nicholaev and Chertova (1962) found a correlation with the same weather conditions in the summer while no such correlation was found in the present work. The reaction of _Arvicola_ to periods of cold noted by Impens et al. (1965), Myllymäki (1969) and Lund (1970) of increasing the proportion of below ground activity was also found in the present work although the voles always came above ground at some time during the 24 hours. Although the voles were unable to feed underground by extending their burrows to new food supplies in the present study the ability to store food within the nest did exist. It is thought unlikely that _Arvicola_ in England remains confined below ground for periods of longer than 1-2 days at a time.

It seems probable that the reduction of activity and the slight diurnal preference in reaction to the short photoperiod in the winter would result in a saving in energy requirement by the avoidance of unnecessary energy expended on activity and also of the most severe night-time cold. The present results are in accordance with this. However if the voles were unable to find sufficient food to cover the increased metabolic cost of low winter temperatures during a daily duration of activity adequate for their requirements during the summer then it could be imagined that an increase in foraging activity might be necessary if torpor was to be avoided. The provision of food stores might suffice to overcome the demands of the short-term periods of severe weather experienced in England but in a climate of long-term cold these might be too rapidly exhausted to provide a reliable food resource. Should long-term periods of severe cold occur the alternatives would be either hibernation, an increase in foraging activity, or the development of a subterranean mode of life. Such differences in climate,representing a corresponding change in food demand, might account, in part, for the variability of the estimates of the duration of daily activity in published work. That this might be generated by increasing the frequency of activity cycles per day in rodents smaller than Arvicola and not by increasing the duration of activity of each activity cycle could reflect the likelihood of hypothermia in a small mammal if it were to experience external cold for too long a period at a time. Increasing severity of cold may have a similar effect on activity periodicity to that of decreasing size, in both cases the frequency may be increased and the cycle duration shortened.

The importance of huddling in a group may be important in reducing the energy expenditure of individuals both by raising the nest temperature and by effectively reducing the surface area to body mass ratio. Little is known however of the social organisation of microtine rodents, especially in winter. Stebbins (1972) reports finding up to seven individuals of *Clethrionomys* in a single nest in winter but such reports are isolated and further knowledge of microtine social organisation would be valuable. In *Arvicola* Zonov and Tugulov (1963) claim that only one individual is normally found in a single nest in winter and Mehl (1950) states that *Arvicola* generally live in separate burrows and that the young rarely contact the mother after reaching maturity. Work is presented in Section 2.2.2 which suggests that this may not be so in *A. t. amphibius*, but a more detailed investigation is necessary.

Reference is rarely made by workers to the age of their experimental animals; this might be particularly important in long term studies. In the present work the voles under study were representative of the dominant section of the wild population from season to season. Sub-adult voles were brought into the enclosures in early autumn and studied until after breeding in the following summer when they were replaced once more by sub-adults. On one occasion an old female was studied through a second winter. Her level of activity was low throughout the winter, rarely exceeding five hrs/day, and the intra-diel periods of activity were more than usually disrupted by short periods of rest. Hamar et al. (1970a) comment that adult *A. t. scherman* show fewer activity cycles/day than nearly full-grown specimens but that the duration of the activity/activity cycle in the former is longer. Further study is needed into the effect of age upon activity; animals of different ages may account for part of the contrasting nature of published work.

The result in the present observations indicating that solitary individuals were less active than accompanied ones, and the result of Grodziński (1963) that diet may be an important regulator of the duration and modality of daily activity, are both factors which will increase the differences encountered in comparative analysis of rodent activity patterns.

Clethrionomys, which may become almost totally diurnal when associated with a nocturnal murid competitor (Brown, 1956) and *Arvicola*, which may become almost totally nocturnal when affected by persistent human day-time interference (Duckett, unpubl.), demonstrate the ability of microtines to adapt to locally important external factors which together with their ability demonstrated here and by Nicholaev and Chertova (1962) to adapt their activity with respect to short-term weather fluctuations, signifies a flexibility of activity pattern which should be fully appreciated. It may be that in laboratory experiments the external influence of some factor, for example photoperiod, takes on an importance which it fails to exert in the wild condition. Not only will other influences be largely eliminated but that of photoperiod will be enhanced as the laboratory animal may be exposed to its influence at all times whereas in the wild situation the influence is only effective when the vole is already above ground and active. It is concluded that the complex influence of the wild condition, of weather, of changing photoperiod, of age, of the influence of inter and intra-specific stimulation, will all tend to disrupt a polyphasic daily rhythm of activity necessitated by the demands of small rodent metabolism.

CHAPTER 2

THE QUALITY AND INTENSITY OF EXTERNAL ACTIVITY

2. The Quality and Intensity of External Activity.

Introduction

Although accounts of Arvicola behaviour are fairly numerous (Barrett-Hamilton and Hinton, 1911; Dean, 1947; Ryder, 1962; Ashby et al., 1969) they are generally confined to descriptions of discrete complexes of activity complete in themselves but lacking a formal context in the total daily behavioural pattern. This is true in the literature of small mammals generally, however Crowcroft (1966) has studied social interactions in the mouse Mus musculus and P. I. V. Sewell (in Ashby, 1972) observed a single Clethrionomys glareolus over many hours and produced a qualitative account of the proportion of time the vole spent on a variety of behavioural types. Sewell's results show that 29% of the vole's day was passed in deep sleep, 14% in light sleep, 19% awake and resting, 10% awake and alert, 13% grooming, and 15% in feeding and exploration. Clethrionomys spent 35% of the day in activities which would normally have taken place above ground while the remainder of the time the vole would have been largely immobile in its nest. Of all the above-ground activity approximately equal proportions were spent on Resting-Alert and on Grooming, about 29% in each case, while the remaining 42% was given over to feeding and exploration. Sewell's observations were carried out with the animal contained in a box illuminated by white light by day and by red light at night, but as Ashby (1972) points out the quality of activity can be much altered by intra-specific interaction and this was precluded in Sewell's experiment.

The scarcity of data on rodents of the type illustrated by P. I. V. Sewell is a result both of its labour-intensive nature but principally of its difficulty of execution in the natural situation where the animals are obscured by cover and frequently moving. In the present study an attempt was carried out to record the proportions of the types of behaviour demonstrated by Arvicola in the wild using a stop watch and a pair of field binoculars, but the ease of observation of the voles while they were swimming and the difficulty of observation once they had climbed out of the water and into the littoral vegetation rendered this method grossly inaccurate and the attempt was abandoned. It was decided therefore to observe the voles in captivity.

Method

A small, bird observation hide was set up some 2 m. from the second, double enclosure system described in Section 1, so that it faced the exits to the exterior of the two burrows (Plate 2). The method of observation was to approach the enclosure as quietly as possible; to enter the hide and await the emergence of one or other of the two voles. Information as to a suitable time for observation was obtained from the previous week's activity records, consequently the time of observation varied with season and individual but the observations were always carried out during the hours of daylight.

On emergence the sex of the vole was noted and a stop watch operated throughout a discrete period of behaviour and returned to zero when this behaviour altered, and the duration of the previous item written down. A mimimum total duration of 30 minutes was required for the period over which observations of behaviour were recorded for it to be regarded as a single behaviour sample.

When the total period of observations failed to reach 30 minutes the behaviour items were added to a subsequent period of observation until a sample of 30 minutes duration was obtained.

The enclosure was watched for periods of from 2 - 3 hours at a time and even though this period of observation was timed as far as was possible to co-incide with a period of vole activity it was usual for the voles to be active for only approximately one third of these periods.

A problem of vole identification occurred during the months when both animals were allowed access to either burrow system; it is not the writer's experience that pelage colour or body shape is a reliable indicator of sex as suggested by Ryder (1962) especially in young individuals. Neither is the presence or absence of an ear tag a reliable guide as these tags may be removed by the animal concerned. To solve this problem one of the two voles inhabiting the enclosure was chosen specifically for peculiarities of colouration, of which the most frequent in A. t. amphibius is that of a white tip to the tail (Stoddart, 1969a). This method removed all doubts as to the sex of the individual under observation.

Items of behaviour were entered under twelve headings, Resting, Grooming, Feeding, Foraging, Exploration, Gnawing (when disassociated from feeding), Burrowing, Social Contact, Running, Climbing, Swimming and Diving, but a more precise description was noted on the occasions when behaviour either fell outside these descriptions or when it referred to a particular aspect of them. An example of this is the taking of material into the nest. This was generally entered under foraging as it could not always be ascertained as to the function of this behaviour. When the material was carrot then it was assumed that the behaviour was of a foraging/feeding association, whereas when it was dead leaves then a foraging/nest building association was deduced. However the material was frequently grass blades and stems and here the precise function of this foraging behaviour was uncertain.

The type of behaviour reflected in these headings is as follows.

Resting

Defined as a period of no locomotory activity and without a function described under another heading. It occurred mainly during:-

i) Watching and listening before or after emergence from a burrow.

ii) Pauses between other types of activity.

iii) Periods of recovery after a previous period of exhausting activity.

iv) Periods of light, dozing sleep.

Grooming

Care of the pelage, mainly seen after emergence from the burrow and after a period of water immersion.

i) Scratching of flanks with hind feet, grooming of back and ventral fur with the forefeet, grooming of fur with the teeth and snout.

ii) Removal of water from the fur after a period of immersion by shaking.

Feeding

The biting off, eating, chewing and swallowing of food while the vole is stationary.

Foraging

i) The carrying of materials from one place to another, includes the transport of mud, food and nest building materials.

ii) Scrabbling about in mud was entered under this heading as a sub-heading when it was not more obviously associated with another classification.

Exploration

Slow locomotory movement, which may or may not be obviously investigatory in nature.

Gnawing

Usually regarded here as a sub-heading of burrowing, much of which is done with the teeth. This activity was generally confined to the structure of the enclosure itself and may be a bi-product of captivity.

Burrowing

Periods of active excavation of earth, some overlap with foraging on occasion. Burrowing is conducted with the fore and hind limbs, with the teeth and with the snout.

Social Contact

Any active and deliberate contact between individuals, not merely unintentional collision.
Running, Climbing, Swimming, Diving.
Self descriptive, exhausting locomotory movements

It was felt that further subdivision of behavioural description would have been counterproductive as the observations were of value here primarily for their information of the relative energy demand of above-ground activities. To this end the twelve descriptive headings were grouped under three additional headings on the basis of apparent energy demand.

1.) Low Energy Demand

Includes- Resting and feeding.

2.) Intermediate Energy Demand
Includes Grooming, foraging, exploration and some gnawing activities.

3.) High Energy Demand
Includes some gnawing activities, burrowing, social contact, running, climbing, swimming and diving. Such activities are regarded as potentially exhausting in nature even when continued for periods of only short duration.

Validity of the Method

i). Range

The restrictions of the home range and the absence of a natural population of Arvicola in the immediate vicinity will undoubtedly result in an alteration of some behaviour characteristics in the experimental voles when compared with their wild behaviour patterns. Not only may some aspects of behaviour diminish or fail to appear but others may be strongly demonstrated within the enclosure while they may be infrequent in the wild. For example although the voles were not observed to gnaw on pieces of wood provided for this purpose they did frequently gnaw at the wire mesh and wooden framework of the enclosure. This behaviour is likely to be a response to the restricted locomotory range within the enclosure and may to some extent compensate for the reduction in exploratory behaviour which would result from this restriction. In any event gnawing forms only a small proportion of the total above ground activity.

Some voles develop the habit of repeated periods of diving, to and from set vantage points in the enclosure, where they rest briefly before recommencing the activity. No reason for this behaviour can be deduced except that either of play or of compensation for the reduction in range.

It is not known to what extent the size of the enclosure reduces locomotory activity, and it is hoped that the compensatory behaviour described above may reduce this discrepancy.

ii). Nutritional Value

The observations of voles feeding within the enclosure were largely restricted to observations of voles consuming carrots. In the wild the voles would be feeding primarily upon grass and since the two foods differ markedly in form this may result in differences in the time required to consume a given calorie requirement between the wild and enclosure conditions. However observations of voles feeding upon grass in the enclosure suggested that the periods of individual feeding are of similar duration in both foods and it is considered that grass and carrots are of similar calorific value in terms of fresh weight food (as argued in Section 1). It is considered therefore that differences in food will not result in marked differences in feeding behaviour between the enclosure and wild situation.

iii). Time

No observations were carried out during the hours of darkness. J. Harling (see Ashby, Harling and Whiles, 1969) watched A. t. amphibius in the wild by torchlight at night but the authors have not commented on any significant differences in activity beyond noting the collection of nest material to take place only during the hours of daylight. There seems little reason why activity should vary in quality between day and night although ranging behaviour might be less hazardous if carried out during the dark. However this may not be reflected in behaviour in the enclosure where the potential range exploration is necessarily limited.

iv). Record

No items of shorter duration than one second were recorded, such items did take place occasionally but they were not a typical feature of vole behaviour.

2. The Variety and Quality of Behaviour.

Results

2.1 The Seasonal Analysis of Behaviour.

The voles in the double enclosure, separated from each other by a wire partition, were watched on 37 occasions during 1972 and 1973. The observations commenced on 2 May 1972 using a male vole in one and a female in the neighbouring burrow system. On 6th May 1972 the wire partition was removed and within 24 hours the male had moved his sleeping quarters into the female burrow system. On approximately 15th June a litter was born from which six young were weaned, all of which survived to maturity. In October 1971 these original adults were removed and replaced by first year individuals taken from the wild, once again a male and a female vole. The partition between the two halves of the enclosure was initially sealed but was re-opened at the end of January 1973. Within 24 hours the female had moved into the male burrow system. The male escaped from the enclosure in March and was replaced initially by a second female but in late March a male vole was introduced and shortly afterwards the second of the two females was removed. The observations came to an end in June 1973. Twenty-eight samples of behaviour taking place outside the burrow systems were obtained, each of at least thirty minutes duration, nine samples during the winter, ten during ths spring, six during the summer and three during the autumn. The results were analysed on a seasonal basis.

The data were analysed in detail for the following three purposes:

1.) To ascertain whether a difference existed between the sexes in the duration of discrete items* of behaviour, in

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* The term "discrete item" in this section refers to a period where a particular type of behaviour, for example, "Grooming" is carried on without interruption from the

the winter and spring, and between adult and juvenile voles in the summer.

Since the sample frequency distributions of individual item duration were invariably positively skewed the non-parametric Median Test was used to compare two distributions with the median of their combined distribution. In the notation + refers to the number of samples where the item duration exceeded the combined median and - to the number of items that fell below it. Ho that there is no sexual difference in the duration of the discrete behaviour items is tested against H_1, that a difference exists.

2.) To ascertain whether a difference existed between the groups of behaviour in the duration of the discrete items of each behaviour type. The Median Test was employed as before. Ho that there is no difference in the duration of discrete behaviour items between behaviour groups is tested against H_1, that a difference exists. In both 1) and 2) $n_1 + n_2 > 40$ in all comparisons and as there is no prediction as to direction the test is two-tailed.

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commencement of that period until it is ended by a change in vole behaviour. These "items" of behaviour are usually short in duration, frequently lasting for less than ten seconds but they can be longer in such activities as feeding where they may last for several minutes. The term "item duration" refers to this period of time, from the commencement to the end of the particular type of behaviour.

3.) To ascertain the percentage of the total activity spent in each behaviour group and to note any sexual or age differences in the concentration of behaviour.

The total activity has been separated into six groups: Resting, Grooming, Feeding, Exploring, Digging and Swimming. In the following text a capital letter denotes the group of related types of behaviour and not an individual constituent part. Feeding includes both feeding and foraging, Digging, both digging and gnawing, and Swimming includes swimming, diving, climbing and running.

The mean and median, the latter with 95% confidence limits, of the item duration of each behaviour group in seconds are given below, with the data for both sexes combined. The means of the male (m.) and female (f.) components are also shown, as is the total range of item duration encountered for each behaviour grouping.

2.1.1. Winter Season. (2 voles; 1 male,1female, 9 samples)

The median and mean item duration length in seconds for each behaviour group are given below:

	Resting	Grooming	Feeding	Exploring	Digging	Swimming
Median	7	5	15	6	8	3
95% Limits	7-9	4-6	12-22	5-7	6-10	3-4
Mean	15.9	8.0	79.6	7.4	12.0	5.1
Mean	m. f. 18.4 12.8	m. f. 7.8 8.4	m. f. 83.1 71.4	m. f. 8.5 5.5	m. f. 7.6 19.6	m. f. 4.4 6.0
Range	2-530	1-135	1-740	2-30	3-65	1-35

1.) In the following comparisons Ho that there is no difference between the sexes in the duration of discrete items of behaviour is tested against H_1 that a difference exists.

Comparison	+m	+f	-m	-f	$n_1 + n_2$	Chi^2 d.f.=1	P	result
Resting	135	105	136	109	485	0.01	>0.05	n.s.
Grooming	48	37	68	42	195	0.37	>0.05	n.s.
Feeding	47	19	51	22	139	0.00	>0.05	n.s.
Exploring	23	11	27	19	80	0.34	>0.05	n.s.
Swimming	139	139	201	116	595	10.33	<0.01	**

There are too little data to enable a comparison to be made for the Digging group of behaviour.

The single significant result that the duration of each Swimming item of behaviour was of longer duration in the female than in the male, was significant at the 1% level. However as only one animal of each sex was present in the comparison the difference may be one between individuals rather than between sexes.

2.) In the following comparisons Ho that there is no difference in the duration of respective items of behaviour is tested against H_1 that a difference exists.

Comparison	+	+	−	−	$n_1 + n_2$	Chi^2 d.f.=1	P	result
	1	2	1	2				
1.Feeding 2.Resting	84	173	55	312	624	26.3	< 0.001	***
1.Feeding 2.Digging	77	9	62	29	177	10.8	< 0.01	**
1.Digging 2.Resting	21	240	17	245	523	0.3	> 0.05	n.s.
1.Resting 2.Exploring	240	27	245	53	565	6.2	< 0.05	*
1.Exploring 2.Grooming	40	85	40	110	275	0.7	> 0.05	n.s.
1.Grooming 2.Swimming	102	216	93	379	790	15.0	< 0.001	***

It is concluded from these data that the median duration of items of behaviour may be related as follows: Resting < Feeding, significant at the 0.1% level, Digging < Feeding, significant at the 1% level, Exploring < Resting, significant at the 0.5% level, and Swimming < Grooming, significant at the 0.1% level. There were no significant differences between the median period of Digging and of Resting activity, nor between those of Exploration and Grooming.

The median duration of an item of behaviour may be summarized relative to the behaviour groups as follows: Swimming < Grooming = Exploration < Resting = Digging < Feeding.

3.) The total percentage of activity which falls into each of the six groups was as follows

	Resting	Grooming	Feeding	Exploring	Digging	Swimming
Male	30.9	5.6	50.5	2.6	1.1	9.2
Female	33.0	8.0	35.3	2.0	3.3	18.3
Total	31.6	6.4	45.3	2.4	1.9	12.3

The largest differences between the sexes were those of feeding and swimming, however as only one individual of each sex was observed these may reflect differences between individuals and not between sexes.

2.1.2. Spring Season. (5 voles; 2 male, 3 female, 10 samples).

The median and mean item duration in seconds for each behaviour group are given below.

	Resting	Grooming	Feeding	Exploring	Digging	Swimming
Median	10	5	25	6.5	20	3
95% Limits	8-10	5-6	20-35	5-10	12-25	3-3
Mean	15.5	9.3	74.7	9.2	29.0	3.8
Mean	m. f.	m. f.	m. f.	m. f.	m. f.	m. f.
	16.5 15.0	6.6 10.2	64.7 81.6	9.0 9.3	28.5 29.4	3.6 3.9
Range	1-213	1-140	1-640	1-45	1-250	1-37

1.) In the following comparisons H_o that there is no difference between the sexes in the duration of discrete items of behaviour is tested against H_1 that a difference exists.

Comparison	+ m	+f	-m	-f	n_1 + n_2	Chi^2 d.f.=1	P	result
Resting	59	135	82	154	430	0.72	> 0.05	n.s.
Grooming	14	65	21	53	153	1.89	> 0.05	n.s.
Feeding	33	46	31	41	151	0.00	> 0.05	n.s.
Exploring	30	49	37	42	158	0.93	> 0.05	n.s.
Digging	16	18	18	22	74	0.00	> 0.05	n.s.
Swimming	34	134	100	286	554	1.75	> 0.05	n.s.

It is concluded that there was no significant difference between the sexes in the median duration of discrete items of behaviour in any of the behaviour groups.

2.) In the following comparisons Ho that there is no difference in the duration of the respective periods of behaviour is tested against H_1 that a difference exists.

Comparison	+ 1	+ 2	- 1	- 2	n_1 + n_2	Chi^2 d.f.=1	P	result
1. Feeding 2. Resting	115	195	43	305	658	53.7	< 0.001	***
1. Feeding 2. Digging	77	30	72	47	226	2.8	> 0.05	n.s.
1. Digging 2. Resting	51	195	29	305	580	16.3	< 0.001	***
1. Resting 2. Exploring	195	44	305	114	658	6.0	< 0.05	*
1. Resting 2. Grooming	264	59	225	112	660	18.5	< 0.001	***
1. Exploring 2. Grooming	82	79	76	99	336	1.6	> 0.05	n.s.
1. Grooming 2. Swimming	109	169	69	386	733	53.0	< 0.001	***

It is concluded from these data that the average duration of items of behaviour may be related as follows:

Resting $<$ Feeding, significant at the 0.1% level;

Resting $<$ Digging, significant at the 0.1% level;

Exploring $<$ Resting, significant at the 5% level;

Grooming $<$ Resting, significant at the 0.1% level;

Swimming $<$ Grooming, significant at the 0.1% level.

There was no significant difference between the average item durations of Feeding and Digging, nor between those of Grooming and Exploring. The average duration of discrete items of the various types of behaviour can therefore be ranked as follows:

Swimming $<$ Grooming = Exploring $<$ **Resting** $<$ Digging = Feeding

3.) The percentage of the total activity which falls into each of the six behaviour groups was as follows:

	Resting	Grooming	Feeding	Exploring	Digging	Swimming
Males	28.9	3.1	44.7	6.4	11.8	5.1
Females	28.3	7.7	43.0	4.8	7.0	9.3
Total (m & f)	28.5	6.1	43.6	5.3	8.7	7.8

The percentages of the total activity in each of the behaviour groups were very similar in the two sexes. It is concluded that these data show no sizeable differences between the sexes in these relative proportions.

2.1.3 Summer Season (9 voles; 4 adults, 5 juveniles. 6 samples)

The median and mean item duration for each behaviour group are given below. The combined mean is subsequently separated into that representing adults (a) and that representing juveniles (j).

	Resting	Grooming	Feeding	Exploring	Swimming
Median	6	3	25	5	3
95% Limits	5-7	3-5	20-35	5-10	3-3
Mean	13.9	8.3	97.3	10.8	4.4
Mean	a j	a j	a j	a j	a j
	7.9 18.7	11.7 4.1	107.9 64.6	10.6 11.1	3.9 5.0
Range	1-285	1-75	1-955	1-125	1-25

The data for Digging are few and are not included.

1.) In the following comparisons Ho that there is no difference between adult and juvenile voles in the duration of discrete items of behaviour is tested against H_1 that a difference exists.

Comparison	+a	+j	-a	-j	n_1+n_2	Chi^{2}df=1	P	result
Resting	44	94	78	64	280	14.19	<0.001	***
Grooming	44	14	26	42	126	16.46	<0.001	***
Feeding	50	11	45	20	126	2.11	>0.05	n.s.
Exploring	36	9	31	18	94	2.44	>0.05	n.s.
Swimming	86	111	145	123	465	4,55	<0.05	*

These results show that juveniles underwent longer individual items of Resting than did adults, significant at the 0.1% level, but shorter individual items of Grooming, significant at the 0.1% level. Juveniles also showed longer items of Swimming, although the difference was less pronounced, significant at the 5% level only. The adults had rather longer individual items of Feeding and Exploring behaviour but the differences are not significant. It is concluded that juvenile behaviour displayed a trend of increasing duration of individual items of Resting and Swimming, but decreasing duration of individual items of Grooming.

2.) In the following comparisons Ho that there is no difference in the duration of the respective items of behaviour is tested against H_1 that a difference exists.

Comparison	+ 1	+ 2	- 1	- 2	$n_1 + n_2$	Chi^2 df=1	P	result
1. Feeding 2. Resting	93	90	33	200	416	63.5	< 0.001	***
1. Resting 2. Exploring	148	45	142	49	384	0.2	> 0.05	n.s.
1. Exploring 2. Grooming	45	46	49	80	220	2.4	> 0.05	n.s.
1. Grooming 2. Swimming	58	197	68	268	591	0.4	> 0.05	n.s.
1. Exploring 2. Swimming	63	197	31	268	559	18.1	< 0.001	***
1. Resting 2. Grooming	148	46	142	80	416	6.9	< 0.01	**

It is concluded from these data that the median duration of items of behaviour may be related as follows: Resting < Feeding, significant at the 0.1% level; Swimming < Exploring, significant at the 0.1% level; Grooming < Resting, significant at the 1% level. There is no significant difference between the median item duration of Resting and Exploring, Exploring and Grooming or Grooming and Swimming. The median duration of a discrete item of behaviour was therefore related between the behaviour groups as follows:

Swimming < Exploring = Resting < Feeding
=
= Grooming <

3.) The percentage of the total activity which falls into each of the six behaviour groups was as follows:

	Resting	Grooming	Feeding	Exploring	Digging	Swimming
Adults	7.3	5.9	74.2	5.2	0.9	6.5
Juveniles	43.7	3.3	29.0	4.4	2.8	16.8
Adults and juveniles	19.5	5.1	59.1	4.9	1.5	9.9

There are notable differences here in the group proportions between adults and juveniles. While at 7.3% the adult level of Resting behaviour was very much below the usual level for the year of 28-32%, the juvenile percentage at 43.7 was in contrast very high. The situation was the reverse in Feeding behaviour. Usually the percentage for this lies between 40-50%; in the adults in summer it was very high at 74.2%, while in the juveniles at 29% it was unusually low. The intensity of Swimming behaviour differed less widely from the usual levels for the year as a whole but nevertheless the percentage in juveniles was markedly higher than that of adults.

These results quantify what was apparent during observation, that in summer the adult voles spent an unusually great proportion of the time feeding while juvenile behaviour was largely comprised of bursts of high activity followed by long periods of rest. The juveniles were also more timid than the adults and spent a considerable proportion of their above-ground activity remaining stationary on emergence from the burrow, listening, sniffing and watching, before a period of more vigorous activity commenced.

2.1.4. Autumn Season (2 voles; 1 male, 1 female, 3 samples)

The median and mean item duration for each behaviour group are given below. The autumn data are few and have not been separated with regard to sex.

	Resting	Grooming	Feeding	Exploring	Digging	Swimming
Median	10	5	20	5	11	5
95% Limits	7-10	5-7	12-43	5-10	7-17	3-7
Mean	15.7	7.4	72.9	9.1	14.7	5.9
Range	2-280	1-45	2-665	2-30	2-56	1-20

1.) The data were too few to allow the duration of discrete items of behaviour in the two sexes to be compared.

2.) In the following comparisons Ho that there is no difference in the duration of the respective periods of behaviour is tested against H_1 that a difference exists.

Comparison	+ 1	+ 2	− 1	− 2	$n_1 + n_2$	Chi^2 df=1	P	result
1. Feeding 2. Resting	33	73	17	104	227	8.63	< 0.01	**
1. Resting 2. Grooming	98	22	79	64	263	19.51	< 0.001	***
1. Feeding 2. Digging	29	11	21	22	83	3.91	< 0.05	*
1. Digging 2. Resting	17	73	16	104	210	0.82	> 0.05	n.s.
1. Grooming 2. Swimming	40	88	46	96	270	0.01	> 0.05	n.s.
1. Exploring 2. Swimming	11	88	12	96	207	0.05	> 0.05	n.s.

It is concluded from these data that the median duration of items of behaviour may be related as follows: Resting < Feeding, significant at the 1% level; Digging < Feeding, significant at the 5% level; Grooming < Resting, significant at the 0.1% level. There was no significant difference between the average item durations of Digging and Resting, Grooming and Swimming, or Exploring and Swimming. The average duration of the discrete items of the various types of behaviour can therefore be ranked as follows:

Swimming = Exploring = Grooming < Resting = Digging < Feeding.

3.) The percentage of the total external activity which falls into each of the six behaviour groups was as follows:

	Resting	Grooming	Feeding	Exploring	Digging	Swimming
Total	31.4	7.2	41.2	2.4	5.5	12.4

The distribution of activity between the behaviour groups was similar to that in winter and spring.

2.1.5 Annual Summary

The median item duration for each behaviour group is given below for each season, together with the annual mean and standard error of the medians.

	Resting	Grooming	Feeding	Exploring	Digging	Swimming
Winter	7	5	15	6	8	3
Spring	10	5	25	6.5	20	3
Summer	6	3	25	5	-	3
Autumn	10	5	20	5	11	5
Median mean	8.25	4.5	21.25	5.6	13.0	3.5
S.E.	1.2	0.6	2.8	0.4	4.4	0.6

The mean item duration for each behaviour group is given below for each season, together with the mean of the four seasons and its standard error.

	Resting	Grooming	Feeding	Exploring	Digging	Swimming
Winter	15.9	8.0	79.6	7.4	12.0	5.1
Spring	15.5	9.3	74.7	9.2	29.0	3.8
Summer	13.9	8.3	97.3	10.8	-	4.4
Autumn	15.7	7.4	72.9	9.1	14.7	5.9
Annual Mean	15.25	8.25	81.1	9.1	18.6	4.8
S.E.	0.5	0.5	6.4	0.8	6.5	0.5

In both medians and means there was a remarkable seasonal similarity. The Digging behaviour group showing the greatest variability, largely as a result of the frequency of gnawing at the enclosure frame increasing when animals were separated from each other. In Summer, when there was no partition between the two halves of the enclosure gnawing was considerably reduced.

The range of item duration in seconds for each behaviour group is given below for each season, together with the range over the year as a whole.

	Resting	Grooming	Feeding	Exploring	Digging	Swimming
Winter	2-530*	1-135	1-740	2-30	3-65	1-35
Spring	1-213	1-140*	1-640	1-45	1-250*	1-37*
Summer	1-285	1-75	1-955*	1-125*	-	1-25
Autumn	2-280	1-45	2-665	2-30	2-56	1-20
Annual Range	1-530	1-140	1-955	1-125	1-250	1-37

In the table * denotes the greatest observed range. The maximum range of 530 seconds for Resting occurred at the only time a vole was seen to go into a light sleep outside the burrow. The only behaviour group likely to have been underestimated in range to any considerable extent is that of swimming. Under natural conditions voles have been observed to continue swimming for over two minutes at a time.

In only one instance of eleven comparisons examined was a significant difference observed between the sexes in the item duration of a behaviour group. In this instance only a single individual of each sex was included in the data, the difference may therefore have been one between individuals and not between sexes.

The percentages for the six groupings for males (m.) and females (f.) are given below.

	Resting		Grooming		Feeding		Exploring		Digging		Swimming	
	m.	f.	m.	f.	m.	f.	m.	f.	m.	f.	m.	f.
Winter	30.9	33.0	5.6	8.0	50.5	35.3	2.6	2.0	1.1	3.3	9.2	18.3
Spring	28.9	28.3	3.1	7.7	44.7	43.0	6.4	4.8	11.8	7.0	5.1	9.3

In general the percentage figures for males and females were very similar. The greatest differences occurred in Grooming and Swimming where the percentages for females were consistently higher than for males. It is concluded that the activity of males and females, both in the average duration of items of behaviour and in the percentage of group activity was broadly similar.

The differences between the behaviour of adults and juveniles were as concluded in section 2.1.3.

The average duration of the discrete items of the various groups of behaviour can be ranked as follows:

Winter: Swimming < Grooming = Exploring < Resting = Digging < Feeding
Spring: Swimming < Grooming = Exploring < Resting < Digging =
Feeding
Summer: Swimming < Exploring = Resting < Feeding
=
= Grooming <
Autumn: Swimming = Exploring = Grooming < Resting = Digging <
Feeding

Swimming always had the lowest item duration but not always exclusively so. The values for Grooming and Exploring were generally significantly greater than for Swimming and similar to each other. That for Resting was always significantly greater than that for Grooming and usually greater than for Exploration. The median value for Feeding was always significantly greater than Resting, and Digging occupied a position intermediate between the two.

The percentage of the total above-ground activity devoted to each behaviour group is illustrated seasonally in Figure 16, together with the average of the samples when combined. Differences did exist between the seasons but there was no marked seasonal trend, what differences there were appeared most pronounced in Summer and Autumn and may have been due to the low sample sizes of these seasons.

As stated in the introduction the behaviour groups have been allocated to one of three further groupings with regard to their supposed relative energy expenditure. Group 1, the least energy costly of the three, includes Resting and the feeding component of the Feeding group. The intermediate Group 2 contains Grooming, Exploration and the foraging component of the Feeding group. Group 3 is deemed to be the most costly in terms of energy expenditure and includes the Digging, Social Contact and Swimming groups.

The means and standard errors of these three groups are given in Table 7, for each season and also for the year as a whole. They are calculated directly from the individual samples. Groups 1 and 2 have also been combined to give a group of low and medium energy-expenditure activity.

Figure 16

The seasonal changes in the composition of above-ground Activity.

The total above-ground activity has been separated into seven behavioural components and the percentage of time spent in each type of activity is shown for each season and for the year as a whole.

Sg = Spring
Sr = Summer
An = Autumn
Wr = Winter
Av = The Year as a whole

The behavioural group : 'Swimming' includes swimming, diving, running and climbing.

'Digging' includes digging and some gnawing activities.

'Feeding' includes feeding and foraging.

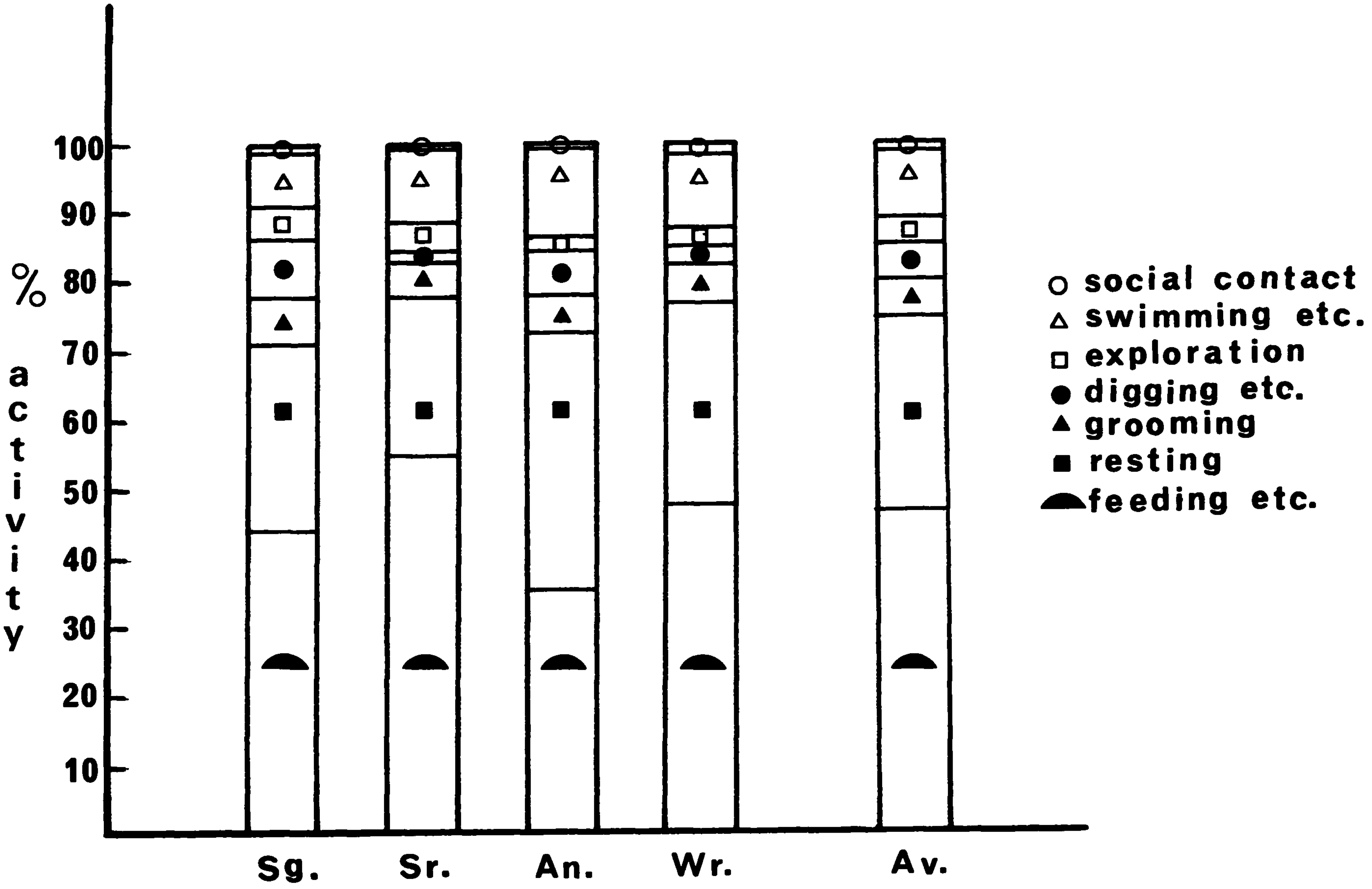

% activity
100
90
80
70
60
50
40
30
20
10
Sg.
Sr.
An.
Wr.
Av.
○ social contact
△ swimming etc.
□ exploration
● digging etc.
▲ grooming
■ resting
feeding etc.

Table 7 Energy-expenditure groups 1, 2,1 & 2 and 3 as a percentage of total above-ground activity

Season	n	Group 1		Group 2		Groups 1&2		Group 3	
		Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
Winter	9	74.75	2.09	10.38	1.85	85.13	1.89	14.93	1.91
Spring	10	66.33	5.38	18.21	3.05	84.54	2.66	15.49	2.65
Summer	6	75.81	3.28	11.28	2.63	87.09	3.59	12.89	3.57
Autumn	3	71.53	4.47	9.17	3.17	80.70	3.91	19.27	4.11
Combined Total	28	71.61	2.17	13.24	1.47	84.85	1.32	15.16	1.32

The parametric t test has been employed to compare the seasonal differences between groups. Those groups the means of which differ most widely are examined, and also other groups where the means are further than two standard errors apart.

Group	Comparison	t	d.f.	P	result
1	Spring Summer	1.505	14	>0.05	n.s.
2	Autumn Spring	2.055	11	>0.05	n.s.
2	Winter Spring	2.195	17	<0.05	*
3	Summer Autumn	1.172	7	>0.05	n.s.
1 & 2	Autumn Summer	1.204	7	>0.05	n.s.

There are no significant differences between the seasons in Group 1, $t = 1.505$, d.f.= 14, when the extremes of Spring and Summer are compared, $P = > 0.05$.

The extremes of Group 2 are not significant, $t = 2.055$, d.f.= 11, $P => 0.05$, however a comparison between Winter and Spring gives $t = 2.195$, d.f. =17, $P = < 0.05$, this result is significant at the 5% level. A difference exists in Group 2 activity between Winter and Spring.

There are no significant differences between the seasons in Group 3, $t = 1.172$, d.f.= 7, $P = > 0.05$, when the extremes of Summer and Autumn are compared.

When Groups 1 and 2 are combined to give a group of behaviour requiring low and medium energy expenditure they produce a group which varied little with season, the maximum difference of the means being only 6.39%. A comparison yields t = 1.204 between Autumn and Summer, d.f.= 7, P=>0.05, the difference is not significant.

Figure 17 shows the seasonal changes in the combined Groups 1 and 2, and the high energy-expenditure Group 3. The heights of the columns are fairly similar between seasons and, as has been noted above, do not show a significant difference in either case. Figure 17 also shows the seasonal percentages of the total activity which are devoted to Feeding. These percentages differed more widely than those previously, particularly between Summer and Autumn. A comparison between the two yields t= 1.103, d.f.= 7, P=>0.05, the difference is not significant and may reflect the low number of samples in these two seasons.

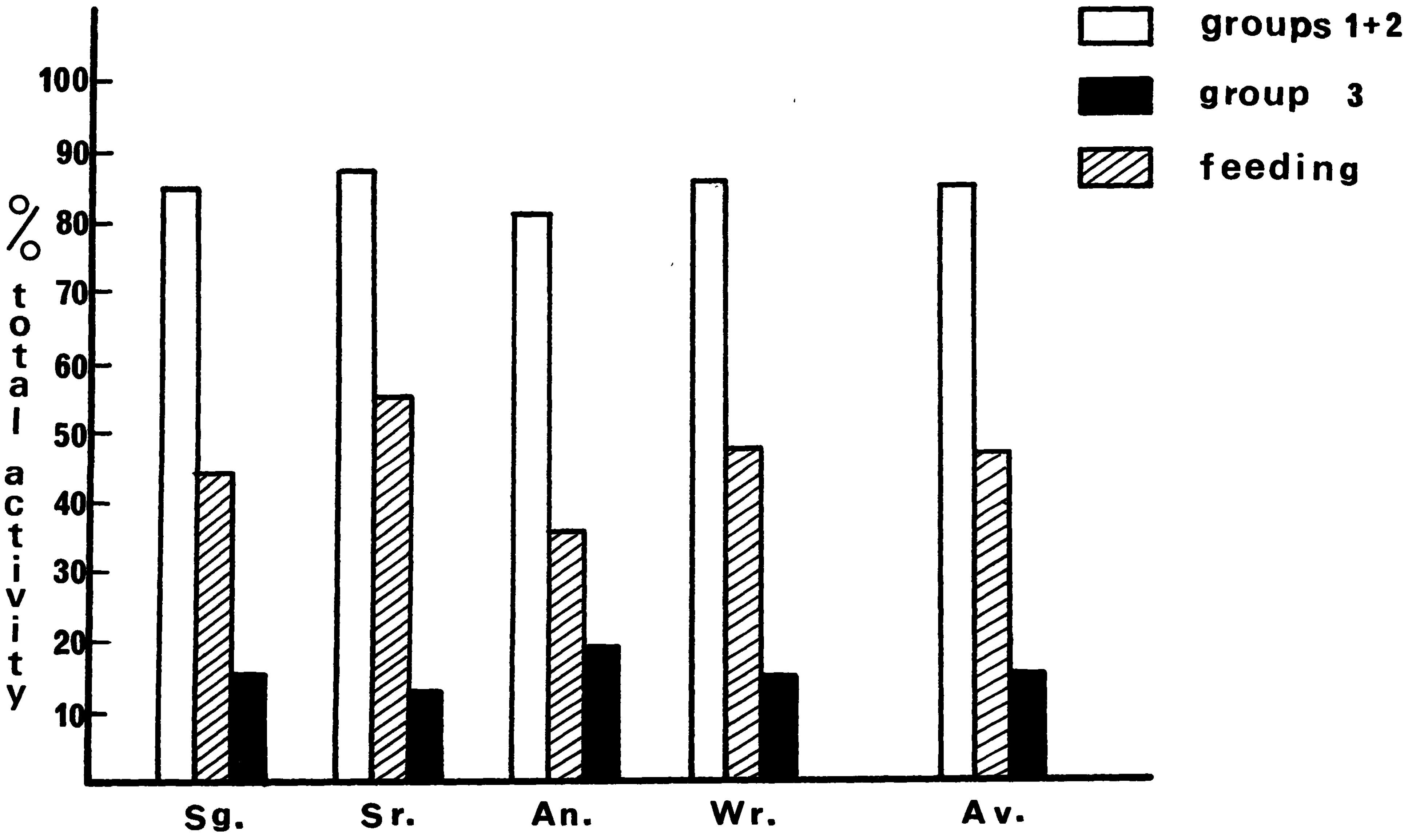
It is concluded from the data presented above that although differences did exist in the proportion of time spent Feeding between summer adults and winter adults, necessitated by the reproductive costs of pregnancy and lactation, and that the behaviour of juveniles was markedly different from that of the adults, the Summer data did not differ significantly from that during the remainder of the year. The levels of low and intermediate activities combined, and high activity, varied little seasonally, and the percentage of time spent Feeding per hour of activity

Figure 17

Seasonal changes in the energy-expenditure groupings of Activity.

The total above-ground activity has been separated into two groupings and each is expressed as a percentage of the whole. The first of the groupings (groups 1 & 2) represents the categories of behaviour likely to result in low or moderate energy expenditure while the second grouping (group 3) represents the categories of behaviour likely to result in a high expenditure of energy. The first grouping includes Resting, Feeding, Grooming and Exploration behaviour, while the second grouping includes Digging, Social Contact and Swimming behaviour. The percentage of above-ground activity passed in Feeding behaviour is also shown separately in the figure as a shaded column. The percentages of the total above-ground activity engaged in energy-expenditure groups 1 & 2, Feeding activity, and energy-expenditure group 3 are shown for each season and for the year as a whole.

Sg = Spring
Sr = Summer
An = Autumn
Wr = Winter
Av = The Year as a whole


groups 1+2
group 3
feeding
% total activity
100
90
80
70
60
50
40
30
20
10
Sg.
Sr.
An.
Wr.
Av.

remained fairly constant. It is concluded that the voles do not significantly alter the quality of activity, in broad terms, from season to season and that the most important seasonal differences will therefore be occasioned by the changing duration of above-ground activity, the behaviour pattern of which remains fairly constant.

It would appear therefore that the more important non-reproductive variable in terms of seasonal changes in energy requirement lies in the relative duration of daily activity and not in the behavioural composition of that activity.

Discussion on Section 2.1

Sewell (in Ashby, 1972) found in a laboratory study that for the types of behaviour of Clethrionomys which would be expected to take place above ground the respective proportions of time engaged in each were 26.3% Resting, 34.2% Grooming and 39.5% Feeding plus Exploration. In the present study the respective figures would be 28.2%, 5.7% and 66.1%. The principal difference between the two species concerned is in the proportion of time spent Grooming. This difference may be accounted for partially by the fact that all Grooming in Sewell's study was assumed to have taken place above ground whereas a proportion might well have taken place within the nest in the wild, and that the simple laboratory environment leads to boredom, which is frequently countered by an increase in personal grooming. In the present study the relatively low figure for Grooming of 5.7%

included the time spent in the shaking and brushing of water from the fur after the frequent periods of immersion in the stream. It would be expected therefore that the proportion of time spent grooming by the terrestrial _Clethrionomys_ would be even lower than this value.

Figure 17 includes the seasonal percentages for the proportion of time active spent Feeding because of the importance of this behaviour group in an energetic study. It can be seen that the voles do not increase the Feeding percentage in winter at the expense of less energetically rewarding activities, particularly Swimming. However whereas in the enclosures the quality of food remained constant throughout the year, in the natural conditions it may be sufficiently poorer in quality in winter to require that the voles extend the duration of their Feeding behaviour at the expense of other activities. However the grazing activities of the voles themselves tend to create areas of short green sward at the water's edge. There is little reason to doubt that this grass is of good quality; whether it is sufficient in quantity to satisfy the voles' requirements during the winter without an increase in Feeding behaviour is not known.

2.2. Behaviour: Social Behaviour

Two aspects of social behaviour which are relevant to the present thesis are commented upon here; the increase in activity duration due to social stimulation, and the cohabitation of voles in the same nest.

2.2.1 Social Stimulation

It has been concluded in section 2.1. that juvenile voles demonstrate a pattern of activity outside the nest which is dominated by long periods of rest alternating with short but frequent periods of high energy activity. On coming to the entrance of the burrow after a period of sleep in the nest the juvenile vole hesitates to leave the burrow prior to commencing a period of activity in the open. Frequently the young vole will approach the entrance several times and after a period of 2 - 3 minutes, during which it surveys the exterior, it will back away again and disappear into the burrow. After several such visits to the entrance the juvenile will eventually leave the burrow and dive into the water, remaining submerged for 7 - 10 seconds before surfacing and climbing out onto a mud bank. It will then groom briefly, rest for a few seconds and either repeat the performance, possibly several times, or run back to the burrow and return to the nest. This behaviour is typical of voles up to three months of age. Longer spells of exploration and feeding outside the nest are few in number in comparison with those of the adults. But even at this age the vole becomes less timid if an adult or other juvenile is present outside the nest at the same time, such accompaniment leads to short periods of swimming and diving behaviour being replaced by longer periods of feeding, grooming and exploration. The voles therefore appear to gain in confidence from the presence of a parent or sibling.

The behaviour of adult voles when alone shows some similarity to that of the juveniles. The same timidity in first leaving the burrow can be observed, being followed very regularly by a spell of diving, grooming and resting. Each sequence consists of 5-15 seconds of diving, 25 seconds being the longest observed period of submergence, 1-5 seconds of grooming and 10 - 20 seconds of rest, before the cycle restarts. On the emergence of a second vole however the nature of the activity changes. The second vole is less cautious in its emergence from the burrow if it is able to see its companion already active outside, and although it too may indulge in a period of diving and swimming from time to time the two voles will soon settle down to longer periods of exploration and feeding. The maximum period a vole was observed to feed without a change in behaviour was in the order of sixteen minutes.

It seems probable therefore that the conclusion of section 1.3 that accompanied voles are active for a greater proportion of each day than solitary ones is a result of a gain in confidence from the presence of a conspecific resulting in a longer and more relaxed period of activity. This conclusion is distinct from one that might suppose that voles increase the duration of their total daily activity as a result of engaging in activity with each other. Social contact such as squeaking, boxing with the paws, and of chasing each other rarely lasts for longer than sixty seconds during each half hour period of activity and may be virtually absent altogether. It is not considered that such contact is important in the duration of diel activity.

2.2.2 Cohabitation.

Mehl (1950), Zonov and Tugulov (1963) and Lund (1970) indicated that Arvicola was largely a solitary vole except for the period immediately prior to and during breeding, and that, for the remainder of the year the nest is inhabited by one vole only. Observations made during the course of the present study suggested that this conclusion may not apply to A. t. amphibius.

Within 24 hours of the partition being removed in May 1972 the male vole had taken up residence with the female in her nest chamber. It remained in residence until a few days after the estimated time of birth of a litter in mid June, when it returned to its original burrow. Within ten days it had returned to the female burrow and the eight animals now present occupied the latter for two months until late August. By the end of this period the young were beginning to enter the male's former burrow, occupying it on occasion for a few hours at a time, and the old male was also seen to return to it intermittently. This situation continued until late September when the voles were removed from the enclosure. Towards the end of this period some animosity was seen to develop between an individual adult temporarily in possession of a burrow and another adult entering it.

During the winter of 1972 the two sections of the enclosure were kept separated, but the partition was removed at the end of January 1973. Within 24 hours the new female had joined the male in his burrow and it remained there until March. In March the male escaped and a second female was introduced into the empty burrow. It occupied it for some two days before joining the existing female in the male burrow. Shortly afterwards a male was introduced into the empty burrow. It remained there for 1 - 2 days before entering the burrow inhabited by the two females, displacing the newer and smaller of the females which left the communal burrow and occupied the empty one. A few days later this female was removed. The remaining male and female voles then occupied the same nest until June when the experiment came to an end.

This evidence, fragmentary though it is, suggests that it is more usual for voles to share nests at all seasons of the year than to live singly, even when an empty nest is available, but that perhaps nests are not usually shared by more than two adult voles. It remains uncertain whether it is usual for females to share nests, or whether the male voles usually leave the breeding nest temporarily at the time when the litter is born. Since nest sharing during the winter may provide a valuable saving in energy expenditure, a greater understanding of such social interactions would be valuable.

CHAPTER 3

THE DAILY AND SEASONAL THERMAL EXPERIENCE OF *ARVICOLA*

3. The Daily and Seasonal Thermal Experience of *Arvicola*.

Introduction.

Existing data on the temperatures experienced by small mammals in the wild are few. Grodziński and Górecki (1967) suggest ambient temperatures in measuring Average Daily Metabolic Rate of 20°C. for rodents from the temperate climatic zone and of 10 - 15° C. for those of the sub-arctic. In their opinion, "The nest provides a relatively constant air temperature which is higher than the soil temperatures at the given depth." Trojan (1969) used the ambient temperature at a depth of 20 cm. in his calculation of nest temperature of *Microtus arvalis*. The soil temperature at 20 cm. was found to be 0.0°C. in the month of January, compared with a surface temperature of -1.0°C., and 19.0°C. in July compared with a surface temperature of 20°C.

Stebbins (1971, 1972) recorded the temperatures of the insulated nest boxes of *Peromyscus* and *Clethrionomys* situated above ground level but beneath the snow cover in Alberta and the North West Territories of Canada. He found that in Alberta these temperatures varied between -6°C. and 1°C. during the winter while at Heart Lake at Latitude 61°N they did not rise above -5°C. from mid November until late March, and from late December until late February lay between -9°C. and -13°C. Stebbins (1971) records that *Peromyscus* used nests outside the insulated nest boxes for most of January and February where the mice were frequently noted to be in a torpid condition.

The work of Trojan (1969) and Stebbins (1971, 1972) indicates that the ambient experimental temperatures suggested by Grodziński and Górecki (1967) may be valid for the warmer part of the year only.

Daniel (1964) measured the nest temperature of Clethrionomys glareolus in Czechoslovakia during a period of 32 days commencing recording after the birth of a litter. The nest temperature varied within the range of 17 - 19°C., and this result accords well both with the summer figure used by Trojan (1969) and the suggested data of Grodziński and Górecki (1967). Daniel's recordings were carried out from an artificial nest chamber and burrow system created from brass wire netting with mesh diameter 3 x 3 m.m. The nest chamber was in the form of a cube of dimension 12 cm. and was sited so that its ceiling was 10 cm. beneath the soil surface. The burrow was 35 cm. in length and 2.5 - 3 cm. in diameter.

Cotton and Griffiths (1967) investigated the temperature fluctuations in the nests of Clethrionomys glareolus in the laboratory at a range of external temperature. They reported that the temperature of the interior of the nest when it was occupied by a single vole was 10°C. higher than the external temperature when this was 10°C., and 13°C. higher when the external temperature was 0°C. When a pair of voles shared the nest the nest interior was 14.5°C. higher than external when the external temperature was 10°C., and 19°C. higher when the external temperature was 0°C. The temperature at the periphery of the nest was found to be 5°C. higher than the external temperature of 10°C., and 7°C. higher than the external temperature of 0°C. when the nest was occupied by a single vole. When two voles shared the nest the rise in nest peripheral temperature was found to be 7°C. at the external temperature of 10°C., and 10°C. at the external temperature of 0°C.

The periphery of the nest was therefore found to be between 5 and 6°C. cooler than the interior of the nest when it was occupied by a single vole and between 7.5 and 9°C. when it was occupied by a pair of voles, at external temperatures between 0 - 10°C.

There is therefore a degree of agreement in the published work on the nest temperatures of small European voles, particularly for the estimate of this temperature during the summer where a range of between 17°C. and 22°C. may be predicted. However it is not known to what extent the data for small voles may be applicable in a study of the much larger Arvicola. Even for small voles the meagre data for the nest temperature during winter and the variability in temperature estimates resulting from the positioning of the recording probe within the nest and from the number of animals sharing the nest suggest that further study is needed.

Method

The method used in the present study employed the burrow systems and temperature recorders described in Section 1. The Cambridge Recorder utilized in the first enclosure drew two traces simultaneously, (Shown in Plate 3) one of the temperature in the burrow chamber and the second of the external shade temperature at ground level. This second probe was protected from the influence of the sun by a well-ventilated wooden box partially enclosing the entire recording instrument. The technique employed to create a model for the daily temperature experience of each vole was to note at hourly intervals whether or not a vole occupied the nest chamber and to record the chamber temperature if it did so, but if it had left the burrow system the fact was noted and the vole assumed to have been experiencing the shade temperature of the surface. Hourly means for each period of 20 days were derived for the shade surface temperature (External temperature), the temperature of the bank surface during those periods when the voles were active outside the burrow and therefore experiencing the external temperature (External Experienced temperature), the temperature of the nest when occupied by a vole (Nest Experienced temperature), and the temperature of the nest when the vole was absent (Nest Unoccupied temperature). These means were calculated over a period of two years, each year providing 18 "20 day" period means.

Relevance of the Method

i.) Burrow System

It has been concluded in Section 1 that the burrow systems employed represented fairly accurately the burrows of wild individuals. The utilization of a fairly wide mesh, 0.5 cm., permitted the air of the nest chamber to make contact with the surrounding soil over the greater part of the chamber's surface area, allowing rapid heat exchange between the nest chamber air and the soil. The system also permitted some modification of the burrow and nest chamber temperature by the activities of the voles themselves, for example nest insulation and the blocking and unblocking of tunnel exits. They were however unable to create ventilation shafts and other subsidiary openings, although these were provided in the first enclosure and had the effect of increasing diurnal variation in nest chamber temperature. Furthermore the enclosed voles survived healthily for long periods in these burrow systems; there were no enclosure deaths during either of the winters 1971-72 or 1972-73 and a litter of six individuals was raised to maturity during the summer of 1972. It is considered that the results gained from the method are a fair representation of the wild condition.

ii). Size

The results gained from the method refer principally to individuals above 100 gms. as the chamber dimensions were designed to represent those of adult voles. Smaller animals in such a chamber would record lower Nest-Experienced temperatures owing to their lower heat output but might in the natural situation experience the higher temperature by either reducing the effective volume of the burrow by introducing more nesting material into it or by occupying a smaller burrow. However, it is probable that in many cases Arvicola of this size would still occupy the maternal burrow and are, in any event, confined as a factor to the summer and early autumn seasons.

iii.) Actual Experience

(1) Because the temperature recording probe is situated laterally and ventrally in the nest chamber there is a risk that on some occasions it will be more greatly influenced by the occupants' presence than on others depending upon the vole's sleeping position, however the probe is large, some 20 cm. in length, and the alteration in the temperature record effected by the vole's changes of position inside the nest chamber seems on inspection to be of the order of 0.5°C or less. A corollary to the positioning of the probe is the problem of the relevance of the nest chamber temperature to the actual thermal experience of the animal. The quantity of nesting material excavated from the nest chamber appears to occupy a volume similar in extent to that of the vole itself, circa 300 cc.; it seems probable that the temperature within this nest will be considerably higher than that of the surrounding air of the nest chamber. This discrepancy in temperature between the nest and surrounding nest chamber would be greatest if the nest were spherical with the vole

sleeping in the centre, however the author has noted that on excavation the vole nests are frequently cup-shaped and open to the air dorsally, the insulation afforded thereby being reduced considerably. Also the nest may, in the laboratory, be dispensed with entirely, the material being used instead to block the burrow entrance, the vole sleeping without bedding, huddled in one corner of the nest chamber. Trojan (1969) has reported that Microtus arvalis construct their nests with great care at low temperatures but cease to be careful in nest building at 25 - 30°C. when the nests are seldom used and are often destroyed.

= C-dl [illegible]

It seems probable therefore that the extent of inaccuracies occasioned from the placing of the recording device would change with temperature and with the behaviour of the individual vole, and a correction does not seem possible. However the swift rise in temperature when the nest was re-occupied after a period of activity would suggest that there was a fairly free passage of heat through the nesting material, especially as the increase quickly levelled out after the period of initial rise. This suggests that a thermal equilibrium is speedily reached and maintained within the chamber. The level of the difference between the temperature surrounding the vole in the nest and the temperature of the air of the nest chamber remains uncertain.

(2) It is assumed that on emergence from the burrow a vole will experience the shade temperature of the bank

surface. To a considerable degree this must be justified as the marginal littoral vegetation of the stream is usually of a height sufficient to enclose the vole entirely. Also the vertical nature of the banks ensure that one or other is likely to be shaded at any particular time although this may be subject to the directional orientation of the stream. Activity at night and the general cloudiness of English weather (Table 1 shows that even in June, the sunniest month, only one quarter of each day enjoys sunshine and this is reduced to one eighteenth in December) will ensure that errors due to sun temperatures will be small. Water cooling while swimming in contrast may be of considerable temporary importance especially in winter. Although it is not thought that swimming occupies much more than 15% of all external activity, with the activity itself producing a considerable supply of body heat, it is quite possible that the assumption of a surface shade temperature here will produce an error. However it is clearly not possible to allow for factors of sun temperature and water cooling with the equipment employed. The two factors should to some extent counterbalance each other.

iv.) The 20 Day Period

The 20 day period was employed for its advantage in sensitivity over the monthly period. Periods of shorter duration than 20 days were thought likely to be too easily influenced by successive phases of cyclonic weather and in consequence would distort seasonal trends by superimposing temporary fluctuations upon them.

3. Temperature Experience

Results

3.1 Period means of Nest and Soil Surface temperature

The shade temperature of the bank surface (External temperature), the actual external temperature experienced by the voles during their periods of above-ground activity (External Experienced temperature), the temperature of the nest chamber when the nest is occupied by a vole (Nest Experienced temperature), the temperature of the nest chamber in the absence of the vole (Nest Unoccupied temperature), and the temperature experienced by the vole at all times (Mean Experienced temperature) are given in Table 8 for the successive 20 day sample periods. Although termed "20 day" periods these samples varied in their individual duration from 18 - 21 days as a result of the differing number of days in the calendar months. By altering the length of the "20 day" period to terminate at the end of a month, or at the tenth or twentieth day of a month, the data for successive years refers to the same calendar period, this would not be the case if the sample periods were terminated after exactly 20 days. The data in Table 8 refer to the record of two years from May 1971 - May 1973.

The data will be discussed in two principal sections, the first dealing with the External and the External

Experienced means and the second with the Nest temperature means.

Table 8. Temperature Means for the Successive 20 day Periods in °C.

Period	External	External Exp'd	Nest Exp'd	Nest Unocc'd	Mean Exp'd
11-31 Jan	2.24	3.02	10.02	9.82	7.59
1-20 Feb	3.07	3.54	10.26	9.75	8.41
21 Feb-10 Mar	3.19	4.00	10.15	10.04	8.49
11-31 Mar	5.27	5.36	11.43	10.85	9.85
1-20 Apr	5.75	6.14	12.64	12.28	10.72
21 Apr-10 May	8.43	8.32	13.97	12.98	12.25
11-31 May	10.01	10.21	16.88	15.68	14.82
1-20 Jun	10.35	10.03	17.46	17.33	15.12
21 Jun-10 Jul	13.60	12.30	18.39	17.56	16.26
11-31 Jul	14.20	13.49	20.04	19.33	17.53
1-20 Aug	13.09	12.63	18.86	17.83	16.86
21 Aug-10 Sep	12.52	11.10	18.88	17.76	16.67
11-30 Sep	10.52	9.81	17.64	16.37	15.70
1-20 Oct	8.77	8.48	15.36	15.15	13.87
21 Oct-10 Nov	7.30	7.47	14.10	13.70	12.56
11-30 Nov	2.85	3.42	10.43	9.9	8.65
1-20 Dec	5.36	5.39	11.13	10.67	9.70
21 Dec-10 Jan	3.38	3.86	10.65	10.01	8.95

3.1.1 External Temperatures

It can be seen from Table 8 that the External mean temperature rose steadily from a figure of 3.19°C. in late February and early March to a maximum of 14.20°C. in late July. The mean External temperature then fell, again fairly steadily, reaching a level of 7.30°C. in late October and early November, following which an unusual combination of two severe Novembers (those of 1971 and 1972) resulted in a sharper fall over the latter part of November to 2.85°C. The temperature rose subsequently to a winter norm of approximately 3 - 4°C.

From the period 21 October - 10 November until that of 1 - 20 April the External Experienced mean temperature exceeded the External mean temperature, the difference ranging from 0.03 to 0.81°C. (1-20 December and 21 February - 10 March respectively). It will be seen from Figure 18 that the magnitude of the differences between External and External Experienced temperature appears to depend upon the magnitude of the External temperature.

During this winter period where the External mean temperatures fell below 4°C. they were exceeded by the External Experienced temperatures by a mean of 0.62°C; when however the External mean temperatures rose above 4°C. they were exceeded by the External Experienced temperatures by a mean of only 0.17°C. These differences may result from both the slight diurnal preference of activity described in section 1.4 and also from the reduction in activity during periods of severe cold referred to in Section 1.5. Both these tendencies will result in the vole avoiding the most severe winter temperatures, those occurring during the night and those during the coldest spells of weather, and thus experiencing an external temperature higher than the External mean temperature. The voles may benefit from the higher External Experienced temperature by a reduction in the cost of thermo-regulation but the differences are not great even during the coldest spells of winter and it is not certain whether such substantial changes in behaviour, as noted in sections 1.4 and 1.5, are justified by the reduction in energy expended in thermoregulation or whether more critical factors are involved.

From the period 21 April - 10 May until that of 1 - 20 October the relationship between External and External Experienced means was reversed, External temperatures being slightly higher than those experienced by the voles. There was a single exception, the period 11 - 31 May had an External Experienced mean 0.20°C. higher than the corresponding External mean. With this exception the External means exceeded the External Experienced means by between 0.11°C. (during 21 April-10 May) and 1.42°C. (during 21 August - 10 September).

In the late spring and early summer when the External means lay between 8 - 10°C. the External Experienced means were closely similar but as the External mean rose above 11°C. a relative decrease occurred in External Experienced temperature, a decrease which reached a maximum in late summer. This relative decrease continued to occur in the autumn below the 11°C. level observed to be the transitional temperature in the spring. In the period 1 - 20 October where the External mean temperature was 8.77°C. the External Experienced mean temperature was only 8.48°C., a decrease of 0.29°C.

At External temperatures exceeding 12°C., the means of late June until early September, the excess of External temperature over that Experienced was at its greatest.

The mean difference during this period was 0.97°C. compared with the difference of 0.36°C. for those remaining periods of late spring and early autumn for which the External means lay between 8°C. and 12°C., excluding the exceptional period 11-31 May.

This low level of External Experienced temperature compared with External temperature, in summer particularly, may have resulted from the strong nocturnal tendency at the time referred to in section 1.4. By avoiding the warm external temperatures of the early afternoon the voles lowered the temperature they experienced throughout the summer below the External temperature mean. There are no clear energetic reasons why they should do this. The cause may be a dislike of bright sunlight as suggested previously or an avoidance of diurnal predators.

It is concluded that the relationship between External temperatures and External Experienced temperatures falls into four seasonal categories. The exception of the period May 11 - 31 to this summary is noted. At temperatures below 4°C., during the winter, the External Experienced mean exceeds the external mean by an average of 0.62°C. At higher temperatures during winter the External Experienced mean approximates more closely to the External mean being on average only 0.17°C. higher. In late spring and autumn where the External temperature lies between 8 - 12°C. the External Experienced mean falls below the External mean, a difference averaging 0.36°C., a difference which increases to an average of 0.97°C. during the summer as the External mean rises above 12°C.

The absolute range in External temperature over the two years of the study was from -11°C. to 28°C., and the absolute range of External Experienced temperature was from -10°C. to 28°C. The maximum observed daily range of External temperature was 21°C., the minimum daily range less than 1°C.

3.1.2 Nest Temperatures

The Nest Experienced temperatures exceeded the External temperatures by 4.79 - 7.78°C. during the year as a whole, with a mean difference of 6.58 ± 0.19°C. The difference was rather higher during the winter, when it lay between 5.77°C. and 7.78°C., than during the remainder of the year, when it lay between 4.79°C. and 7.12°C., but the seasonal variation in the difference was not marked. The mean Nest Experienced temperatures kept within the range of 10-12°C. between 11 November and 31 March and at no time fell below 10°C. During the late spring the Nest Experienced temperatures rose rapidly in conjunction with the rise in External temperature reaching a maximum of 20.04°C. in the period 11-31 July, when it exceeded the External temperature by 5.84°C. The absolute range of Nest Experienced temperature over the two years of the study was 5-26°C.

The temperature of the unoccupied nest was lower than the Nest Experienced temperature by between 0.11°C. and 1.27°C., the former difference occurring in the period 21 February - 10 March and the latter in the period 11 - 30 September. The mean difference over the year as a whole was 0.63 ± 0.09°C. The difference between the two values tended to be smaller in autumn and winter than in the remainder of the year, but there was considerable variability in its magnitude. The absolute range of Nest Unoccupied temperature over the two years of the study was 5 - 25°C.

When the nests were unoccupied the intra-diel variation in nest temperature was small, never being greater than 2.5°C. and usually less than 1.5°C. The maxima and minima of daily nest temperature occurred several hours after the corresponding extremes of External temperature.

When the nests were occupied the changes in nest temperature effected by the presence and absence of the vole caused a greater temperature fluctuation, usually 1 - 3°C., than that resulting from external temperature variation and over a very much smaller period of time. While within the nest the vole experiences a very stable ambient temperature and one which is usually higher than the external temperature at the time, even during summer. In contrast on emergence from the burrow the vole may encounter temperatures 20°C. lower than it had been experiencing only a few seconds earlier, and if it then dives into near freezing water it may encounter a cooling load of even greater severity. In winter therefore the voles experience long periods of rest at relatively high and stable temperatures followed by rapid and sometimes considerable reductions in temperature at the beginning of each period of external activity. In summer the changes in temperature on emergence are generally less severe, and the external temperatures themselves are closer to the voles' zone of thermal neutrality. In this season the change from a dark burrow to the glare of bright sunlight may be a more disturbing experience than the change in ambient temperature, at least during the late morning and early afternoon.

3.1.3. Soil Temperatures.

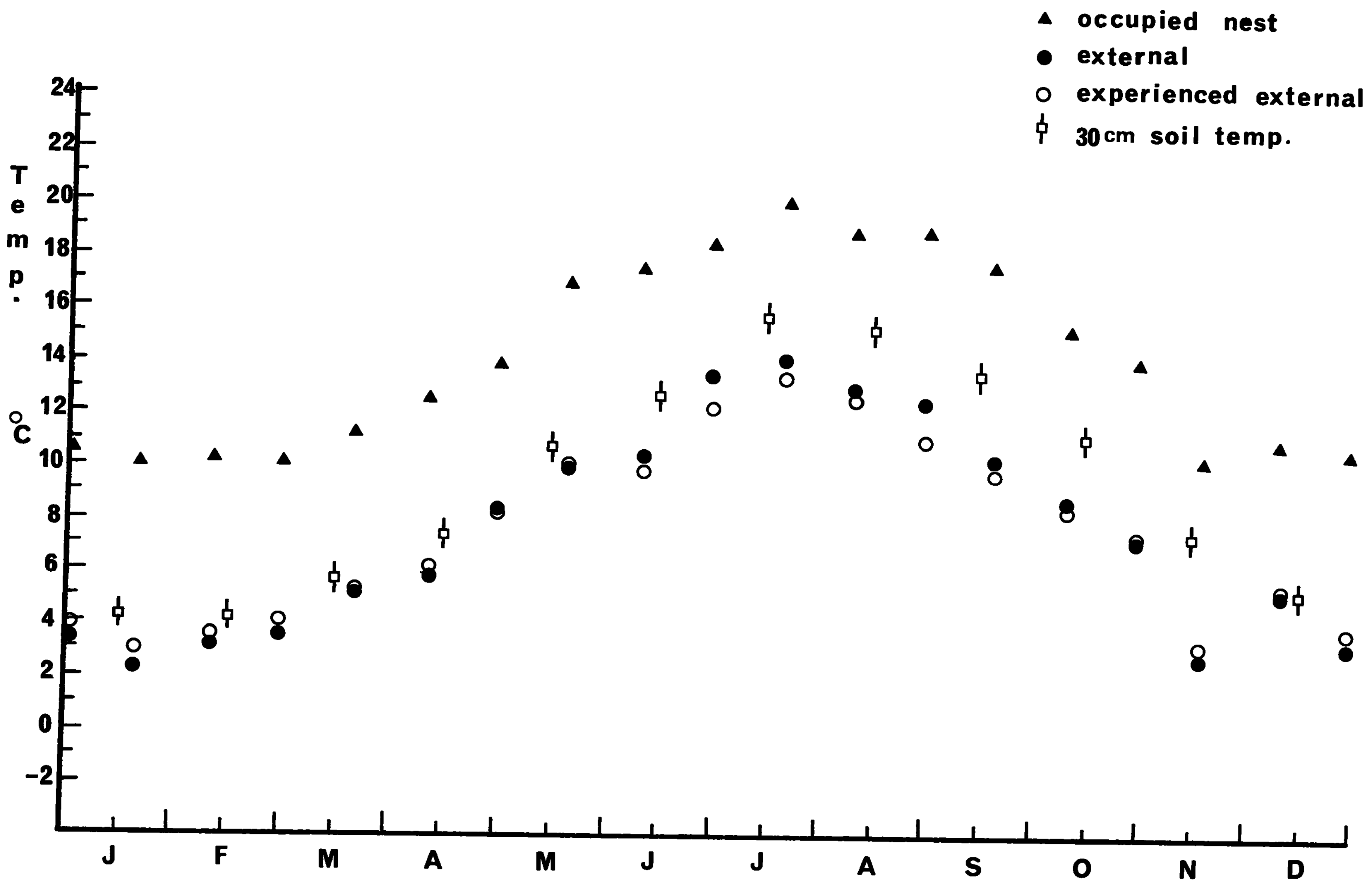
The Durham Observatory present data for the mean monthly temperature of the soil at a depth of 30 cm. These means are included in Figure 18. It will be seen that in winter this parameter is more closely associated with the corresponding External temperature than with Nest Experienced temperature, being rarely more than 2°C. higher than the former prior to the late summer. The soil at this depth is seen to cool more slowly than the air in late summer and autumn, and by the end of the latter season the mean soil temperature at 30 cm. is approximately midway between the External and Nest temperatures. By December however the temperature at 30 cm. has fallen once more to a level less than 2°C. higher than the External temperature.

The depth of 30 cm. approximates closely to the depth of the nest in the enclosures and it may be seen from Figure 18 that for the winter, spring and early summer

Figure 18

Changes in vole-experienced temperature, with time of year.

The mean temperature in °C over periods of approximately 20 days are shown for the temperature of the vole-occupied nest, for the temperature of the bank surface (External) and for the temperature of the bank surface at the time when the vole was active outside the burrow (Experienced External). The mean temperature of the soil at a depth of 30cm. at monthly intervals is also shown. The soil temperature data was calculated from figures presented by the Durham Observatory. The temperature data were recorded over the two year period from May 1971 to May 1973.


▲ occupied nest
● external
○ experienced external
30cm soil temp.
Temp. °C
24
22
20
18
16
14
12
10
8
6
4
2
0
-2
J
F
M
A
M
J
J
A
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O
N
D

seasons mean soil temperature at this depth is little better than the External mean as an estimate of nest temperature. It is concluded from these data that soil temperatures taken at depths corresponding to the siting of rodent nests are considerably different from nest chamber temperatures experienced by the voles.

Discussion on Section 3.1

The records of the mean Nest Experienced temperature in the winter mainly concern records of single animals in each nest. When a nest became shared its temperature rose 1 - 2°C. within 24 hours and retained that differential over a nest inhabited by one individual throughout the year. Such an increase might well provide a considerable saving in energy expended on thermo-regulation even if the voles did not come into actual huddling contact with each other. For the remainder of the year the data concerns records from solitary, shared and family nests, a mixture that is thought to represent the natural condition as accurately as was feasible.

Comparison with other work is rendered difficult by the differing climates of the study areas. While agreeing with Grodziński and Górecki (1967) that the temperature of the occupied nests of small rodents is higher than that of the soil at the same depth the writer considers that their figure of 20°C. for the mean experienced temperature in the Temperate zone for measuring A.D.M.R. seems far too high and that their figure for the sub-arctic zone of

10 - 15°C. seems more appropriate for all but Mediterranean Europe. The assumption of Trojan (1969) that soil temperatures may be used as an alternative to nest temperatures appears inaccurate; he instances a July temperature at 20cm. of 19°C. when the surface temperature is 20°C., while in the present work a nest temperature of 20°C. at 30 cm. depth was recorded when the corresponding surface temperature of the exterior was 14.2°C.

In the present study Nest Experienced temperatures exceeded the External temperatures by a mean for the year as a whole of 6.58°C. This result is very similar to that reported by Cotton and Griffiths (1967) for the temperature of the nest periphery of <u>Clethrionomys glareolus</u> in the laboratory. These authors found that for a range of external temperature from 0 - 10°C. the temperature of the nest periphery was 5 - 7°C. higher than the external temperature when the nest was occupied by a single vole, and 7 - 10°C. higher when the nest was occupied by a pair of voles.

3.2. Tabulation of Temperature and Activity Experience.

The data available from Sections 1, 2 and 3 can be used to draw up a model record for each "20 day" period in which the total number of hours in each period are allocated an ambient temperature and prevailing level of activity by employing the mean figures calculated previously.

The entire temperature data for several animals over two years was available for each 20 day period. The data were already divided into resting and active components by the method of recording the data as Nest or External Experienced temperature throughout that period since while in the Nest the animals are presumed to be resting and while outside the burrow they are presumed to be active.

Because the data are for several voles over two years, the records will greatly exceed in number the 20 day x 24 hour records for each 20 day model period. The total data are converted to the 20 day model by multiplying each temperature record in both resting and active ranges of temperature by the expression $\frac{n}{N}$ where N is the number of hourly records in the total data for each 20 day period and n is equal to the 20 day period x 24 hours. To increase the clarity of explanation for this and subsequent conversions an example is given of a 20 day period taken from hypothetical total data. The data appear as a range of activity and rest temperatures each containing a number of hourly records.

Example

	External Experienced Range (Active)								Nest Experienced (Resting)				
°C.	5	6	7	8	9	10	11	12	13	14	15	16	17
hrs	7	37	79	91	65	53	27	6	58	190	250	219	70
Total hrs.	(365)								(787)				

In the example N = 1152. As the 20 day period of the example is in fact 21 days the number of hours in the model, n, is 21 x 24 = 504. Each temperature record is therefore multiplied by $\frac{n}{N} = \frac{504}{1152} = 0.4375$. The result of each conversion is rounded to the nearest whole number.

	External Experienced (Active)								Nest Experienced (Resting)				
^{o}C.	5	6	7	8	9	10	11	12	13	14	15	16	17
x 0.4375	3	16	35	40	28	23	12	3	25	83	109	96	31
Total hrs.	(160)								(344)				

In the compilation of the temperature experience data the division into resting and active sections was achieved by dichotomising the data into rest or activity at hourly point intervals while in the compilation of the duration of daily activity data it was achieved by summing the actual duration of activity and rest. The estimates of the daily proportion of activity is never identical in the two calculations. Since the estimate of the proportion of daily activity achieved by summing the actual duration of activity and rest utilizes the entire data it is the more accurate estimate. A correction is therefore applied by multiplying each activity record of the temperature range by $\frac{p}{P}$ where p is the proportion of diel activity estimated in Section 1.2 and P the proportion estimated from the temperature experience data. A similar correction is applied to the resting record of the temperature range by multiplying each by $\frac{q}{Q}$ where q is the proportion of diel rest estimated in section 1.2 and Q the proportion estimated from the temperature experience data.

In the example P = 160/504 = 0.3175 and Q = 0.6825. From the hypothetical data in section 1.2 let us suppose that p was found to be 0.30 and q to be 0.70. Therefore the activity range is multiplied by p/P = 0.9449, and the resting range by q/Q = 1.0256. The result of each conversion is rounded to the nearest whole number.

	External Experienced (Active)									Nest Experienced (Resting)				
	5	6	7	8	9	10	11	12		13	14	15	16	17
x0.9449	3	15	33	38	26	22	11	3	x1.0256	26	85	112	98	32
Total:	504		(151)							(353)				

In the revised figures P = 0.2996 compared with the expected figure of 0.30, an approximation which is acceptable.

The activity data are then divided into two sections, a combined low and medium energy expenditure component (groups 1 and 2 of section 2.1), and a high energy expenditure component (group 3 of section 2.1). Each member of the activity range is multiplied by $\frac{a}{A}$ where "a" is the proportion of the total activity spent in low and medium energy expenditure activity as estimated in section 2.1 and "A" is the total activity. In each case the relevant seasonal estimate of "a" is used and not the yearly mean. This choice was rather arbitrary but the difference is not great.

In the example group 1 and 2 of Section 2.1 was found to be 84% of the total. Consequently $\frac{a}{A} = \frac{84}{100} = 0.84$. The members of the activity range are multiplied by 0.84 and rounded to the nearest whole number. The result gives the number of hours spent in activities of groups 1 and 2, the number of hours spent in group 3 is then found by subtracting each result from the pre-conversion figure.

	External Experienced (Active)									Nest Experienced (Resting)						
°C	5	6	7	8	9	10	11	12		As before	13	14	15	16	17	
x0.84	3	13	28	32	22	18	9	3	(128)		26	85	112	98	32	
Group 3	0	2	5	6	4	4	2	0	(23)							(353)

The results calculated by this means are a fair estimation of the experimental and observational data, splitting the total number of hours in this period of 21 days into the components of Rest, Low Energy Activity, and High Energy Activity, and each of these components into their likeliest range of experienced temperature. It will be seen however that the timing of the 20 day periods of the temperature estimation do not directly correspond to the monthly means of p and q of the diel activity duration estimation of section 1.2. In the calculation where the entire 20 day period falls within a discrete month p and q are assumed to be equal to those of that month, where the 20 day period occupies part of two months the mean of the adjacent months is used.

The three component ranges were calculated for each of the 20 day periods but when calculating respirometry costs it was found that the mean of each range sample was as good a model as the entire range, the difference in the result being negligible. This is discussed in greater detail in Section 5.4.

In the example the mean of the temperatures measured at hourly intervals is 8.285°C. for External Experienced and 15.071°C. for Nest Experienced temperature. The result may be summarised as follows:

Rest		Low Energy Active		High Energy Active	
hrs	°C.	hrs	°C.	hrs.	°C.
353	15.071	128	8.285	23	8.285

The result for the eighteen 20 day periods calculated to include the conclusions of Sections 1 - 3 are given in Table 9.

Table 9. The component breakdown of each 20 day Period for Activity and ambient temperature

Period	Rest		Low Energy Active		High Energy Active
	hrs.	°C.	hrs.	°C (both activities)	hrs.
11-31 Jan	378	10.02	109	3.02	17
1-20 Feb	348	10.26	113	3.54	19
21 Feb-10 Mar	317	10.15	100	4.00	15
11-31 Mar	373	11.43	111	5.36	20
1-20 Apr	338	12.64	121	6.14	21
21 Apr-10 May	334	13.97	126	8.32	20
11-31 May	348	16.88	134	10.21	22
1-20 Jun	329	17.46	128	10.03	23
21 Jun-10 Jul	312	18.39	142	12.30	26
11-31 Jul	311	20.04	163	13.49	30
1-20 Aug	326	18.86	128	12.63	26
21 Aug-10 Sep	361	18.88	121	11.10	22
11-30 Sep	361	17.64	96	9.81	23
1-20 Oct	376	15.36	85	8.48	19
21 Oct-10 Nov	387	14.10	93	7.47	24
11-30 Nov	358	10.43	100	3.42	22
1-20 Dec	360	11.13	104	5.39	16
21 Dec-10 Jan	378	10.65	107	3.86	19

These results are used later for assessing the respiratory costs for their respective periods.

CHAPTER 4

THE MODEL POPULATION

4. The Model Population: Introduction

Purpose of the Model Population

(1.) In order that the experimental data for respiration rate in Section 5 for the parameters of bodyweight, temperature and activity may be utilized in the estimation of Arvicola energy flow along a stretch of stream it was necessary to investigate a natural population of A. t. amphibius to assess the following criteria.

i) Seasonal changes of population density.

ii) Changes in bodyweight of the individuals in the population.

iii) The fecundity of the population. This requires details of the number of pregnancies, the size of the litter in each pregnancy, the duration of pregnancy and lactation, and on the survival rate of young voles.

(2.) An investigation of a natural population is also necessary to disclose the productivity of the population, which combined with respiratory cost will provide a figure for the energy assimilated by that population. Such a productivity figure requires information on:

i) The increase in bodyweight of existing members of the population.

ii) Production resulting from reproduction and the growth of new members of the population.

Population Structure of *Arvicola*.

(1.) Reproductive Cycle. Although there is some variation in the figures published the work of Perry (1943), van Wijngaarden (1954) and Stoddart (1968, 1971) are in basic agreement concerning the growth and reproductive cycle of *Arvicola.* Perry (1943) who worked principally on *A. t. amphibius*, describes the reproductive organs of both sexes as resembling those of *Clethrionomys glareolus* as described by Brambell and Rowlands (1936) and Rowlands (1936). Breeding is interrupted by winter when the males become non-fecund and the females anoestrus. The females have a poly- oestrous cycle like the white rat and *Clethrionomys*. They are non parous until March. In that month half are in di-oestrus. Males become fecund in February and mating takes place towards the end of March. One or more infertile cycles may occur in the female before pregnancy takes place. There is a post partum oestrus and the females may become pregnant while lactating in the spring, but rarely do so later in the year. If the animal fails to become pregnant at the post partum oestrus it enters upon a lactation anoestrus. The first pregnancies occur in April with the maximum number taking place in May. None occur after September, when the lactation anoestrus passes into a winter anoestrus without further ovulation. The gestation period is variously described as being between 20 - 28 days (Herfs, 1939; Ryder, 1962). The first lactations occur in May, lasting for 13 - 20 days and cease after September when the winter anoestrus starts. Winter anoestrus ceases in

December.

Stoddart (1968) found that over 50% of females of A. t. reta in Aberdeenshire were pregnant by late May, that the maximum frequency of pregnancy was reached in June and that no pregnancies occurred after September. These figures reveal a population attaining the maximum frequency of pregnancies approximately one month later than the voles studied by Perry (1943) the majority of which were obtained from Shropshire, a reflection perhaps of the cooler climate experienced by the former.

Perry (1943) states that animals born early in the year may breed in the same season and that most become fecund by the end of their first summer. Stoddart (1968, 1971) records no breeding in the year of birth which may be a result of the later commencement of the breeding period. Adults of both sexes begin to cease being fecund in August - September, a process complete by December.

Stoddart (1968) found that young animals increased in weight until October when the increase ceased at a mean bodyweight of 140 g., and the bodyweight declined slightly until February, to a mean of 125 g. By March the animals had increased in weight once more reaching a maximum in May at a mean of 195g, which, discounting changes due to pregnancy, remained stable thereafter until December when a slight decline could be noted. This spring increase in bodyweight was also recorded by Perry (1943), and Brambell and Rowlands (1936) note a similar occurrence in Clethrionomys glareolus, as does Evans (1973) in Microtus agrestis.

Perry (1943) records an average number of 5.7 embryos in each pregnancy for A. t. amphibius while van Wijngaarden (1954) found a mean of 4.9 for A. t. terrestris, and Stoddart (1968, 1971) one of 6.4 for A. t. reta.

Van Wijngaarden (1954) reports an annual mean number of 4.4 litters per female and an average litter size of 3.8* young, while Stoddart (1968) records mean figures of 2.2 and 5.5 respectively, with 86% of the females surviving to produce a second litter and 36% surviving to produce a third. Meylan and and Morel (1970) found mean litter sizes for A. t. scherman of 4.4 from 5 litters in 1966 and 4.05 from 19 litters in 1968.

Stoddart (1968) weighed newborn young and found values within the range 4.5 - 5.08 g., while Perry (1943) who weighed foetuses found the largest to weigh 8.45 g. These data suggest that the females investigated by Perry (1943) would have given birth to rather larger young than did those of Stoddart (1968).

(2.) Growth and Density

Stoddart (1968, 1971) measured the growth rate of young voles in the laboratory and was able to create a growth curve correlating age with weight which he considered

*not seen in original, reported in Stoddart 1968.

to maintain accurate correlation for several weeks after birth. He obtained mean bodyweights for the first six weeks of circa 13, 22, 46, 63, 78, 86 grams. The young opened their eyes at 7 - 8 days of age and weaning started after approximately two weeks.

Pelikán and Holišová (1969) estimated the density of a population of A. t. terrestris by snap trapping as being 4.0 - 7.9 per 100 m. of stream in 1966 and as 6.3 - 9.3 per 100 m. of stream in 1967. Pelikán et al. (1971) however found rather lower densities of 0 - 4 voles per 100 m. of stream and 0 - 2 voles per 100 m. along the edge of ponds. Van Wijngaarden (1954) found a maximum density of 15.4 voles/100 m. of stream in the Netherlands. However most continental data concern Arvicola whose home range is confined to agricultural land and so cannot be compared directly with fluvial populations. Myllymäki (1969) records densities varying from 62/ha - 260/ha in southern Finland and Mehl (1950) found a density of 16/ha in normal years in Germany, rising to 100-300/ha in peak years. Lund (1970) states, "Regular population cycles are not known in the Netherlands, Germany or Denmark but 5 - 7 year cycles are recorded for West-Siberian populations and Ognev (1949) found 3 - 4 year cycles near N. Dwina. 'Crash' phenomena have never been directly observed in water vole populations whereas severe decimation of numbers may have been caused by external factors, e.g. unfavourable weather conditions. An internally induced decrease in population as in the case of other Microtinae like the field vole and the lemming is not reported in this species." Lund records that in the winter of 1961-62, 32.6% of the voles in his enclosures died while in the winter of 1962-63, an exceptionally severe winter throughout northern Europe, this figure rose to 51.4%.

Not all populations of British Arvicola are confined to the banks of streams. Davis (1970) reported that on a few occasions A. t. amphibius had become abundant locally in England and had spread into arable fields, orchards and gardens. Southern and Crowcroft (1956) described a terrestrial form of A. t. amphibius living on an island in the Humber estuary and isolated from freshwater as having developed a burrowing habit similar to that of A. t. scherman. They note that there were no moles or rats on this island.

Whereas the population densities of Arvicola do not appear, from the published data, to be prone to the same marked fluctuations characteristic of the populations of other voles and lemmings it is clear that over a period of a few years the population density may change markedly, increasing tenfold in some cases (Mehl, 1950; Myllimäki, 1969). The primarily fluvial habitat of the English water vole however, coupled with a large size that might be reflected in more extensive home ranges and a subsequent reduction in density, suggests that the published data for continental subspecies and possibly even A. t. reta may not be directly applicable in the present study. It was considered desirable therefore to investigate the density of an Arvicola population in Durham.

Site of Study

The stream chosen for the study of the model population was the Woodham Burn, a tributary of the River Skerne and ultimately of the River Tees. The location studied was at Low Copelaw Farm, near Newton Aycliffe some 17 km. south of Durham City, Ordnance Survey Ref. NZ296264, latitude 54°37'N., longitude 1°32'W., and at an altitude of approximately 230' (70 m.). At this point the Burn flows almost due North-South and varies little from 3 m. in width. The present course of the stream follows a dyke cut during the last century which diverted the water flow from the original meandering course. The Burn has silt-clay banks rising to between 40 - 150 cm. in height at a distance of 1 m. from the water's edge and is flanked by earthern artificial levées approximately 2.5 m. above mean water level at a distance of 3 - 4 m. For short stretches the bank soil loses its silt fraction and becomes a heavy clay.

When at mean water level the stream varies in depth from 10-70 cm. with a mean of 40 cm. and is floored principally by sand, which may grade into silt or gravel according to the rate of stream flow. This is slow and linear except over the shallows which occur at infrequent intervals along the stream's length. In summer, after a period of dry weather, the rate of flow may become almost imperceptible while in winter, after periods of prolonged heavy rain or rapid snow melt, it can become turbulent with the water level rising up to 1 m. above its usual level. At all times the water shows some turbidity. This increases rapidly after a period of rain.

Where the stream's banks are vertical they are devoid of vegetation. The banks are continually being undercut by the action of the water and this, in conjunction with the burrowing of Arvicola and the trampling of domestic cattle, causes frequent slumping into the water. Where slumping has occurred, and it is the more usual state of the banks, vegetation is continuous from the levée to the water's edge and may extend into the water as reed growth during the summer. The banks are largely devoid of trees and woody shrubs with the vegetation cover being dominated by grasses and locally by a few herbaceous dicotyledons. Principal among the grasses are Poa pratensis L., Agrostis gigantea Roth, Lolium perenne L. and Arrhenatherum elatius (L.) T. & C. Presl. The proportion of dicotyledonous plants varied seasonally but never exceeded 30% of the dry weight of the total bank vegetation biomass. The most important of these at all seasons was the nettle Urtica dioica L. although the Balsum Impatiens glandulifera Royle became important in the summer, as to a lesser extent, did Brassica rapa L., Lamium album L., Epilobium hirsutum L., Conium maculatum L., and Cirsium arvense (L.) Scopoli. Marginal vegetation was confined to the reed Sparganium, and, less importantly, to the cress Nasturtium officinale R. Brown. Submerged vegetation was, apart from algae, almost entirely absent at the point of study. The vegetation of the stream banks is described more fully in Section 6. Part of the stretch of Woodham Burn studied is shown in Plates 4 - 6.

Zejda and Zapletal (1969) concluded from a survey of stream preference of Arvicola in central Moravia, Czechoslovakia, that: (1) streams with muddy floors are preferred over those floored by stones or sand; (2) loamy banks are preferred to stony, paved or sandy banks; (3) banks covered with vegetation are preferred to those devoid of vegetation; (4) banks covered by grasses, reeds and herbs are preferred to those growing shrubs and trees; (5) banks which are slightly undermined and in excess of 1 m. in height are preferred, whereas banks less than 0.5 m. in height are lightly colonised; (6) a stream depth of 0.2 m. and over is preferred to shallower brooks, and slowly flowing water over a flow in excess of 0.5 m./sec; (7) stream floors covered with vegetation are preferred to those devoid of it; (8) marked variability in water level reduces the number of water voles present; (9) mowing the vegetation reduces the number of water voles present.

It can be seen that Woodham Burn satisfies most of the conditions of Zejda and Zapletal (1969) the principal exception being the fact that the stream floor is devoid of plant growth and that the bank vegetation is cut back once annually at the end of July. Generally however it may be concluded that Woodham Burn represents an excellent habitat

Plates 4-6

Woodham Burn. The site of study of the model population.

Plate 4

April

Plate 5

July - before scything

Plate 6

August - after scything

for Arvicola. The features of a slowly flowing, turbid stream of fairly stable water depth reflect the drainage area of the Burn which comprises the low, glacial boulder clay plains of South Durham, a pattern in marked contrast to that of the streams of North Durham where the tributaries of the rivers Wear and Tyne flow rapidly in shallow, pebble-strewn courses from the uplands of the Pennines to the west. The principal practical disadvantage in studying the vole populations of these streams and of the lowland reaches of the Wear and Tyne themselves is the likelihood of a rapidly fluctuating water level responding to weather conditions away from the immediate locality. This is a hazard to traps set at the water's edge, and to any animals they may have caught. Woodham Burn was chosen as the site of the model population for the reason of its local drainage area as well as for those habitat qualities previously mentioned.

Method

The aim was to trap, mark for identification, and assess weight and sexual status of the entire trappable Arvicola population along a short stretch of the Woodham Burn, 380 m. in length, at all seasons of the year.

Trap Design

The traps employed, a diagrammatic example of which is shown in Diagram 2, were constructed from a design described by Lockie (1966) for catching weasles Mustela nivalis L., using 1 cm. plywood with the exception of the back which was made of perspex and could be removed to allow access to the tre~~d~~adle and trigger mechanism lying closely anterior to it. Exterior trap dimensions were 30 x 22 x 20 cms. In the description which follows the abbreviations in parenthesis are those employed in Diagram 2, to which they refer. At the front end of the trap is an aluminium door (d) which closes over the entrance hole (e) when permitted to fall and which is raised by a nylon line (l) attached to a hole in its upper surface. This nylon line passes exteriorly along the midline of the trap to within 5 cm. of the perspex back (b) at the rear and then re-enters the trap through a 1 cm. diameter brass cylinder, the ring sheath (rs), set into its roof. The ring sheath projects into the trap interior for 3 cm. The nylon line is kept from abrading the wooden roof of the trap by cylindrical strips of perspex or brass, the line guides (lg), situated at intervals along its path. The line is nowhere enclosed externally as such an enclosed pathway might become blocked with mud after periods of flooding. At its posterior end the nylon line is attached to a 3 cm. brass wire, the ring shaft (rsh), which at its opposite end is formed into a ring (r) which engages the trigger mechanism (t). An aluminium strip 2 cm. in width is placed approximately 3 cm. from the rear of the inside of the trap. This strip, which forms part of the tre~~d~~adle (tr), extends almost the width of the trap and is laid horizontally. Welded to it at its midpoint is a second smaller strip 3 cm. in width which rises vertically from the horizontal plate for 1.5 cm. To

Diagram 2

The design of the live-trap

A

Design of the trap viewed in longitudinal section.

B

Design of the trap viewed from the front.

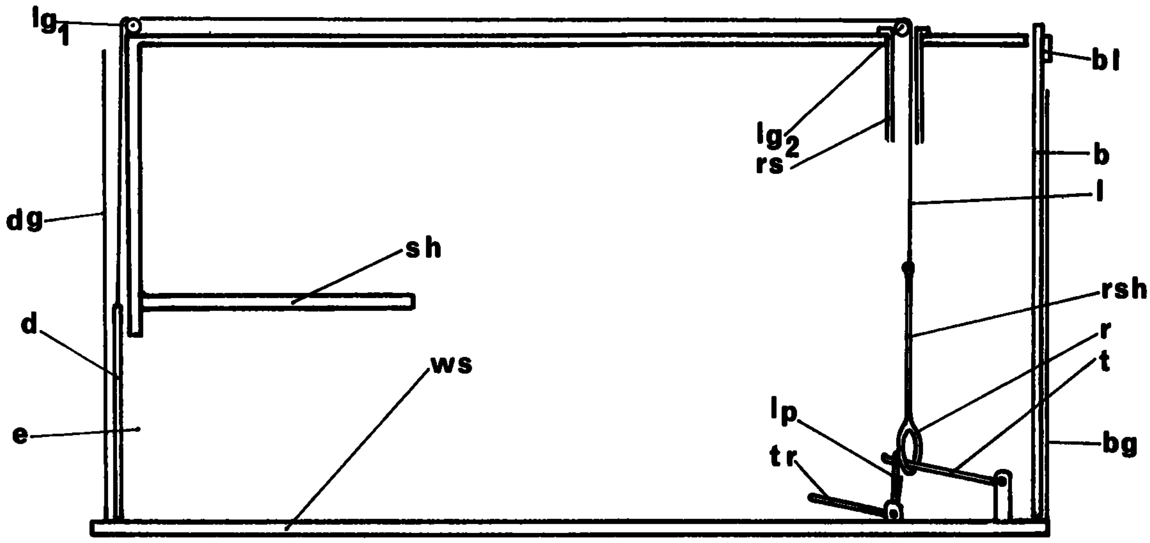
C

Design of the trap viewed from the rear with the perspex back removed.

Key

b	perspex back
bg	perspex back guide
bl	perspex back lip
d	trap door
dg	trap door guide
e	entrance hole
l	nylon line
lg_{1-2}	line guides 1 and 2.
lp	treddle loop
r	ring
rs	ring sheath
rsh	ring shaft
sh	sleeping shelf
t	trigger
tr	treddle
ws	wooden shell

A


lg1
bl
lg2
rs
b
l
dg
sh
rsh
d
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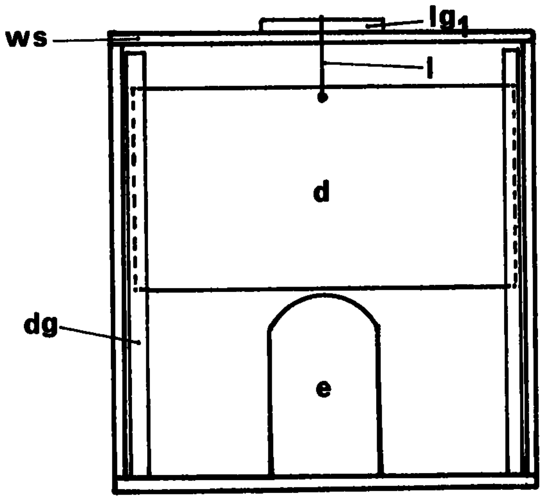
t
ws
lp
e
tr
bg


lg1
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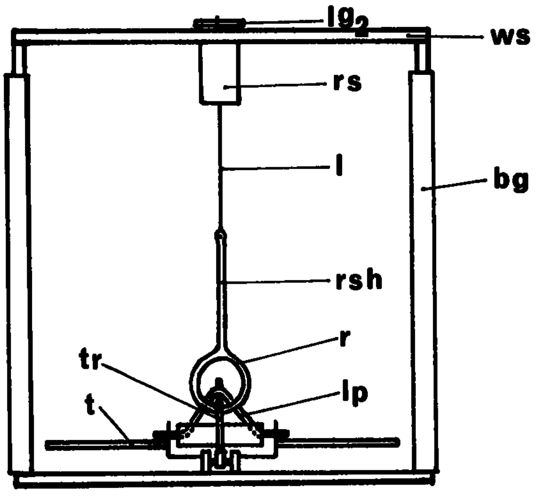
B


lg2
ws
rs
l
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rsh
r
tr
lp
t

C

this vertical strip of aluminium is attached a loop of wire (lp) which exceeds it in vertical height and also projects horizontally on each side as two short end pieces at its base. These basal pieces slot into sockets in a strip of aluminium screwed to the wooden floor, so that the entire treadle mechanism (tr) may be tilted backwards and lifted clear of the trap floor. A strip of wire acting as a trigger (t) is held loosely at the rear end by a support screwed to the trap floor immediately anterior to the perspex back so that it may be raised and lowered without undue friction. The aluminium door is then raised by pulling the brass ring down posterior to the wire loop of the treadle and kept there by the insertion of the trigger which passes through both ring and loop tilting the horizontal plate of the treadle clear of the floor; this plate lies furthest anterior of the treadle mechanism. The trap is baited with carrot placed between the treadle and the perspex back, and a small piece of carrot is also placed at the entrance hole. The vole is attracted by the bait at the trap entrance and proceeds along the length of the trap to the remainder of the carrot and in doing so steps upon the treadle, springing the trigger and releasing the brass ring. This rises up into the protecting ring sheath. The aluminium door falls closing the trap.

Inside the trap a wooden ledge is fixed above the hole entrance at the anterior end and on this is placed dried grass to serve as bedding material, additional food may also be placed on this ledge in winter. The advantages of this trap are the simplicity of construction and cheapness of materials, combined with good insulation against night chilling; voles were found to survive a frost of -10°C. Disadvantages include the relatively rapid erosion of the traps by the vole gnawing, especially around the entrance hole, and also the size and weight of the traps which made the setting out of a trap line a laborious process. The former objection would be removed by lining the interior of the trap with aluminium sheeting, this increases trap life but also initial cost. The lining of the anterior end at least was found to be very worthwhile. The attachment of the ring wire to the nylon thread is protected by its retraction into the ring sheath. But for this protection the thread would almost invariably be bitten through by the vole before release and it would be necessary to rethread the trap before re-use.

The traps were placed at the water's edge on natural ledges formed as a result of bank slumping, or on ledges deliberately provided for this purpose should the former be absent, and where possible were sited at frequently used latrines or where footprints were abundant (Plate 7). The traps, 35 - 70 in number, were set approximately 10 m. apart in winter and 5 m. apart in summer, a minimum of three traps was provided for every estimated vole in the study area. They were stationed permanently and were tied by wire or thick nylon twine to 1.5 m. bamboo stakes driven deep into the bank. This method enabled the traps to survive frequent flooding and losses were confined to the

Plate 7

Trap in situ.

The trap is placed close to the water's edge and held in position by strong nylon twine tied to bamboo stakes in order to restrict flood damage. The small mud bank on which the trap is sited is being used by the voles as a latrine.

Plate 8

The Respirometry Chamber.

The vole shown in the chamber is a large male of circa 300g bodyweight.

destruction of both stakes and traps by bank slumping.

The traps were set in the morning and emptied on the morning of the following day. Approximately 80 gms. of carrot food was found to be adequate provision for the voles for the maximum duration of trapping time.

Arvicola is a relatively large, vigorous rodent which is difficult to handle gently enough to avoid harming it without at the same time being bitten or allowing it to make its escape. For this reason the technique of using Diethyl Ether as a general anaesthetic suggested by Lockie and Day (1964) and employed on Arvicola by Stoddart (1968) was used throughout the study. It was not found necessary first to remove the animal from the trap into a polythene bag as suggested by Stoddart (1968) as with the traps used the voles could be etherized in situ. Ether vapour was blown into the trap from a wash bottle until the vole had reached the state of being unable to move without staggering. This state was usually induced by the effect of six deep exhalations through the wash bottle. The vole could then be removed by a gloved hand, weighed in a polythene bag of known weight with a "Pesola" 300 g. or 500 g. spring balance, examined to determine identity, sexual state, and condition of pelage for details of moult and scarring. By the time it was released into the stream the vole had usually recovered from the anaesthetic sufficiently to swim or dive rapidly to a nest burrow.

On first capture the vole was marked for future identification by ear tagging using the method described by Stoddart (1968) employing Monel metal, serially numbered, ear tags produced by the National Band and Tag Co. of Newport, Kentucky. These were fixed to the thickest basal part of the ear with a small pair of pliers. This procedure was apparently painless to the etherized animal and rarely accompanied by struggling and never by bleeding. On no occasion was infection seen to occur as a result of marking by ear.tagging. Both ears were tagged as tags occasionally pull free but during regular trapping it was very rare for both tags to be lost and certain identification of individuals could be maintained.

Initially the stretch of stream under observation was trapped on successive days as it was considered that enough animals may have escaped capture on the first occasion to produce a large error in the population estimates. Early results showed however that the records of the second trapping were little different from those of the initial trapping, the principal discrepancy being not one of individuals captured but of their condition. After the second trapping voles were found to have lost as much as 15% of their previous bodyweight and to show a decline in the condition of the pelage apparently induced by over-grooming in the trap. In view of this deterioration caused by repeated capture and because very little additional information was being gained by the second trapping, this was discontinued.

The usual procedure was to divide the stretch of stream studied into two approximately equal halves. On the first day of the trapping session those traps of the first half were set and the voles caught were released on the second day when the traps of the second half were set. Voles caught in these traps were released on the third day. These trapping sessions were repeated at intervals of approximately ten days from late spring until the end of the breeding season in the autumn. The frequency of trapping was then reduced gradually reaching a minimum of once monthly in winter. This reduction in trapping frequency was a result both of the stabilising population level and of the need to avoid trapping under conditions of cold and wet weather that might deplete the population by trap deaths. This was particularly important in view of the number of voles in total being small. In the winter trapping generally took place only within periods of mild but settled weather. Even in summer care had to be taken to avoid trapping during a period of heavy rain. Several trapping sessions had to be cancelled or abandoned as a consequence of the likelihood of the voles being drowned by a rise in stream level during the night.

Validity of the Method

i.) Trapping

The method was found to be very successful in all respects. The voles were greatly attracted by the carrot bait even on first introduction and displayed great trappability even when young; the present writer agrees with Stoddart (1968) that the likelihood of an animal being trapped on the first occasion the traps are set exceeds 70% and indeed under low population densities in winter this figure approaches 100%. Under a program of frequent trappings therefore those voles which escaped capture on one occasion would almost certainly be caught on that following and its presence in the population was assumed for the former trapping session if it had previously appeared in the population a maximum of 20 days earlier. Only when trapping sessions are at a much longer interval will the possibility of untrapped voles develop as a source of error, the accurate timing of death or emigration of a vole during this period being open to doubt. This may be true of winter. when, necessarily, trapping sessions may be postponed by hard weather or the likelihood of flood, however it is at this season that the population density is low and the capture likelihood rises as argued above.

ii) Anaesthesia

No voles died from the effects of the anaesthetic when this was administered directly into the trap. However it must be emphasized with Stoddart (1968) that the animals should not become immobile as recovery is not certain when this state has been induced. Normally recovery is rapid, the animals apparently behaving normally within seconds of release.

iii.) Marking

Identification by ear tagging was found to be effective and tag losses were usually due to poor placing of the tag on the ear. Captive animals were never seen to worry or pull at the tags while grooming or show any signs of discomfort.

iv.) Newborn Mortality

There remains however a reservation about the practice of trapping during the breeding season when the nursing female may be removed from the litter for up to 24 hours with resultant loss of food and body heat to the young. This is a feature of trapping rarely mentioned by those who employ it in estimating population dynamics. The survival rate of the young might be directly affected by the trapping procedure itself. There may be a case for instituting a control reserve area, trapped only prior to and immediately following the breeding season as a method of comparison.

v.) Range Overlap

With an animal whose range is linear and which is not completely territorial there will be some overlap in the distribution of individuals and the implied error of this when considering a stretch of stream of only 380 m. was encountered at the outset. To reduce this source of error the trapping line was in fact developed to encompass the ranges of three adult male Arvicola in the spring of 1971, the total range of the three individuals concerned being ascertained by trapping beyond them. The study area was restricted to a stretch of stream marginally shorter than the estimated total range length of these three adult males. This resulted in: (1) the exclusion of other male voles from the trapping area, male voles displaying a distinct territorality, (2) a slight underestimate of the feeding and locomotory range of the three adult males studied. The second consequence noted above is a disadvantage but it should be remembered that the portion of the range left untrapped is essentially a region of overlap between the ranges of the voles studied and of voles outside the study population. This area of overlap therefore may be considered to represent only half the value as a food source, per unit area, of an uncontested part of the range, it being assumed that two neighbouring voles are in contention for this disputed area. It was considered that the slight disadvantage of reducing the estimation of the total range of the three adult voles below that which was observed to occur naturally was more than counterbalanced by the advantage of reducing the error caused by the inclusion of individuals, normally inhabiting ranges outside the study area, within the estimate of the study population.

4. The Model Population

Results

4.1 The Structure of the Population

4.1.1 Seasonal changes in Biomass

The trapping in 1971 commenced in early February and was discontinued in late November to avoid trap deaths due to cold, with consequent interference with the population structure. Trapping was recommenced in the late spring of 1972 on a similar stretch of stream some 400 m. downstream from that used formerly, not to obtain population data but to provide animals for respirometry experiments. However each animal caught was tagged and recorded in the usual way so that by October 1972 the age of each member of the population was known. By late October the population structure and total biomass approximated closely to that of October 1971; the population of this second section of stream was retrapped from late November 1972 until January 1973 to complete the twelve month sequence of the model population.

A continuous sequence of bodyweight data for each individual vole was extracted from the crude trapping data. The trapping data contained gaps in its record of particular individuals as each trapping session would only catch 70 - 90% of the population as explained previously. The weights of the voles at the time when they were absent from the catch data were estimated as an average of their bodyweight determined from the trapping sessions immediately prior to and following the unsuccessful trapping session. When trapping data was not available for a vole for more than 30 days however its residence within the population was assumed to be discontinuous, no such interpolation was carried out, and the vole was omitted from the intermediate data.

Study of the population resulted in the conclusion that the adult females were normally delivered of two litters annually. The first litters occuring approximately one month before the second litters. The bodyweight for each individual at 10 day intervals was estimated from the continuous data, and the totalled biomass of adults, of first and of second litter juveniles was found at each interval.

There was some evidence of young from a late litter being born outside the study area which may have represented a third litter. On one occasion a precocious pregnancy of a juvenile female from an early litter occurred and young born late in the summer may all result from such pregnancies.

There is no evidence to suggest that such late pregnancies occurred frequently in the population as a whole and neither a third litter nor a precocious pregnancy occurred in the study area of 1971.

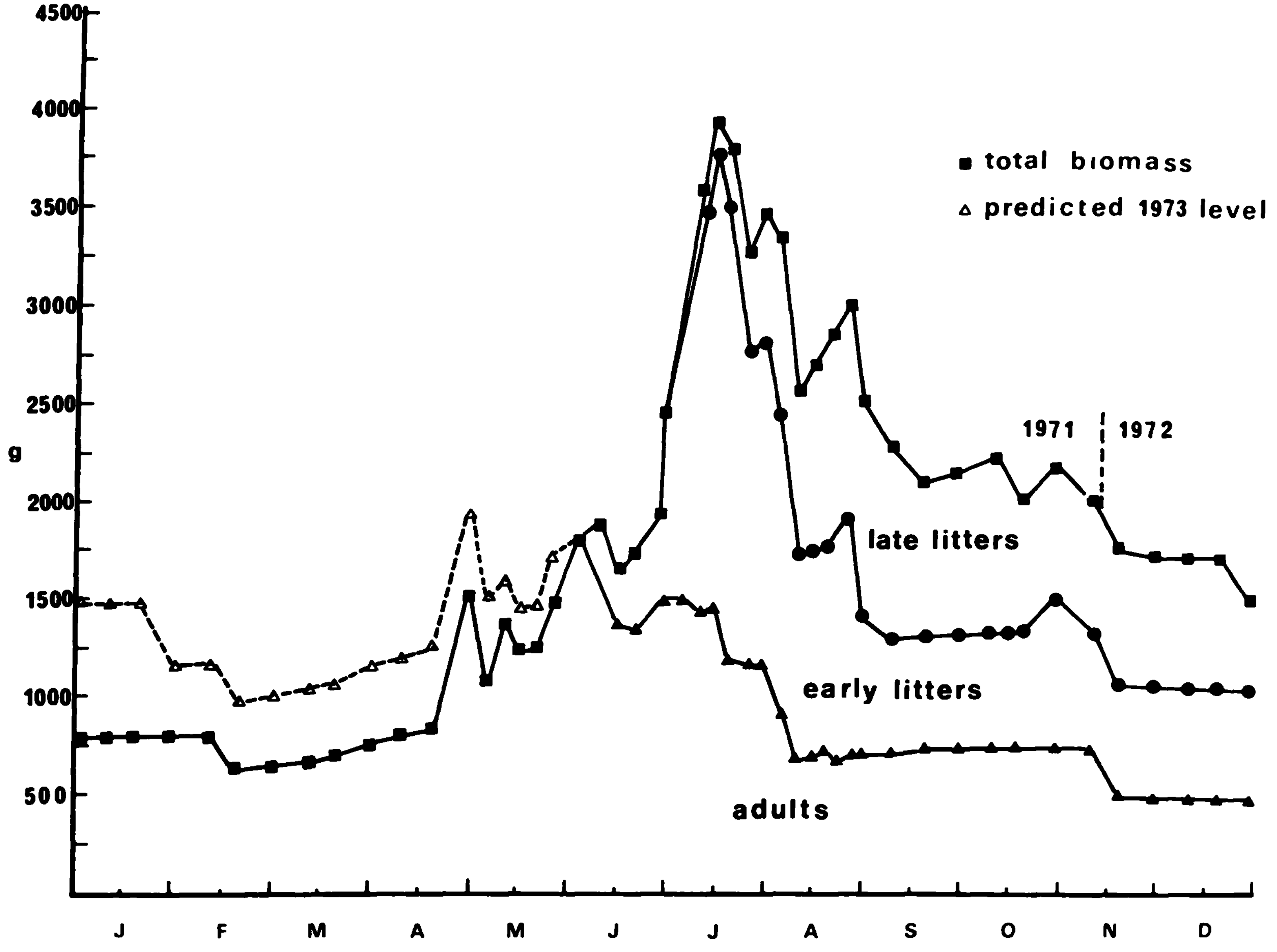
Figure 19 shows the estimate of population biomass, principally during 1971, with the points drawn at 10 day intervals. It will be observed from the figure that although the population biomass was fairly similar in November 1971 and 1972, the difference being a reduction of one adult female in 1972, the difference between late January 1973 and early February 1971 was considerable. The winter of 1972/3 was exceptionally mild and it is thought that mortality was unusually low during this period. However an immigration of voles from outside the study area in early May 1971 suggested that surplus voles were available elsewhere along the stream in 1971; after this immigration the number of resident adult voles in the study area increased from four to six. It may be that the population of voles in February - April 1971 was unusually low and that, as a result, this stretch of stream became attractive to transient individuals moving from more crowded and territorially competitive stretches such as that studied in 1972-3. The reason for the difference in biomass in late winter and early spring between 1971 and 1973 cannot be decided definitely however and consequently two distinct biomass figures for 1971 and 1973 have been estimated from January until after the spring dispersal. The two estimates have been assumed to become equal after the period of immigration in late May, when it is felt that the movement of transient individuals will bring a fairly even and stable vole density along the stream as a whole.

In January the population comprised the survivors of those individuals present at the end of the previous autumn. It consisted of a few old individuals which were experiencing their second winter and of a larger number of young voles

Figure 19

Changes in the biomass of the Model Population.

The figure shows the biomass of the model population (in grams) over the calendar year at 10 day period intervals. The total biomass is sub-divided into adult biomass, and the biomass of the First Litter juveniles and of the Second Litter juveniles. From February until early November the biomass is estimated from the trapping results of 1971 with the figures for January estimated by extrapolation. From early November onwards the biomass figures are calculated from trapping results obtained in 1972, this data continues until the end of January 1973. The January 1973 biomass total is shown by a broken line in the figure and is continued by extrapolation until early June when it is assumed to approximate to the 1971 figure.


■ total biomass
△ predicted 1973 level
1971
1972
late litters
early litters
adults
g
4500
4000
3500
3000
2500
2000
1500
1000
500
J
F
M
A
M
J
J
A
S
O
N
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from both the early and late litters of the previous summer. The mortality during the months of November - April particularly affected the old individuals described above which had disappeared from the population by late March. In March, April and May the young adults increased in weight and in the latter month there was an influx of voles from outside the study area. This influx was comprised principally of males but occasional females were also included. A male and a female became established in the existing population, the remainder of these transients left the study area within 14 days of their arrival.

By late May three pairs of voles were evenly distributed along the study area and by early and mid June each of the females was observed to be heavily pregnant. The first juvenile was trapped in mid-June, probably a result of an early pregnancy outside the study area, this vole was not trapped subsequently. By late June and early July the juveniles from the first litters began to make an appearance in the traps. These juveniles grew rapidly and by mid and late July they dominated the population biomass. During late July and early August the numbers of adult voles were depleted by the loss or emigration of two adult males and at this time the earlier of the second litters began to make an appearance. The juveniles from the first litters continued to dominate the population until mid-August when their numbers were depleted either through death or emigration. This period was also the time of the maximum number and rate of growth of the juveniles from the second litters but by early September these also showed a decline in numbers, but nevertheless by a small margin formed the greatest proportion of the biomass.

The population structure changed little from September until the end of the 1971 trapping season in November, occasional losses of individuals during the autumn being balanced in terms of biomass by the continued growth of the juveniles. In the 1972 season however the growth of what may now be considered to be young,adult voles had virtually ceased by December and little change was noted in the population structure throughout the winter. Those old adults which had survived into the late autumn also survived the winter of 1972-73, the only loss to the population during this period being one sub-adult, derived from the second litter cohort, in late December.

The population structure has been analysed further in two subsequent sections. The first of these concerns adult voles and the second the juveniles.

4.1.2 The Adult Component

The adult component of the population here comprised all individuals which entered the new year either as old or young adults. Since the old adults had died by late March the young adults formed the entire adult component from April onward. The life history of these voles is followed until December; no voles born during the summer of a given year are included in the adult component.

Figure 20 shows firstly the mean weight of adult voles with its 95% confidence limits taken from the actual trapping data of 1971, 1972 and 1973. In the calculation of the standard errors two corrections are made to compensate for the inaccuracy inherent in small sample sizes. Bessel's correction is applied to the variance, $\sigma^2 = S^2 \times \frac{n}{n-1}$ where n is the sample size, and a second correction is applied in determining the standard error from the sample standard deviation where $S.E. = \frac{\sigma}{\sqrt{n-1}}$ and not $\frac{\sigma}{\sqrt{n}}$. Objection might be made to the use of a parametric statistic in data where the members of a sample could be considered to be taken from two populations with possibly significantly different means, those of early and late litters, and in the early part of the year also from a third population, the old adult component. However in small samples the arithmetic mean is probably a better indication of the average than the median, and the use of a parametric statistic in circumstances where data of this kind is analysed is general practice.

From January until March the means for young adult and old adult components have also been given separately, no confidence limits are shown for the old adult means as only two individuals were present. It will be seen however that both in early February and also in mid-March the mean for the old adult occurred outside the 95% confidence limits of the mean for young adults.

The mean bodyweight of overwintering adults showed an increase in March, an increase which became more pronounced

Figure 20

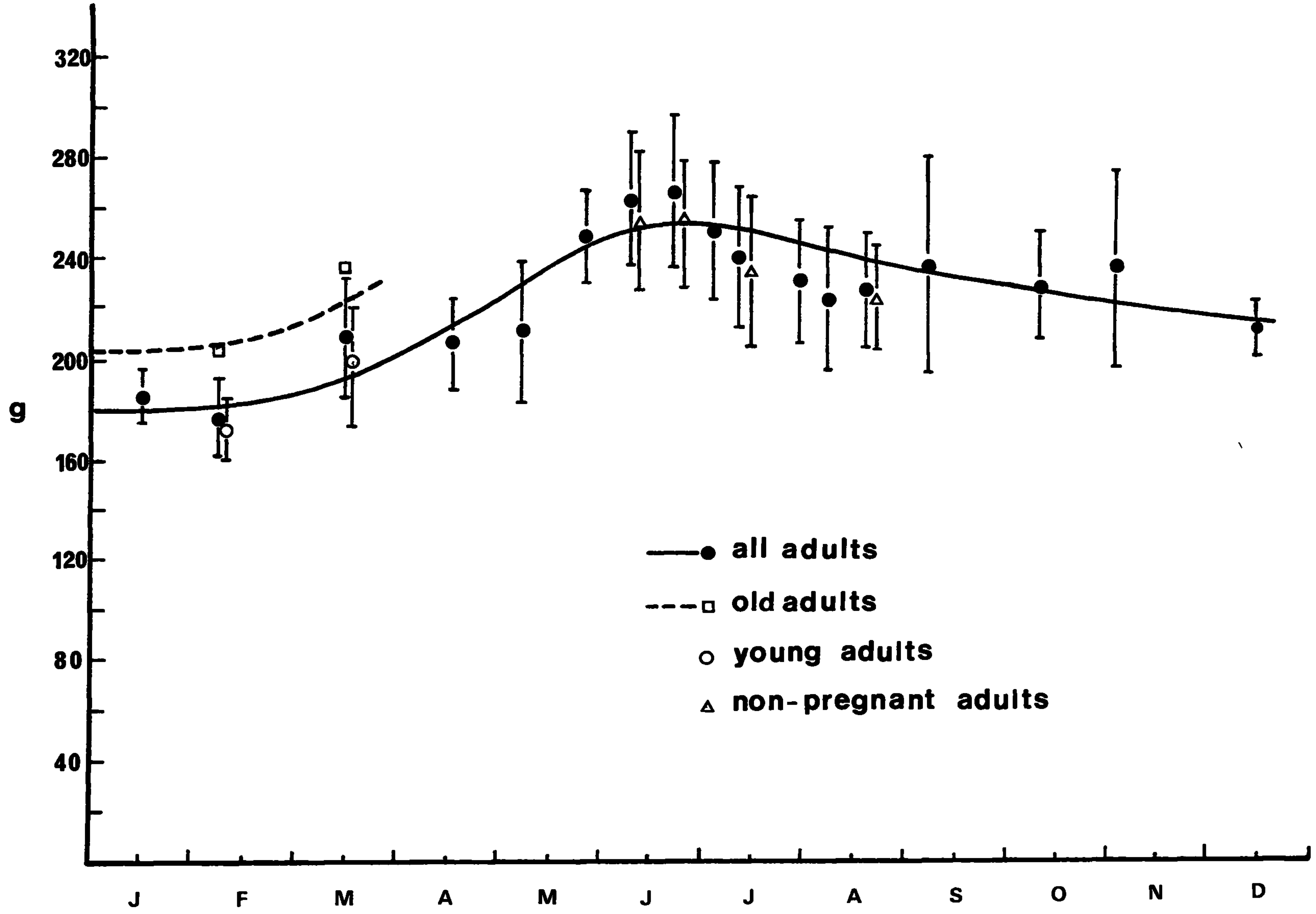
Changes in the mean bodyweight of adult voles with time of year.

The mean bodyweight of voles born in previous years is shown at intervals during the year. The means are shown together with their 95% confidence limits; the trend line has been drawn by eye.

old adults - adults which have survived two winters.

young adults - adults which have survived one winter.

non-pregnant adults - pregnant females are included in the estimation of the mean but at their bodyweight immediately prior to pregnancy.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non-pregnant adults

in late spring until a maximum bodyweight was reached in mid-June. During the summer months the means included pregnant females, in these months alternative means are also given for comparison where these pregnant females are included at their estimated non-pregnant bodyweights. The maximum bodyweight recorded was for a male of 320 g. in mid-July; 315 g. was the highest bodyweight recorded for a pregnant female and 285 g. for a non-pregnant female.

The means of adult bodyweight at intervals throughout the year have been compared by the parametric t test. Since the sample sizes were small there is a possibility that the variances of the two samples may be unequal thereby invalidating the test. Such a possibility was examined by the variance ratio distribution, F. (Campbell, 1967). The t test was carried out where the F test failed to give a significant result at the 5% level, the variances were then considered to be similar. Degrees of freedom were assumed to be $n_1 + n_2 - 2$.

Comparison

Date	Mean	S.F.	Date	Mean	S.E.	t	d.f.	P	result
Feb 6	176.5	6.3	Apr 16	205.75	9.1	2.643	20	<0.05	*
Apr 16	205.75	9.1	May 24	247.75	9.1	3.264	19	<0.01	**
May 24	247.75	9.1	Jun 10	263.5	13.5	0.967	20	>0.05	n.s.
Jun 10	263.5	13.5	Oct 11	229.3	9.6	2.064	15	>0.05	n.s.
May 24	247.75	9.1	Dec 15	211.3	4.7	3.559	13	<0.01	**
Feb 6	176.5	6.3	Dec 15	211.3	4.7	4.428	15	<0.001	***
* Feb 15	172.0	6.4	Dec 15	211.3	4.7	4.949	13	<0.001	***
* Mar 15	199.2	13.4	Dec 15	211.3	4.7	0.852	7	>0.05	n.s.

*In these two comparisons young adults only in February and March are tested against the means of old adults in the following December. No comparison is carried out between means when the 95% confidence limits of one mean encompass the second mean. In these cases the differences are assumed to be non-significant.

Seasonal Changes in the Adult Component

Overwintering voles entered the new year at a bodyweight of approximately 180 g. (185.7 ± 4.5). The two old adults surviving in February had a mean weight of 203 g., a figure outside the 95% confidence limits of the young adults at that time (Upper Limit 184.8 g). Both old adults had increased in weight by March to a mean of 236 g. which remained outside the 95% confidence limits of the young adults (Upper limit 226 g). The latter had also increased in weight but not significantly so. After the disappearance of the old adults by April the young adults (henceforward "adults") continued increasing bodyweight so that by mid-April they were significantly heavier than in early February, $t = 2.643$, $P = < 0.05$. Growth continued into late May when a mean weight of 247.75 g. was attained, significantly heavier than in mid-April, $t = 3.264$, $P = < 0.01$.

The females became heavily pregnant from late May onwards but even so although an adult maximum of 265.7 was reached in late June, this was not significantly heavier than the level of late May, the non-pregnant mean in late June being 245 g. A slight decline in mean sample bodyweight was apparent in late summer, autumn and early winter but the mid-October mean of 229.3 g. was not significantly lighter than either mid-June, $t = 2.064$, $P = > 0.05$ or late

June, $t = 2.155$, d.f. = 12, $P = > 0.05$. By mid-December many of the adults had disappeared from the population, those that remained had a mean bodyweight of 211.3 g., significantly lower than the mean for late May $t = 3.559$, $P = < 0.01$, due both to the selective loss of one or two of the heaviest individuals and to the slight weight reduction of those remaining in the population. It will be seen that the two animals which survived a second winter remained fairly heavy, a mean of 203 g. being recorded in February as noted above.

The mean bodyweight of adults in December 1972 was significantly greater than it had been in February 1971, $t = 4.949$, $P = < 0.001$, but not significantly higher than it had been in March 1971, $t = 0.852$, $P = > 0.05$.

4.1.3 The Juvenile Component.

Between June 5 - 20 each of the three adult females of the model population were found to be in an advanced state of pregnancy. Approximately one month later, between July 9 - 21, this was repeated. The times of the two pregnancies were more or less synchronous in the various females and in consequence the young from these pregnancies have been separated into two cohorts, the first and second litter juveniles. However the estimated range in date of birth of approximately two weeks, in the first litters in particular, will create a considerable variability between the time of first capture of the young from each litter and in their relative bodyweight for some time afterwards.

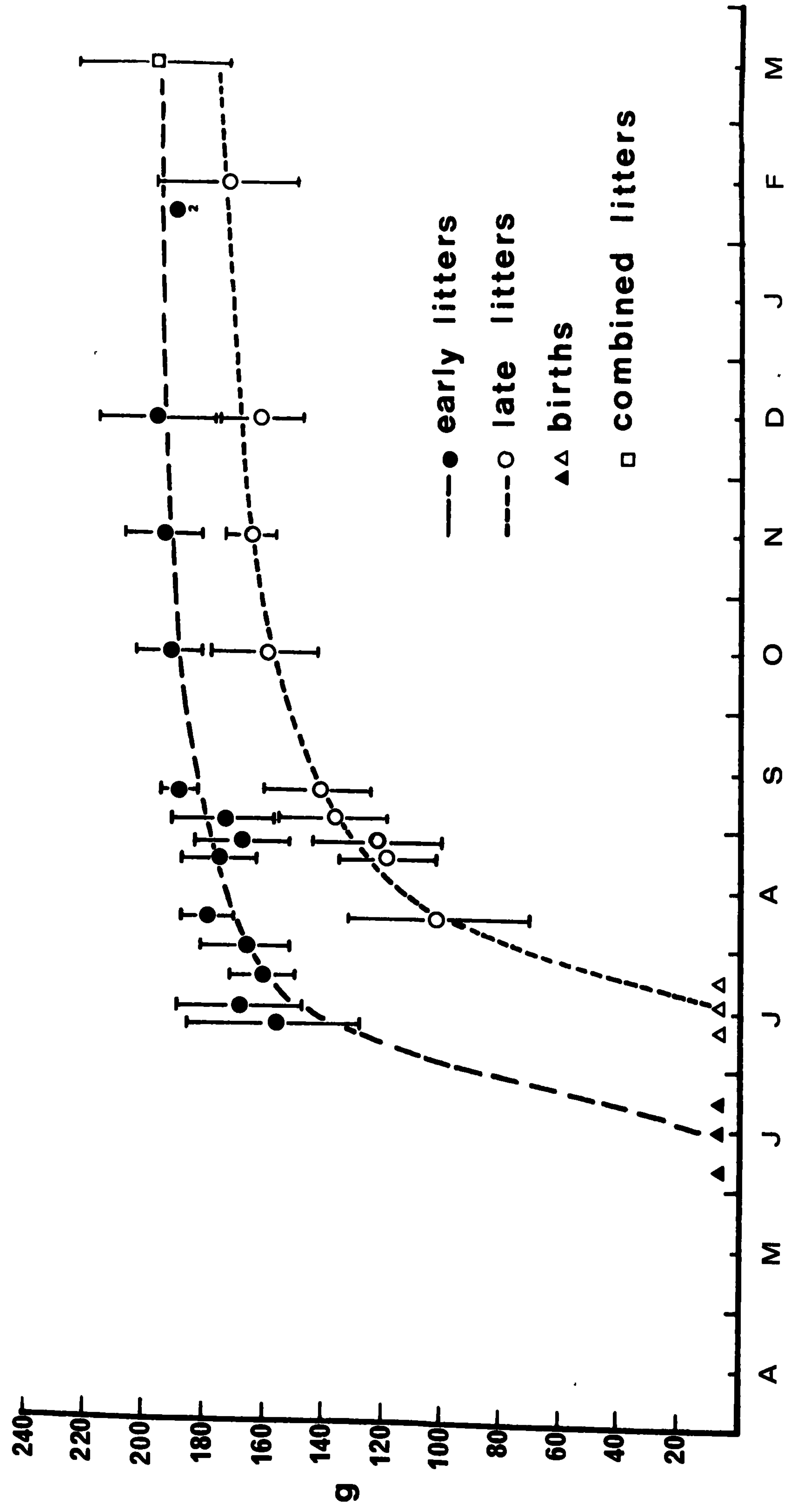
Figure 21 gives the data for the mean weights of the juveniles of the First and Second litters. First litter juveniles began to make an appearance in the trapping catches from early July. On no occasion was a member of this cohort caught weighing less than 120 g. Stoddart (1968) reports that the young of the first litters were of this order of weight on first capture. In the present study the weight at first capture of first litter juveniles was greater than the weight at first capture of the second litter juveniles, but the qualification must be added that the trapping session which first recorded the first litter juveniles was delayed by several days as a consequence of a rise in stream level after heavy rain, a delay that would exacerbate any differences in bodyweight between the vole litters at first capture.

There is some doubt however that the First Litter juveniles did in fact originate from the pregnancies which were observed to occur between 5 - 20 June since the growth rate of 140 g. in 30 days, indicated in Figure 21, is far in excess of the figure of 60 - 70 g. for 30 days given by Stoddart (1968, 1971) for A. t. reta in the laboratory, even allowing for the larger average size of voles in the present study (plus 25 - 45% depending on season). If the second litter juveniles corresponded to the pregnancies of 9 - 21 July a reduced but still considerable rate of growth of 110 g. in 30 days is indicated. While the writer has observed that juvenile voles in the laboratory do grow far less rapidly than expected from growth rates measured in the field,

Figure 21

Changes in the mean bodyweight of Juvenile voles.

The figure shows the mean bodyweight (in grams) of First and Second Litter voles from the age of approximately 30 days until the February of the following year. One further mean is shown, in March, here the individual bodyweights of the two litters have been combined. Except in one instance where the mean was of two individuals only (signified by '2') the means are shown with their 95% confidence limits. The trend lines have been drawn by eye.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indicating that the keeping of voles in the laboratory results in retarded growth (indeed, adult voles tend to lose weight in the laboratory), these rates of growth do appear unusually high. An alternative explanation would be that the second litter juveniles were the result of the first pregnancies, and that the pregnancies of the First Litter juveniles went unrecorded. If this were the case then the young of the second observed pregnancies either went unrecorded until they reached maturity or were annihilated by flood or other catastrophe before they attained trap-capture size. Since pregnancy is normally accompanied by a sharp increase in weight it is considered unlikely, though possible, that pregnancies earlier than those of June 5 - 20 escaped notice. It is considered highly improbable that all or part of an entire cohort should achieve maturity without becoming trapped at some time. Destruction of a cohort by flood at an early age is possible but no such flood was recorded in late July or early August 1971. The set of circumstances necessary for the Second Litter juveniles to be derived from the pregnancies of June 5 - 20 do not seem probable and in the absence of further information the high growth rates indicated by Figure 21 were accepted.

The Second Litter juveniles exhibited consistently lower first capture weights than the First Litter juveniles. Weights at first capture of under 80 g. were frequent, under 60 g. occasional, and one weanling of 38 g. was caught by hand as it was swimming along the stream.

Figure 21 shows that the mean weights of 1st and 2nd litter juveniles were significantly different at least until January. After this time low numbers of First Litter juveniles rendered a comparison impossible. However since the 95% confidence limits of the Second Litter juveniles encompass the mean (of two voles) of First Litter juveniles in mid-February the difference in means at this time would not have been significant.

Little growth was observed in either juvenile group between October and the end of the winter.

The parametric t test has been used to separate the means of First and Second Litter juveniles during the summer and autumn. Corrections were made with respect to small sample size both to the variance and in the calculation of the standard error. The variance ratio distribution was tested for significance and the t test was employed when the F.test was non-significant at the 5% level. Degrees of freedom are calculated as $n_1 + n_2 - 2$.

Comparison

Date	First Litters		Second Litters					
	Mean	S.E.	Mean	S.E.	t	d.f.	P	result
Aug 20	176.0	6.2	119.6	8.2	5.486	9	<0.001	***
Sep 6	181.3	5.6	140.2	5.7	5.144	28	<0.001	***
Oct 15	193.0	4.8	160.0	7.7	3.637	15	<0.01	**
Nov 15	195.6	4.7	166.0	3.7	4.949	9	<0.001	***
Dec 15	198.0	10.6	162.7	8.2	2.634	5	<0.05	*

The results show that at least until the end of December the First Litter juveniles were heavier than their Second Litter counterparts, the differences being significant at the 5% level or higher. As has been suggested earlier the differences in mean bodyweight appear to have ceased to be significant by mid-February.

When comparing the bodyweight of the First and Second Litters at the same age the First Litters were presumed to be 30 days older than the Second Litters and the parametric t test used to compare the groups approximately one month apart.

Comparison

Date	First Litters		Date	Second Litters		t	d.f.	P	result
	Mean	S.E.		Mean					
Jul 20	160.7	5.2	Aug 20	119.6	8.2	4.233	14	<0.001	***
Aug 6	180.1	3.4	Sep 10	142.3	8.9	3.968	12	<0.01	**
Oct 15	193.0	4.8	Nov 15	166.0	3.7	4.455	10	<0.01	**
Nov 15	195.6	4.7	Dec 15	162.7	8.2	3.481	9	<0.01	**

The results demonstrate that for the first five months of age at least the First Litter juveniles were significantly heavier than the Second Litter juveniles, the results are significant at the 1% level or higher. Since, as has been noted earlier, the difference between the juvenile groups failed to achieve significance in February then significance between the groups at equivalent ages will be lost between 5 and 7 months of age. Experience gained from monitoring the growth of individual animals suggested that the difference in weight between the litter groups disappeared during the increase in bodyweight in the spring. Some of the largest summer individuals were derived from the Second Litter group but had weighed less than 150 g. the previous

February. Such individuals added up to 100 g. to their bodyweight between March and the end of May.

The First Litter juveniles may be separated from the adult component by the t test.

Comparison

Date	Adults		First Litters					
	Mean	S.E.	Mean	S.E.	t	d.f.	P	result
Sep 6	236.3	21.9	181.3	5.6	2.433	8	<0.05	*
Oct 2	229.3	10.4	199.0	7.5	2.363	8	<0.05	*
Nov 15	237.3	18.8	195.6	4.7	2.152	8	>0.05	n.s.
Dec 15	211.3	4.7	198.0	10.6	1.147	5	>0.05	n.s.

The differences in bodyweight between adults and First Litter juveniles were significant in early September and early October at the 5% level, but had ceased to be significant by mid-November, although the adult mean at 237.3 was still greater than that of the juveniles at 195.6 g. By mid-December the means were not significantly different and were closer, the adults at 211.3 g. and the juveniles at 198 g.

The adults were significantly heavier than the Second Litter juveniles at least until mid-December where the respective means were 211.3 ± 4.7 (adults) and 162.7 ± 8.2 (juveniles), $t = 5.142$, d.f. 4, $P = < 0.01$. The combined sample size of 6 was however very small.

Summary to Section 4.1.3

The First Litter juveniles born between 5 and 20 June grew very rapidly, reaching a mean weight of 140 g. after the first 30 days, 170 g. after 60 days and 184 g. after 90 days. Their growth rate then slowed down and at five months of age their mean bodyweight was approximately 195 g. and stayed at this level throughout the winter.

The Second Litter juveniles born from 9 - 21 July grew less rapidly, attaining 110 g. at 30 days, 145 g. at 60 days and 160 g. at 90 days. At five months of age their mean bodyweight was approximately 170 g.

The Second Litter juveniles were not only significantly lighter than the First Litter juveniles at least until the following January, but were also significantly lighter than their First Litter counterparts at a given age for the first five months of their life. By mid-February, however, when the Second Litter juveniles were 7 months old, the difference in weight was no longer significant.

First Litter juveniles were significantly lighter than adult voles at least until the end of October and Second Litter juveniles were significantly lighter than the adults at least until the end of December.

4.1.4 Sex Differences in Bodyweight

A comparison of the bodyweights in February of male and female young adults gave values of $t = 1.292$, d.f. $= 12$, $P => 0.05$, the mean weight of the nine males being 183.3 ± 7.4 g. and that of the five females being 164.2 ± 12.8. The difference between the two means is not significant.

In late July the mean bodyweight of seven First Litter males was 162.0 ± 8.0 g. and of five First Litter females 158.5 ± 8.0g. The 95% limits of each mean encompass the other mean. The difference is not significant.

Although the sample sizes were small in both cases it appears that in non-reproducing animals there is insufficient evidence to conclude a significant difference between the mean bodyweight of males and females although that for the males was the larger. The figures of the First Litter juveniles are suspect as they represent individuals born over a period of two weeks and considerable individual weight variability may not be equally represented in both male and female groups.

4.2 Tissue Production of the Model Population

Tissue production has been calculated in terms of biomass at "10 day" period intervals, periods which actually varied in duration from 8 - 11 days. Deviation from the 10 day norm occurred for the period from the 21st to the last day of the month, where the month contained 28 or 31 days. The error in production estimate caused by this deviation is very small. Production was calculated from the continuous estimate of the weight of individual voles referred to in Section 4.1 by deducting from each vole's maximum biomass during period t2 the maximum biomass observed during the previous periods. An exception to this procedure was made in the case of individual females during their second pregnancy where instead the maximum biomass of the previous post-natal period was deducted from the maximum biomass during period t2 of the second pregnancy. An example of these calculations is given below using hypothetical data.

Example

Period	t1	t2	t3	t4	t5	t6	t7
Maximum Weight g. (W)	190	200	195	230	200	230	200
Production g.		10	0	30	0	30	0

In the example an overwintering female increased in weight from a maximum during t1 of 190 g. to a maximum in t2 of 200 g; Production t2 = Wt2 - Wt1 = 10 g. The maximum of the next 10 day period is 195 g. the female has lost weight slightly; Production t3 = Wt3 - Wt2 = -5 g. This negative production is ignored being presumed to be due to fluctuations of ingested material in the vole's gut and not to a loss of body tissue; Production t3 = 0 g. The production so far has been in spring growth, at the end of t4 the female has become heavily pregnant reaching a maximum weight of 230 g; Production t4 = Wt4 - Wt2 = 30 g. Wt2 and not Wt3 is deducted as the former is the previous maximum. The female gives birth during t5 and Production t5 = Wt5-Wt4 = - 30g Such a negative production has not in fact taken place as the newborn young remain within the nest; Production t5 = 0 g. The female becomes heavily pregnant again in t6 where production t6 = Wt6-Wt5 = 30 g. The post natal maximum Wt5 is used here and not the previous maximum Wt4 as the production is from a second pregnancy. Production t7 = Wt6-Wt7 = -30 = 0g.

For adult animals errors due to including ingested material as production are not great as they are offset by the fact that the maximum at Wtl also includes a proportion of ingested material. If this proportion is a constant of vole bodyweight then the ingested material of a small vole may be substantially less than a large one. The error will be at its greatest in the estimation of production of juveniles where the ingested material at tl is virtually zero and the proportion of the bodyweight biomass at its growth maximum that is in fact ingested food will be counted as tissue production in its entirety. No correction is made with regard to this error during the "10 day" estimate but a correction has been applied to the annual total. This correction assumes that ingested material will be a constant of 10% of bodyweight when the vole is weighed, a figure suggested by the weight loss observed when newly captured voles were kept without food for twenty hours. In adults the correction is applied in the form of $\left(\frac{Wt2}{10} - \frac{Wt1}{10}\right) x\ 1.526$ which is deducted from the calculated annual Calorie production estimate where Wtl and Wt2 are the minimum and maximum 10 day period maxima, and 1.526 is a Calorie conversion constant. In juveniles the correction applied is in the form of $\frac{Wt2}{10}$ x 1.455 which is deducted from the calculated estimate of annual Calorie production, where Wt2 is the maximum observed biomass and 1.455 a Calorie conversion constant.

No negative production is assigned to old adults approaching their second winter. The decrease in bodyweight during the second autumn and winter referred to in Section 4.1 is as much a reflection of the death of large individuals as of an actual reduction in bodyweight. If a reduction in bodyweight were to occur the problem would arise as to whether previous growth could be regarded as production or as a metabolizable food reserve for the future. A reduction in the water content of the body tissues in winter relative to the summer has been observed to take place in shrews by Górecki (1965), in Apodemus flavicollis by Sawicka-Kapusta (1968) and in Microtus agrestis by Evans (1973). The last author also found a reduction in fat content in Microtus in late winter but found that fat levels are very low in non-reproducing animals at all times of the year. It is assumed here that the maximum tissue production should be taken as the production estimate and any reduction in biomass during the winter was regarded as a reduction in water content.

No figure for the production of milk has been included in the present production data. The cost of lactation is included in the data for respiration costs. Although the production of milk could be regarded as true production no figures are available from which it could be estimated.

Newborn young have been assumed to weigh 7 g. This represents a figure rather higher than that of 4.5 - 5.08 g. observed by Stoddart (1968) for A. t. reta but less than the maximum for embryos of 8.45 g. for A. t. amphibius reported by Perry (1943). Not only are adult A. t. reta some 25%

smaller in terms of bodyweight than A. t. amphibius of similar age but young born in the laboratory shortly after capture may have been born somewhat prematurely under the laboratory conditions of rather greater stress than would occur naturally.

Trapping estimates gave the mean number of young weaned per litter in the First Litter group as 5.3 and in the Second Litter group as 4.3. These figures are very similar to the estimates of litter size of 4.05 - 4.4 for A. t. scherman given by Meylan and Morel (1970), and of 5.5 for A. t. reta by Stoddart (1968) and similar to the mean number of embryos per litter of 5.7 for A. t. amphibius found by Perry (1943). No correction is made for pre-weaning mortality. Such losses, if they occurred, would constitute a very small component of the total production estimate. The writer does not consider that such a correction would be justified in the absence of relevant data.

There remain the important possibilities however both that voles were recorded as being part of the resident population when in fact they were derived from outside the study area and also that some individuals may never have been caught at all. As described in the discussion of method validity in Section 4 the total ranges of the three adult males were discovered by trapping and the study area reduced slightly in an attempt to prevent the capture of males whose territories might partially overlap those of the males resident in the study area. This procedure was successful with regard to the adults, no "foreign" voles being caught except during the spring immigration, and could be expected to be successful with the juveniles, the range of which would almost certainly be more limited than that of the adults. However as the juveniles grow so there might be a tendency for them to range further from the nest, a tendency resulting both from a growth in territorality on their part and from competition from their parents and siblings. Any attempt at emigration resulting from such pressures from within the study area could well however be counterbalanced by similar pressures on the juveniles of neighbouring areas so that although increased activity and aggression might be displayed by the adult and juvenile population of the study area little permanent emigration could occur without a reciprocal immigration of juveniles from outside the study area. The trapping results suggest that the population was in fact remarkably static, the same voles being retrapped time and time again. It cannot however be proved that some range overlapping did not occur so frequently that it was assumed that an individual actually resident outside the study area was a member of the study area population. It cannot be proved either that some individuals native to the study area were never caught however high the trapping success of the remainder. If both errors do occur then they will tend to counterbalance each other.

In view of the estimation of the adult biomass in spring described in Section 4.1.1 from, firstly, the numbers of voles present in February 1971 and, secondly, those in

January 1973, two estimates of tissue production are given for each 10 day period from January until June. Similarly two estimates of total annual production are given.

The conversion of biomass into its calorific equivalent was achieved by the use of estimates of the calorific value of freshweight biomass of small rodents of different ages made by Górecki (1965, 1967), Kaczmarski (1966) and Chew and Chew (1970). The conversion figures from these sources used in this study are given below together with a description of the period in the vole's life when each is applied.

	kcals/g Freshweight	
Unborn young, placental membranes , voles <20 g.	1.03	(Chew and Chew, 1970)
Weanling voles 20 - 80 g.	1.43	(Kaczmarski, 1966)
Young voles 80 g. until February	1.455	(Górecki, 1965, 1967)
Adult voles, Spring and Summer	1.526	(Górecki, 1965, 1967)

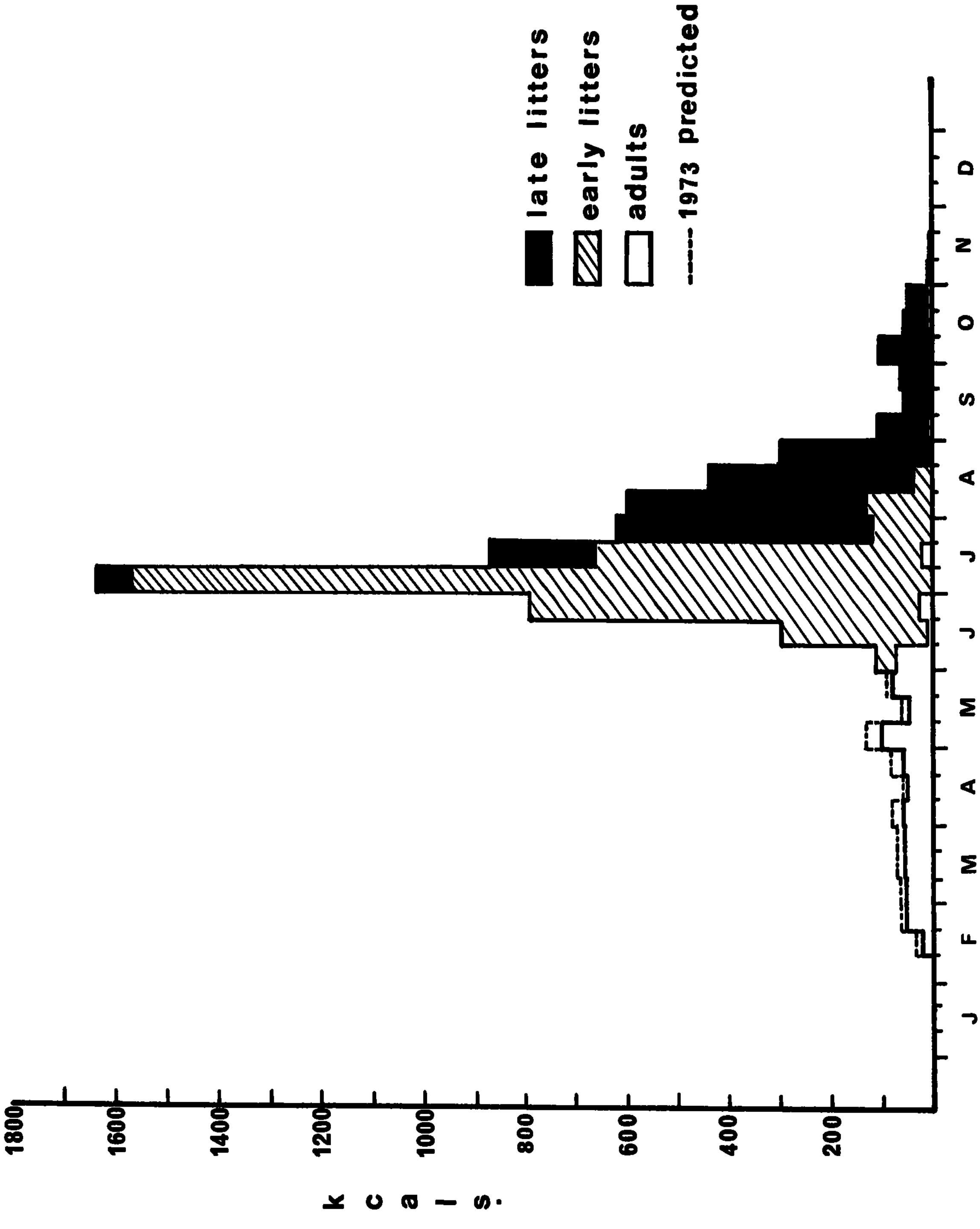
Figure 22 shows the tissue production of the population for 10 day periods for the entire year.

Production began in mid and late February through the adult component increasing in bodyweight, a rate of increase that reached a maximum of 102 kcals/10 day period in early May. Evans (1973) has found that the spring increase in bodyweight of Microtus agrestis is due largely to muscular growth as the percentage of protein per gram of lean bodyweight increased markedly at this time of year. Other

Figure 22

Changes in the tissue production of the model population with time of year.

The figure shows the tissue production of the model population in kcals for consecutive periods of approximately 10 days. The production is sub-divided into the components of adult, First Litter juvenile and Second Litter juvenile production. The higher estimates for adult production predicted for 1973 have been shown as the broken line.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increases will be in the development and growth of the reproductive organs and in the increase in the percentage of water in the tissues; there may also be some skeletal growth but there is little or no deposition of fat in Microtus in the spring except in pregnant females (Evans, 1973). Adult tissue production fell in late May as the spring growth passed its maximum, and early in June it was replaced by the production of embryos by the females. This was reduced after the young were born in Mid-June but again became important in the production of the second litter embryos in late June until mid-July. After late July no further production was observed from the adult component.

The first of the litters was born in early June and the remainder of the First Litter group were added within a fortnight. The growth of First Litter young exceeded the adult production by mid June by which time it had risen to 287 kcals/period. By early July the production of the First Litter juveniles exceeded the highest rate of adult production by a factor of ten and dominated the population production completely. This reached its maximum for the year of 1,640 kcals/10 day period in early July. During this 10 day period the earliest of the Second litters was born and by mid-July the Second Litter young accounted for nearly a quarter of the total population production. The latter had now fallen to 874 kcals/period.

By late July the production of the First Litter juveniles was much reduced. By this time they were 5 - 7 weeks old. Many had disappeared from the population entirely, and the growth rate of the remainder had slowed considerably. The Second Litter juveniles now dominated the population production and continued to do so until the end of the autumn. The Second Litter juveniles however were fewer in number than those of the First litters and, as described in Section 4.1, their rate of growth was markedly slower. For these reasons their maximum production never equalled that of the First litters in early July and was extended over a longer period. Population production fell in mid- and late-September to 60-65 kcals/period as the First litter production ceased and the Second litter production declined through falling numbers and reduced rates of growth. Production continued at a low level throughout October being by then almost entirely composed of Second Litter production. This virtually ceased in November and no production was recorded from December until early February.

The production of newborn and suckling young and of juveniles for 2 - 3 weeks after weaning relative to that of adults and larger juveniles is lower if expressed in calorific terms than as fresh weight as a result of the higher water and relatively lower fat content of the former (Górecki, 1967). As the juveniles increase in size the relative proportions of bone, protein, fat and water in their tissues gradually approach those of the adults.

The annual population production without a correction for ingested material was estimated to have been 6,780 (actual figure was 6,781.5) kcals/380 metres of stream in 1971 and 6,950 (6947.2) kcals in 1973, the latter figure being based on the predicted population for that year. This represents a production of 8.92 and 9.14 kcals/m^2. With a correction for ingested material applied the annual production was estimated at 6,030 (6,030.5) and 6,180 (6,177.2) kcals/380 m. of stream for 1971 and predicted 1973 populations respectively. This represents a production of 7.93 and 8.13 kcals/m^2. The reduction is in fact slightly greater than 10% as the error for ingested material was estimated at the "old" juvenile calorific value of 1.455 kcals/g fresh weight while a large proportion of the total juvenile production was calculated at the lower values for "newborn" and "weanling" voles, 1.03 and 1.43 kcals/g fresh weight respectively. The difference however is small amounting to less than 1.1% of the uncorrected estimate.

The contribution of adult and juvenile production to the total annual production for the observed and predicted estimates was as follows:

	Observed 1971		Predicted 1973	
	kcals	%	kcals	%
Adults	777.4	11.46	943.1	13.58
1st Litters	3,609.1	53.22	3,609.1	51.95
2nd Litters	2,395.0	35.32	2,395.0	34.47

It will be seen that not only did the First Litter juveniles represent the highest single component of the annual production but also that their contribution was greater in total than those of the adults and Second Litters combined. The Second Litter juveniles given their slightly lower numbers and slower growth rate, which for the majority results in a smaller size at death, contributed rather over a third of the total, while the adults contributed 10-15%.

The adult production can be regarded as having two components, that resulting from individual growth and that from the growth of embryos and placental membrances. The two components have been separated below.

	Individual Production		Embryo Production	
	kcals	%	kcals	%
Observed 1971	578.6	74.4	198.8	25.6
Predicted 1973	744.3	78.9	198.8	21.1

The predicted estimate for 1973 is the more accurate as the observed 1971 value included the embryo production of one female without recording her previous individual production. It may be concluded from these figures that the adult production resulting from individual growth was four times greater than the production of embryos and placentae.

Summary to Section 4.2

Adult production commenced in mid-February with the resumption of the growth of individuals and reached a maximum in early May. By late May individual growth had almost ceased and adult production was limited to the first pregnancies of late May to mid-June and to the Second pregnancies of late June to mid-July. Adult production ceased after mid-July.

First Litter production commenced in early June, rose to a maximum in early July when the total production was also at a maximum, and dominated the total production from mid-June until mid-July.

Second Litter production commenced in early July, rose to a maximum in late July and early August and continued at a reduced level until the end of October. All production had ceased by early December.

The adult component represented 10 - 15% of the annual total, the First Litter component 50 - 55% and the Second Litter component 32 - 37%.

The annual production total was estimated at between 6,030 (6,030.5) and 6,180 (6,177.2) kcals per 380 m. of stream or 7.93 - 8.13 kcals/m^2.

It is calculated that 78.9% of the adult production resulted from individual growth and 21.1% from the growth of embryos and placental membranes.

Discussion on Section 4.2.

The conversion figures used in the expression of freshweight biomass production as its heat equivalent are derived from the published work of several authors for a variety of small rodents other than Arvicola. Inter specific differences in the values are however small (Górecki, 1967) variation depending more on age and season. The components of water content, fat and protein varying more widely in their relative proportions with age and season than they do with species. In the present study the most relevant data has been used. Where possible the data for microtines and for Microtus in particular are favoured. However it will be realised that if the calorific value of a large juvenile is 1.455 kcals/g while that for a small juvenile is 1.43 kcals/g then the production in biomass necessary to change a small juvenile into a large one will have to be greater in calorific value than 1.455 kcals/g to effect the overall calorific value of 1.455 kcals/g of a large juvenile. An example to illustrate this is calculated below for the production of a vole from conception to its maximum first year biomass of 180g.

For the first 20 g., the vole production was estimated at 1.03 kcals/g = 20.6 kcals; for the next 60 g. (20 - 80 g. bodyweight) its production was estimated at 1.43 kcals/g = 85.8 kcals; for the last 100 g. (80 - 180 g. bodyweight) its production was estimated at 1.455 kcals/g = 145.5 kcals. The total in the calculation, 20.6 + 85.8 + 145.5 = 251.9 kcals. However at 180 g. the actual calorific value of the vole is 180 x 1.455 = 261.9 kcals, an increase of 4% on the previous estimate.

A correction along these lines is not possible however without accurate data on the changes in protein, fat, skeleton and water components of the growing voles, and are not appropriate when it is remembered that the conversion figures are in themselves only estimates. Nevertheless it could be considered that the final production estimates are 3 - 4% lower than their real value.

Apart from lactation, the cost of which is estimated in Section 5.3.2, no data is included for other components of secondary production such as hair growth during the seasonal moults and the scent secretions of the flank organ. The significance of this uncounted production is not known.

The above limitations in the computation of the production are unlikely to be as important an influence in miscalculation as errors in the determining of the vole population where each juvenile represents 3 - 4% of the total production. It is not possible to estimate confidence limits for the estimate of annual production. The real value of production is unlikely to lie within less than ± 10% of the calculated value and may lie only within ±30%.

The conversion figure from kcals/380 m. of stream to kcals/m^2 is here taken to be 1/760 on the basis of the assumption of Ryder (1962) that the lateral range from the water's edge is 1 metre on both banks. However if the stream itself is included in the calculation of vole range this conversion factor should be 1/1900 given that the stream is 3 m. wide. The first figure represents production/m^2 of feeding range and the second production/m^2 of locomotory range. The second may be derived from the first by multiplying it by 0.4.

4.3 Population Density

The estimated vole population along the 380 m. stretch of stream varied from a minimum of four animals in the spring of 1971 to a maximum of 22 in mid-July 1971. These figures refer to the trappable population which is confined to those animals foraging outside the burrow system and which are feeding themselves. With suckling young included, the total population in mid-July would have been 30. These figures correspond to vole densities of 1.1 - 5.8 voles per 100 m. of stream for the trappable population and 1.1 - 7.9 for the total population, inclusive of suckling young.

In terms of area these densities are equivalent to 55 - 290 per hectare of feeding range for trappable animals and 55 - 395/ha for the total population. The equivalent figures for locomotory range are 22 - 116 per hectare for trappable animals and 22 - 158/ha for the total population.

4.4 Population Structure Summary

The composition of the population for each 20 day period as described in Section 3 can be estimated, including such details as the average bodyweight of each vole during that period, the precise number of days when the vole was present in the population during that period, and the number of days during each period that a female was lactating. Such data cannot be summarised accurately, but the number of voles in the adult, lactating adult, First Litter juvenile and Second Litter juvenile components are given below for each of the 20 day periods. These data do not include the numbers of suckling young which, for the purposes of assessing energy demand, have been regarded as a component of the lactating female.

They do however include the occasional transient voles which, although not considered to be part of the population in terms of production, which has been accumulated elsewhere, nevertheless feed within the study area while they reside within it. Consequently these transients add to the population demand in energy assimilated for respiration and have been included in the estimation of that demand in Section 5.5. In Table 10 each asterisk refers to one female lactating during the 20 day period specified.

Table 10. Voles present in the Population for each 20 day Period.

	Adults		Juveniles	
Date	Observed 1971	Predicted 1973	First Litters	Second Litters
11-31 Jan	5	7		
1 - 20 Feb	5	7		
21 Feb-10 Mar	4	7		
11 Mar-31 Mar	4	7		
1-20 Apr	4	7		
21 Apr-10 May	8	10		
11-31 May	5	6		
1-20 Jun	7 **			
21 Jun-10 Jul	6 ***		17	
11-31 Jul	6 ***		16	6
1-20 Aug	5 **		9	13
21 Aug-10 Sep	3		6	8
11-30 Sep	3		3	6
1-20 Oct	3		3	6
21 Oct-10 Nov	3		4	4
11 Nov-30 Nov	2		3	4
1-20 Dec	2		3	4
21 Dec-10 Jan	7 (Total no. of voles)			

Discussion on Section 4

Lund (1970) found that winter mortality of Arvicola was higher in severe winters than during mild ones. The unusual mildness of the winter of 1972-73 may have been a cause of the high vole survival noted. The lower number of adults caught during February 1971 may have resulted from the lower temperatures during the winter of 1970-71 which, while not severe, was substantially colder than 1972-73. Lund (1970) also found that male voles were twice as likely as females to change the location of their burrow systems during the year, and that the change of territory occurred much more frequently in the early breeding season, the months of April and May, than at any other time of the year. This is in agreement with the observations of the present study that male immigration was observed to occur in late April and early May.

There have been previous records of Arvicola, along with other microtines, increasing in bodyweight at the beginning of the breeding season (Southern, 1964, Stoddart, 1968). This increase was prominent in the present study where the early February mean of 176.5 ± 6.3 g. had risen to 247.75 ± 9.1 g. by late May, an increase of some 40%.

Perry (1943) found the first pregnancies of A. t. amphibius to occur in April and that the greatest proportion of pregnancies took place in May. Stoddart (1968) found that the respective dates for A. t. reta were a few weeks later, the maximum frequency of pregnancies occurring in June. None of the females in the present study became pregnant during April, but all had become pregnant by late May. Given the small number of females under study this result could accord with the data of either of the two previous workers.

The mean litter size is given as 3.8 for A. t. terrestris by van Wijngaarden (1954), as 5.5 for A. t. reta by Stoddart (1968, 1971) and as 4.05 - 4.4 by Meylan and Morel (1970) for A. t. scherman. No comparable figures are available in the present study. The estimates of trapped and therefore weaned animals result in a mean of 5.3 for First Litters and 4.3 for Second Litters. Six young born to a female in an activity enclosure were observed to survive weaning successfully, these young resulted from a first pregnancy of the season.

The mean number of litters per female is given as 4.4 by van Wijngaarden (1954) for A. t. terrestris and 2.2 by Stoddart (1968) for A. t. reta. In the present study the mean number of litters was estimated as 2.0 in the observed population but the possibility of a third pregnancy is not ruled out although it was not observed.

Arvicola have been found to breed in the year of birth by Herfs (1939), van Wijngaarden (1954) and Perry (1943) but not in the populations studied by Stoddart (1968, 1971) and Lund (1970). In the present study a precocious pregnancy of a first year female was observed to take place on one occasion, outside the study area in 1972.

Stoddart (1968, 1971) found that juvenile A. t. reta achieved a bodyweight of 60 - 70 g. at the age of 30 days in the laboratory. In the present study a higher rate of 140 g. for this period is indicated for First Litter juveniles and 110 g. for Second Litter juveniles. The substantial difference between these figures and those of Stoddart (1968, 1971) may be a result of the rather smaller size of adult A. t. reta when compared with adult A. t. amphibius together with the laboratory condition under which the former were kept. This may have resulted in the premature birth of young as a result of handling stress and a slower rate of growth which the writer has observed to be a feature of juveniles kept in the laboratory, in comparison with individuals of the same weight in the wild, although Stoddart (1968, 1971) did not find this to be so.

Stoddart (1968, 1971) found that no juvenile born after July 1 contributed to the breeding stock of the following year. In the present study the number of Second Litter juveniles surviving until December exceeded by one the number of First Litter juveniles and while it is not certain that these contributed to the breeding stock of the following year it seems likely that they did so.

Pelikán and Holišová (1969) and Pelikán et al. (1971) found the density of A. t. terrestris to vary between 0 and 9.3/100 m. of stream, while van Wijngaarden (1954) found the maximum density of A. t. terrestris to be 15.4/100 m. of stream. These figures refer to animals of trappable age. The corresponding figures in the present study were

1.1 - 5.8/100 m. of stream, which show fairly good agreement with those of Pelikán and Holišová (1969) and Pelikán et al. (1971).

Much of the continental data concerning Arvicola density refers to populations occupying pasture and cultivated ground. Myllimäki (1969) gives figures of 62 - 260/hectare in Finland, Mehl (1950) suggests the figure of 16/ha as the density for normal years in Germany rising to 100 - 300/ha in peak years, while van Wijngaarden (1954) suggests a figure of 18/ha in Holland. Comparable figures in the present study would be 55 - 290/hectare of feeding range and 22 - 116/ha of locmotory range. Such densities are similar to those observed by Myllimäki (1969) but rather higher than those of Mehl (1950) for a normal year and those of van Wijngaarden (1954). It seems probable that densities of Arvicola living in fluvial habitats will be higher than those of woodland and agrarian habitats both because a greater proportion of the habitat is likely to be of high suitability as a food source, since ploughing and grazing might reduce this suitability in the agrarian habitat, and because in fluvial habitats emigration to areas of lower vole density is restricted by their reduced availability and by possible harassment from territorial males beyond the emigrating vole's own range.

The purpose of studying the population dynamics was the combined one of tabulating the numbers, bodyweight and sexual state of the population for a calendar year, and of calculating its productivity. This immediate purpose has been achieved but the important questions of whether the stretch of stream studied was typical of the stream as a whole, and whether the 1971 season was a typical year as far as vole dynamics are concerned remains largely unstudied. However it was found that the numbers and structure of the autumn population in 1971 were similar to those of a neighbouring stretch of stream of equal length in the autumn of 1972. This similarity gives some grounds for confidence that vole density between years and between stretches of stream were not changing by a large factor. Nevertheless it must be remembered that the immigration of only one breeding pair in the early spring might have increased the population size and the annual population production by one third. It is possible that a mild winter resulting in a high juvenile survival rate might cause a large increase in the size of the population the following summer beyond its normal level. Other factors that might have a considerable effect on population density from one year to the next would include the occurrence of a flood at a period of synchronised lactation among females which might result in the destruction of a litter group. Between stretches of stream differences in water depth and rate of bank collapse together with localised competition from colonies of Rattus norvegicus, and differences in grazing quality, could all cause dissimilarities in Arvicola density.

Nevertheless any study of rodent energetics is of limited value unless the laboratory data gained from a number of individual animals can be related to the field situation in terms of the impact that the population is likely to have upon its food source. To accomplish this some knowledge of the population structure and productivity is necessary even if the result from a limited study tends towards the atypical either in the choice of year or in the choice of study area. It is unlikely that the results given here give a precisely representative figure but it is also considered unlikely that they are wildly inaccurate. It is the size of the population rather than its structure that will constitute the likeliest source of error, so that the figures in terms of numbers and productivity could be multiplied by a suitable constant if and when they are found to be unrepresentative of the mean condition. It is suggested that annual production of any population of A. t. amphibius may be roughly estimated by discovering the number and density of female voles prior to the commencement of the breeding season in April and multiplying the total by 2,000 to give a figure for the total population production in kcals/yr.

CHAPTER 5

RESPIRATORY COST FOR THE PARAMETERS OF SIZE, TEMPERATURE, ACTIVITY AND SEXUAL STATE

5. Respiratory cost for the parameters of Size, Temperature, Activity and Sexual state.

Introduction

The construction of the Daily Energy Budget (D.E.B.) for each member of the model population at regular intervals throughout its lifetime, necessary for the evaluation of Arvicola importance in relation to its food source, requires an empirical investigation of the parameters affecting Arvicola metabolism. In the present study these parameters were simplified to interpret the relevance of: i) Size and Age, ii) Ambient temperature and seasonal acclimatisation, iii) Intensity of Activity, and iv) Sexual state.

The relationship between whole animal metabolism and bodyweight in mammals is usually expressed as: $M = kW^b$ where M is the metabolic rate, W the bodyweight, k a constant distinctive of a given species, in the order of 10 - 12 for mammals (Prosser and Brown, 1961) and which Grodziński (1961) considers to be lower for rodents, between 8 - 10, and b a power in the order of 0.73 (Prosser and Brown, 1961). This relationship approximates closely to that of Meeh's (1879) formula expressing surface area in terms of mass as $S = kW^{0.67}$ where S is the surface area, W the mass, and k the constant. Poczopko (1965) examined the value of k in rats from birth to death and found it to change rapidly with age in young rats, from 7.4 to 10.35 as the rats increased weight from 5 - 27 g., but only from 10.35 - 11.37

during a weight increase from 27 - 320 g., this reflecting the stabilisation of rat shape at an early age.

Blaxter (1962) suggests an interspecific mean of heat production at Basal Metabolic Rate (B.M.R.) of 70 kcal/kgW$^{0.73}$ to which specific estimates may be compared. His data for domestic sheep suggest that during the first week of life the metabolic rate is approximately twice this mean falling to the expected level at 15 weeks, after which period he calculated a further decline to 59 kcal/kgW$^{0.73}$ at 4 years of age. He interprets published work as indicating that the growing animal's metabolism is proportional to a higher power of their weight than it is in the same animal when older.

These data refer to metabolism measured as B.M.R. which requires that the animal be at its thermo-neutral temperature, that it be in a post absorptive state where the heat generated by the Specific Dynamic Action (S.D.A.) of food is nil, and that it be in a state of rest (Kleiber, 1961). Kleiber considers that the thermoneutral zone is circa 16 - 20°C for dogs and rabbits, 30°C. for rats, and 36°C. for hairless mice. At ambient temperatures below these the animal must produce additional metabolic heat to keep its body temperature from falling below the range of 36 - 38°C. which is fairly constant for all homoiothermic mammals, being ca. 37.6°C. in whales and 37.8°C. in shrews (Kleiber, 1961). In mammals thermoregulation can be maintained by: 1) altering the blood supply to the skin,

2) Piloerection, 3) Secretion of sweat, 4) altering the respiratory frequency and 5), altering the Metabolic rate.

Not only is the thermoneutral temperature lowered as thermal insulation increases but the degree of increase in metabolic rate with decreasing environmental temperature is also reduced (Kleiber, 1961). The muskrat *Ondatra zibethicus* L. maintains a subcutaneous temperature of 37°C. while swimming in icy water largely as a result of the air entrapped in its fur, the fur comprising 21% of its bodyweight (Johansen, 1962). In general mammals adapt to cold by developing more effective thermal insulation by increasing subcutaneous fat and pelage thickness; by reducing the blood flow to the peripheral tissues; by acclimation of peripheral tissues to temperatures below those of the deep body interior; and by increasing their metabolic rate. (Hart and Héroux, 1955; Hart, 1956, 1964).

Kleiber (1961) has expressed the rate of cooling of a mammal as being proportional to the reciprocal of the cube root of bodyweight. $C = \frac{W^{2/3}}{W} = W^{-1/3}$, and Blaxter (1962) has investigated the properties of pelage insulation which increases with hair density, and with thickness but at an ever decreasing rate. He has also examined the importance of the pelage-air interface. He concludes that the insulation provided by this interface against thermal conduction decreases by a factor of 4 when wind speed increases by a factor of 20. The insulation is reduced further by the wind entering the pelage itself.

Increases of heat production in the resting animal are due to shivering and non-shivering thermogenesis (Kleiber, 1961). In most mammals shivering is the only readily demonstrable method of increasing heat production during rest (Kleiber, 1961), first involving the fascicular muscles and later the larger muscle groups of the limbs where the contraction appears in the form of rigours (Blaxter, 1962). Since the heat generated by fascicular muscle contraction is released at the body periphery Blaxter has considered that it is inefficient in thermoregulation. In rodents also shivering appears to be the most important heat source in non-cold acclimatised animals but Hsieh and Carlson (1957) demonstrated an increase of metabolic rate in rats at low environmental temperatures in the absence of shivering. The sympathetic nervous system and the secretion of Noradrenaline are both implicated in the development of non-shivering thermogenesis which appears as a factor in newborn and cold acclimatised rodents and in the latter develops gradually during exposure to cold and is proportional to the decrease in temperature (Janský, 1973). The material oxidised to produce the additional heat during shivering and non-shivering thermogenesis is considered by Blaxter (1962) to be almost entirely body fat but Janský (1973) considers that skeletal muscle and the viscera may make a greater contribution than body fat as a source for providing the additional heat in non-shivering thermogenesis. The increase in energy expenditure in response to lowering environmental temperature has been investigated for the following small mammals:

Reithrodontomys (Pearson, 1960), Pitymus (Gębczyński, 1964), Neomys (Gębczyńska and Gębczyński, 1965), Clethrionomys (Górecki, 1966), Spalax (Górecki and Christov, 1969), Microtus (Trojan, 1969; Bashenina, 1969), Arvicola (Droždž et al., 1971) and reviewed for several genera including Micromys and Apodemus by Grodziński and Górecki (1967). Although experimental technique and experimental temperature varied, a fairly constant increase of energy expenditure of 100 - 150% could be observed for the majority of these genera when the ambient temperature had been lowered from the near thermoneutrality of 30°C. to 0°C.

Increases in metabolic rate due to voluntary muscular activity can exceed B.M.R. by a factor of 3 to 10 in man during walking or running and by a factor of 20 in a trained sprinter for a short period of time (Janský, 1965). Similar increases have been found for rodents which have been forced to run intensively in a treadmill. Janský (1959) found a Working Metabolic Rate in Microtus arvalis 5.7 times higher than B.M.R. and 4 times higher for Clethrionomys glareolus, these figures were increased to 6.5 and 7 times higher respectively during the most intensive short term exercise.

During low intensity activity the metabolic rate of the humming bird increased by a factor of 2.5 above its resting level and this rose to 6.1 during hovering flight. The ratio of metabolic rate of high as compared to moderate intensity activity was 2.35, a figure similar to that of 2 for man and indicative of a fairly stable ratio for animals ranging in size between humming bird and horse (Odum, 1960a).

A comparison of energy costs incurred during sleep and during short periods of unstimulated maximal activity can be made during measurement of Average Daily Metabolic Rate (A.D.M.R.) in a large respirometry chamber, enclosing nest chamber, food and activity wheel. The ratio of maximum to minimum values of oxygen consumption during A.D.M.R. measurement was found to lie between 1.5 and 2.1 for a variety of species of *Pitymys*, *Clethrionomys*, *Microtus* and *Peromyscus* by Pearson (1947). Gębczyński (1964) found a value of 1.6 for *Pitymys subterraneus*, Grodziński (1966) values of 1.5 in *C. rutilus* Pallas and 1.6 *M. oeconomus*, and Górecki (Grodziński and Górecki, 1967) values of 2.1 and 2.0 in *C. glareolus*. Under natural conditions however these animals would encounter a more varied and stimulating environment and the above values probably more accurately represent the "moderate" work of Odum (1960a).

The principal difference in energy expenditure between rodent sexes in non-reproducing animals is probably a result primarily of variability of size and activity although some periodic change may occur as a result of the oestrous cycle in females and possibly also from a corresponding rhythm in males. Trojan (1969) has found in *Microtus arvalis* that even during pregnancy energy expenditure increases are no greater than would be expected solely from the increase in weight of the pregnant female. Blaxter (1962) found that the heat production of the lamb foetus was 30 kcal/kg/day, which was about normal for that of the adult ewe at rest, but that within 24 hours of independent life and often within six hours of birth the lamb's metabolism was three times this level. Blaxter (1962) concludes that, "There is some evidence that the major increase occurs only after the lambs have suckled. In any event the metabolism of the lamb in utero is closely similar per kg. of weight to that of the adult ewe. It is thus understandable that in practical trials it has proved difficult to measure any increase in the energy needs of the pregnant animal per kg. of her total weight."

The cost of lactation is however considerable. Kaczmarski (1966) estimated that a female C. glareolus had to assimilate an additional 364 kcal during the 36-38 day period of pregnancy and lactation above its control rate and that of this 289 kcal were assimilated during the 18-20 days of lactation, an average increase for lactation of 92% above the metabolic rate of the non-pregnant female. Migula (1969) found an even higher cost in M. arvalis where the lactating female required an average increase in the rate of assimilation of energy of 133%. Kaczmarski calculated that for the entire period of pregnancy and lactation C. glareolus required an increase of 58% of the assimilated energy required by the non-breeding female.

The metabolic rate of young rodents has received attention particularly in the study of the development of thermoregulation. Taylor (1960) failed to notice shivering in young rats until about 19 days after birth and piloerection at cold temperatures only after two weeks while noting that there was some response to cold even in very young rats. This was indicated by increased oxygen consumption suggesting the action of non-shivering thermogenesis even at this early age. Poczopko (1961) observed no constriction or dilation of skin blood vessels in rats until the fourth day after birth. This control over heat loss continued to improve until the rat was 20 days old. The situation appears similar for young rabbits where isolated young were unable to maintain their body temperature at birth but were able to do so at 20°C. when six days old and at 8°C. by the age of 12 days (Poczopko, 1969). Hill (1947) noted a gradual improvement in temperature regulation of young rats after birth which continued until they reached an age of 60 days. At 60 days of age they commenced a period of maximum resistance to cold which continued until approximately day 300 whereupon resistance to cold showed a slow decline in effectiveness until death.

The dependence of rodent litters on nest insulation and the body heat of adults and siblings during the early days of life when their temperature regulation is poor indicates the importance of the precise thermal experience of individuals in the nest. Poczopko (1969) examined the nest temperature of a litter of baby rabbits kept in an unheated shed which varied in temperature between 2 and 31°C. The temperature of the bottom of the nest beneath the rabbits varied within the range 24-33°C. whereas that among the animals themselves was close to their body temperature and that in the upper part of the nest remained within the limits of 20 - 26°C. Slightly lower temperatures (19 - 23°C.) were recorded in the upper part of the nest when it was occupied by new born rabbits and there was some manipulation of the nest to counter changes in ambient shed temperature. The latter phenomenon was also reported by Trojan (1969) for M. arvalis.

The influence of group huddling on metabolism has been investigated by Ponugaeva (1960, reported in Grodziński and Górecki, 1967) who found that voles, mice and rats (e.g. M. arvalis, C. glareolus, Mus musculus, Rattus norvegicus) if kept in groups of 3 to 5 animals decrease their nesting metabolism by 8 - 17%, an effect reported to be due both to thermal economy and psychological relaxation. Trojan (1969) reports for M. arvalis that at 5°C. groups of from 2 to 5 animals showed no reduction per capita over voles kept singly while groups of 6 - 8 animals showed a reduction of 25% at this temperature. The reduction is markedly less at 20°C. Pearson (1960) investigating the value of the nest in energetic cost concludes that resting metabolism is 17% higher when no nest is present at intermediate temperatures and 24% at 1°C. There is however some evidence to suggest that when allowed to build nests solitary rodents lose heat at no greater rate than they do when huddled (Gębczyńska and Gębczyński, 1971) and although there must be some benefit to the group in the reduction of thermoregulation cost when the ambient temperature of the nest chamber is raised, the actual social organisation of rodents outside the breeding season is still too poorly documented to permit definite conclusions on the importance of group huddling on energy economy.

R.M.R. values determined from respiration estimates and energy assimilation values from food ingestion measurements have been found to be within 1 - 3% of each other but both are substantially higher than A.D.M.R. respiration values (Gębczyński, 1965, 1966; Grodziński and Górecki, 1967; Drożdż, 1968). Drożdż (1968) found these differences to vary from 11.5 - 22% in an examination of several rodent species and suggested that it was the absence of a nest in the first two techniques in association with the possible unnatural excitement of animals confined in small spaces which accounted for the discrepancy. In the present study respiratory cost was evaluated using a modification of the R.M.R. technique and it is hoped that the design of the experiments, while making physiological comparison more difficult by the introduction of unquantifiable variability, for example in vole restlessness and the efficiency of the use of nest materials, will nevertheless represent a more justifiable approximation of the ecological reality.

Method

The apparatus used to determine metabolic rate was the Kalabukhov-Skvortzov respirometer described by Górecki (1968a) and which although of a closed circuit type has been modified to permit the determination of A.D.M.R. by Gębczyński (1963). In the present study the apparatus was used in unmodified form only.

The abbreviations employed in the following description are those used in Diagram 3_1 where the Kalabukhov-Skvortzov respirometer is shown. The apparatus consists of a vertical 800 c.c. graduated burette of uniform diameter (5 cm.) with the tap, t1, uppermost and the lower end sealed. (It is an advantage to have also a second tap, t2, at the lower end.) A narrow bore glass tube, a1, leads horizontally from the left of the burette 7 cm. from the lower end for 4 cm. and then bends vertically for 3 cm. To this vertical section is fitted a rubber tube, into the distal end of which is fitted a polythene funnel, F, placed so that the top edge of the funnel is at the same level as the top of the burette. The funnel is held in place by a brass retaining ring screwed into the wooden back support onto which the burette and pressure valve are also fastened. A second glass tube of similar bore, a2, leads horizontally from the right of the burette 6 cm. above the sealed end for 6 cm. and is attached by rubber tubing, which can be closed by the tap t3, to the tube, V1. The tube V1 projects from the left of the water pressure valve PV, which it enters horizontally before bending vertically for 2 cm., V2. The joint between the tube and valve is sealed. The water pressure valve consists of a vertical glass cylinder 3 cm. in diameter which at its upper end, V3, is extended into a graduated "U" tube manometer, m, and at its lower end, V4, into a tube of similar bore 7 cm.

Diagram 3

Kalabukhov-Skvortzov Respirometer

1

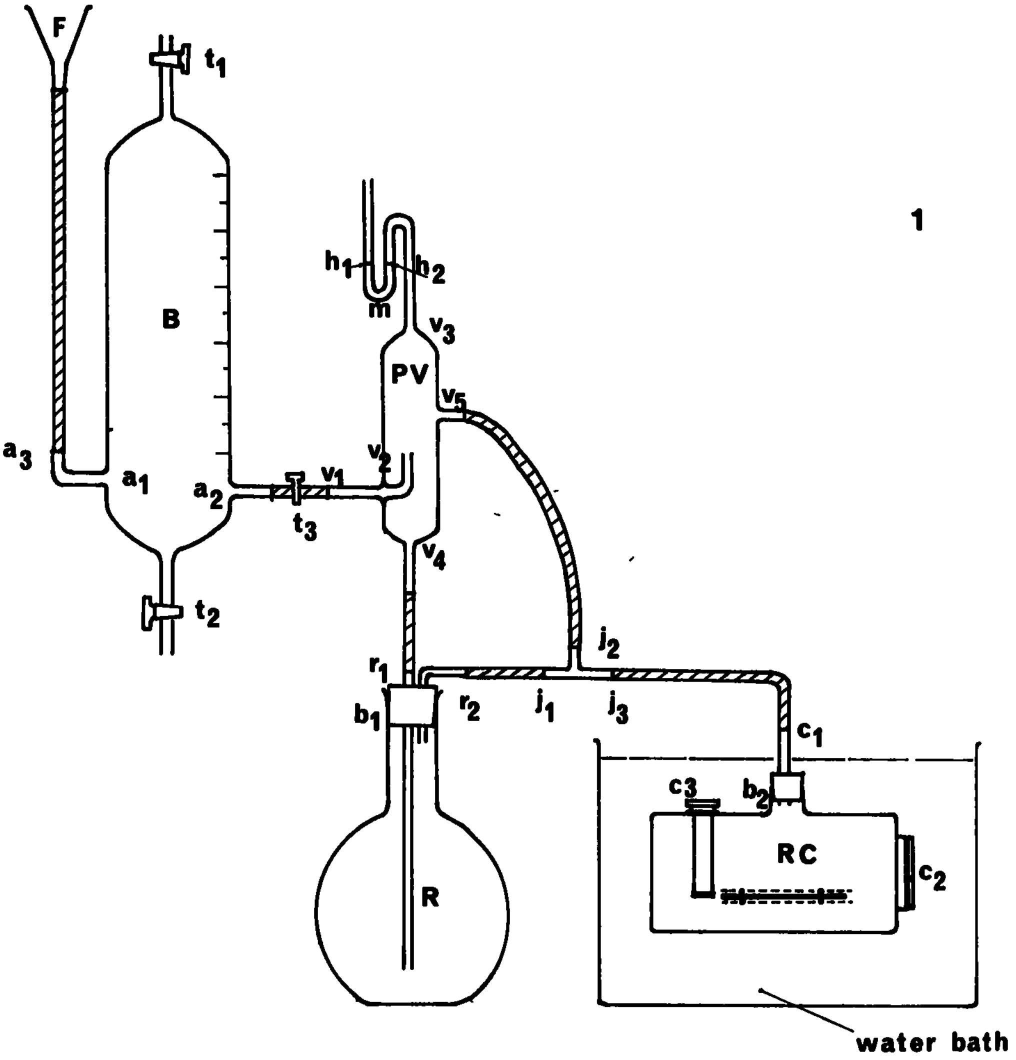
Diagram of Kalabukhov-Skvortzov respirometer. Dimensions and operational procedure are given in the text.

Key

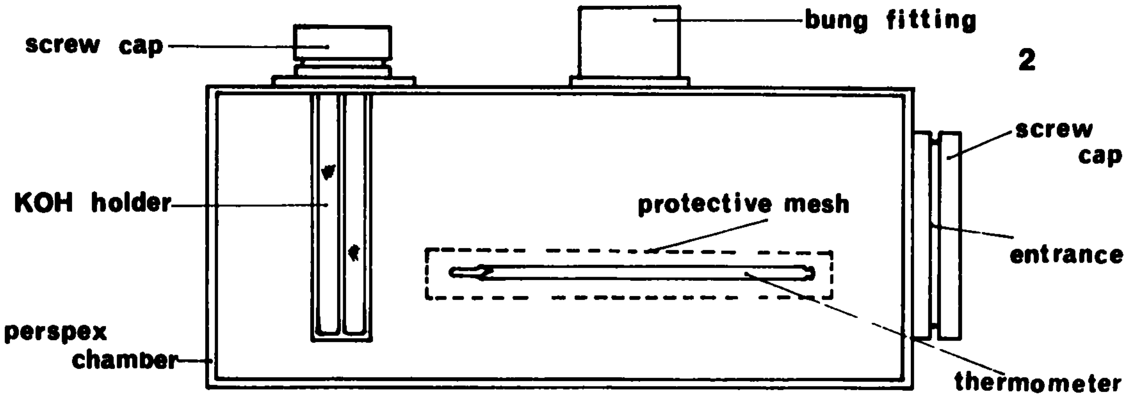
a_{1-3}	burette arms	m	manometer
B	burette	P V	pressure valve
b_{1-2}	rubber bungs	R	oxygen reservoir
c_{1-3}	respirometer chamber exits	r_{1-2}	reservoir exits
F	funnel	R C	respirometry chamber
h_1, h_2	manometer reading levels	t_{1-3}	taps
j_{1-3}	't' joint arms	v_{1-5}	pressure valve exits

2

Respirometry chamber in side view. Dimensions and details of construction are given in the text.


F
t_1
B
a_3
a_1
a_2
t_3
v_1
v_2
t_2
h_1
h_2
m
v_3
PV
v_5
v_4
r_1
b_1
r_2
j_1
j_2
j_3
c_1
c_3
b_2
RC
c_2
R
water bath

1


screw cap
bung fitting
screw cap
KOH holder
protective mesh
entrance
perspex chamber
thermometer

2

in length. A fourth exit, V5, leaves the water pressure valve towards the top right. The lower tube, V4, is connected by a piece of polythene tubing to the tube r1, which enters the oxygen reservoir, a 3 litre flask, R, for all but 5 cm. of its length through a sealed rubber bung, b1. A second reservoir tube, r2, leaves the flask and bends horizontally connecting to a glass "T" joint at j1 via a length of polythene tubing. Similar tubing connects the "T" joint at j2 to the tube V5 of the pressure valve and the "T" joint at j3 to a glass tube, C1, inserted into the rubber bung, b2, which fits into the respirometry chamber, RC.

The respirometry chamber in which the animal is placed is traditionally a desiccator sealed with vaseline but the difficulty of introducing and removing a large unetherised rodent such as Arvicola, and of replenishing the CO_2 absorbant without first removing the animal prompted the design of a respirometry chamber more suited to the animal concerned.

The respirometry chamber figured in Diagram 3_2, has a rectangular cross section of dimension 15 cm. wide, 10 cm. in height and 25 cm. in length having a capacity of 3750 cc. and was constructed of 0.5 cm. perspex. The bung, b2, fits into an aluminium cylinder of diameter 3.5 cm. which is sealed to and opens into the interior of the chamber 10 cm. from the front end. It is an advantage if this entrance is closed to the interior by a wire mesh screen to prevent interference with the bung by the animal, or the latter's escape. The admission entrance of the chamber, C2, consists of a circular aluminium entrance of internal diameter 5.5 cm. into which is screwed an aluminium sealing cap. The entrance is rendered airtight by screwing the cap against an internal rubber "O" ring. Traditionally the alkali for absorbing expired CO_2 in this respirometer is placed beneath the animal and separated from it by a layer of perforated zinc. In the present design however the alkali, Potassium hydroxide flake, is placed inside a gauze cylinder, of internal diameter 2 cm., 8.5 cm. in length and with a mesh of 0.7 mm.. This cylinder has a minimum surface area of 53.4 cm^2; the actual surface area of alkali presented by the flake KOH is many times larger. The gauze tube has a proximal lip of diameter 3.0 cm. which rests inside the brass screw C3, set 4.5 cm. from the posterior end of the chamber, and is sealed by a brass screw cap and associated rubber "O" ring. All entrances to the chamber C1, C2, C3 are centred along the midline of the chamber. A thermometer is set horizontally but away from direct contact with the perspex, along one longitudinal side of the chamber, and is protected from the animals by wire mesh (See Plate 8).

The maximum volume of gas in the reservoir, chamber, water pressure valve and connecting tube is 7050 c.c.

The respirometer is set up and a test run conducted as follows: The apparatus is attached to a wooden support stand and set up as shown in Diagram 31 so that the height of V2 is marginally greater than that of a1. The determination is made in a room of constant temperature to within ±1°C. and the experimental chamber at least is set in a water bath at that temperature. The tap t2 remains closed throughout the experiment and is used only for draining residual water after the completion of the experiment or as required.

Tap t1 is opened and tap t2 is closed. Water is poured into the funnel from a flask kept at experimental temprature and the burette, B , is filled to the top of the gradation marks or as required. Tap t1 is well lubricated with rubber grease and is then closed to seal the burette. The rubber tube at a_3 is removed and excess water in the funnel drained; the tube is not replaced. A check is then made on the level of water at a3 to ensure that it does not drip. This would indicate a leak at t1 and will introduce an error into the experiment. When the level of water at a3 is seen to be stable the tap t3 is opened. The water level at a3 will drop and water will rise into V2 and equilibrium become established. If air bubbles pass a1 at this stage, V2 is raised until they cease and the water level at a1 remains in the horizontal or vertical sections of the tube.

The "U" tube manometer, m , is partially filled with water. The water level in the manometer is then taken, as is also a barometric reading, B1. The air in the reservoir flask R. is replaced by oxygen either by displacement of water with compressed medicinal oxygen, an operation which required the opening of the oxygen valve for 22 - 27 seconds, or more simply by displacement of air for a longer period, 60 seconds, to ensure complete replacement. The tubes r1, r2, are sealed and the oxygen cooled to experimental temperature by the transfer of the reservoir flask to the constant temperature room. The temperature may be checked by the insertion of a thermometer through r1.

The gauze cylinder C3 is filled with 20-25 g. of flaked Potassium hydroxide (KOH) placed in position and sealed with the brass cap. The entrance C2 is also sealed and the bung b2 pushed into position. The connections j1, j2, j3 and V5 are completed and need not henceforward be disconnected. The respirometry chamber, RC, which is maintained at the experimental temperature, may now be placed in its water bath so that all entrances below C1 become covered. The chamber is then checked for leakages and these, if any, sealed.

The tubes r1 and r2 are then unsealed, any change in the volume of oxygen resulting from temperature changes during acclimation to experimental temperature being replaced immediately by air at experimental temperature and r1, r2 are connected as shown in Diagram 3_1.

A trial experiment may now follow to evaluate the effect of the pressure changes taking place in the constant temperature rooms due to the heating and cooling systems and to the air disturbance caused by persons entering and leaving the room. The level,(L1) of the water in the burette, is read at time T1 and again (L2) at T2, the difference in readings representing the volume of water which has been displaced through V2 into R during that period and which represents a value varying with apparatus design and experimental conditions. Normally water displaced per hour represents less than 1% of displacement resulting from vole respiration.

In the respiration experiment the vole is transferred from the darkened coffee jar which serves as a temporary retreat into the respirometry chamber by gently vibrating the jar when its exit is placed against the entrance of the chamber. This is usually sufficient to effect voluntary transfer. Nesting material in the form of 15 - 20 g. of cotton wool is placed in the chamber and the entrance C2 sealed; at this stage there is no alkali in C3 and the bung b2, is not in place. The vole is then allowed to acclimatise to experimental temperature and to construct a nest, this acclimatisation period was never less than one hour. In R.M.R. experiments the water bath is blacked out.

At the start of the experiment, KOH is placed in the gauze cylinder C3, this and the bung, b2, are fixed in position and the respirometry chamber placed in the water bath and checked for leaks; r1 and r2 are connected. The introduction of the alkali at this stage unsettles the vole and a period of 30 minutes is therefore allowed to elapse before the first reading, L1, is taken. The second reading, L2, is taken 60 minutes later.

Oxygen is used up by the vole and the carbon dioxide expired is absorbed by the KOH. A slight lowering of experimental pressure results which is demonstrated by the raising of the interior manometric level h2 above that of the open tube, h1. When this pressure is lowered sufficiently (after about 30 - 60 seconds) the remaining water in a1 will be drawn into the burette and bubbles of air will rise intermittently thereby displacing water at the top of the burette which flows out of V2 and into the flask R.

At time T1 the bubbles should be rising freely, the difference in mm. of the water levels of h1 and h2 is recorded. This difference will remain fairly stable until the end of the 60 minute experiment time, T2, when the barometric pressure is retaken (B2). The voles were weighed prior to each experiment. At the end of the experiment the voles normally entered the dark coffee jars freely, but this process could be facilitated by gently blowing on them through the bung aperture. The calculation of oxygen consumption/g weight/hr at S.T.P. dry gas is as follows:

Where

$T = T_2 - T_1$ duration of experiment = 1 hr.

$B = \frac{B_1 + B_2}{2}$ mean Barometric pressure, mm. Hg

$h = h_2 - h_1$ manometric pressure, mm. Hg where 1 mm Hg = 13.6 mm H_2O.

$EP = B - h$ experimental pressure

$VP =$ saturated vapour pressure of water at experimental temperature

$P2 = EP - VP$ Experimental pressure corrected to dry gas

$P1 =$ 760 mm. Hg

$K1 =$ 273°C

$K2 =$ Experimental temperature in degrees absolute

$V1 = L_1 - L_2$ Volume of water displaced during experiment in cc.

W = Weight of vole in grams.

Then the volume of O_2 consumption at S.T.P. dry gas

$$= \frac{V1 \times P2 \times K1}{P1 \times K2}$$

the volume of O_2 consumption at S.T.P. dry gas/hr

$$= \frac{V1 \times P2 \times 273}{760 \times K2 \times T} = V$$

the volume of O_2 consumption at S.T.P. dry gas/hr/g. =

$$C = \frac{V}{W} \quad cc. \ O_2/g/hr$$

The oxygen consumption expressed in cc. O_2/g/hr was converted into kilocalories by assuming the respiratory quotient, R.Q., for Arvicola to be 0.8 (Droždž et al., 1971), in which case the caloric value of 1 litre of oxygen corresponds to 4.8 kcal.

$$\frac{C \times 4.8}{1000} = 0.0048\ C. \quad kcal/g/hr$$

The Experimental Animals

Sealander (1952) described the importance of previous thermal experience on Peromyscus metabolism and Górecki (1966) concluded that the use of voles acclimatised to laboratory conditions is inadvisable for constructing bioenergetics models. Gębczyński and Olszewski (1963) could find no seasonal changes of the fur of laboratory voles analgous to the increased insulation of the fur of wild Clethrionomys in the winter. The writer likewise observed that Arvicola kept in captivity over the winter months did not undergo a change in pelage of the type found in voles in the wild.

To ensure that the respiratory rates of experimental animals were not affected by laboratory acclimatisation the experiments were conducted upon voles within 4 - 14 days of their capture in the summer series of determinations. They were then returned to the wild and not recaptured for a period of four weeks, intermediate determinations being conducted on animals removed from different stream sections in rotation. This technique was less appropriate in winter when climatic conditions rendered frequent trapping difficult and at that season the period of retention was extended to four weeks. The voles were kept at all seasons in an unheated greenhouse and were supplied with dark coffee jars, to act as substitute burrows, and ample nesting material. The temperature of the greenhouse fluctuated with the prevailing weather conditions from a range of 15 - 25°C. in summer to one of 0 - 12°C. in winter. These fluctuations of temperature were more rapid than those occurring in the burrows, described in Section 3, but were of the same magnitude and could be expected to provide some of the variation in temperature which the voles would have experienced when active outside the burrow system. The experimental voles were fed upon a diet of carrot, cabbage and grass.

The Validity and Relevance of the Method

i.) Metabolic Rate in the Nest

Slonim (1961, in Trojan, 1969) reported that in nocturnal rodents the metabolic rate is 6 - 11% higher in the dark than in the light while in diurnal rodents the rate is depressed by 8 - 9% indicating that R.M.R. should be measured in the light for nocturnal rodents and in the dark for diurnal ones. It seems unlikely however that even in nocturnal rodents sleep actually occurs in any but darkened nests and a state of inactivity in light may not itself produce the full depression of metabolic rate to a resting level. It is not clear (See Section 1.4) whether Arvicola has a strong nocturnal or diurnal activity preference as this changes and is less important in determining whether the majority of activity takes place during the day or night than is the straightforward proportion of day or night within the 24 hours. It was noted throughout this study however that Arvicola activity showed a strong apparent correlation with external stimulation. When deprived of this stimulation voles would spend brief periods grooming and follow them with extended periods of sleep. It was considered that stimulation would be reduced in the dark and in the absence of all edible material. Also it was considered that confinment of the animal in a gauze container as suggested by Górecki (1968a) would produce stress and encourage frustration activities such as gnawing at the gauze itself as suggested by Drożdż (1968).

An equally important consideration is that under natural conditions the voles could be expected to rearrange the nest, feed on stored grass or root material and undertake grooming activities as well as undergoing extended periods of sleep. All these activities take place at a nest environmental temperature not necessarily measured by that of the surrounding nest chamber of Section 3. The nest chamber temperature of the burrow system which has been measured in Section 3 may be regarded as representing the temperature of the Respirometry Chamber of the Kalabukhov-Skvortzov respirometer, that is, the experimental temperature. The temperature actually experienced by the voles inside their nests within the nest chamber of Section 3 has not been measured but it is considered here to have been reproduced within the Respirometry Chamber of the respirometer inside the nests of cotton wool which the voles create during the period of experimental acclimatisation. The quantity of nesting material used by the voles in the wild was found when the burrows were opened up to be similar in volume to that of the animal itself and to that of the 15 - 20 g. of cotton wool provided in the respirometry chamber. It is considered here therefore that both the natural variability of behaviour taking place in the nest chamber and the variability of nest chamber and internal nest temperature have been reproduced in the design of the respirometry experiment. Therefore if the respirometry experiment was conducted at temperature T, in the dark, within the 3750 cc.. respirometry chamber, with sufficient nest material provided, then the metabolic rate should be a close approximation of that produced at the temperature T recorded in the enclosure nest chamber.

The R.M.R. of previous investigators is not strictly comparable to the R.M.R. calculated in the present work because of, (1) the lack of physical constraint on the animal and (2) the provision of a nest, so the term Nest Metabolic Rate (N.M.R.) adopted by Trojan (1969) has been used in its place.

ii.) Respirometer Error

(1.) Animal Heat Production

The heat produced by the experimental animal will, if not immediately removed by conduction through the respirometry chamber walls and into the water bath, produce a reduction in obserbed oxygen uptake by causing the air within the respirometry chamber to expand and create a pressure increase partially counter-balancing the decrease from CO_2 absorption. Such a possible error is difficult to investigate. Although a thermometer was fitted inside the chamber the readings may be depressed below the true level by proximity to the perspex wall, or raised above it by the proximity of the sleeping vole. Consequently temperature readings showed some variability but a rise of 0.5°C. above ambient was that most frequently noted after the 1½ hour experimental run. Assuming an error of 0.5°C. for the 3,750 cc.. chamber, the remainder of the apparatus remaining at ambient, an under-estimate of circa 3% in oxygen consumption would occur for adult voles. This error appeared constant for all ambient temperatures under investigation and would probably be of a similar order for small voles where a reduced heat production is directly proportional to a reduced oxygen uptake.

(2.) Experimental Pressure Variability

The constant temperature rooms in which the experiments were conducted themselves have temperature confidence limits of between ±0.05 and ±1°C., and pressure variabilities were caused both by the operation of heating and cooling apparatus and by the opening and closing of the room doors. Trial experiments, in the absence of voles, indicated a mean over-estimate of 1.95% for oxygen consumption of 200 cc/hr and one of 0.975% for oxygen consumption of 400 cc./hr, the usual upper and lower limits of observations.

Assuming the errors caused by the heating of the respirometry chamber by the voles' body heat and by the change of pressure in the constant temperature room to act in concert, they will tend each to compensate the other resulting in a net underestimate of 1 - 2%. Even if this was on occasion not the case, it appears unlikely that errors due to experimental design exceeded 3%.

iii.) Saturated Vapour Pressure

It is customary practice (Dixon, 1951; Górecki, 1968a) to assume that respirometry measurements are conducted at 100% realtive humidity and to correct the volume of oxygen consumed to dry gas to compensate for this. Such an assumption would be open to some criticism in this case. Certainly the gas contained in the oxygen reservoir can be expected to be at 100% humidity especially if filled by displacement of water, and if by air by the retention of 20 ml. of water in the flask bottom, moreover it will be kept at this humidity by the splashing of water drops into it as absorbed oxygen is replaced. The humidity of the respirometry chamber is however open to question. At the commencement of the experiment it can be expected to be at ambient humidity, circa 60% but the introduction of an animal exhaling water vapour and at the same time of a water absorbing alkali will have an effect which is problematical and which will depend on both animal size and experiment duration. At temperatures of 3°C. or below condensation was invariably observed on the chamber interior walls and a humidity at 100% deduced. At temperatures of 10°C. and above however condensation was rarely if ever observed. Error due to the correction for saturated vapour pressure when in fact subsaturation was maintained will increase with ambient temperature and the maximum error assuming a 50% humidity for the apparatus as a whole is circa 2% at 30°C. If it is assumed that the respirometry chamber itself is at 50% humidity then this error is reduced to 1%. Any such error will result in an underestimate of oxygen consumption; it is unlikely that it approaches even 1% at experimental temperatures below 20°C.

It is considered therefore that experimental error, as opposed to vole variability, will at no time exceed 3 - 4% of measured consumption and since the source of this error is difficult to quantify and, apart from (2.) may not in fact exist, no correction was applied.

iv.) Carbon Dioxide Diffusion Rates

It is not altogether clear from the literature whether the diffusion rate of CO_2 into the alkali is likely to be a limiting factor in oxygen consumption estimates as Dixon (1951) has suggested it may be in respirometers of different design, this is especially surprising in view of the data suggesting a decline in O_2 consumption per capita when the grouping effect of a large number of experimental animals is investigated. The rather different method whereby the alkali is presented to exhaled gases in the current study necessitated an examination into whether experiments as performed were in any way influenced by an absorption limitation.

The maximum rate of experimental absorption observed occurred during the investigation of activity costs when a rate of 605 cc. O_2/hour was reached. The maximum total absorption observed was one of 683 cc.. for an exceptionally large male, 320 g. at 3°C., measured during the summer. It was felt that the measurement of the absorption of two adult voles enclosed together and consequently considerably excited over a longer period of time would give a better guide to diffusion limitations than would the direct absorption of CO_2 gas which would not encompass other aspects of the usual experimental variability. Results showed the apparatus capable of absorbing CO_2 at the rate of at least 1080 cc. O_2/hour and that a total absorption of at least 1600 cc. was possible without reduction in absorption rate below the rate expected. Even though these rates do not represent the maximum possible for the respirometer they nevertheless represent excess capacity ratios of at least 1.7 for rate of diffusion, and 2.34 for total diffusion. It is therefore considered that neither the rate nor capacity of CO_2 diffusion represented a limiting factor in any of the experiments.

v.) Experimental Gas Concentrations

(1.) The design of the Kalabukhov-Skvortzov respirometer assumes that the concentrations of oxygen and nitrogen of inhaled gas are maintained throughout the experiment at similar if not identical levels to those of the air. This assumption is probably correct as the coefficient of diffusion between oxygen and air is relatively low, and the narrow bore and substantial length of connective tubing coupled with the counterflow of oxygen introduced by the lowering of pressure in the respirometry chamber as a result of CO_2 absorption will probably render negligible the loss of nitrogen from the chamber.

Additional nitrogen entering the oxygen reservoir when the seals r1, r2 are removed as a result of the lowering of interior pressure after cooling to ambient temperature, will not raise the percentage of nitrogen in the O_2 reservoir above a maximum of 6% of the total gas content. This represents a reduction in oxygen concentration in the respirometry chamber after 500 cc. of oxygen has been transferred and absorbed of less than 1%. Since Taylor (1960) has demonstrated that reductions in oxygen concentrations of up to 6% have little effect upon oxygen consumption of rodents, the calculated reduction in oxygen concentration of 1% is not considered to be a possible source of error.

Similarly Taylor (1960) found that oxygen concentrations of up to 50% in inhaled air had a negligible effect upon oxygen consumption. In consequence it is doubtful whether there would be any effect on oxygen consumption even if the oxygen and air were to become perfectly mixed throughout the respirometer.

(2.) The withdrawal of carbon dioxide by the alkali from the air supply surrounding the experimental vole might be considered to result in an atypical condition of gas concentration if it is assumed that in the natural nest chamber carbon dioxide may well build up to substantial concentrations to which the voles may have adapted their metabolism. McNab (1966) investigating the gas condition in the burrows of fossorial rodents where differences from external air concentrations could be expected to be the most severe, found oxygen concentrations of 15 - 20% and carbon dioxide concentrations of 0.5 - 2.0%. Irving (1938) found that the respiratory rate of diving mammals such as the Beaver and Muskrat was independent of carbon dioxide concentration in inhaled air until a level of 10% was reached. Since the semi-aquatic Arvicola is also likely to possess, at least in part, this tolerance of carbon dioxide it seems unlikely that the vole will be affected by burrow concentrations of less than 2%. The removal of CO_2 altogether by the alkali is therefore unlikely to affect the respiration rate, especially as the vole must spend 25 - 35% of its life in the very low CO_2 concentrations of the open air.

(3.) The conclusions of Hart (1950) on Peromyscus that heat and carbon dioxide production are independent of the relative humidity of air have been accepted without further investigation.

vi.) Vole Weight.

Voles were weighed prior to the experiment when some ingested material would be present in the gut to enable closer approximation with the weights of trapped animals in the model population when this would also be the case. The weighing of animals in a post absorbant state might produce an overestimate of energy expenditure when applied to field data.

give an exponential curve of the oxygen consumed/g/hr at each experimental temperature, these in turn being transformed into a straight line by plotting the log of Respiration in $cc0_2$/g/hr against the log of total bodyweight in grams.

The resulting regressions are shown in Figures 23 - 28. It can be seen that the experimental variability did not alter with change in weight. The data satisfies the requirements of parametric regression analysis that the trend should be a straight line, that the parameter of the x co-ordinate should be uninfluenced by changes in the y parameter, that the scores should represent measurement in at least an equal interval scale, and furthermore that scores are from a bivariate normal population (Bailey, 1959; Campbell, 1967).

The correlation coefficient r was calculated for the regression of the oxygen consumption/g/hr on bodyweight, and the significance of r tested by the t test with n - 2 degrees of freedom, where n is the number of paired samples in the correlation. Where t is significant at the 5% level the correlation coefficient has been shown to be significant. The parametric regression analysis permits the calculation of the slope (b) and the intercept (a) giving a regression line from the relation of $y = bx + a$. The regression lines drawn in Figures 23 - 28 were obtained in this way. All the regression analyses in this and subsequent sections were carried out using an Olivetti 101 programmed calculator.

The regression equations for N.M.R. for the summer population are given below for each of the experimental temperatures. R = respiration in cc. O_2/g/hr and W = bodyweight in grams. The correlation coefficient r and its test of significance t are also given.

Temp°C	n	Regression Equation	r	t	P
3	43	log R = 1.595-0.544 log W	-0.955	20.68	< 0.001
10	41	log R = 1.606-0.587 log W	-0.950	18.96	< 0.001
15	54	log R = 1.386-0.516 log W	-0.878	13.23	< 0.001
20	27	log R = 1.120-0.415 log W	-0.920	11.71	< 0.001
25	13	log R = 1.091-0.407 log W	-0.840	5.13	< 0.001
28	44	log R = 1.265-0.492 log W	-0.864	11.10	< 0.001

Regression lines drawn from these equations are shown in Figs. 23 - 28. All the correlations were significant at the 0.1% level. It is concluded that the consumption of oxygen/g/hr increased with decreasing bodyweight at all the experimental temperatures. It is seen that the slopes of the regression equations varied little between the maximum and minimum experimental temperatures. (-0.544 ± 0.026 at 3°C. and -0.492 ±0.044 at 28°C.) the mean slope at 3°C. lying within the 95% confidence limits of that at 28°C. and the principal difference lying in the value of the intercept (1.595± 0.054 at 3°C. and 1.265± 0.092 at 28°C.) which was at a higher level at lower temperatures where the uptake of oxygen was increased to supply heat for thermoregulation.

The value of log R can therefore be calculated at any bodyweight between 55 - 320 g without extrapolation, for each of these experimental temperatures. For any given bodyweight between 55 - 320 g. 5 points can be calculated giving log respiration values at 3°, 10°, 15°, 20° and 28°C. (25°C. is excluded as the experimental sample was small and the experimental range only 140 - 300 g.) A regression line

Figures 23 and 24

The rate of oxygen consumption of the summer vole population while resting - regression of respiration on bodyweight.

Figure 23

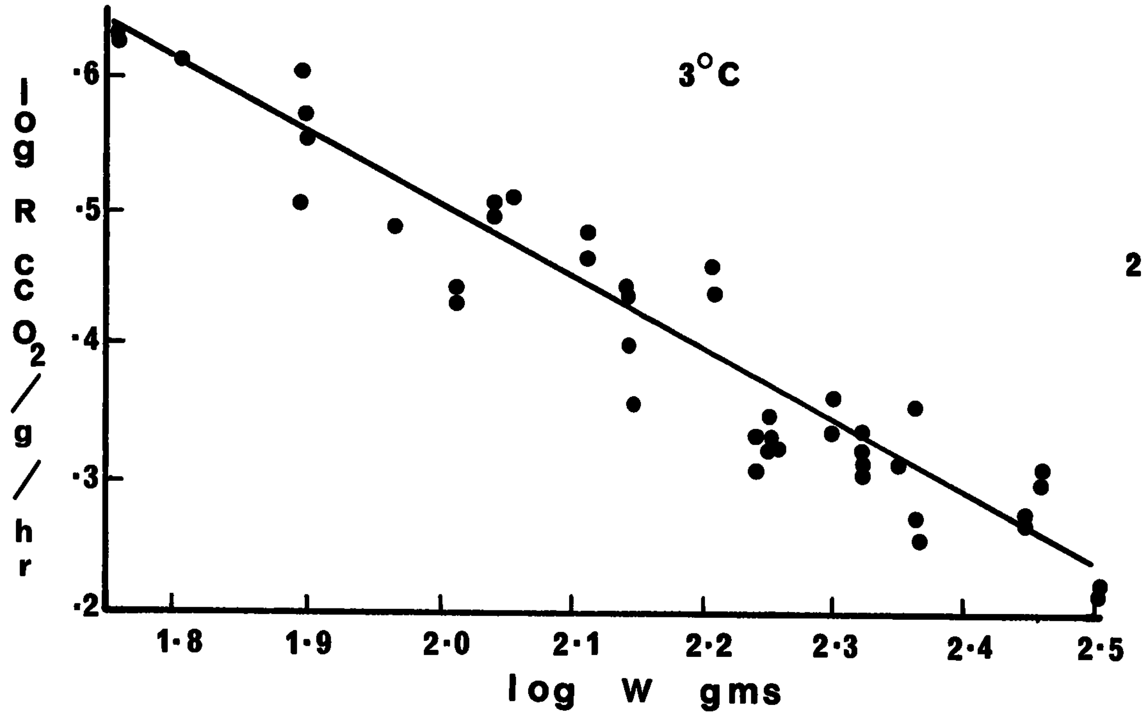
Regression of log respiration (log cc.O_2/g/hr) on log bodyweight (log gms) at 3°C.

$$\log R = 1.595 - 0.544 \log W.$$

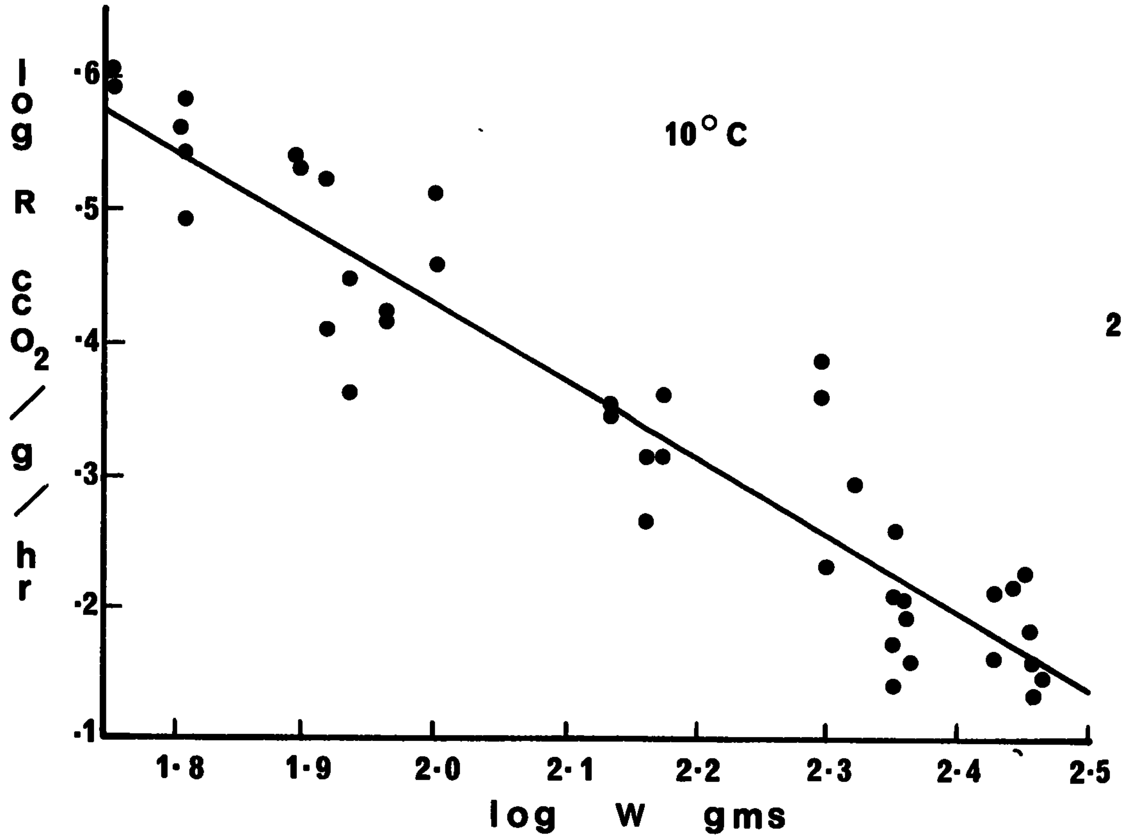
Figure 24

Regression of log respiration (log cc.O_2/g/hr) on log bodyweight (log gms) at 10°C.

$$\log R = 1.606 - 0.587 \log W.$$


3°C
log R cO_2/g/hr
·6
·5
·4
·3
·2
1·8
1·9
2·0
2·1
2·2
2·3
2·4
2·5
log W gms

23


10° C
log R cO_2/g/hr
·6
·5
·4
·3
·2
·1
1·8
1·9
2·0
2·1
2·2
2·3
2·4
2·5
log W gms

24

Figures 25 and 26

Rate of oxygen consumption of the summer vole population while resting - regression of respiration on bodyweight.

Figure 25

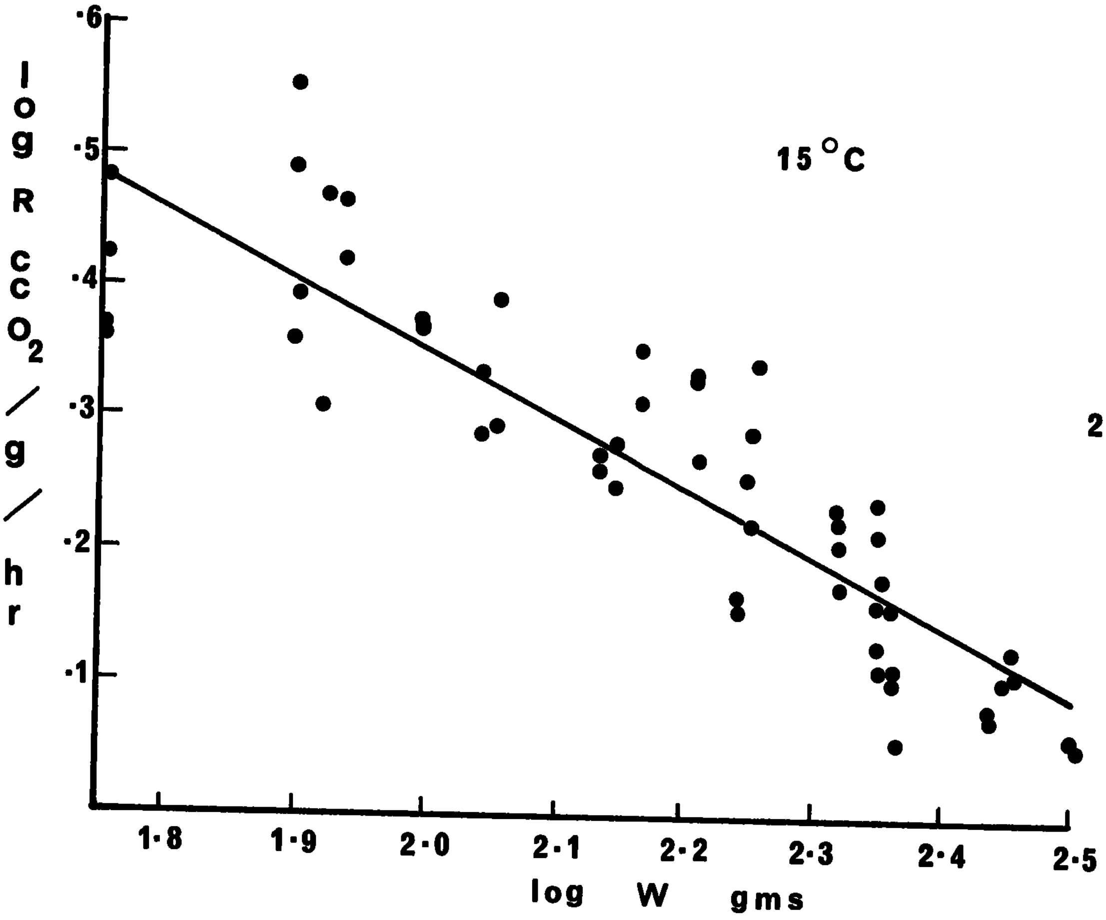
Regression of log respiration (log cc.O_2/g/hr) on log bodyweight (log gms) at 15°C.

$$\log R = 1.386 - 0.516 \log W.$$

Figure 26

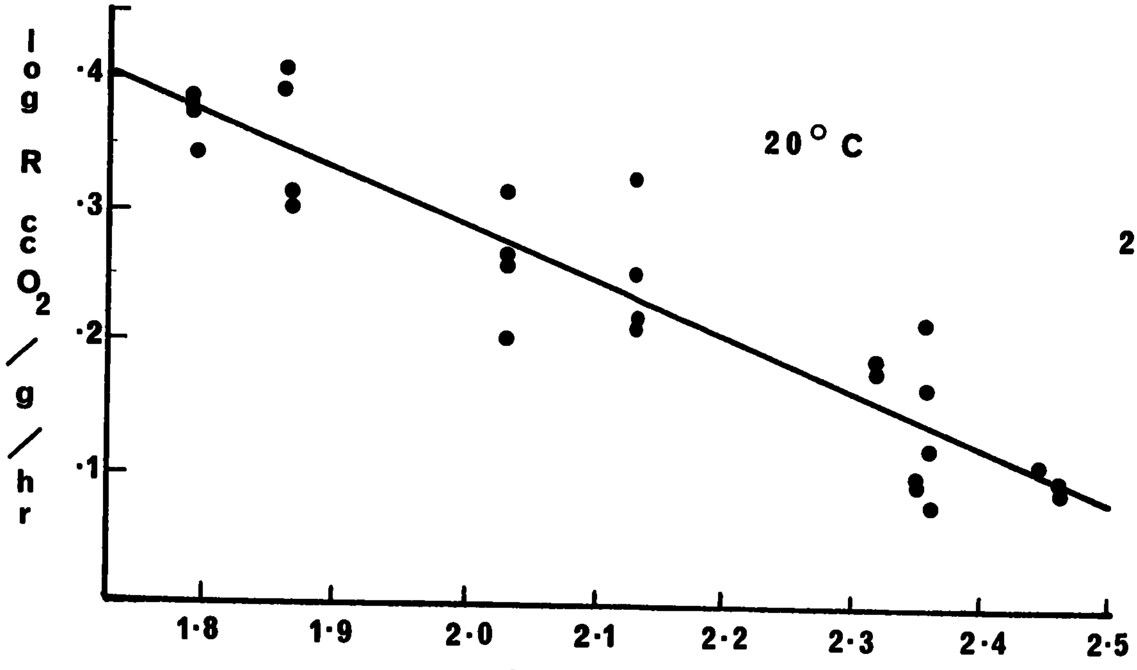
Regression of log respiration (log cc.O_2/g/hr) on log bodyweight (log gms) at 20°C.

$$\log R = 1.120 - 0.415 \log W.$$



log R ccO2/g/hr
·6
·5
·4
·3
·2
·1
15 °C
1·8
1·9
2·0
2·1
2·2
2·3
2·4
2·5
log W gms

25



log R ccO2/g/hr
·4
·3
·2
·1
20 °C
1·8
1·9
2·0
2·1
2·2
2·3
2·4
2·5
log W gms

26

Figures 27 and 28

Rate of oxygen consumption of the summer vole population while resting - regression of oxygen consumption on bodyweight.

Figure 27

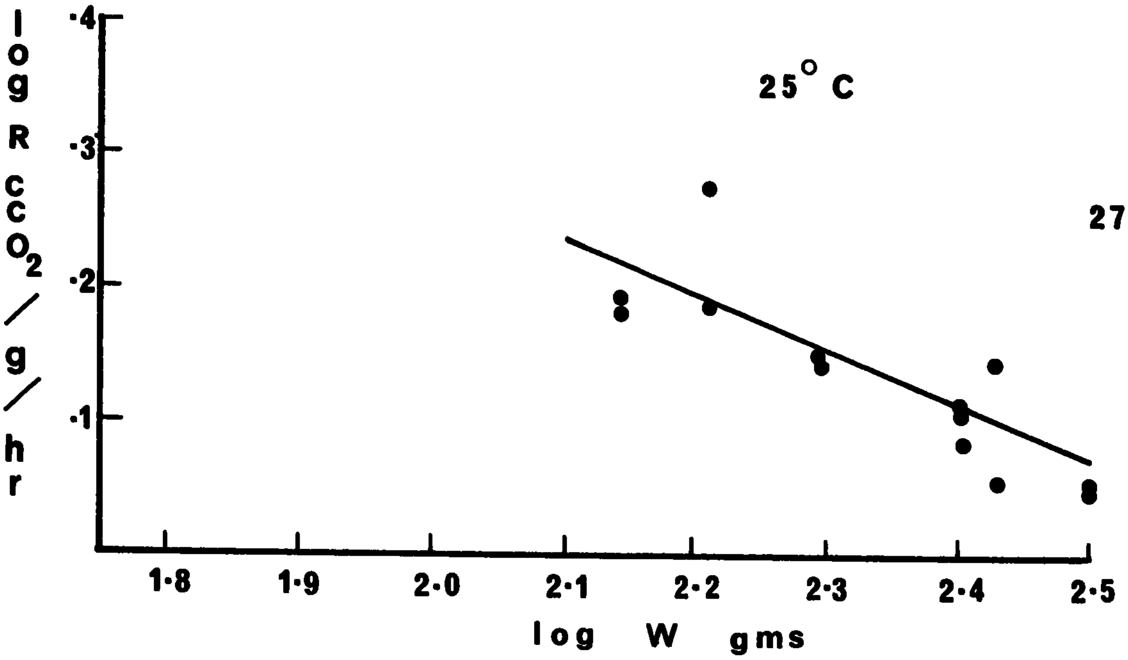
Regression of log respiration (log $cc.0_2/g/hr$) on log bodyweight (log gms) at 25°C.

$$\log R = 1.091 - 4.07 \log W.$$

Figure 28

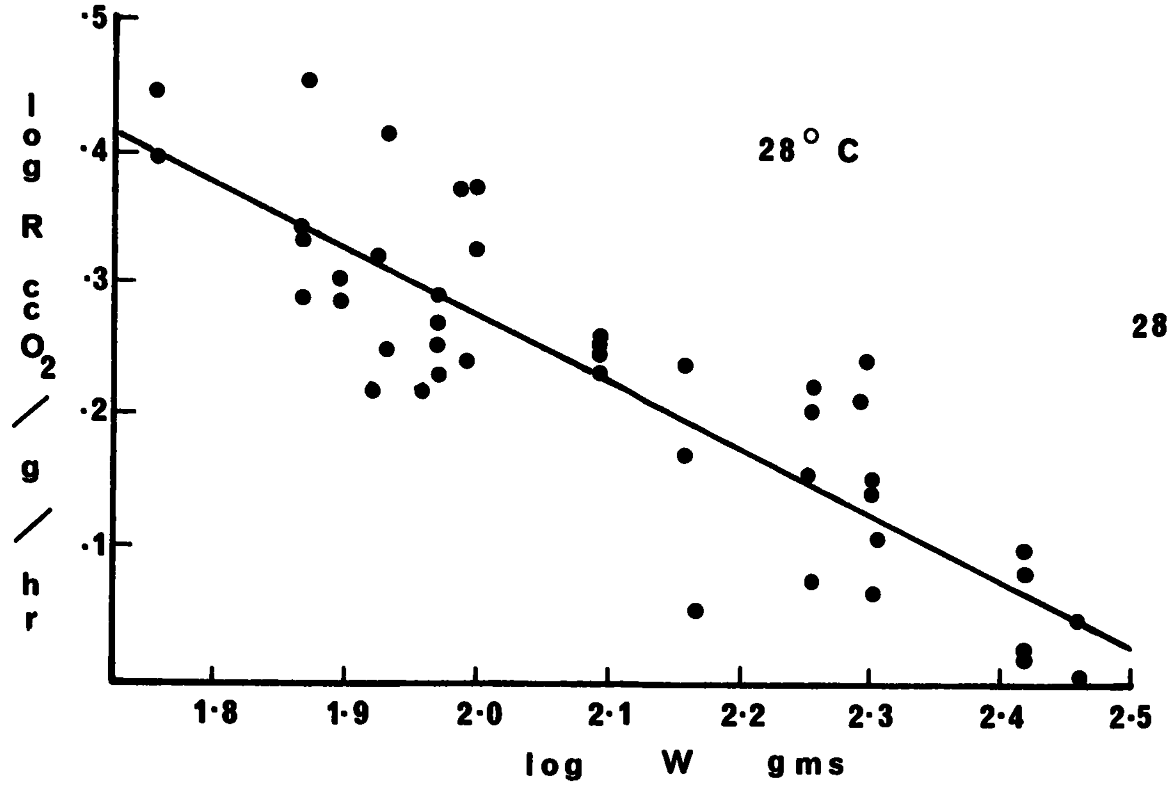
Regression of log respiration (log $cc.0_2/g/hr$) on log bodyweight (log gms) at 28°C.

$$\log R = 1.265 - 0.492 \log W.$$



log R cO$_2$ / g / hr
·4
·3
·2
·1
25° C
1·8
1·9
2·0
2·1
2·2
2·3
2·4
2·5
log W gms

27



log R cO$_2$ / g / hr
·5
·4
·3
·2
·1
28° C
1·8
1·9
2·0
2·1
2·2
2·3
2·4
2·5
log W gms

28

may now be calculated between Respiration and Temperature where bodyweight is held constant. Log R is plotted against log K (experimental temperature in degrees Absolute). Such equations were calculated at bodyweights from 60 - 320 g. at 20 g. intervals. An extrapolated equation was also calculated for the bodyweight of 40 g. These equations are given in Table 11. All the correlation coefficients exceeded -0.92 which for 3 d.f. is significant at the 5% level. R = respiration cc.O_2/g/hr, K = temperature in degrees Absolute.

Table 11. Regression Equations of log Respiration Rate on log Temperature for given Bodyweights.

Bodyweight grams.	log R =	a	+	b	log K
40		18.937	-	7.465	
60		17.706	-	7.001	
80		16.789	-	6.654	
100		16.086	-	6.389	
120		15.535	-	6.181	
140		15.070	-	6.006	
160		14.596	-	5.825	
180		14.260	-	5.699	
200		13.893	-	5.560	
220		13.604	-	5.451	
240		13.343	-	5.352	
260		13.410	-	5.386	
280		12.897	-	5.185	
300		12.695	-	5.109	
320		12.424	-	5.005	

These regression equations refer to voles between 55 - 320 g. bodyweight at a temperature range between 276 - 301°K. It is concluded that a negative correlation existed between temperature and respiration at all bodyweights between 55 - 320 g. It will be seen from Table 11 that the range of constants for the intercept, a, and also

for the slope, b, were functions of bodyweight.
If regression equations can be calculated for "a" on log bodyweight and for "b" on log bodyweight then $\log R = a + b \log K$ could be transformed into the more general equation of $\log R = (a_1 + b_1 \log W) + (a_2 + b_2 \log W) \operatorname{Log} K$ where Respiration is expressed both in terms of temperature and bodyweight in the same equation. Log W in grams is therefore plotted against a, and against b.

$a = 30.3 - 7.1 \log W$, r -0.999 $P = < 0.001$ 13 d.f.

$b = -11.8 + 2.7 \log W$, r 0.999 $P = < 0.001$ 13 d.f.

log Respiration may therefore be expressed in terms of log absolute temperature and log bodyweight as:

$$\log R = (30.3 - 7.1 \log W) + (2.7 \log W - 11.8) \log K$$

for voles between 55 - 320 g. and at temperatures of 276-301°K.

The oxygen consumption of a vole of any bodyweight and at any temperature between the experimental limits could then be calculated. This was carried out for voles at 20 g. intervals between 60 and 320 g. and also for the extrapolated value for 40 g. bodyweight and at 1°C. intervals from 3 - 28°C. together with the extrapolated values for 0, 1, 2, 29 and 30°C. A summary is given in Table 12 where the antilog of the calculated value is shown, respiration is expressed as cc.O_2/g/hr. Values are plotted at 5° intervals from 0-30°C.

Both the 0°C. and 30°C. figures are derived from extrapolation but as the extrapolated values are only 3° and 2°C. respectively outside the experimental range of 25° it is considered that any error is likely to be small.

Table 12. Nest Metabolic Rate for the Summer Population

Respiration in ccO_2/g/hr

Temperature °C.

Weight g.	0*	5	10	15	20	25	30*
40*	5.65	4.93	4.30	3.81	3.32	2.94	2.59
60	4.49	3.95	3.47	3.10	2.72	2.44	2.16
80	3.80	3.37	2.97	2.67	2.37	2.12	1.90
100	3.33	2.96	2.63	2.38	2.11	1.91	1.71
120	3.01	2.69	2.39	2.17	1.94	1.75	1.59
140	2.75	2.46	2.20	2.00	1.79	1.63	1.47
160	2.55	2.29	2.06	1.87	1.68	1.53	1.39
180	2.38	2.15	1.93	1.76	1.59	1.45	1.32
200	2.23	2.01	1.82	1.66	1.50	1.37	1.25
220	2.11	1.91	1.73	1.59	1.43	1.31	1.20
240	2.02	1.83	1.66	1.52	1.38	1.26	1.16
260	1.95	1.77	1.60	1.47	1.33	1.22	1.11
280	1.85	1.68	1.52	1.40	1.28	1.17	1.07
300	1.78	1.62	1.47	1.36	1.23	1.14	1.04
320	1.71	1.56	1.42	1.26	1.19	1.10	1.01

*Extrapolated results.

Although the slopes of the regression lines of Respiration rate on bodyweight only varied slightly over the temperature range of 3° to 28°C., the increase in oxygen consumption with fall of temperature from 25° to 5°C nevertheless varied in degree in voles of different sizes. For example the oxygen consumed by a vole of 60 g. was estimated as 2.438 cc./g/hr at 25°C. and as 3.945 at 5°C. which is an increase of 61.8%, while the respective increase for voles weighing 120 g. was 53.7%, 48.3% for those of 180 g., 45.1% for those of 260 g. and 41.8% for those of 320 g. These figures suggest that not only did small voles consume a greater volume of oxygen/g bodyweight than large voles but that they showed a greater relative increase in metabolic rate on exposure to cold.

This greater relative increase is reflected in the calculation of the average percentage increase of oxygen consumption per 1°C. fall from the experimental maximum at 28° to the experimental minimum at 3°C. The percentage increase of respiration/g/hr at 3°C. over that at 28°C. is divided by the temperature difference, 25°, to give a percentage increase of oxygen consumption per 1°C. fall in temperature. This percentage increase is given below for a range of vole bodyweight.

Bodyweight g.	% Respiration increase/ fall of 1°C.
60	3.35
120	2.84
180	2.56
260	2.38
320	2.18

Kleiber (1961) suggested that interspecific data could be compared by expressing the daily energy demand in terms of kcals/kg $^{0.75}$. This is achieved by dividing the energy demand obtained experimentally by the bodyweight expressed as kilograms raised to the power of 0.75. Kleiber, (1961) gives conversion tables to kg$^{0.75}$ for a wide range of bodyweights (Kleiber, 1961; Appendix 24). If, for example, a vole of bodyweight 200 g. had an energy demand of 30 kcals/day, its metabolic rate could be expressed in terms of kcals/kg$^{0.75}$ as follows: 200 g. expressed as Kg$^{0.75}$ = 0.30. The energy demand in kcals/Kg$^{0.75}$ is therefore 30/0.30 = 100 kcals/kg$^{0.75}$/ day.

The daily respiration demand of a resting vole within the nest for voles of 60, 180, 260 and 320 g. at 5° and 30°C. expressed as kcals/kg$^{0.75}$ is given below:

Bodyweight (g)	Energy demand (kcals/kg$^{0.75}$/day)	
	5°C.	30°C.
60	223.4	122.4
180	160.6	98.4
260	145.3	91.3
320	134.6	87.5

It is seen that even when metabolic rate is expressed as kcals/kg$^{0.75}$ small voles had a substantially greater energy demand than adults.

Figure 29 shows the relationship in daily energy demand at a range of temperatures between 3 - 28°C. expressed as kcals/kg$^{0.75}$ for a vole of 180 g.bodyweight. If this relationship can be extrapolated to 0°C. and 30°C. as indicated in the figure it will follow that the energy demand increased by approximately 80% over the 30° fall in temperature. Turkheim and Delost (1968) reported that the point of thermoneutrality of Arvicola was approximately 30°C.

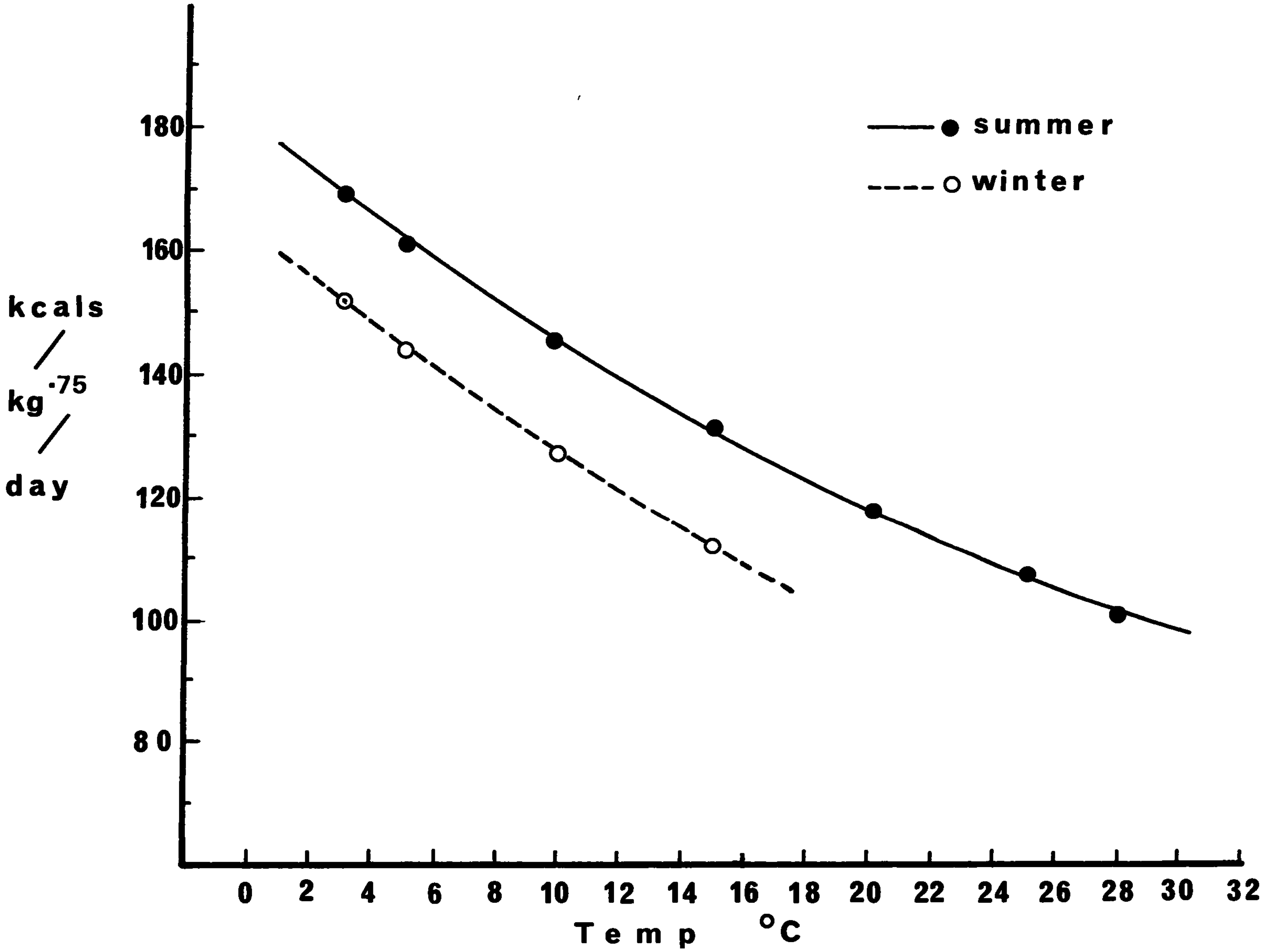
Summary to Section 5.1.1

The energy demand increased with a reduction in temperature, and increased per gram bodyweight as the vole

Figure 29

Comparison of the respiration of the summer and winter vole populations while resting.

The oxygen consumption of voles of 170-190g bodyweight expressed as kcals/kg$^{0.75}$/day are plotted against temperature. The values of voles from summer and winter populations are shown separately.



summer
winter
kcals / kg·75 / day
180
160
140
120
100
8 0
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
32
Temp °C

size decreased.

Although the slopes of the Respiration/g bodyweight to bodyweight regression did not vary substantially from 3° to 28°C. it appears that the respiratory rate of small voles increased at a faster rate with fall of temperature than that of adult voles. The mean percentage increase in respiratory rate for a 1°C. fall in temperature over the entire temperature range varied from 2.18% at a bodyweight of 320 g. to 3.35% at one of 60 g.

The regression of the metabolism of the whole animal in cc. O_2/hr on bodyweight is given by the expression $R = 18.4\ W^{0.51}$ at 28°C.

Nest Metabolic Rates have been calculated over the temperature range 3 - 28°C. and for voles varying in size from 55 - 320 g. Respiration may be evaluated in cc./g/hr by the general equation of:

$$\log R = (30.3 - 7.1 \log W) + (2.7 \log W - 11.8) \log K$$

where respiration (R) is expressed in terms of both bodyweight (W) in grams and temperature (k) in degrees Absolute.

5.1.2 Winter Population

The experiments investigating Nest Metabolic Rate for the Winter population were carried out from January 1973 until March 1973. The total of 12 individual voles used in the experiments were all animals experiencing their first winter and ranged in weight from 135 - 220 g. No distinction was made between the sexes. The experiments were carried out at

3°, 10° and 15°C., temperatures which correspond to the range of nest chamber temperature experienced during the winter. No time was available to conduct experiments at 20°C. and 28°C. to provide a comparison with the summer data. The experimental conditions were the same as those for investigating the summer N.M.R. A total of 16, 22 and 20 experiments were carried out at 3°, 10° and 15°C. experimental temperatures respectively, and the results as cc.O_2/g/hr were calculated as previously.

The regression equations for Respiration expressed as cc.O_2/g/hr plotted against bodyweight in grams are given below for each of the experimental temperatures.

Temp °C.	n	Regression Equation	r	t	p
3	16	$\log R = 1.385 - 0.484 \log W$	-0.507	2.200	< 0.05
10	22	$(\log R = 0.787 - 0.243 \log W)$	-0.353	1.767	> 0.05
15	20	$(\log R = 0.875 - 0.310 \log W)$	-0.397	1.838	> 0.05

At 3°C. the correlation coefficient is significant at the 5% level, but those at the other experimental temperatures are not significant at this level as a result of the natural variability of the individual voles being large in relation to the metabolic advantage possessed by the heavier animals within a fairly restricted range of bodyweight. Furthermore the total number of experiments conducted was not large, and the majority were carried out on voles of between 170 - 190 g. bodyweight. The significant result at 3°C. has the regression equation of $\log R = 1.385 - 0.484\ W$, or $R = 24.3\ W^{-0.48}$. This is similar to that at 15°C. for the Summer data where $R = 24.3\ W^{-0.52}$. However the ranges in weight at the two seasons are substantially different so the two sets of data are not comparable.

In the analysis of the respiration regression on temperature the point estimates of respiration at 3°, 10° and 15° were not estimated from the weight regressions as they were during the summer since two of the three did not have significant correlations. Instead the Respiration data for voles of between 170-190 g. bodyweight were plotted individually against temperature in degrees absolute, so that at each of the three experimental temperatures a range of log respiration values in cc. O_2/g/hr was plotted against log temperature, for all the experimental voles between 170 - 190 g. This limited range of bodyweight was chosen because it included the majority of voles present during this season and because the range is so narrow that any differences in metabolic rate/g weight due to size are likely to be very small.

Log Respiration in cc .O_2/g/hr was plotted against log temperature in °K.

Weight (g)	n	Regression Equation	r	t	P
170-190	31	log R = 17.561-7.069 log K	-0.77	6.524	<0.001

The resulting correlation coefficient is significant at the 0.1% level. The regression line, together with the individual point results are shown in Figure 30. Fig. 30 also shows a second regression line calculated from the results already mentioned combined with those obtained from an additional series of experiments conducted at and below freezing point. The latter experiments were carried out in a constant temperature cabinet at a range of temperature between -3° and 3°C. with the water column in the respirometer replaced by 95% water and 5% commercial antifreeze. Control experiments at 15°C showed this to have no effect upon the measurement of respiration rate. However the experiments were difficult to conduct without a rise in temperature occuring when the cabinet door was opened to take the initial reading at T_1, even when the surrounding air temperature was as low as 5°C. Although the interior of the cabinet was protected from the loss of cold air by a double layer of polythene sheeting, some error may have been caused by warming and therefore by the expansion of, the gas in the apparatus, and thus tending to affect the reductions in volume resulting from respiration.

The regression of respiration on temperature recalculated for the total range of -3°C. to 15°C. is given below:

Weight (g)	n	Regression Equation	r	t	P
170-190	39	$\log R = 14.26 - 5.72 \log K$	-0.78	7.527	<0.001

The correlation coefficient is significant at the 0.1% level. The slope of this second equation is less steep than that for the range 3° - 15°C. only, and the intercept for the equation -3° to 15°C. is at a lower level than that previously calculated for the range 3° - 15°C.

Figure 30

Regression of log respiration (log cc.O_2/g/hr) on log temperature (log°K) for voles of 170-190g bodyweight from the winter population while resting.

The data ~~is~~ are calculated twice, firstly for respiration values between 3° and 15°C and secondly for respiration values between - 3° and 15°C

3° - 15°C range. log R = 17.561 - 7.069 log k

-3°- 15°C range. log R = 14.26 - 5.72 log k

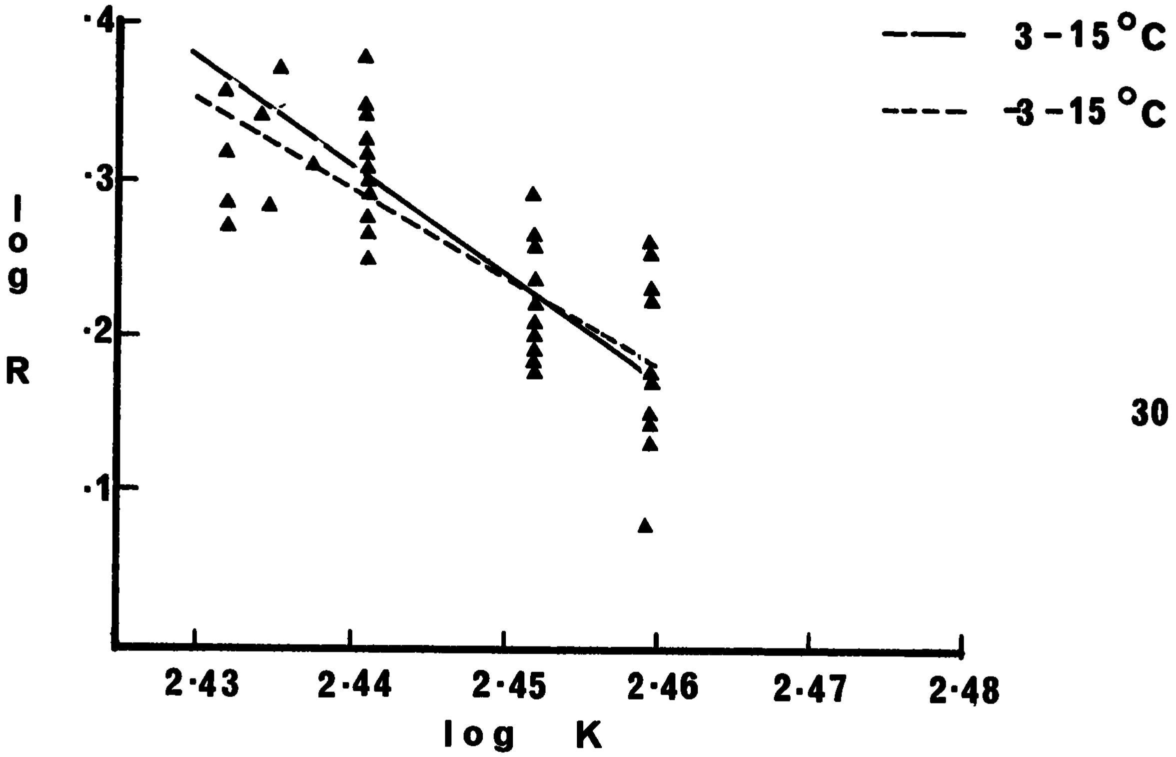
Figure 31

Regression of log respiration (log cc.O_2/g/hr) on log temperature (log °K) for voles between 170-190g bodyweight from the summer population while resting.

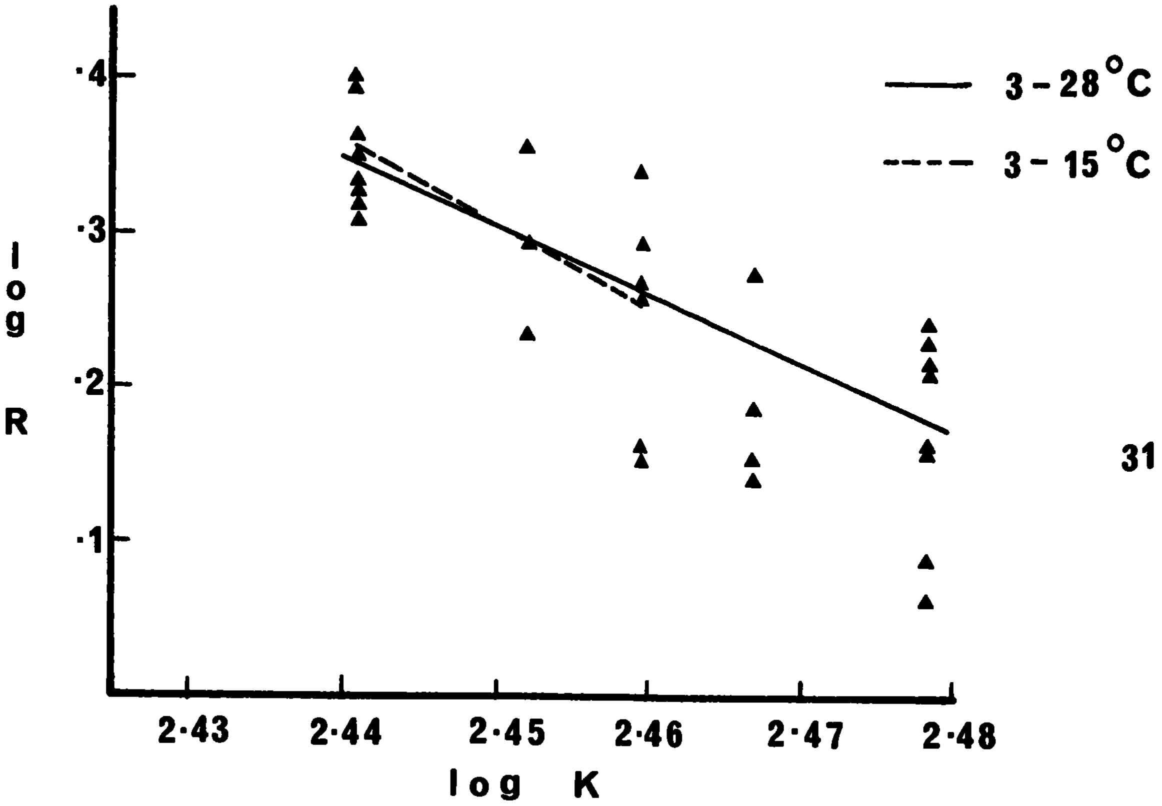
The data ~~is~~ are calculated twice, firstly for respiration values between 3° and 15°C and secondly for respiration values between 3° and 28°C.

3° - 15°C range. log R = 13.63 - 5.44 log k

3° - 28°C range. log R = 11.06 - 4.39 log k


3 - 15°C
-3 - 15°C
·4
·3
·2
·1
log R
2·43
2·44
2·45
2·46
2·47
2·48
log K

30


3 - 28°C
3 - 15°C
·4
·3
·2
·1
log R
2·43
2·44
2·45
2·46
2·47
2·48
log K

31

Regression °C.	Slope	Intercept
3° - 15°C	-7.069 ± 1.084	17.561 ± 2.66
-3° - 15°	-5.72 ± 0.76	14.26 ± 1.86

However the slope and intercept of the -3° to 15°C. regression both fall within the 95% confidence limits of the respective figures for those for 3 - 15°C. Such an apparent reduction in oxygen consumption would be the expected result of a slight expansion of gas within the apparatus if this occurred after the constant temperature cabinet door had been opened to take the initial water level reading.

The oxygen demand in cc./g/hr may be calculated at 1°C. intervals from the regression equation $\log R = 17.561 - 7.069 \log K$. Calculated values in cc./g/hr are given below at 5°C. intervals for a vole of 180 g. As well as values between the experimental temperature range of 3°- 15°C. extrapolated values (marked *) are also given at 0°, -5° and -10°C. These are not used in the computation of N.M.R. They are however utilized later in the computation of the Active Metabolic Rate. (Section 5.2)

°C	-10*	-5*	0*	5	10	15
cc .O_2/g/hr	2.84	2.50	2.19	1.93	1.70	1.50

The amount of oxygen consumed was 1.502 cc. at 15°C. and 2.030 cc. at 3°C., an increase of 35.15% over a 12°C. fall in temperature.

The energy demand for a vole of 180 g. bodyweight expressed as kcals/kg$^{0.75}$/day can be graphed against temperature as described in Section 5.1.1. The result of this calculation, shown in Figure 29, can be compared with the results calculated for the summer, shown on the same figure. Both sets of data refer to a mean vole bodyweight of 180 g. The results for the winter population showed a range in daily energy demand from 152.0 kcals/kg$^{0.75}$ at 3°C. to 112.4 kcals/kg$^{0.75}$ at 15°C.

Summary to Section 5.1.2

N.M.R. was investigated for voles of bodyweight ranging from 135-220 g. at 3°, 10° and 15°C. Of the three regressions of respiration/g/hr on total bodyweight only that at 3°C. proved to be significant at the 5% level, the equation was $\log R = 1.385 - 0.484 \log W$.

The regression equation for voles between 170-190 g. bodyweight for Respiration/g/hr on temperature (°K) was $\log R = 17.561 - 7.069 \log K$. This represents an average increase in respiration over the 12° experimental range of 2.929% for a 1°C. fall in temperature.

Energy demand for a 180 g. vole expressed as kcals/kg$^{0.75}$/day ranged from 152.0 kcals at 3°C. to 112.4 kcals at 15°C.

5.1.3 Comparison between Summer and Winter N.M.R.

The regression line for the winter season data of Respiration/g/hr plotted against temperature for a temperature range of 3 - 15°C., which is log R = 17.561-7.069 log K, may be compared with the regression for the summer season where this is derived by plotting the individual respiration results at 3°, 10° and 15°C. of voles between 170 - 190 g. against the respective temperature in °K. The Summer regression, both for the temperature range of 3 - 15°C. and also for the range 3 - 28°C, is shown in Figure 31. The details of the regression equations are given below.

Regressions for Summer Data. Respiration on Temperature (°K) for voles 170 - 190 g.

n.	Temp °C	Regression Equation	r	t	P
17	3° - 15°	log R = 13.63-5.44 log K	-0.65	3.346	<0.01
29	3° - 28°	log R = 11.06-4.39 log K	-0.76	6.114	<0.001

Compared with the regression for the winter population over the range 3 to 15°C. that for the summer population over this range was less steep and had a lower intercept value, but in each case the slope and intercept for the winter regression lie within the 95% confidence limits of those of the summer regression. This lack of significance can be attributed to the small number of experiments on which the summer regression is based (17) and the considerable degree of data variability.

	Winter	Summer
Slope	-7.07 ± 1.08	-5.44 ± 1.63
Intercept	17.56 ± 2.66	13.63 ± 3.98

It will also be seen from Figure 31 that the slope of the regression for the summer data over the range 3° - 28° C.

was less steep than that of the summer regression for the range 3° - 15°C. (-4.39 ± 0.72 and -5.44 ± 1.63 respectively), and that the intercept of the 3° - 28°C. regression was at a lower level than the 3° - 15°C. regression (11.06 ± 1.77 and 13.63 ± 3.98 respectively), but both the slope and intercept of the 3° - 28°C. regression lie within the 95% confidence limits of the slope and intercept for the 3° - 15°C. regression.

Whereas the percentage increase in respiration costs for each 1°C. fall in temperature from 15°C. to 3°C. has been estimated at 2.93%/1°C. for the winter population, the corresponding figure for a member of the Summer population weighing 180 g. was 2.17%/1°C. The difference between the two, which reflects the steeper slope for the winter data, suggests that, for voles of a given weight, the respiration rate in winter rose more steeply with fall of temperature than in summer, although as stated earlier the difference between the slopes for summer and winter regressions is not substantial.

The relative proportions of summer and winter energy demand expressed as kcals/kg$^{0.75}$ (shown in Figure 29) are given below at a range of temperature. The winter level is expressed as a percentage of the summer level.[*]

	Temp °C			
	3°	5°	10°	15°
Winter level as % of Summer level	90.8	89.7	87.5	85.6

The mean level in winter was thus 9 - 15% below that of the Summer.

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[*] The summer figures were derived from the regression of Respiration on Temperature at constant bodyweight given in Section 5.1.1.

It is concluded from the data as a whole that the respiration rate in summer, for a vole of given bodyweight, exceeded that in winter by approximately 12%.

5.2 Active Metabolic Rate (A.M.R.)

5.2.1 Low Energy Activity

Low energy activity results from those categories of behaviour which are allocated to groups 1 and 2 of Section 2. These include alert resting, feeding, foraging, grooming and exploring. When measuring low energy activity the cotton wool nesting material was removed from the Respirometry Chamber and replaced by sawdust to a depth of about 3 cms. Food in the form of carrot and cabbage was placed in the chamber and this was brought into the experimental temperature room together with the experimental voles, which had been placed in small cages without food, for two hours before the commencement of the experiment. The two hour period of acclimatisation allowed the chamber to attain the temperature of the experiment and to allow the vole metabolism to become adjusted to that temperature. The provision of food and sawdust in the chamber was intended to provide a feeding and foraging stimulus for the voles which had been kept without food for two hours previously to encourage the development of an activity period at the beginning of the experiment.

At the commencement of the experiment the voles were transferred to the Respirometry Chamber which was then connected to the respirometer. The chamber was placed in the water bath but was not blacked out so that its interior was well lit and the animal could be observed from above. The initial reading was taken about five minutes after the respirometer connection had been made. This time lapse was sufficient to allow the system to reach experimental equilibrium but insufficient for the animal to become bored with its environment. Each experiment lasted for 45 minutes.

A stop watch was used to time the length of each discrete item of activity and of the behaviour type involved. However this qualitative data was difficult to analyse and a simple record of the duration of all low energy activity would have been sufficient to satisfy the analysis that was carried out. It was usual for the voles to begin to explore the experimental chamber within minutes of its connection to the respirometer. They would forage and dig in the sawdust and spend some time grooming before settling down to a sustained period of feeding. Little sign of handling stress was observed, and the voles took no notice of the experimenter provided he remained still. After about twenty minutes of sustained activity it was usual for the voles to make a depression in the sawdust in which they curled up to sleep, re-awakening subsequently from time to time to renew feeding or grooming.

The experiments were carried out in March and April 1973. Five individual voles were used each having a bodyweight in the range 170 - 190 g. No distinction was made as to sex. Fourteen experiments were completed at an experimental temperature of 3°C. and fifteen experiments at each of 10°C. and 15°C. The Respiration was calculated as the oxygen consumed per hour per individual of circa 180 g. bodyweight. The results have been plotted in terms of the regression of rate of oxygen consumption on the percentage of the duration of the experiment spent in low energy activity. On this basis the intercept should represent a figure which approaches the N.M.R., where activity is negligible, and the respiration at 100% activity should represent continuous low energy activity with an A.M.R. expressed in cc $.O_2$/180 g./hour.

The regressions were calculated as previously except that the co-ordinates were maintained in antilog forms. The regression equations are given below. The point results and regression lines for each experimental temperature are shown in Figures 32 - 34, and the accumulated data for all temperatures in Figure 35.

Respiration is expressed as cc $.O_2$/180 g./hr. and Activity as the activity % of the experimental total where both were calculated in seconds. The calculated regression equations of non-significant regressions have been included below but are shown in parenthesis.

Temp °C.	n	Regression Equation	r	t	P
3	14	$(R = 383.2 + 0.612A)$	0.405	1.536	> 0.05
10	15	$R = 320.0 + 1.530A$	0.850	5.825	< 0.001
15	15	$(R = 319.2 + 1.683A)$	0.442	1.779	> 0.05
Total	44	$R = 339.5 + 1.248A$	0.567	4.461	< 0.001

Neither the correlation coefficients of the 3°C. regression nor the 15°C. regression achieved significance at the 5% level. This had been expected for the 3°C.

Figures 32 and 33

Rate of oxygen consumption during low energy activity

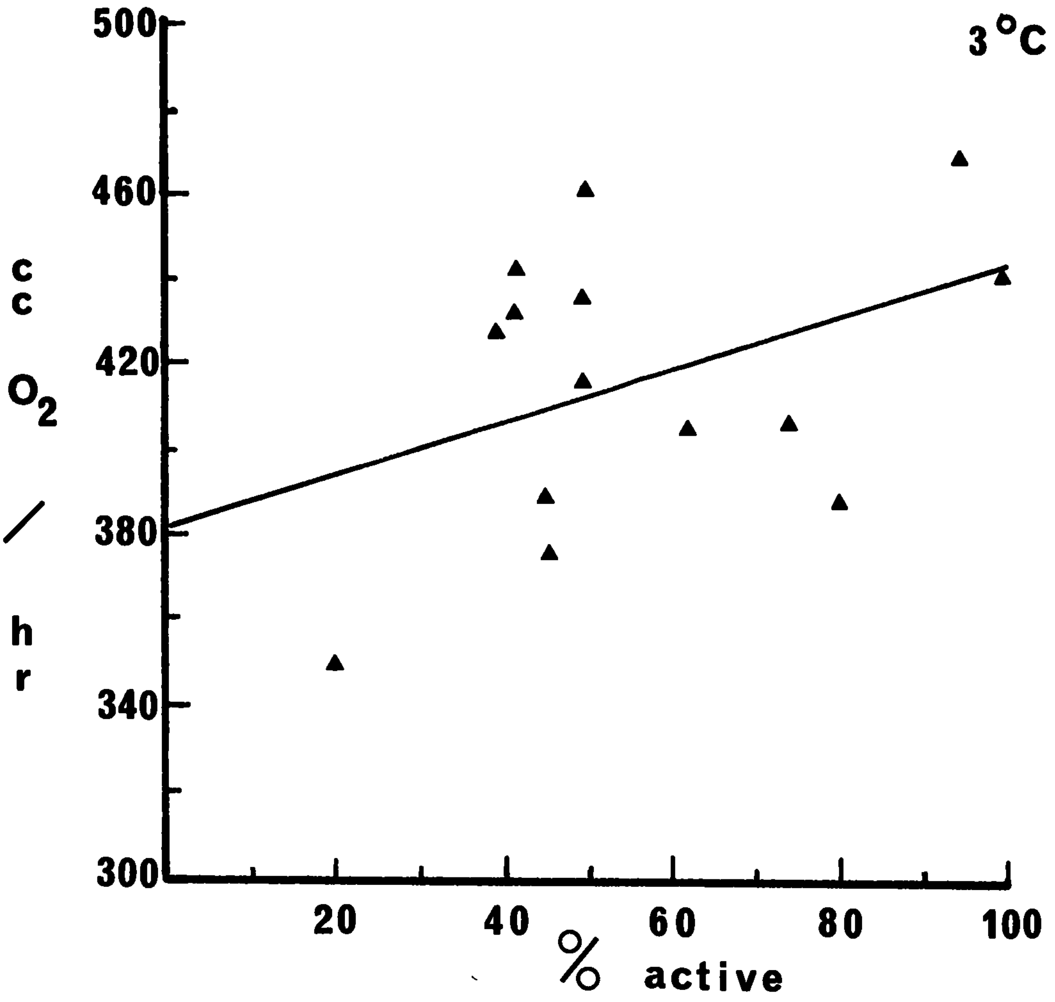
Figure 32

Oxygen consumption in cc.O_2/hr/individual for voles of 170 - 190g bodyweight is graphed against the percentage time passed in low energy activity. The remainder of the time is passed resting. The experiments were conducted in the early spring at an ambient temperature of 3°C. The regression is not significant.

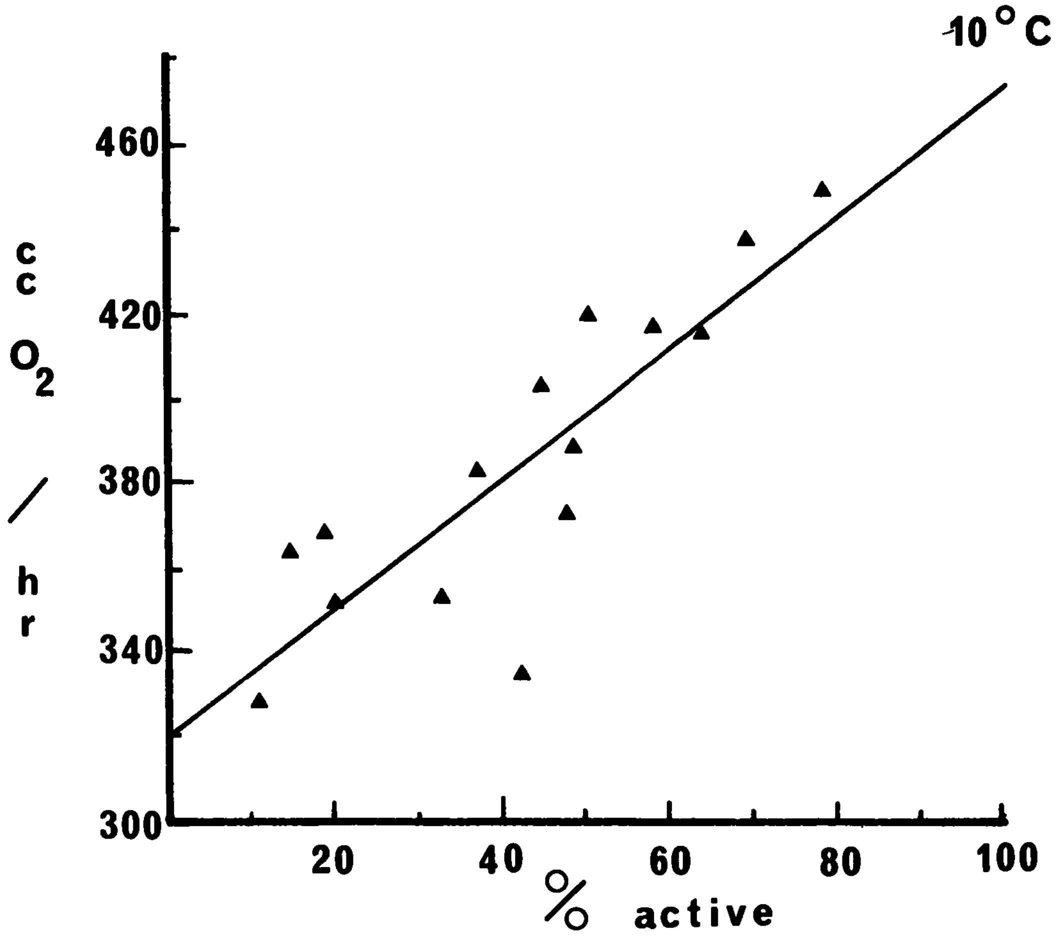
Figure 33

Oxygen consumption in cc.O_2/hr/individual for voles of 170 - 190g bodyweight is graphed against the percentage time passed in low energy activity. The remainder of the time is passed resting. The experiments were conducted in the early spring at an ambient temperature of 10°C. The regression is significant.

$$R = 320.0 + 1.530\ A.$$


3 °C
500
460
420
380
340
300
cc O2 / hr
20
40
60
80
100
% active

32


10 °C
460
420
380
340
300
cc O2 / hr
20
40
60
80
100
% active

33

Figures 34 and 35

Rate of oxygen consumption during low energy activity.

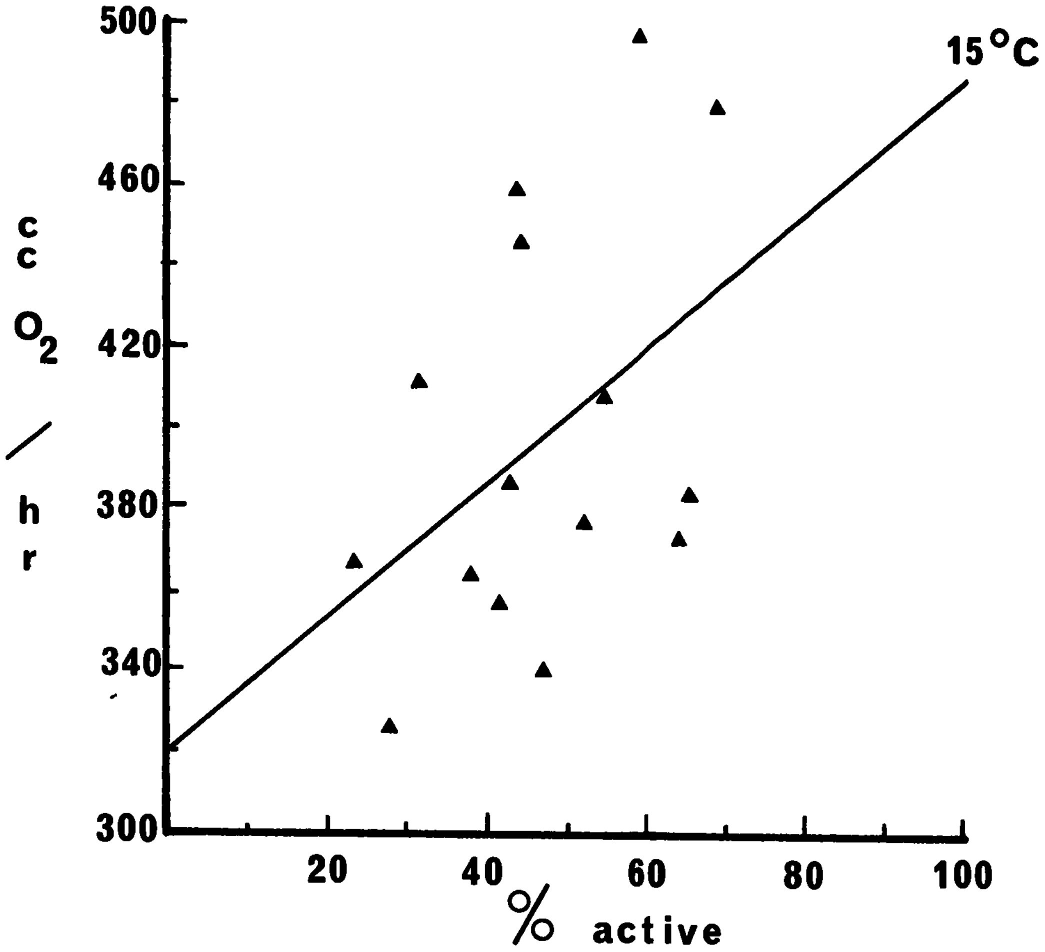
Figure 34

Oxygen consumption in cc.O_2/hr/individual for voles of 170 - 190g bodyweight is graphed against the percentage time passed in low energy activity. The remainder of the time is passed resting. The experiments were conducted in the early spring at an ambient temperature at 15°C. The regression is not significant.

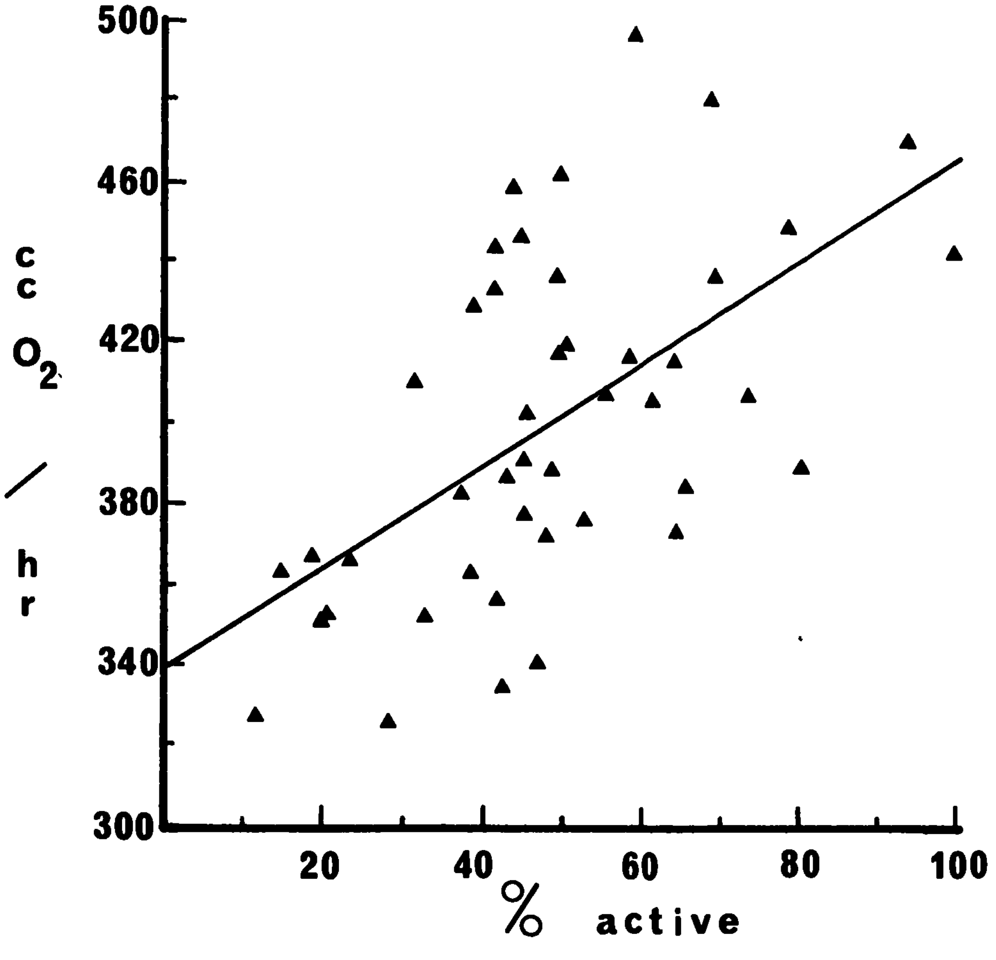
Figure 35

The data of Figures 32-34 are combined. Oxygen consumption in cc.O_2/hr/individual for voles of 170 - 190g bodyweight is graphed against the percentage time passed in low energy activity. The remainder of the time is passed resting. The experiments were conducted in the early spring at ambient temperatures between 3° and 15°C. The regression is significant.

$$R = 339.5 + 1.248 A.$$


15 °C
cc O2 / hr
500
460
420
380
340
300
20
40
60
80
100
% active

34


cc O2 / hr
500
460
420
380
340
300
20
40
60
80
100
% active

35

experiments where it had been assumed that low energy activity would in part replace shivering in thermogenesis for temperature regulation so that an increase in the percentage of activity would only result in a small increase in oxygen consumption over N.M.R. The failure of the 15°C. regression to achieve significance was unexpected, especially as the 10°C. regression achieved significance at the 0.1% level. Figure 33 shows that even in the regression at 10°C. there may be a suggestion that the data scatter was not equal along the entire regression, although this may be an artefact of the limited data.

When the data at the three temperatures are combined, significance is achieved at the 0.1% level with the intercept at 339 cc. and the 100% Activity level at 464 cc. This combined data may be useful when a broad spectrum of temperature is considered and suggests that the regression of increasing oxygen consumption with increasing activity outweighed the differences in oxygen consumption between the range of experimental temperature. The Respiration estimates for the 0% and 100% Activity levels for each of the calculated regressions are given below together with the previously calculated winter values for N.M.R. Respiration figures are in cc. O_2/180 g./hr. The figures calculated from non-significant regressions are shown in parenthesis.

°C.	3°	10°	15°	Data Combined
N.M.R.	365	306	270	314
0%	(383)	320	(319)	339
100%	(444)	473	(487)	464

Expressed as percentage increases over N.M.R., 100%

Activity Metabolism from these figures represented an additional energy expenditure of 21.6% at 3°C., 54.6% at 10°C. and 80.4% at 15°C. When the individual experimental results at all three experimental temperatures are combined the increase of the Combined 100% activity expenditure above their respective N.M.Rs was 27.1% at 3°C., 51.6% at 10° and 71.9% at 15°C.

If the regressions at 3° and 15°C. had been significant it would have been observed that the slope of the regression increased with rise of temperature as had been expected, the increase due to activity not being counterbalanced by a decrease in shivering thermogensis at the higher temperatures where such thermogensis would be of reduced occurrence. Nevertheless it is very unlikely that the maximum oxygen consumption at 3°C. should be lower than at 10°C., the 3°C. result was therefore discarded.

In view of the considerable variability between voles and between the same vole on different occasions it is seen that the number of experiments at each temperature was too small. An appropriate number of experiments would have been at least 30 at each experimental temperature. The differences in respiratory rate between individual voles was a noticeable feature of the experiments and may have been a result of differing reaction to the experimental situation, of differing physical fitnesses and efficiencies, and possibly of varying rates of hormonal secretion probably both of adrenalin and noradrenalin.

The respiratory rate at the 100% level of low energy activity, which includes the range of behaviour in groups 1 and 2, will probably vary with the relative proportions of these groups. For example foraging is likely to require a greater expenditure of energy than alert resting. However, a period of any one kind of behaviour usually lasted for only a few seconds at a time and there was a brief delay in respirometer reaction to oxygen consumption as a result of fluctuations in pressure within the respirometer due to vole body movement. Consequently it was not possible to record the costs in cc. oxygen for each type of behaviour by recording the level of the graduated water column at the beginning and end of each discrete item of behaviour. A further difficulty in making such an analysis results from mammals repaying short term energy debts incurred during periods of activity over the subsequent periods of rest (Janský, 1973).

However it seems likely from the very limited data obtained that the 100% level of low energy Activity Metabolism required at least 470 cc. /180 g./hr at temperatures of 3°C and above and that this figure may in fact have been as high as 520 cc. /180 g./hr. It is considered here that the heat produced by low energy activity was sufficient for thermoregulation, at least down to 3°C. and that no extra heat generation was required for this purpose, even though the vole no longer had the insulating benefit of the cotton wool nesting material. The estimated increase of low energy A.M.R. above N.M.R. at 3°C. of 20 - 30%, is at least as great as the usual estimate for small mice and voles of the energy saving from a well structured nest, (Pearson, 1960, suggests a 24% saving at 1°C., Trojan, 1969, 31% saving at 5°C.) and that at any level of oxygen consumption higher than this shivering thermogenesis can be assumed to have ceased.

An estimate of low energy Activity Metabolic Rate is required if the population respiratory cost is to be estimated. In the estimation of low energy A.M.R. for the winter population a figure of 473 cc/180 g./hr was assumed for 100% low energy activity at 3°C., with the values for 10°C. and 15°C. being kept at their experimentally determined levels of 473 cc., and 487 cc. respectively, there being no clear reason for altering them. A figure intermediate between these latter two estimates, 480 cc../180 g./hr, was estimated for 100% low energy A.M.R. at 28°C. These 100% Activity rates were then divided by the respective N.M.R. in cc.O_2/180 g./hr giving ratios of A.M.R. to N.M.R. These ratios were used as a conversion factor which when multiplied by the corresponding N.M.R. values in cc..O_2/g./hr provided an estimate of A.M.R. in cc.O_2/g./hr.

The ratios of low energy A.M.R./N.M.R. for the winter population are given below at a range of temperature.

	Temp. °C.			
	3	10	15	28
Conversion factor A.M.R./N.M.R.	1.30	1.55	1.80	1.87

The N.M.R. value at 28°C. for the winter was considered to be 257 cc./180 g./hr., the same as its summer value, as 28°C. is assumed to be near or within the thermoneutral zone in both seasons.

The regression of the Conversion factor (C) on temperature (°K) was then calculated, employing the logarithm of each, giving the resulting equation:

$$\log C = 4.021 \log K - 9.675.$$

The Conversion values for the summer population were calculated similarly to those of the winter population, estimating the 100% low energy A.M.R. at 480 cc.O_2/180 g./hr, with the appropriate N.M.R. values for 3°, 10°, 15°, 20° and 28°C. calculated from the data of section 5.1.1. The assumption is made here that at 100% low energy A.M.R. no shivering thermogenesis takes place in the summer population. The summer N.M.R. for a 180 g. vole at 3°C. is established from section 5.1.1 as 407 cc.O_2/hr. The A.M.R. rate of 480 cc./hr represents a 17.9% increase. This figure is similar in magnitude to the energetic saving represented by the provision of a well structured nest according to Pearson (1960), although Gębczyńska and Gębczyński (1971) suggest a higher figure. It is possible therefore that in the absence of a nest, 100% low energy activity metabolism provides just sufficient heat at 3°C. for thermoregulation and that no more energy need be expended by shivering thermogenesis for this purpose. In consequence the proposed A.M.R. rate of 480 cc./180 g./hr. is considered a reasonable approximation. At lower temperatures, however, for example at temperatures below 0°C., it seems probable that low energy activities of this kind would not provide sufficient heat for thermoregulation.

The regression of the Conversion ratio (C) against temperature ($^{\circ}$K) for the summer data gave the regression equation:

$$\log C = 5.793 \quad \log K \; - \; 14.062.$$

These regressions give a factor which when multiplied by the relevant N.M.R. provide an estimate of low energy A.M.R. A range of these conversion factors are given below for summer and winter.

$^{\circ}$C	-10	-5	0	5	10	15	20
Winter Constant	1.135	1.224	1.318	1.418	1.524	1.635	1.752
$^{\circ}$C	0	5	10	15	20	25	30
Summer Constant	1.122	1.246	1.381	1.529	1.690	1.862	2.046

5.2.2. High Energy Activity

No experiments were conducted into high energy activities such as those in the behaviour group 3 as described in Section 2. No normal behaviour of such high activity could be encouraged in the experimental chambers. In the absence of any experimental data as a guide in the estimation of high energy A.M.R, an estimate was derived from published work in conjunction with the low energy A.M.R. results described in the previous section.

Estimates of maximum and minimum A.D.M.R. values gave ratios varying from 1.5 - 3.1 in a variety of mice and voles (Pearson, 1947; Gębczyński, 1964; Grodziński, 1966; Górecki, in Grodziński and Górecki, 1967; Hansson and Grodziński, 1970). The environment represented by the chamber in which the A.D.M.R. experiments were conducted is rather limiting for locomotory exercise and consequently the lower figure of this range of ratios may be too low as an estimate of the kind of high energy activity involved in Burrowing, Diving and Swimming, while the figure of 2 and 2.35 for the ratio of high energy activity to moderate energy activity ascribed to man and hummingbirds respectively (Odum, 1960a) may be too high in view of the fact that climbing, vigorous gnawing and social contact have also been included in the high energy category.

It was considered that a ratio of High Energy Activity to N.M.R. of 2.8677 at 28°C. for both the summer and winter populations was a reasonable estimation being at the upper end of the range of A.D.M.R. ratio values quoted above but not as high as the high energy expenditure rates quoted by Odum (1960a) being 1.54 times the low energy A.M.R. of 1.8677 times N.M.R. at 28°C. The rate of 2.8677 times N.M.R. when applied to a vole of 180 g. bodyweight is equal to an oxygen consumption at 28°C. of 737 cc./hr. This level of oxygen consumption was expected to be independent of temperature at least from 3° - 28°C. and possibly to a much lower temperature.

The rate of 737 cc.O_2/hr was divided by the corresponding N.M.R. for a range of temperatures for the summer and winter populations. The same figure for the maximum respiration level of 737 cc ./hr was chosen for both populations as the energy demand of high energy activity is considered to be independent of pelage thickness. The logs of these ratios were then plotted against the log of temperature (°K). The regression equations of the two conversion constants are given below.

Winter Population. $\log C = 3.864 \log K - 9.102$

Summer Population. $\log C = 5.727 \log K - 13.717$

As in section 5.2.1 C gives the oxygen consumption/g/hr of high energy A.M.R. at any given temperature when multiplied by the N.M.R. in cc.O_2/g/hr at that temperature. A range of constants for both populations are given below at 5°C. intervals.

°C.	-10	-5	0	5	10	15	20
Winter Population C.	1.774	1.906	2.048	2.196	2.354	2.519	2.693

°C	0	5	10	15	20	25	30
Summer Population C.	1.721	1.907	2.113	2.337	2.580	2.841	3.124

In the winter population where the voles are of similar size the High Energy A.M.R. is equal to $\frac{737}{180}$ x Wg. in cc..O_2/Vole/hour, where W. is the vole bodyweight at any weight between 170 and 190 gms. In consequence the conversion factor (C) need not be used. In the summer however the range of bodyweight is much greater and the conversion factor (C) was employed to take account of any change in respiration rate resulting from variation in bodyweight.

Discussion on Section 5.2

Alexander (1962) found that at low temperatures when the resting metabolism was at its maximum, the relationship between the respiration rate and the bodyweight of lambs approximated to $R = aW^1$. It is possible to infer from this that where shivering thermogenesis is at its maximum respiration rate is proportional to bodyweight and not to body surface area. It is possible therefore that voles undergoing a measure of muscular activity will show a relationship between respiration and weight in which the slope of the regression line is closer to unity than is the case with N.M.R. Furthermore this approximation to unity would be expected to be closer with high energy activity than with low energy activity.

If Active Metabolic Rate is calculated for voles of bodyweights different from 180 g. by the equation $R = aW^1$ however certain inconsistencies arise, if the low energy A.M.R. for a 180 g, vole is assumed to be 480 cc../hr and high energy A.M.R. to be 737 cc ./hr. For example a 100 g. vole at 5°C. in summer has an estimated N.M.R. of 300 cc./hr. If low energy A.M.R. is calculated from $\frac{480}{180}$ x 100 cc./hr, the $R = aW^1$ relationship, the resultant value of 266.7 cc./hr is obtained, a value lower than N.M.R. and clearly unacceptable. Similarly if the high energy A.M.R. is calculated from the

$R = aW^1$ relationship the value of R is equal to $\frac{737}{180} \times 100$ cc. = 409.4 cc./hr. This respiratory rate is not substantially greater than that of 360 cc./hr which would be expected if the cotton wool nesting material, which permitted a metabolic saving of 20% (Pearson, 1962) had been omitted when measuring N.M.R. That is 360 cc. would be the expected R.M.R. in the absence of nesting material, an absence inherent in the calculation of A.M.R.

Both these figures calculated assuming $R = aW^1$ are considered too low to be acceptable. It is therefore concluded that either the slope of the regression of respiration on bodyweight is not equal to unity when the voles are active, or that the levels of low and high energy A.M.R. which have been estimated here are much too low. In consequence the conversion constants of low and high energy A.M.R. have been used in conjunction with the N.M.R. figure to give respiration figures for voles of all bodyweights between 55 and 320 g. These figures therefore incorporate the relationship between respiration and bodyweight which was calculated for N.M.R. in Section 5.1. For the 100 g. vole at 5°C. in summer the value of R calculated by the conversion constant and N.M.R. figure method would be 374 cc./hr for low energy A.M.R., and 572 cc./hr for high energy A.M.R. If the actual relationship between respiration and bodyweight for active animals has a slope closer to unity than in resting animals then the estimations of A.M.R. by the conversion constant x N.M.R. method will result in a slight overestimate of respiration for voles smaller than 180 g. and a compensating underestimate for voles larger than 180 g.

It is concluded that the relationship between N.M.R. and low and high energy A.M.R. should be more thoroughly investigated, especially with regard to the relationship between respiration and bodyweight at high levels of activity.

It has been assumed in this Section that the generation of heat by voluntary activity replaces thermogensis by shivering at low temperatures. Although this seems a reasonable assumption, experiments by previous authors (Hart and Héroux, 1955 and Janský, 1959) have indicated that the metabolism of animals when active shows a similar increase in magnitude above resting metabolism at low temperatures as at high temperatures. This additive effect of activity on metabolic rate however appears to be confined to animals which normally encounter severe cold in the wild or which have become acclimatised to cold. For example Janský (1959) found that <u>Microtus arvalis</u> showed this additive effect while <u>Clethrionomys glareolus</u> did not and he concluded that it was the difference in habitats between the two species which required <u>Microtus</u> to become more acclimatised to colder conditions than <u>Clethrionomys</u>, which lived in nature under more sheltered conditions.

It seems likely that the additive effect noted above is a result of the heat produced by voluntary activity failing to replace the thermogenesis effected not by shivering but by noradrenalin secretion. Since Arvicola has been shown (Sections 1 and 3) to spend approximately 75% of the winter at temperatures of 10°C. or above it is questionable that the voles need to acclimatise to cold by noradrenalin secretion, and if they were to do so the figures of Janský (1973) suggest that the increase in metabolism by this means of voles acclimatised at 10°C. would be slight.

In consequence of this it is concluded that Arvicola should not show the additive effect on metabolic rate of the additional energy requirements of activity at low temperatures, and that the initial assumption that voluntary activity replaces thermogenesis by shivering is valid.

5.3 Metabolic Cost of Pregnancy and Lactation.

It had been hoped that estimates independent of published work could have been made of the metabolic cost of both pregnancy and lactation from data obtained from pregnant females brought into the laboratory and housed within the respirometry chambers. The chambers, containing hay and cotton wool as nesting material, were blacked out and placed inside larger laboratory cages within which water and food were provided in excess of requirements. The pregnant females were thereby encouraged to give birth within the respirometry chambers which were to have been transported to the experimental situation and there tested for the oxygen consumption of mother and young without directly handling either.

Several pregnant females were brought in from the wild and took up residence within the artificially darkened respirometry chambers but both the females which were observed to give birth devoured their young within twenty four hours of parturition. On the first of these occasions it was considered that a respirometry experiment on the day prior to birth which was intended to evaluate the maternal respiratory cost in late pregnancy, might have occasioned unusual stress for the female and possibly initiated a premature birth. Subsequent females were therefore not experimented upon while pregnant, but even so no young survived the first day of birth. The lack of respiratory data for both pregnancy and lactation in the present study necessitates that an estimate of this important energetic cost be made from published work.

5.3.1. The Metabolic Cost of Pregnancy

The observations of both Blaxter (1962) on sheep and Trojan (1969) on Microtus suggest that the tissues of young in utero respire at the same rate per unit weight as the mother, and that it is only after birth and particularly after the young first begin to suckle that an increase in metabolism above that of the maternal tissue actually occurs. Kaczmarski (1966) found in Clethrionomys the increase in food assimilation of the female in pregnancy above that of the non-pregnant female to average 24% over the 18 day period of the pregnancy as a whole. This appears to indicate an increase in total energy cost during pregnancy in excess of the combined effect of a rise in total respiration due to bodyweight increase plus the calorific value of the young and placental membranes at birth. For example Trojan (1969) reports that in *Microtus arvalis* the pregnant female shows a 9.93% increase in respiration over the non-pregnant female. If a similar increase were to be assumed for *Clethrionomys*, then over an 18 day pregnancy, the respiratory cost to the pregnant female at the increased weight plus the calorific value of 10.34 kcals/pregnancy (Kaczmarski, 1966) of the young and placental membranes at birth would represent an energetic cost of 13.21% higher than that of the non-pregnant female. This figure however is little over half that which Kaczmarski (1966) reported for the average increase of food assimilation of a pregnant female over a non-pregnant female.

Migula (1969) found *Microtus arvalis* to increase its food assimilation during pregnancy by 32% compared with the non-pregnant female. However the non-pregnant females were kept in an experimental chamber without nesting material, while this was provided in the chambers of the pregnant females. The respiration rate of the non-pregnant females was reduced by 20% to allow for the absence of nesting material and to permit a comparison with the data for the pregnant females. The experiments were conducted at 20°C. At this temperature Trojan (1969) found that in *Microtus arvalis* the provision of a nest reduces the energy requirement by only 11.1%. If a reduction of 11.1% instead of 20% had been made, Migula's (1969) figures for pregnancy cost of an increase above the non-pregnant female demand of 32%, and for lactation cost of 133%, would have been closer to Kaczmarski's (1966) figures for C. glareolus of 24% and 92% respectively.

In the present study it is assumed that the pregnant female will have an increased energy requirement of 24% above that of the non-pregnant female. In the calculation of the energy requirement of pregnant females the weight of the female immediately prior to pregnancy was estimated and the respiration rate for a vole of this weight was calculated and multiplied by 1.24 over the period of pregnancy. This period was estimated at 25 days on the basis of the investigations of Herfs (1939) and Ryder (1962) which suggest a period ranging from 20 to 28 days.

From the energy requirement calculated by the means described above the maximum tissue production of embryos and placental membranes was deducted as these had already been included in the estimate of tissue production in Section 4.2, and the remainder is entered as the respiratory cost of the pregnant female.

Summary to Section 5.3.1

The total energy assimilation of the pregnant female (E) is estimated as being 1.24 times the energy respired by a non-pregnant female (e), on the basis of the estimate of Kaczmarski (1966) on Clethrionomys, over a gestation period of 25 days.

$$1.24e = E$$

The maternal respiration cost (m) is assumed to be equal to the total energy assimilation cost minus the tissue production of embryos and placental membranes (P) which has been included in the production estimate of section 4.2

$$m = E - P$$

5.3.2. The Metabolic Cost of Lactation

Kaczmarski (1966) found the cost of lactation in Clethrionomys glareolus to represent an average increase of 92% as compared with that of the non-breeding control female over a period of 18 days.

In the present study Kaczmarski's (1966) figure is assumed and the daily energy demand of a non-breeding female of the same bodyweight as the lactating female is multiplied by 1.92 to give an estimate of the total energy requirement of the lactating female. The period of lactation is assumed to be 18 days in Arvicola also, on the basis of the estimates of Ryder (1962) and Stoddart (1968) of between 13 and 20 days.

However a large percentage of this energy requirement represents the production of milk which is in turn assimilated by the suckling young and used for their growth and respiration. Trojan (1969) has estimated the respiratory cost to the lactating female in M. arvalis as being 20.4% above that of the non-breeding female of the same weight. In the present study this percentage has been assumed to apply to Arvicola and regarded as being a true respiration increase of the mother.

Thus the energy assimilated by the lactating female is regarded as being 1.92 times the energy assimilated by the non-lactating female of the same bodyweight. The true respiration increase of the lactating mother is regarded as being 1.204 times the energy assimilated by the non-lactating female. The difference in calories between the total lactation demand and the respiration of the lactating mother is attributed to milk production and is included here in the energy demand of the suckling young and not of the mother.

The digestibility of milk by the suckling young is assumed to be 100%. While no figures are available concerning the assimilation efficiency of milk by suckling voles, it can be expected to be of a very high order. The tissue production of the young from birth until weaning has already been included in the population production calculation of Section 4.2. It is therefore deducted from the lactation cost attributed to the suckling young. The remainder of this cost represents the respiration costs of the young prior to weaning.

Summary to Section 5.3.2.

The total energy assimilated by the lactating female (E) is estimated as being 1.92 times the energy respired by a non-breeding female of the same weight (e) for a period of 18 days, on the basis of Kaczmarski's (1966) investigations on Clethrionomys glareolus.

$$1.92e = E$$

The maternal respiratory cost (m) is assumed to be 1.204 times the energy respired by a non-breeding female of the same weight (e), on the basis of Trojan's (1969) investigations on Microtus arvalis.

$$1.204e = m$$

The energy ingested by the suckling young as milk (y) is estimated by subtracting the maternal respiratory cost from the total energy assimilated.

$$E - m = y$$

The assimilation efficiency of milk by the suckling young is assumed to be 100%, the assimilated energy (Y) therefore being equal to the ingested energy.

$$Y = y = E - m$$

The assimilated energy of the young is equal to the sum of their tissue production (P) and their respiration (r).

$$P + r = E - m$$

The tissue production of the young has been estimated previously in Section 4.2 and is deducted from Y to give r, which is expressed as the energy respired by the suckling young.

$$r = E - m - P$$

Discussion on Section 5.3

Kaczmarski (1966) did not continue the investigation of the energy assimilated by the lactating female after weaning.

In the present study it is assumed that the very high levels of energy consumption at the end of lactation on the 18th day fall immediately to the non-breeding level. Such an immediate return to the control figure in energy assimilation seems unlikely however and the level of post-weaning, maternal energy assimilation requires further study.

The level of respiration of both pregnant and lactating females has been calculated on the assumption that the females concerned do not differ in their mean level of activity from non-breeding females. This assumption is considered to be realistic although in the enclosure pregnancy the external activity of the mother was reduced considerably for two or three days following parturition.

It is possible that the respiratory cost of both breeding and non-breeding females in Kaczmarski's (1966) experiments was artificially low since food was provided and no foraging activity was required by the voles to gain an adequate supply of food. This would have the effect of increasing the relative costs of pregnancy and lactation when expressed in terms of the requirements of a non-breeding female. In the wild however additional foraging activity may be required of the voles to satisfy the costs of reproduction which would have the effect of increasing the relative energy costs of the breeding female in terms of the requirements of the non-breeding female.

Further study is required to investigate the external activity levels of pregnant and lactating females.

5.4 The Daily Respiration Demand (D.R.D.)

In this and in the subsequent sections on daily and 20 day period energy requirement the data on metabolic rate calculated in Sections 5.1 to 5.3 are related to the duration of rest, of low and high energy activity and to the temperature at which these activities take place. Section 3.2 has dealt with the number of hours during each 20 day period which the average vole spends resting within its nest, the mean temperature of the nest, together with the number of hours spent in low and high energy activity outside the nest, and the mean external temperature at which they take place.

The method used to calculate the mean temperature for the 20 day period from the range of temperatures and their frequency has been described in Section 3.2. It had been expected that the use of the original data would produce a more accurate estimation of the daily respiration demand than would its calculation from the sample mean multiplied by the total number of hours in the sample. In fact however the estimates of the total respiration cost of the model population calculated for seven 20 day periods during the winter by each method differed by only 0.076 ± 0.033%, an error which was less than the rounding-off errors inherent in the calculation of the number of hours of low and high energy activity for each 20 day estimate in the first instance. Since the calculation using the data on mean temperature is very much quicker and simpler than that using the entire data all subsequent daily and cumulative energy budget estimates were calculated using the mean experienced temperature and not the range of temperature.

The daily respiration demand for a vole during a "20 day" period is calculated by summing the energetic cost of rest, and of low and high energy activity. A hypothetical example is given below for a vole of 200 g. bodyweight during the summer season.

Example

"20 day" period of 20 days = 480 hrs.

Rest hrs.	Rest mean temp °C.	Low energy Activity hrs.	Low energy Activity mean temp °C	High Energy Activity hrs	High Energy Activity mean temp °C.
300	20	150	12	30	12

	Rest	Low energy Activity	High Energy Activity
Rate/g	N.M.R.	N.M.R. x C_1	N.M.R. x C_2
ccO_2	1.496	1.761 x 1.438	1.761 x 2.200
"20 day" /g.	(1.496) 300	(1.761 x 1.438) 150	(1.761 x 2.200) 30
200 g.	200(1.496)300	200(1.761 x 1.438)150	200(1.761 x 2.200)30

D.R.D. ccO_2

$$\frac{200(1.496)300}{20} + \frac{200(1.761 \times 1.438)150}{20} + \frac{200(1.761 \times 2.200)30}{20}$$

D.R.D. ccO_2 4,488 + 3,798 + 1,162

D.R.D. kcals 9,448 x 0.0048 = 45.35 kcals

5.4.1 Seasonal Changes in D.R.D. for a vole of Standard Bodyweight.

The mean daily respiration cost for a non-breeding vole weighing 180 g. was calculated for each 20 day period throughout the year on the basis of the mean temperature values and activity proportions summarised in section 3.2, and assuming the N.M.R. and A.M.R. rates calculated for the summer and winter populations of sections 5.1 and 5.2. Two 20 day periods were omitted. These were the periods nearest the change of N.M.R. from the summer to winter population rates as it was considered that this change would be gradual. The change from the winter pelage to that of the summer is estimated to occur at May 1, and from the summer pelage to that of the winter at November 1, the approximate periods of spring and autumn moult reported by Buhlow (1970).

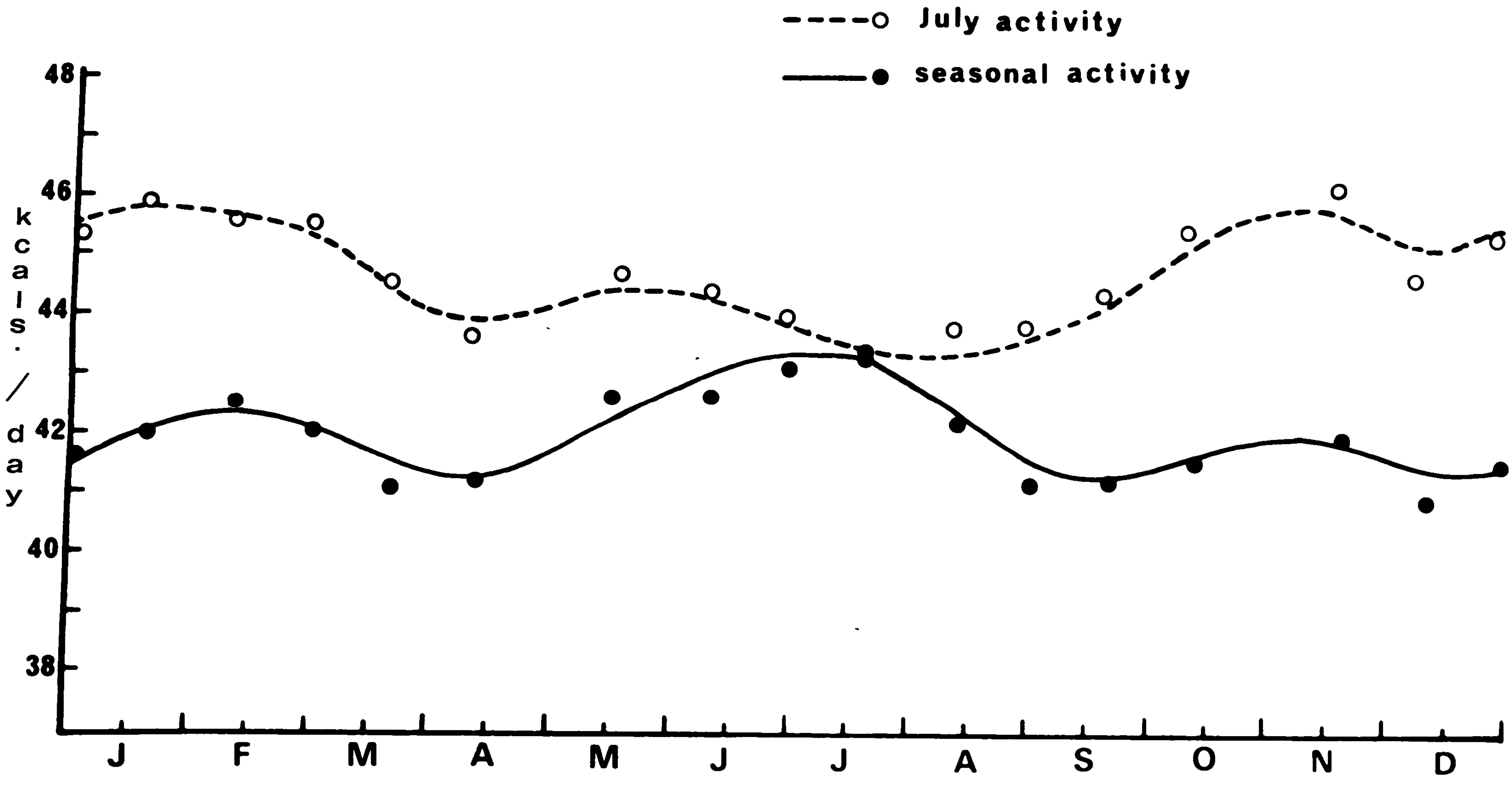
The result of these "20 day" calculations are divided by their constituent number of days and converted to their calorific equivalent to give the D.R.D. for a vole of 180 g. at regular intervals throughout the year. These periodic estimations of D.R.D. are shown in Figure 36. A trend line, drawn by eye, which evens out the more localised temperature and activity fluctuations has been added.

The D.R.D. rose from a level of 41.6 kcals in early January to a winter maximum of 42.5 kcals in mid-February. This was followed by a decline to a level of 41.15 kcals in late March and early April. In late spring the D.R.D. increased once more and it continued to do so until mid-summer. The maximum for the year of 43.3 kcal was reached in late July. The D.R.D. then decreased to a minimum of 41.15 kcals in the late summer and rose again to a level of 42.1 kcals in November, whereupon it declined slightly to the early January level of 41.6 kcals.

Figure 36

Variation in the Daily Respiration Demand of a non-breeding vole of 180g bodyweight with time of year.

The Daily Respiration Demand expressed in kcals/ individual for a non-breeding vole of 180g is estimated at 20 day intervals throughout the year. The D.R.D. has been estimated twice, firstly with the parameter of the duration of daily activity permitted to vary seasonally and secondly with this parameter fixed at the July level of 9.1 hrs/day. A spring moult is assumed to occur at the beginning of May and an autumn moult at the beginning of November. The estimated D.R.D. at these two periods has been omitted. The trend lines have been drawn by eye.


July activity
seasonal activity
kcals./day
48
46
44
42
40
38
J
F
M
A
M
J
J
A
S
O
N
D

These fluctuations between 41.15 and 43.3 kcals/day are a result of the interaction of the seasonal variation in pelage thickness, in temperature and in the duration and intensity of activity.

Figure 36 shows also what the estimated D.R.D. would have been had the duration and intensity of activity remained static at the July level throughout the year.

The minimum D.R.D. would then have occurred during mid-summer (43.3 kcal) and the maximum during late autumn (46.3 kcal). The level of the D.R.D. would then be an inverse function of the seasonal temperature pattern except between April and May, where the rise in D.R.D. resulted from the relatively high summer metabolic rate, probably a consequence of the spring moult. The autumn moult was not indicated by a distinct break in the curve like that in the spring as the relative reduction of late autumn metabolic rate was outweighed by unusually cold temperatures during this period. The cold Novembers of 1971 and 1972 resulted in a higher D.R.D. occurring at this period than in January as the latter month in 1972 and 1973 was relatively mild.

A comparison between the estimations of D.R.D. where the activity variable is excluded with those where it is included will help to explain the irregular pattern of the seasonal trend of the latter.

Thus the increase in the duration of activity between early January and February resulted in a rise in D.R.D. between these months while between February and mid March a decrease in the duration of activity coupled with an increase in nest and external temperature resulted in a decline in D.R.D. in the latter period. An increase in temperature had the effect of counter-balancing an increase in activity between mid March and mid April with little resulting change in D.R.D. while in May and June the advantage of rising temperature was outweighed by increased activity and a thin summer pelage, factors which together caused a seasonal rise in D.R.D. Increased activity outweighed the advantage of rising temperature to cause a further rise in D.R.D. in July.

In August and early September the decrease in activity resulted in a decrease in D.R.D. while the temperature, although falling below the July maximum, was still fairly high. Falling nest and external temperature outweighed the effect of reduced activity in October where a rise in D.R.D. occurred. A further rise in D.R.D. took place in November where the effect of falling temperature and slightly increased activity was only partially offset by the increase in pelage thickness. The milder weather of December resulted in a slight fall in D.R.D., a fall which was reversed in the more severe weather of January.

If the duration and intensity of activity which took place in July were to be continued in January the D.R.D. of the vole would be 9.11% above the actual estimated figure for the latter month.

In the late spring and late autumn when the change from summer to winter metabolic rates takes place, the summer rate of metabolism exceeded the winter rate by an average of 9.4%. This increase, which is calculated including both N.M.R. and A.M.R. for the same period at both the summer and winter metabolic rates, ranged from 8.10 - 10.73%.

The increase in pelage thickness combined with the reduction of the duration of diel activity resulted in a saving in D.R.D. during mid-winter of 17 - 20% in comparison with the summer respiration levels. That this saving in fact resulted in an actual reduction in D.R.D. from July to January of only 2.9% was entirely due to the increase in respiratory cost caused by the low winter nest and external temperatures.

Summary to Section 5.4.1

The daily respiration demand of a non-breeding vole of constant bodyweight varied seasonally as a result of changes in pelage thickness, temperature, and the duration and type of external activity over a range of 2.15 kcals or approximately 5% of the mean D.R.D. over the year as a whole.

Three periods of relatively high energy demand, above 42 kcals/day, were observed, these being in late winter, in the first half of the summer and in late autumn. The last mentioned was perhaps a response to the cold weather at this time during the study period. Three periods of reduced energy demand, below 41.5 kcals/day, were noted, one in early spring, the second in late summer and the third in early winter, the last mentioned perhaps resulting from the unusual mildness of the weather at this time. The D.R.D. in summer is considered to be as high or perhaps higher than during the winter.

The energy saving to the voles resulting from the increase in pelage thickness and the reduction in activity, which were of a similar order of magnitude, appear to have compensated almost exactly the fall in environmental temperature in winter and kept the D.E.B. at a stable level throughout the year.

Discussion on Section 5.4.1.

The increased thickness of the fur in winter will mean that, in a vole of a given bodyweight, the proportion of the bodyweight which is metabolically active during the summer is greater than it is during the winter. A vole of 180 g. therefore would show a higher respiration rate during the summer than during the winter even within the zone of thermoneutrality, as in summer its naked bodyweight would be greater. There will be a tendency therefore to increase the summer respiration cost artificially above the winter level in Figure 36.

5.4.2. Changes in the Daily Respiration Demand with Age.

Figure 37 shows the estimated D.R.D. for a non-breeding vole from the time of weaning until death. The weight at weaning is here taken to be 45g. and the vole is assumed to to follow the duration and intensity of activity of the population as a whole. This activity estimate is probably incorrect when applied to voles younger than 8 weeks of age (see Section 2.1). However no data is available to allow a more accurate estimate of activity at this early age. The changes in nest and external temperature and in the condition of the pelage are included in the calculation and it is assumed that the young vole is a member of the first cohort of the breeding season and is weaned by approximately June 10. The initial rates of growth assumed are lower than those suggested in Section 4 and are intermediate between these and the rates suggested by Stoddart (1968).

The D.R.D. is calculated to be 23.0 kcals on weaning at approximately 18 days of age. By 5½ weeks the vole has grown to 107 g. and has a D.R.D. of 34.1 kcals. This has increased to 40.7 kcals at 8 weeks when the vole is 160 g. The first five weeks after weaning therefore correspond to an increase in weight by a factor of times 3.56 and an increase in D.R.D. by a factor of times 1.77 or approximately half the rate of increase of the weight.

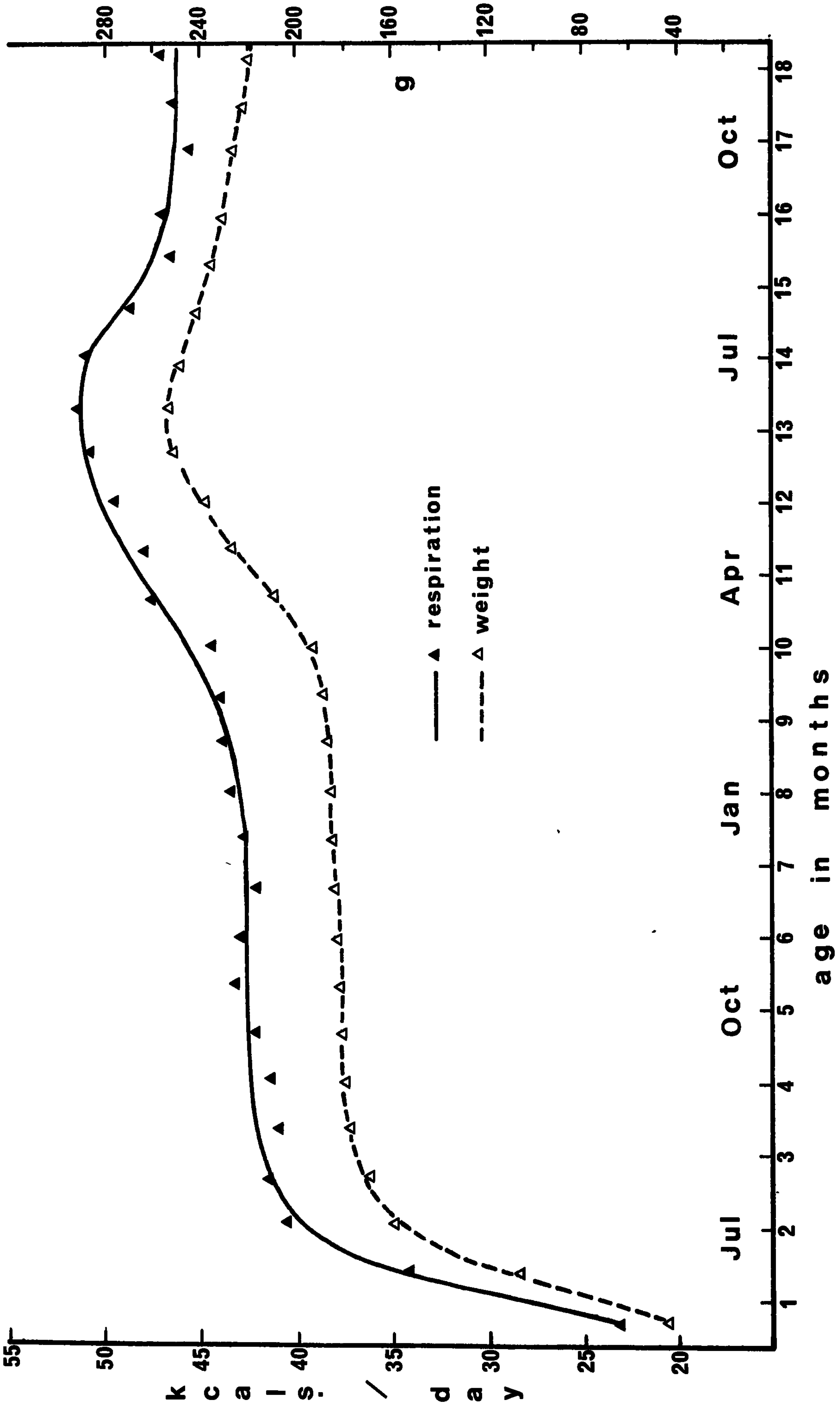
From the age of 8 weeks to that of approximately 9 months, the period of autumn and winter, the bodyweight increases from 160 g. to 186 g., and the D.R.D. from 40.7 kcals to 43.8 kcals. Here, over a period of 7 months, the increase in D.R.D. is only 7.6%. This phase represents a period of respiratory stability.

In early spring the vole begins to grow once more and reaches a maximum bodyweight in June of 254 g. at the age of

Figure 37

Changes in the Daily Respiration Demand of a non-breeding vole with age.

The Daily Respiration Demand of a non-breeding vole expressed in kcals/individual has been estimated at 20 day intervals from the approximate time of weaning until that of death. In the calculation the parameters of temperature, activity and moult are assumed to reflect those of the population as a whole. At each interval the approximate bodyweight of the vole has also been shown. The trend lines have been drawn by eye.


k cals. / day
55
50
45
40
35
30
25
20
g
280
240
200
160
120
80
40
respiration
weight
Jul
Oct
Jan
Apr
Jul
Oct
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
age in months

13½ months, and a maximum D.R.D. of 51.29 kcals. This represents an increase in bodyweight of 36.6% over 4½ months and an increase in D.R.D. of 17.1%, approximately half the rate of increase of the weight, as in the previous summer.

After 14 months of age both bodyweight and respiration decline, until at the age of 18 months, at the commencement of the second winter, the bodyweight has decreased to 218g. and the D.R.D. to 47.0 kcals. Gębczyński (1965) has already reported that the respiration rates of old animals tend to be below those of young adults of similar weight. No correction is made for this possibility in Figure 37, the D.R.D. at ages greater than 16 months may therefore be unduly high.

5.5 The Respiration Demand of the Model Population.

The total respiration for every vole in the model population was calculated over each 20 day period individually in the way demonstrated in the example of Section 5.4, and the values obtained were summed to give the population respiration for that 20 day period. Where a vole was observed to inhabit the study area for only part of the 20 day period its contribution to the population respiration was assessed on the basis of its assumed duration of residence in the population.

The cost of reproduction was calculated in the manner described in Section 5.3 and added to the population cost where appropriate.

Since most voles weighed between 170 and 190 g. in the winter the respiration of these voles was assessed in simple proportion to their bodyweight. The respiration of voles outside this weight range was calculated assuming the respiration per gram bodyweight to follow the relationship $R = aW^{-50}$.

From the 11 January until 31 May the population respiration was calculated, firstly on the data for the observed 1971 population, and secondly for the predicted 1973 population data, as described in Section 4.

The respiratory cost of the model population for the 380 m. stretch of stream at 20 day period intervals is given in Table 13. It has been divided into separate adult, first litter juvenile and second litter juvenile components where appropriate. The respiration totals for the predicted data for 1973 are given in parenthesis.

Table 13. The Respiration Cost of the Model Population for the 20 day Periods.

Period	Total kcals	Adult	First Litters	Second Litters
11-31 Jan	4,841.8 (6,586.8)			
1-20 Feb	3,781.4 (5,462.7)			
21Feb/ 10 Mar	2,660.1 (4,203.0)			
11-31 Mar	3,374.8 (5,217.4)			
1-20 Apr	3,550.5 (5,421.9)			
21 Apr/ 10 May	4,869.2 (6,398.5)			
11-31 May	5,263.5 (6,269.5)			
1-20 Jun	7,368.3	7,190.5	177.8	
21 Jun/ 10 Jul	13,271.7	6,206.9	7,010.4	54.4
11-31 Jul	18,609.4	6,071.1	10,421.7	2,116.6
1-20 Aug	14,415.1	3,357.1	5,572.6	5,485.4
21 Aug/ 10 Sep	12,189.2	2,908.9	3,759.1	5,521.2
11-30 Sep	9,577.5	2,857.0	2,576.7	4,143.8
1-20 Oct	9,257.4	2,831.6	2,600.3	3,825.5
21 Oct/ 10 Nov	9,876.4	3,099.5	3,271.7	3,505.2
11-30 Nov	7,723.1	1,921.3	2,607.9	3,193.9
1-20 Dec	7,485.8	1,870.2	2,513.6	3,102.0
21 Dec/ 10 Jan	7,281.2			

Annual Total

145,396.4(156,614.9) kcals/380 m. of stream

The annual total represents respired energy of 191.3 (206.1) kcals/m^2 of feeding range or 76.5 (82.4) kcals/m^2 of locomotory range. The adult component comprised 50.85 (54.4)% of this annual total, the first litter juveniles 27.9 (25.9)%, and the second litter juveniles 21.3 (19.8)%.

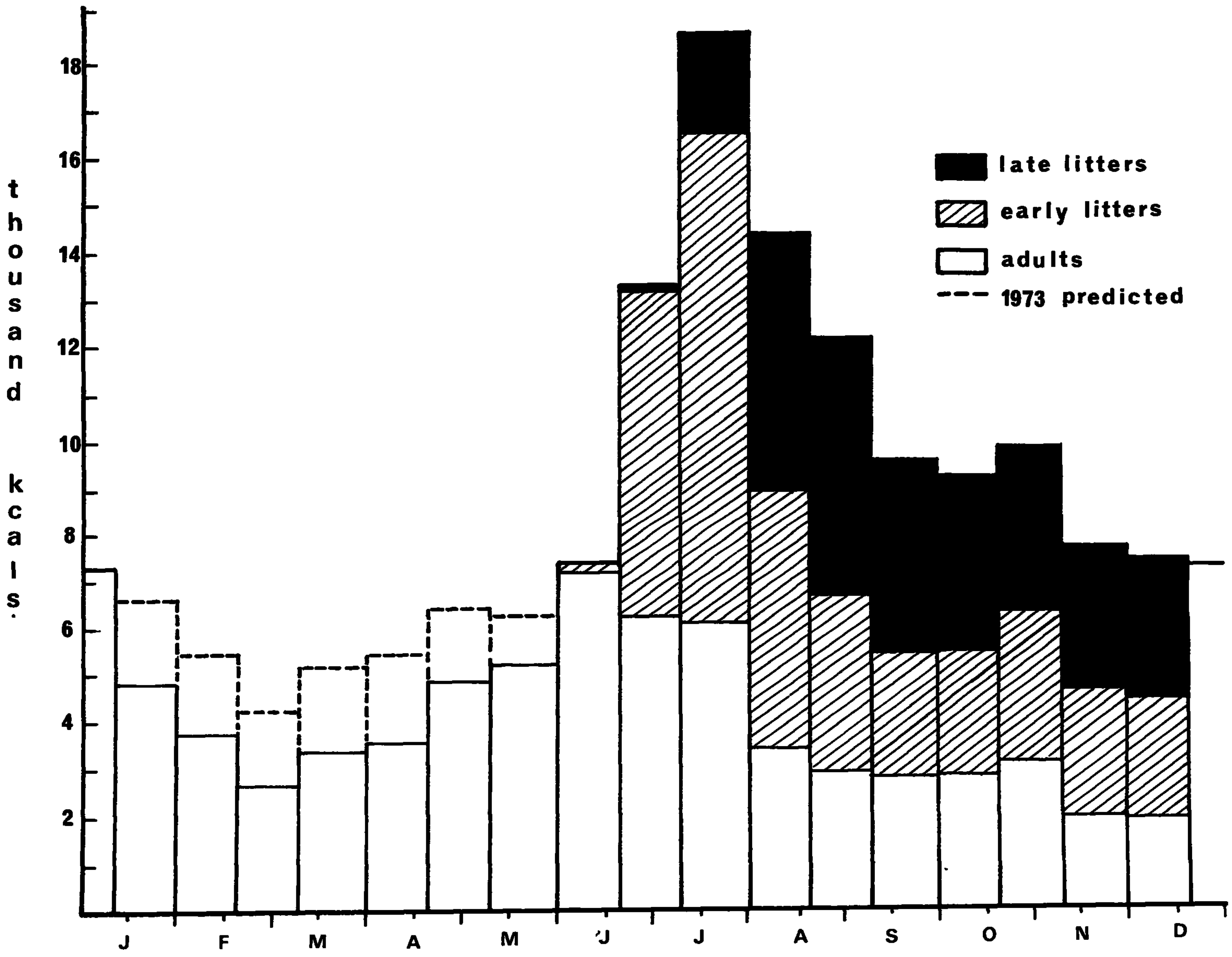
The 20 day changes in population respiration are shown in Figure 38.

The combined respiration of young and old adults fell from 346.7 kcals/day for the period Dec. 21-Jan. 10 over the

Figure 38

Changes in the Respiration Demand of the model population with time of year.

The respiration demand of the model population expressed in thousands of kcals is estimated for consecutive periods of approximately 20 days. The total respiration demand has been subdivided into components for adults, First Litter juveniles and Second Litter juveniles. The respiration demand for the predicted 1973 population has also been shown.


thousand kcals.
18
16
14
12
10
8
6
4
2
J
F
M
A
M
J
J
A
S
O
N
D
late litters
early litters
adults
1973 predicted

subsequent weeks of late winter, owing to the decrease in the number of voles, to reach a minimum for the year, during the period Feb. 21 - Mar. 10, of 147.8 (233.5) kcals/day.

The increase in the weight of individuals during the spring resulted in an increase in population respiration to a level of 177.5 (271.1) kcals/day for the period 1 - 20 April. From April 21 - May 10 continued growth combined with the short term spring immigration of male voles resulted in a further increase in population respiration to 243.5 (319.9) kcals/day.

The short-term immigration of May increased the resident population of the study area by two individuals. The addition of these two voles plus the advanced state of the first pregnancies resulted in a rise in population respiration to 368.4 kcals/day during the period 1 - 20 June. This total includes the respiration of the first of the suckling young, some 8.9 kcals/day. The first litter juvenile component rapidly increased in importance and during the period 21 June - July 10 constituted 52.8% of the population respiration. The population respiration during this period had risen to 663.6 kcals/day and included a component of 2.7 kcals respired by the first of the second litter juveniles.

The maximum population respiration of 886.2 kcals/day was reached during the period of 10 to 31 July. The adult component here comprised 32.6% of the total, the first litter juveniles 56.0% and the second litter juveniles 11.4%.

During the period 1 - 20 August a decline in the numbers of adults and first litter juveniles was only partially compensated by the growth of second litter juveniles and consequently the population respiration fell to 720.8 kcals/day. By the period 21 August - 10 September the component from the second litter juveniles constituted 45.3% of the total and represented the largest individual component both for this period and for those subsequently until the components ceased to be distinguished from 21 December onwards. The population respiration had fallen to 580.4 kcals/day during 21 August - 10 September and continued to decline owing to the decrease in population numbers being only partially counterbalanced by the growth of the juveniles.

The annual population respiration total of 145,396.4 (156,614.9) kcals/380 m. of stream may be used to give a better approximation of the population respiration of vole populations from other streams and in other years when it is expressed in terms of kcals per pre-breeding female vole. The numbers of female voles may then be assessed prior to breeding in late March or early April and the population annual respiration total estimated for a given area by multiplying the number of females by 48,465.5 (52,205.0) kcals, the result calculated here per pre-breeding female. It is suggested that an approximate mean of these figures, namely 50,000 kcals/pre-breeding female, be employed in this respect.

Table 14 gives a summary of the population daily respiration demand in kcals for each 20 day period and also the percentage of the total represented by the adult, first litter juvenile and second litter juvenile components, where these are appropriate.

Table 14. Daily Respiration Demand of the Model Population.

Period	kcals/day	% Adults	% 1st Juveniles	% 2nd Juveniles
11-31 Jan	230.6 (313.7)			
1-20 Feb.	189.1 (273.1)			
21 Feb-10 Mar.	147.8 (233.5)			
11-31 Mar.	160.7 (248.4)			
1-20 Apr.	177.5 (271.1)			
21 Apr-10 May	243.5 (319.9)			
11-31 May	250.6 (298.5)			
1-20 Jun	368.4	97.6	2.4	
21 Jun-10 Jul	663.6	46.8	52.8	0.4
11-31 Jul	886.2	32.6	56.0	11.4
1-20 Aug	720.8	23.3	38.7	38.0
21 Aug-10 Sep	580.4	23.9	30.8	45.3
11-30 Sep	478.9	29.8	26.9	43.3
1-20 Oct	462.9	30.6	28.1	41.3
21 Oct-10 Nov	470.3	31.4	33.1	35.5
11-30 Nov	386.2	24.9	33.8	41.3
1-20 Dec	374.3	25.0	33.6	41.4
21 Dec-10 Jan	346.7			

Discussion on Section 5

The amount of published work on the respiration and energy budget of Arvicola is small. Turkheim and Delost (1968) investigated the temperature range of the thermoneutral zone of Arvicola caught in late summer and acclimatised in the laboratory at a temperature of 20°C. They concluded that the thermoneutral zone lay between 28° - 31°C. in males and between 29° - 31°C. in females, with the minimum oxygen consumption being attained at 30°C. in both sexes.

In the present study the maximum experimental temperature used during the summer season was 28°C. Since nesting material was made available to the voles, which would have had the effect of raising the temperature slightly in their immediate vicinity, it is considered that the 28°C. experimental temperature was within the *Arvicola* zone of thermoneutrality.

Furthermore the findings of Turkheim and Delost (1968) that no difference exists in the oxygen consumption of male and female voles of similar bodyweight at basal metabolism seem to justify the assumption made in the present study that no correction is necessary with regard to the sex of the vole per se except during pregnancy and lactation.

Drożdż et al. (1971) conducted a comprehensive study of the R.M.R., A.D.M.R. and food assimilation efficiency of the spring and autumn populations of *A. t. terrestris*. The population they studied had a bodyweight range of 39 - 124 g. comprising both young and growing animals and in this last respect their investigation was comparable with the present study. However the average bodyweight of 104 g. of these voles during the growing season (Pelikán unpubl. in Drożdż et al. 1971) is in marked contrast to that of the present study in which a vole of 104 g. would have been only 4 weeks of age.

Drożdż et al. (1971) found the regression of respiration in cc.O_2/g/hr on bodyweight at R.M.R. to range between $75.0W^{-0.67}$ at 0°C. and $15.3W^{-0.44}$ at 20°C. In the present study the N.M.R. regression of respiration per unit weight on bodyweight for the summer population was found to range between $39.4W^{-0.54}$ at 3°C. and $12.3W^{-0.41}$ at 25°C. These figures are close to the level suggested by Hansson and Grodziński (1970) as being typical of the regression of respiration per unit weight on bodyweight of small rodents, when measured at A.D.M.R., which tend to oscillate round a level of $18W^{-0.50}$.

In the present study the regression of respiration rate of the whole animal (in cc. O_2/hr.) on bodyweight was found to be $18.4W^{0.51}$ when measured in the thermoneutral zone (28°C.). A weight exponent of this magnitude is considered by Hansson and Grodziński (1970) to be typical of small rodents. However Gridgeman and Héroux (1965) reported that the respiration to bodyweight exponent of $R = aW^b$ can be an unstable parameter and may be altered by a number of experimental conditions, particularly temperature. The difference between the exponents calculated in the present study and also those of Drożdż et al. (1971) and Hansson and Grodziński (1970) of a range from approximately $R = aW^{0.40}$ to $R = aW^{0.60}$, and the interspecific means of $R = aW^{0.67}$ to $R = aW^{0.75}$ suggested by Brody (1945), Prosser and Brown (1961), and Kleiber (1961) probably reflect the use of both growing and adult animals in the former studies, together with the variety of experimental conditions involved in these studies.

Drożdż et al. (1971) estimated the daily cost of maintenance determined by food assimilation experiments, to range between 126-181 kcal/kg$^{0.75}$ (average 152 kcal/kg$^{0.75}$/day), when feeding on a mixed diet. When corrections have been made for the lower external temperature of the natural population and for the reproductive cost of the population these authors suggest a Daily Energy Budget for a water vole of 104 g. of 25.5 kcals/day or 139 kcals/kg$^{0.75}$/day. The daily cost of maintenance of a vole of 104 g. in the present study would be rather higher, 33 kcals, or 180 kcals/kg$^{0.75}$. A vole of 104 g. in the present study would represent a young juvenile vole of only 4 weeks of age and the D.E.B. would not include a correction for reproductive cost but would include a high activity correction which may not be a realistic estimate for such a young vole.

The D.E.B. for a vole of 180 g. would be approximately 42 kcals, or 152 kcals/kg$^{0.75}$, and for a vole of 250 g. would be 50 kcals, or 142 kcals/kg$^{0.75}$. These figures for adult voles are in better agreement with the results of Drożdż et al. (1971) when expressed as kcals/kg$^{0.75}$/day than were those of a young vole of 104 g.

For adult voles in summer the N.M.R. value of daily maintenance costs at 30°C. would be 87.5 and 98.4 kcals/kg$^{0.75}$ for voles of 320 g. and 180 g. respectively. Such values which represent the nearest approximation to B.M.R. available in the present study are in fairly good agreement with the figure of 70 kcals/kg$^{0.73}$ suggested by Blaxter (1962) as an inter-specific mean to which specific results could be compared.

Drożdż et al. (1971) state that the increase in respiration when the ambient temperature was lowered by 1°C., over the temperature range of 0 - 30°C., amounted to 3.6% in both spring and autumn. In the present study this increase amounted to 2.9% for voles of 170 - 190 g. body-weight during the winter over a temperature range of 3° - 15°C., and from 2.18% (320 g. vole) to 3.35% (60 g. vole) per 1°C. during the summer, over the temperature range of 3° - 28°C. The figures of percentage respiration increase of Drożdż et al. (1971) are rather higher than those of the present study and are likely to reflect both the smaller size of their voles and the lower minimum temperatures in their investigation.

Little work has been published on the active metabolic rates of Arvicola, although Vybíral (in litt. Drożdż et al. 1971) reports that heat losses of the voles in water are higher by approximately 105% than they are during normal external activity on land. Drożdż et al. (1971) assumed that water voles spend 25% of their external activity in the water while the writer considers this figure to be rather high and prefers the estimate of between 10 - 15%. Much of the heat lost while in the water may be compensated for by the energy expended during swimming and in the actions of shaking the body and grooming the fur that follow emergence from the water. These activities are recorded in the present study and included in the estimation of D.E.B. A further correction for heat lost while in the water may thus be unnecessary. The importance of heat losses incurred while swimming or even resting in the water, and which may be particularly pronounced in winter, are still a matter for conjecture.

The estimation of metabolic rate during both low and high energy activity in the present study is far from satisfactory, particularly the latter. Although it is considered that the method employed in the estimation of low energy A.M.R. may yield valuable results when applied over a larger number of experiments, the estimation of high energy A.M.R., particularly when applied to an amphibious vole, presents far greater difficulty.

Although the number of hours which the voles experience at temperatures lower than -5°C. are comparatively few, and the resulting error in estimating the 20 day energy demand likely to be small, the assumption that low energy A.M.R. will be 473 cc./hr. for a 180 g. vole in winter at temperatures as low as -10°C., and that a high energy A.M.R. will be 737/hr. at these low temperatures is open to considerable doubt. The Kalabukhov-Skvortzov respirometer is not suitable for N.M.R. estimation at these low temperatures, nor is it reasonable to expect the experimenter to remain motionless at these temperatures for any length of time in the estimation of low energy A.M.R. The use of the Morrison respirometer together with the automatic measurement of activity (Morrison and Grodziński, 1968) would appear to be necessary for further investigation of N.M.R. and A.M.R. at sub-zero temperatures.

Drożdż et al. (1971) assume that the increase in assimilation costs of reproducing females are in the same proportion in Arvicola as in Clethrionomys and Microtus.

This assumption is also made in the present work, nevertheless an investigation into the reproductive cost to the female Arvicola would have been an advantage had it been possible. Stoddart (1968) successfuly weighed young A. t. reta at frequent intervals from birth until several weeks after weaning without losing the litters through maternal cannibalism. Yet this interference with the lactating female might be expected to present as much stress as would a respirometry experiment. If the pregnant females were placed in a Morrison respirometer and handled as little as possible at the critical period of and subsequent to parturition it is considered that it should be possible to evaluate the reproductive cost to the female Arvicola.

The daily energy budget has been worked out in detail for Clethrionomys glareolus and for Apodemus agrarius by Górecki (1968b, 1969) and evaluated as a function of body size for Microtus agrestis by Hansson and Grodziński (1970). The D.E.B. of these small rodents whose bodyweight ranges from 12-30 g. is usually considered to be in the region of 8 - 16 kcals/day. Since the bodyweight of voles in the present study ranged from 55 - 320 g., nearly ten times greater on average than those of small mice and voles, a comparison of the present results with those of these very small rodents does not seem appropriate.

Drożdż et al. (1971) calculated the D.E.B. for a vole weighing 104 g. as 25.5 kcals, assuming an external activity lasting for 23% of the diel period, while the present estimate of 33 kcals assumes an external activity proportion of 34%. Since the nest and external temperature environments were similar in both estimates it is probably the differences in the proportion of activity which account in part for the differences in estimated D.E.B. between the two studies.

A rodent of similar size to *A. t. amphibius* is the mole rat *Spalax leucodon*. Górecki and Christov (1969) using animals averaging 178 g. in weight, calculated the D.E.B. for this rodent for an autumn day to be 34.6 kcals. In the present study the D.E.B. of *A. t. amphibius* of 180 g. has been found to vary between 41.15 - 43.3 kcals during the year as a whole. Górecki and Christov (1969) comment that the metabolism of fossorial rodents such as *Spalax* is almost invariably lower than that of other groups of rodents and that the B.M.R. of 46.4 kcal/kg$^{0.75}$/day was only 66% of the metabolic rate to be expected from Kleiber's (1961) equations.

The figures presented in the present study therefore suggesting a D.E.B. ranging from 25.5 kcals at 55 g. bodyweight to 50 kcals at 250 g. bodyweight are higher than those of *A. t. terrestris* (Drożdż et al., 1971) by 29.4% and those of *Spalax leucodon* (Górecki and Christov, 1969) by 21.4% although neither result is strictly comparable to the present figure.

Mezhzherin (1964) found the bodyweight of the genus *Sorex* to decrease in winter and concluded that a reduction in size was an advantage to the shrews in the cold season for it reduced the absolute food requirement of each individual at a time when the invertebrate food supply was scarce. No such reduction in size has been noted in Arvicola in the present study, the average vole bodyweight in winter being as high then as at any time in the year with the exception of the spring and early summer. The late autumn and winter does however represent a period of stability in D.R.D. with very little increase in this over a period of nearly six months, from early September until late February. Whether this is a response to a shortage of food or to the unsuitability of the season for entering breeding condition is uncertain.

It is suggested that the figure of 50,000 kcals per pre-breeding female is a useful guide in the estimation of annual population respiration when applied to A. t. amphibius. This figure may be multiplied by the number of females in a given area in late March or early April to give an estimation of the likely population respiration of that area throughout the year.

CHAPTER 6

ESTIMATE OF PRIMARY PRODUCTION AND FLORAL COMPOSITION OF THE FEEDING RANGE

6. Estimate of Primary Production and Floral Composition of the feeding Range.

Introduction

The vegetation within the lateral feeding range of Arvicola represents a food resource which is not being utilized by the domestic cattle and sheep grazing the carrs of Low Copelaw Farm. This vegetation does however carry populations of other herbivorous animals besides Arvicola, principally populations of Microtus agrestis, largely confined to the upper part of the bank, a small number of Gallinula chloropus L. and a variety of herbivorous invertebrates and their predators. In its principal feeding area the Arvicola population is without significant feeding competition from other vertebrates. It was decided to investigate the primary productivity of this zone in its capacity as a food source for Arvicola. It was hoped that an estimate of primary productivity on a seasonal basis would, when compared with the estimate of Arvicola food requirement, demonstrate if and when the food supply becomes a limiting factor in vole productivity. The investigation was carried out to assess:

i. Residual primary production of the lateral feeding range after feeding losses to herbivore populations.

ii. Residual primary production of the lateral feeding range plus feeding costs of Arvicola population, to give an estimate of primary production after feeding losses due to herbivore populations excepting Arvicola.

iii. Proportion of ii. actually available as food to Arvicola population.

Section 6 will be confined to an assessment of i.)The Residual primary production.

Methods Employed in Published Work.

Much published work on primary productivity estimates has been done by quadrat sampling at periods of maximum and minimum growth to give a harvest yield of the difference between the two (Gorham and Pearsall, 1956; Pearsall and Newbould, 1957; Bray et al., 1959; Bellamy and Holland, 1966). Wiegert and Evans (1964) have, however, shown that harvest yields may be insufficient in the estimation of primary production as no allowance is made for changes in dead material from one harvest to the next nor for the material lost from the sample by decomposition, especially in ecosystems with a rapid organic turnover. They have developed a method for estimating the net primary production of the aerial vegetation which requires data on the biomass of dead and living standing crop, at regular intervals, together with data on the rate of decomposition of dead material. Their method may be summarised as follows:

where t = time interval between successive harvests in days

a_1 = standing crop of dead material at first harvest

a_2 = standing crop of dead material at second harvest

b_1 = standing crop of green material at first harvest

b_2 = standing crop of green material at second harvest

r = instantaneous daily rate of disappearance of dead material during t and can be found from the equation $r = \frac{\text{Log e } (Wo/W1)}{t}$ where Wo and W1 are initial and final weights of dead material in a field trial for interval t where no biomass is added during t.

Let the amount of dead material disappearing during an interval = x,

$$1) \quad x = rt\,(a_2 + a_1) / 2$$

and where change in standing crop of green material = Δb

$$2) \quad \Delta b = b_2 - b_1$$

and where the change in standing crop of dead material = Δa

$$3) \quad \Delta a = a_2 - a_1$$

Then since Δa is the change in dead standing crop $X + \Delta a$ is the amount of material added to the dead standing crop = d.

$$4) \quad d = x + \Delta a$$

The production during t/unit area is then given by Y.

$$5) \quad Y = \Delta b + d$$

These expressions require the evaluation of green and dead biomass before and after the interval t together with that of the daily rate of decomposition of dead biomass r during that interval.

Traditionally square quadrats have been used in harvest sampling (Milner and Hughes, 1968), but van Dyne et al. (1963) have demonstrated that the use of circular sampling plots may be advantagous as the perimeter/area ratio is reduced and the "edge effect" less marked. Wiegert (1962) and Wiegert and Evans (1964) have investigated the optimum quadrat size for sampling grasses and herbs in relation to result accuracy and sampling effort and suggest that in Old Field grassland this figure is 0.187 m^2. (Wiegert, 1962), 0.05 m^2 for grasses alone, and 0.2 m^2 for herbs (Wiegert and Evans, 1964). Greig-Smith (1964) used a graph method to investigate the optimum number of quadrat samples in relation to result accuracy and sampling effort and found that above 25 samples there was little difference in subsequent sampling means and that the optimum for accuracy and effort combined was 25 - 30 samples. Milner and Hughes (1968) in their review of primary production methods conclude that the number of sample plots must depend upon the degree of precision required and suggest an error of 10% of the mean as an acceptable standard. Many workers have used contiguous line transect or grouped quadrat sampling to reduce the bias of the edge effect (Pearsall and Gorham, 1956; Wiegert, 1962) but this practice has been challenged by van Dyne et al. (1963).

Edwards (1965) has shown that vegetation samples can be kept in sealed polythene bags for several hours with only small losses of moisture and no significant loss of dry matter. Milner and Hughes (1968) conclude that hand sorting of the material into species should be completed and the sample dried to constant weight as rapidly as possible to prevent the activity of respiratory enzymes in the cut herbage. They suggest drying the cut sample in an air oven at temperatures from 80°C. - 100°C. which will dry the sample quickly without causing the loss of volatile organic compounds.

Method

Forty vegetation samples were cut to ground level with a pair of scissors from a quadrat, of dimension 20 x 30 cm. Twenty of these samples were taken with the 20 cm. dimension placed at the mean water level of the stream, and parallel to it, the samples taken at 20 m. intervals, an equal number from each bank. A further twenty quadrat samples were taken contiguous to the first set with their lower boundary held in common with the upper boundary of the first, in an attempt to reduce the influence of the edge effect. Twenty samples were therefore taken from a position of 0 - 30 cm. from the mean water level and twenty 30 - 60 cm. from it. The quadrat size of 0.06 m^2 is within the optimum quadrat size range suggested by Wiegert (1962) and Wiegert and Evans (1964) for sampling grasses and herbs.

Rectangular quadrats were used in preference to circular ones as the latter could be expected to produce a bias in sampling on what is likely to be a gradient of both species type and primary production in relation to distance from the water's edge.

The cut material from each quadrat sample was placed in a polythene bag and removed to the laboratory where it was washed in lukewarm water over a 1 mm. mesh sieve until no trace of surface soiling remained. Excess moisture was removed by shaking and air drying for a short period whereupon the material was separated into its constituent species and subdivided into three categories; i) green shoots and leaves, ii) mature stems and leaves, iii) dead and decaying material. Each sample was then weighed. In the case of the dicotyledons the entire content of the sample was treated in this way but this was not possible for the grasses owing to the size of the sample and the difficulty of examination. After each sample had been weighed the grass content was gathered together and ten 20 g. subsamples abstracted randomly and separated into green stems and leaves, and into yellowing or dead stems and leaves. All separated material was then weighed and dried in an oven at 100°C. to constant weight. The remainder of the grass sample was dried unseparated to constant weight.

Values of dry weight for the grass sample and for each dicotyledonous species were obtained, subdivided into dry weight content of the green and of the dead tissue components. The proportional representation in the sample of species and tissues was evaluated in terms of dry weight and subsamples of dry weight material in these proportions were ground in a pestel and mortar, redried to constant weight and ashed in a Muffel furnace for 12 hours at 500°C. The mean ash percentage of three such subsamples was then deducted proportionately from the dry weight biomass sample to give a biomass figure in terms of grams, ash-free, dry weight/ m^2.

The freshweight values of each sampling were used to estimate the confidence limits of the mean, and the ash-free, dryweight biomass of green and of dead material were used in the evaluation of primary production. The sampling was conducted at intervals of two months over a period of two years.

The rate of decrease of dead material was investigated by placing samples of recently cut vegetation of known dry weight into 3 mm. nylon mesh bags, which were then sealed and secured by nylon twine to pegs situated near the corners of each bag in a position 60 cm. above the mean water level close against the soil surface. Ten sample bags were placed in position at the time of the sampling and allowed to remain undisturbed for two months. At the end of this period they were taken up, any new growth intruding into them removed, and the contents washed gently over a 1 mm. sieve. Each sample was then dried to constant weight and three subsamples were ashed. The original ash content of the samples was assumed to be that of the initial biomass sample from which they had been taken. The original and final ash-free dryweight of the mean sample was then calculated. Control samples which followed the same experimental procedure but which underwent no period of decomposition were investigated for losses of organic matter in the handling of the samples. As far as could be determined the handling losses during washing, extraction of the sample, and drying, were negligible.

Validity of the Method

i.) Sampling Error

The banks show considerable variability in their vegetation carrying capacity owing to the differences of bank slope and rate of subsidence. In view of the occurrence of fairly extensive areas completely barren of vegetation at infrequent intervals along the stream it was essential that the sample number should be sufficient to produce a mean biomass figure within acceptable confidence limits for the stretch under investigation. Analysis of the fresh weight biomass of the forty samples allowed the estimation of the standard error of the mean. This varied in magnitude from 7 to 12% of the mean, a level close to the 10% suggested as an acceptable standard by Milner and Hughes (1968). It is considered therefore that even in the variable area under investigation forty samples were sufficient to provide an acceptable estimate of mean biomass.

It was not possible to dry the discrete samples to constant weight and in consequence the confidence levels calculated for fresh weight were applied to ash-free, dryweight biomass on a percentage of the mean basis. Where the samples are homogeneous the error caused by this practice should be small and this homogeneity is maintained for the greater part of the year. In the summer however the greater percentage of water in the tissues of reeds and Impatiens will reduce homogeneity but in this case the standard error will be artificially inflated and not reduced. No parametric statistic was applied to this data.

ii.) Grass Composition

As it was only possible to identify grasses to species floristically during the summer months, grass values are assessed together. An estimate of the relative proportions of the various grass species was derived directly from the relative number of inflorescences present for each grass species obtained in the summer samplings; but the reliability of this estimate is not known. During the remainder of the year it was not possible to identify the grass species in the sample, in these seasons the relative importance of the various species was considered to be of the same order as that during the summer.

iii.) Decomposition Mesh Size

Edwards and Heath (1963) have investigated the relative efficiencies of mesh size in decomposition estimates and suggest that a mesh of 7 mm. allows the free passage of all invertebrates but that one of 1 mm. excludes the activity of earthworms which they conclude have an important function in the breaking up of dead material facilitating degradation by micro-organisms. It was considered in the present study that a mesh of 7 mm. would permit the accidental loss of some undecomposed material during rainwater run-off or during a rise of stream water level and indicate losses of organic material higher than that due to decomposition alone to a much greater degree than would be the case of dead material in situ. A mesh size of 3 mm. does not easily permit the loss of undecayed tissue and allows access to all but the largest earthworms. Although the exclusion of the largest invertebrates may be a source of error it was not considered that a mesh size of 7 mm. was justified under the prevailing conditions. The data of Edwards and Heath (1963) suggest that a mesh size of 3 mm. would not underestimate organic decomposition to any appreciable extent.

iv.) Factors Affecting Decomposition

Weigert and Evans (1964) assessing the technique of monitoring decomposition rates from mesh bags consider that they have the disadvantage of measuring the disappearance of unweathered material as opposed to the naturally stratified dead layer of the field; that they limit the entry of larger invertebrates; and that the removal of vegetation in exposing the soil surface when siting the bag may decrease the suitability of the microenvironment as a habitat for decomposer organisms. In the present study it is considered that a sample of material from the alternate monthly sampling will include all states of weathering and decay; that the limiting of entry of large invertebratos will not represent a major error; and that the altering of the microclimate will not be as serious here as it would be in their alternative method which necessitates the removal of all living material from two similar vegetation plots and sampling them in situ at the beginning and end of a time interval.

However in the natural situation dead material may be removed by rainwater or stream flooding to an unknown degree and this factor is likely to introduce a reduction in dead matter over and above that caused by organic decomposition. The magnitude of this loss is unknown.

6. Primary Production and Floral Composition

Results

6.1 The Floral Composition of the Vegetation

The vegetation within the feeding range of the vole was sampled a total of twelve times over a period of two years. The components formed by the Gramineae, the reeds, and the major dicotyledon species were calculated as percentages of the total dryweight biomass of each sample. Table 15 shows the percentages of these plant components expressed as a mean of from two to four samplings for each of the four seasons. The mean of the total number of 12 samplings is also shown as an annual mean. Where three or more samplings are available in the determination of a component percentage mean, the standard error of the mean is also shown.

Table 15. The Floral Composition of the Vegetation as % of Dryweight Biomass.

	Spring	Summer	Autumn	Winter	Annual Mean
Gramineae	74.9±0.9	78.3±3.3	75.3±5.7	83.8	77.4±1.95
Sparganium erectum L.	0.1	0.6	0.5	0.0	0.4±0.2
Urtica dioica	14.9±4.8	10.6±4.1	17.0±5.2	10.8	13.8±2.0
Brassica rapa	2.8	2.4	0.8	2.1	1.9±0.7
Lamium album	2.5	0.9	1.1	0.5	1.3±0.5
Alliaria[*] *petiolata*	0.4	0.4	0.4	0.2	0.3±0.1
Impatiens glandulifera	0.3	1.8	2.0	0.2	1.3±0.5
Epilobium hirsutum	1.3	0.4	1.1	0.0	0.8±0.3
Cirsium arvense	0.8	1.2	1.0	0.0	0.9±0.2
Scrophularia aquatica L.	0.1	1.1	0.1	0.7	0.4±0.2
Conium maculatum	0.3	0.6	0.2	0.0	0.2±0.1
Ranunculus repens L.	0.1	0.8	0.4	0.0	0.3±0.1
Other dicotyledons	1.5	0.9	0.1	1.7	1.0±0.3
Number of samplings	3	3	4	2	12

To compare the relative frequency of occurrence of the various grass species the relative abundance of inflorescences present during the summer was determined. The percentage composition of inflorescences for the frequently represented species is given below.

---

[*] *Alliaria petiolata* (Bieb) Cavara & Grande

Gramineae

	%
Poa pratensis	45.9
Agrostis gigantea	21.4
Arrhenatherum elatius	18.3
Lolium perenne	12.5
Holcus mollis L.	1.2
Alopecurus pratensis L.	0.4
Dactylis glomerata L.	0.4

The grasses dominated the plant community representing over three quarters of the entire plant biomass. Their percentage of the total dry weight biomass varied little between the seasons although in winter, owing to the decline of the dicotyledon floral component, the percentage is slightly above that in the other seasons (see Table 15).

The nettle Urtica dioica formed the second largest component of the vegetation biomass becoming particularly important in spring owing to its growth having started earlier than that of the other dicotyledons and the grasses and in the autumn owing to having been the first dicotyledon to produce substantial new growth after the scything of the banks in summer. This removed both old stems and tall-growing competitors, particularly the balsam Impatiens and the Hemlock Conium. Over 50% of the biomass of nettle in winter was represented by dead material.

The field cabbage Brassica rapa, the dead nettle Lamium album and Impatiens were of some importance but never individually represented more than 7% of the biomass samples. *Impatiens* was of little importance during the spring and reached its maximum growth in summer. It was largely removed by the summer scything and in autumn was represented above ground only by dead stalks.

Cirsium (Thistle), *Epilobium* (Willow-herb), *Alliaria* (Garlic mustard), *Scrophularia* (Figwort), *Conium*, *Ranunculus* (Buttercup) and *Sparganium* (bur-reed) were all abundant during the summer but together constituted less than 10% of the biomass total. Although the reed *Sparganium* is a bulky plant it grew in clusters, tended to be localised in distribution and had a water content in excess of 90%. It also was largely removed by the summer scything.

The other dicotyledons which occurred less frequently in the samplings included *Rumex obtusifolius* L. (Dock), *Stellaria media* (L.) Villar (Chickweed), *Myosotis palustris* (L.) Hill (Forget-me-not), *Galium aparine* L. (Goosegrass), *G. cruciata* (L.) Scopoli (Crosswort), *Nasturtium officinale* R.Br. (Water cress), and *Geranium dissectum* L. (Crane's bill). Taken together they rarely constituted more than 2% of the biomass total although *Galium cruciata* was an important floral component of the plant community higher up the bank.

Summary to Section 6.1

In winter 83.8% of the dryweight biomass was composed of grasses and 10.8% of nettles. New growth particularly of *Urtica dioica* took place in spring. During this season the grass component formed 74.9% of the total, its lowest seasonal value.

In summer the standing crop of the majority of plants was at its maximum and the species diversity of the samples at its greatest. The banks were scythed in late summer. Substantial new growth took place in autumn only in the nettles which formed 17.0% of the biomass at that season.

The mean annual biomass was dominated by grasses (77,4 ± 1.95%) and among the dicotyledons by Urtica (13.8 ± 2.0%).

6.2 Changes in the Biomass of Vegetation with Season.

Table 16 shows the biomass/m^2 of vegetation for each of the twelve samplings, in gms ash-free, dryweight. The living and the dead components are expressed separately. The percentage of the total biomass which is dead and is consequently in a state of decomposition is also given. The number of quadrat samples per sampling was 40 (n = 40).

Table 16. Seasonal Changes in the Composition and Biomass of Vegetation. Gms, ash-free, dry weight/m^2.

Date	Total	S.E.	Green component	Dead component	Dead%
25 Jan 72	96.7	9.2	37.4	59.3	61.3
6 Mar 72	72.8	8.9	35.4	37.4	51.4
11 Apr 73	143.9	18.1	55.4	88.5	61.5
4 May 71	60.9	6.4	(37.4)	(23.5)	(38.6)
7 Jun 72	219.2	18.4	190.5	28.7	13.1
5 Jul 71	292.7	32.3	263.7	29.0	9.9
2 Aug 72	278.9	38.2	222.5	56.4	20.2
2 Sep 71	116.6	9.6	74.5	42.1	36.1
3 Sep 72	250.6	26.0	192.0	58.6	23.4
1 Oct 72	274.6	16.8	215.6	59.0	21.5
30 Oct 71	205.4	17.4	143.5	61.9	30.1
5 Dec 72	207.0	22.4	104.8	102.2	49.4

Figures shown in parenthesis were not measured directly but were estimated from the relevant two adjacent seasonal values.

Figure 39 is drawn from these data with the individual sampling estimates given together with their 95% confidence limits and suggested annual trends of total biomass and dead material biomass added by eye.

The values for 4 May 1971 and 2 September 1971 are anomalous. The figure of 60.9 gms/m^2 for 4 May 1971 is lower than the trend would suggest and was caused largely by bank slumping following flooding during the previous March. The figure of 116.6 gms/m^2 for 2 September 1971 is also lower than the trend would estimate and was again largely a result of a flood during the previous August. The effect of flooding is to (1) cause bank collapse, resulting in large stretches of bank becoming barren of vegetation, (2) remove much decomposing and in the case of 2 September 1971 much scythed material, and (3) cover the remaining vegetation with a thin layer of mud that buries part of the aerial biomass and which may smother and destroy small plants.

If the trend line is drawn so that these anomalous results, in particular that of 2 September 1971 are not permitted their full influence then the curve of total biomass had two growing-season peaks with a minor trough between them in late summer and a major trough extending from late November until early May. The minimum occurred in mid-March and the maximum in late July. This maximum was not measured by sampling. Extrapolation from the June and early July figures suggested a peak of 327 a.f. dw./m^2.

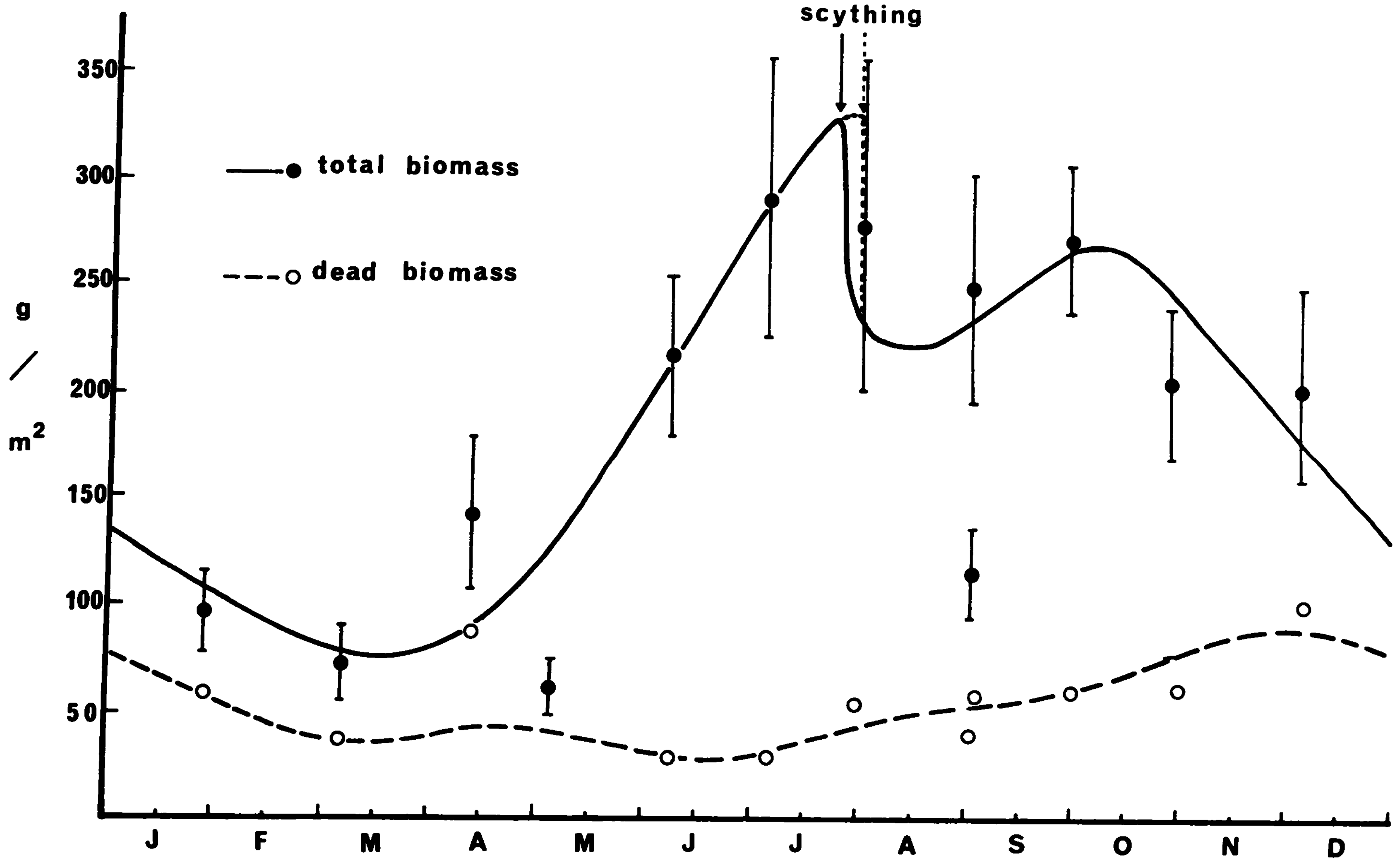
At a date between July 20 - August 1 the banks are scythed each year. Much of the cut material was removed from the water's edge onto the higher levée bank while part fell into the stream. The greater proportion of the aerial vegetation of the larger dicotyledonous plants was removed by the scything together with the reed growth above water level. Most of the grass biomass escaped being cut however with the result that the fall in total biomass, although appreciable, was not drastic. A fall of biomass to 222 gms/m^2 is suggested. This fall was not immediate as some of the cut material remained in situ and would have been available as food for <u>Arvicola</u> until it became dried up after a few days when it would have entered the dead material biomass and begun to decompose. The level of the total biomass in this trough depended partly on the rainfall subsequent to scything as a rise in stream level would have removed most of the remaining cut material and would have tended to bury and smother the remaining aerial vegetation beneath a deposited layer of mud.

New growth, particularly of nettles, took place during the autumn and a second biomass peak of 270 gms/m^2 was reached in early October. Much of the vegetation began to die in November, a process which accelerated in December. The removal of the biomass during flooding in winter, the limited amount of new growth at this season and the removal of growing

Figure 39

Changes in vegetation biomass with time of year.

The estimated means of total biomass in grams of ash-free dry weight/m^2, with their 95% confidence limits, calculated from the two-monthly samplings, are shown together with the means of the dead biomass component. The data include samplings from 1971, 1972 and 1973. The scything of the banks in summer normally takes place at some time between July 20 and August 1. The rate of removal of the scythed material depends on a number of variables (see text). The trend lines have been drawn by eye to suggest a generalised seasonal pattern.


scything
total biomass
dead biomass
g / m²
350
300
250
200
150
100
50
J
F
M
A
M
J
J
A
S
O
N
D

biomass by vole feeding combined with the slow but continuing decomposition of dead material to reduce the total biomass level over the winter and early spring period to an annual minimum of 76 g/m^2 in mid-March.

In late March and April an increase in rate of growth of living tissue resulted in production exceeding the losses due to decomposition, flooding and grazing. Over the period April 15 to May 31, the biomass total doubled and continued to increase at a rapid rate until the scything took place.

The biomass of dead material reached a peak in early December of approximately 92 gms/m^2 and then gradually reduced in amount during the winter through losses from flooding and decomposition to reach a minimum in early spring of 37 gms/m^2. There may then have followed a slight increase as the growth flush of late spring may have added to the biomass of dead material as the older growth died. But if so this was followed by a second decline in biomass of dead material to approximately 30 g/m^2 in early June due to losses from an increasing rate of decomposition (See Section 6.3.1)

The biomass of dead material remained low during the early summer but increased slowly in late summer and early autumn. The scything of the banks in late summer did not result in a marked increase in biomass of dead material as most of the cut vegetation was either removed by hand to a position higher up the bank or carried downstream by a rise in water level. However an increase in dead material in the early autumn would have occurred as a result of scything if the material had not been removed by one or both of these agencies. A gradual rise in the biomass of dead material occurred in late autumn and early winter as the vegetation died back, until the maximum was reached in December.

Discussion on Section 6.2

At each of the twenty positions chosen for sampling the vegetation was cut from the water's edge for a distance of 30 cm. up the bank along a 20 cm. wide band. Included in this sample however was any emergent vegetation found growing within this 20 cm. wide band when it was extended from the water's edge to the midpoint of the river. This additional vegetation was invariably Sparganium and its presence was confined to the summer samplings. No allowance was made in the computation of standing crop per / m^2 for the extra area sampled in this way.

The quantities of Sparganium included were in fact small as the reed was scattered in distribution, being absent along long stretches of the river, and had a high water content of over 90%. In July, the month of its maximum occurrence, the additional reed recorded in this way increased the biomass by 9%.

Although this procedure artificially raised the biomass total in summer, it was considered to be necessary to include the Sparganium biomass that fell outside the sampling quadrat as it represented part of the food resource of the Arvicola population. The feeding range in summer therefore was not restricted to that range spreading inland from the water's edge but extended into what had previously been merely part of the locomotory range. The allowance made for the extended range by the inclusion of its biomass with that of the existing range was a more simple method than attempting to measure the increased range itself and keeping its biomass as a separate component. In strict terms however the biomass figures refer to the vegetation of one square metre of bank plus the area included by the extension of that metre one and a half metres to the mid point of the stream.

6.3 Primary Production

6.3.1 Rate of Decomposition

Each trial to determine the rate of decomposition was undertaken in the field situation and lasted for a period of approximately two months. The results for the six trials given below are expressed as the average percentage decomposition of the sample per day of the trial.

Period	Decomposition %/day
11 Dec - 10 Feb	0.302 ± 0.011
10 Feb - 11 Apr	0.430 ± 0.03
17 Apr - 9 Jun	0.833 ± 0.044
16 Jun - 11 Aug	1.298 ± 0.103
9 Aug - 1 Oct	0.449 ± 0.025
6 Oct - 5 Dec	0.374 ± 0.014

It is seen that during late autumn and winter the rate of decomposition was low, less than 0.4%/day reaching a minimum during the period of 11 Dec - 10 Feb of 0.302%/day In late winter and early spring the rate increased to 0.43%/day.

This rise was followed by a further and more marked increase to 0.833%/day in the late spring and early summer. By midsummer the rate of decomposition had reached the maximum annual level of 1.298%/day, a high rate of decomposition representing a loss of some 78% of the sample over a period of 60 days. By late summer and early autumn the rate of decomposition had fallen dramatically to 0.449%/day. This is a surprisingly large reduction in decomposition rate probably reflecting the low August and September rainfall of 1972 which was only 21.2% and 46.8%, respectively, of the monthly average and which would have dried out the decomposing samples and thereby reduced the activity of earthworms and micro-organisms.

In the calculation of r, the rate of disappearance of dead matter, which is necessary for the evaluation of primary production, the formula $r = \frac{\log e\ (Wo/Wl)}{t}$ is employed as described in the introduction, where Wo is the mass of dead material available at the beginning of a time period t, measured in days, and Wl is the mass of dead material extant at the end of t.

W_1 is derived from the data on decomposition by multiplying the time interval t by the average daily percentage decomposition for the appropriate period. This gives the percentage of the sample decomposed during t. W_1 is found by deducting the result from 100 to give the percentage of the sample remaining after t. Wo/Wl is computed by dividing W_1 thus calculated into Wo, the percentage of the sample available at the beginning of t (= 100).

For example if t = 20 days and the average daily percentage decomposition for the period was found to be 0.5%/day then

$$W1 = 100 - (20 \times 0.5) = 90$$

$$Wo = 100$$

$$\text{Log e } Wo/W1 = \text{log e } 1.111 = 0.1053$$

$$\text{Therefore } r = \frac{0.1053}{20} = 0.0053$$

The use of the figures from average daily percentage decomposition in the calculation of r is justified by their being the best available estimate of the decomposition of the dead biomass component.

This will contain elements added to the sample both very recently and also several months previously.

The average age of the dead biomass component in the vegetation sampling is therefore assumed to be one month, the approximate date when the mean rate of decomposition occurs during the two months of the decomposition trials.
Since the monthly removal of material by decomposition alone is calculated to vary from 9% to 39% depending upon season, this assumption is thought to be a reasonable one.

Discussion on Section 6.3.1

During the decomposition period extending from 16 June to 11 August several days of rain caused the water level to rise above the decomposition samples resulting in their being covered by a thin layer of mud. This, by insulating the samples from the drying influence of the air and so keeping them moist, encouraged the activity of earthworms and micro-organisms. The unusually low rainfall during the period from 9 August to 1 October and the resultant drying out of the samples would slow down decomposition even though the environmental temperature was still relatively high. It is seen that such seasonal changes in the moisture content of the dead biomass component cause differences between adjacent periods almost as great as between those of midsummer and midwinter.

6.3.2 Estimate of Residual Primary Production

Table 17 shows the biomass of green and dead vegetation in gms. ash-free, dry weight/m^2 at intervals during the year. The figures are given for the first day of each calendar month together with the points of maxima and minima of total biomass represented in Figure 39. The estimates of the biomass for green and dead vegetation for each period are derived from the trend lines drawn in Figure 39 and do not represent the data for any individual year but are an estimate of the trends suggested by the data as a whole. The percentage of dead material lost to the sample by decomposition per day is also given in Table 17 for each month. This is derived from the data presented in section 6.3.1.

Table 17. Estimates of Biomass of Vegetation (g. ash-free, dry weight/m^2) and Rate of Decomposition of dead material (%/day).

	Biomass g./m^2		Rate of Decomposition	
Date	Green	Dead	Month	%/day
Jan 1	56	78	Jan	0.302
Feb 1	49	57	Feb	0.36
Mar 1	42	39	Mar	0.43
Mar 14 (Min)	39	37		
Apr 1	42	38	Apr	0.63
May 1	70	49	May	0.833
Jun 1	162	30	Jun	1.065
Jul 1	246	31	Jul	1.298
Jul 22 (Max)	286	41		
Aug 1	189	43	Aug	0.779
Aug 15 (Min)	174	48		
Sep 1	184	52	Sep	0.449
Oct 1	211	57	Oct	0.39
Oct 5 (Max)	212	58		
Nov 1	167	76	Nov	0.374
Dec 1	96	92	Dec	0.316

The difference in green biomass totals between periods (Δ b) is found by subtracting the green biomass total at the beginning of the month (b_1) from the green biomass total at the end of the month (b_2). In the present study the biomass total on the first day of month 1 is subtracted from that on the first day of month 2.

$$\Delta b = b_2 - b_1$$

Δ b is calculated in this way for each month where there is no alteration in the direction of the total biomass trend during the month but where a maximum or minimum occurs between the first and last days of a month then Δ b is calculated by subtracting the green biomass total at the beginning of the month from the green biomass total at the time (day T) of minimum or maximum biomass. The calculation of green biomass production for the next period then takes as its initial green biomass total the biomass at the day of minimum or maximum biomass in the previous calculation (day T) and its final biomass as that of the first day of the next month, so that two figures for Δ b are calculated for each month where a change in the direction of the total biomass trend occurs.

A similar procedure is carried out to estimate the changes of dead biomass. The difference in dead biomass totals (Δ a) has been found by subtracting the total for dead biomass at the beginning of the month (a_1) from that at the end of the month (a_2); a_1 on the first day of Month 1 is subtracted from a_2 on the first day of Month 2.

$$\Delta a = a_2 - a_1$$

For the months during which a maximum or minimum of the total biomass occurs Δ a is calculated using the date of the maximum or minimum biomass as the period interval in the same way as for the calculation of Δ b.

The calculation of the biomass of the material lost to the dead sample by decomposition (X_1) between the first and last days of each period interval is accomplished by the use of the formula

$$X_1 = \left(\frac{a_1 + a_2}{2}\right) . rt$$

where t is the time period in days, and r the rate of disappearance calculated by the method demonstrated in Section 6.3.1.

The Primary Production in gms. ash-free dry weight/m^2 may then be calculated for each period interval as the residual production after losses due to flood removal and herbivore grazing as:

$$\text{Residual Primary Production} = \Delta a + \Delta b + X_1$$

Table 18 shows the calculated residual primary production in gms. ash-free, dry weight/m^2 for each month of the year. Where a maximum or minimum of total biomass occurs during a month both period calculations are given. These figures for biomass production have been converted to their calorific equivalent by multiplying each gram biomass by 4.5 to give the production in kcals. The conversion constant of 4.5 has been calculated as an average of the data presented for the calorific value of green and dead grass by Golley (1961), Weigert and Evans (1964) and Drożdż et al. (1971), assuming an ash content of dry weight/grass of 5%. In the present study the percentage of ash per dry weight grass was found to be approximately 10% even after the sample had been washed thoroughly. If an ash content of 10% were assumed the calorific value of grass per gram ash-free, dry weight would be approximately 4.7 cals. This value however is higher than that found by Golley (1961) of 4.33 kcals/gm ash-free dry weight grass sample and may still contain a silt fraction even after washing. It was decided therefore to use the conversion figure of 4.5 kcals/g ash-free dry weight biomass, the error involved in employing this figure is unlikely to be greater than 5%. Both Golley (1961) and Weigert and Evans (1964) found the calorific value to be slightly lower in dicotyledonous herbs than in grasses and the assumption in the present study of the higher grass value for the 16 - 24% of the total biomass that is represented by herbs will compensate partially for the estimate of ash content which may prove to be slightly low.

Table 18 Residual Primary Production

Date	Production g/m^2		Production $kcals/m^2$	
Jan		-21.3		-95.8
Feb		-19.9		-89.6
Mar	6.9	-2.7	30.9	-12.1
Apr	48.1		216.6	
May	84.8		381.4	
Jun	96.7		435.2	
Jul	62.1	-89.8	279.5	-403.9
Aug	20.6	-4.3	92.9	-19.5
Sep	39.8		179.3	
Oct	3.1	-19.9	14.1	-89.4
Nov		-45.2		-203.4
Dec		-45.3		-203.9
Total	362.225	-248.34	1,630.01	-1,117.53

Theoretically negative production should not exist in the calculation of primary production, losses from the death of green biomass being replaced by equivalent increases in the dead biomass after a correction has been made for the material lost through decomposition, with the result that production estimates should never fall below zero. The causes of the negative production demonstrated in the present data must therefore be due either to sampling error, to inaccurate measurement of the decomposition rate, or to the removal of green or dead biomass by means other than death and decomposition. Although some errors in sampling and estimation of decomposition rate are inevitable, the principal causes of negative production occurring in the present study are considered to be the removal of vegetation by the action of flood water, by herbivore consumption, and by scything. The last was clearly responsible for the 89.8 gm deficit in biomass in late July, which accounted for some 36% of the total negative production.

Visible Primary Production commenced in March at 6.9 g/m^2 and increased rapidly during April and May to reach a maximum of 96.7 g/m^2 in the month of June. The rate of production was almost as high in July at 62.1 g/m^2 over the reduced period of 22 days, before a considerable part of the vegetation biomass was removed by scything. No visible production occurred in the first half of August but during the period 16 - 31 August production had reached 20.6 g/m^2. This level of production was maintained in September with 39.8 g/m^2 for the entire month but fell to the low level of 3.1 g/m^2 in October. No visible production occurred in November or December.

It is considered that 362.2 gms or 1,630.0 $kcals/m^2$ may be regarded as a minimum estimate for the annual total of residual primary production. To this may be added an estimate (Section 8) of the annual yield of plant production which is ingested by the vole population to give an estimate of the minimum net primary production which is available to the voles as a food supply at some time during the year. The fraction of the aerial production which is likely to be selected as food by the vole population is investigated in Section 7.

Discussion on Section 6

Difficulties arise in the estimation of the primary production of streamside vegetation. The ecosystem is rendered complicated by the unstable influence of the stream. Vegetation on the banks is liable to be buried by slumping and by the deposition of mud during flooding which may also remove both dead and green vegetation. Weigert and Evans (1964) developed a correction for the vegetation losses caused by decomposition.

A similar correction for losses due to the action of floodwater was not attempted in the present study and the magnitude of the losses resulting remains unknown.

The scything of the banks in July was a further complication since it removed from the reach of the vole population a part of the production accumulated during the spring and summer which had been included in the production estimate. It is not certain whether or not this lost production should be included in its entirety in the estimate of the vole food supply. If the vegetation had become unpalatable to the voles by dying, (as much of it appeared to do in November) and become unavailable as food by this means then it would certainly have been included in the effective production estimate. In the present study the entire production prior to scything is included in the residual production estimate.

The removal of a substantial biomass of vegetation at infrequent intervals, as is the case during scything and during the more severe floods, will not result in a marked underestimate of primary production even during the growing season if the biomass levels at or near the previous maximum and also at the new minimum have both been measured. The farther the previous and subsequent biomass samplings are from the moment of loss of biomass the greater the probable underestimation of primary production.

In contrast where material is removed at frequent intervals, notably by the grazing of the vegetation by herbivores, an underestimate of primary production will result as the biomass removal is continuous and the lost production may not be measured by sampling.

The theoretical approach for the estimation of primary production of Weigert and Evans (1964) requires that the dry weight biomass of green material be equal to the dry weight biomass of that same material at its death. This is probably true when considering both above and below ground biomass as a whole, and when none of the biomass is removed by grazing, but when the above ground biomass alone is considered it is probably a false assumption. Prior to death part of the non-aqueous component of the plant tissues may be removed from the aerial vegetation to be stored in the root system as a reserve for winter and early spring growth. Should this be the case then the dryweight biomass of the aerial vegetation at death will be less than it had been when alive. Where there is no visible production in late autumn this transfer of cell contents to the root system will result in a negative production estimate.

If the primary production estimated to have been ingested by the vole population is added to the residual primary production, the underestimate of primary production will be largely confined to the material which is ingested by other herbivores together with that lost as a result of minor rises in stream level. It is assumed here therefore that the apparent negative production due to the major rises in water level, to the withdrawal of part of the aerial cell contents to the root system and to the removal of the vegetation by scything is in fact largely illusory, the material thereby lost having been included in the production estimate of earlier periods.

The herbivores of the ecosystem apart from Arvicola include a population of Microtus agrestis, occasional individuals of the more strictly omnivorous Rattus norvegicus, the moorhen Gallinula chloropus, and an invertebrate population which is likely to be dominated by members of the Orthoptera and Hemiptera. The proportion of the primary production ingested by these animals is not known.

Comparisons between the estimate of primary production in the present study with those of other workers is rendered partially inappropriate by the differences in climate, soil type, drainage pattern, floral composition, in the ecosystem management between the study areas, and also by the different methods employed to calculate the primary production.

Golley (1960) estimated the residual above-ground primary production of an area of old Poa grassland in Michigan to be 251-385 g. dry wt/m^2/yr. Odum (1960b) found the same production of an area of old field grassland in Georgia to vary between 300 - 500 g. dry wt/m^2/yr, with the lower figure representing the more stable phases of the grassland succession. Weigert and Evans (1964) found the residual, above-ground primary production of an area of old field grassland in Michigan to vary between 305 - 1064 g. dry wt/m^2/yr, the higher figure being produced on damp alluvial soils. The results of Weigert and Evans (1964) demonstrate the differences in grassland production within a small geographical area resulting from varying conditions of soil type and drainage.

The partially-managed plant community in the present study resembles an old field grassland in some respects and shows some similarities in floral structure to the study areas of Golley (1960), Odum (1960b) and Weigert and Evans (1964) although considerable differences in climate exist between the present study and these others. A corresponding production estimate in the present study would be 381.3 - 402.5 gms. dry wt/m^2/yr calculated assuming a 5% and 10% ash content respectively. The present production estimate therefore shows good agreement with those of Golley (1960), Odum (1960b) and Weigert and Evans (1964).

CHAPTER 7

DIETARY ANALYSIS OF THE MODEL POPULATION

7. Dietary Analysis of the Model Population

Introduction

In any investigation into the impact a feeding population has on its food source it is necessary to determine not only how much food is required, in terms of calories, by the population and how extensive the primary food supply, but also, as accurately as possible, what part of the food source is being ingested and what part allowed to remain untouched in a situation where the food can be expected to be abundant. If selectivity does exist then it may do so either with a preference in the species consumed or with a preference to certain of the plant's tissues over others, or to both preferences concurrently. It would also be of interest to know whether any such grazing selectivity is modified during a seasonal food shortage, should this exist at any time in the natural situation.

To investigate whether the voles are feeding selectively on either certain plant species or on certain plant tissues, it is necessary to know: (i) The proportions in which the plant species and/or their tissues occur naturally. (The Natural Standard). (ii) The proportions in which the plant species and/or their tissues occur in the Arvicola ingested food.

A comparison of the two will indicate whether the population is feeding randomly on the available vegetation or whether food selectivity does take place. A realistic understanding of (i) however presents certain difficulties as to whether it should be estimated on the basis of its natural occurrence per se or on its random occurrence in relation to the normal, non-positively selective, behaviour of Arvicola. If after a period of swimming a vole comes to rest on the bank and is about to commence feeding then whether it ingests randomly will probably depend on the proportions of the various plant species in their surface area coverage of the bank beneath the vole's feet. However this might not be the sum of the vegetation available as further vegetable material may be present in considerable mass above the animal's head, the foliage out of direct reach and attached to the bank by woody stems of minimal bank surface area coverage. It would be considered that this herb layer vegetation is not therefore available and should be excluded from the naturally occurring proportion as it is involving selection on the vole rather than being the subject of the vole's selectivity; conversely it might be reasonable to argue that the animal is capable of felling the woody stems and then consuming large quantities of food that do not exist in the proportions of the natural standard. Beyond this is the question whether the natural standard should be based not on bank surface coverage but on vegetation surface area; a thick grass stand thereby providing a greater proportion of the food supply than one of scattered blades covering the same area of bank and carrying a reduced vole-attracting capacity, thereby encouraging the animal to move off and continue its food search elsewhere. If the proportions of ingested food are measured by an examination of stomach or faecal remains then the digestibility of the food, the relative water, lignin and cellulose content of the various tissues, will also present considerable problems in the comparison with a natural standard where these proportions may not be known.

The difficulty of evaluating the natural standard as it appears to the vole necessitated that it be estimated on the basis of its natural occurrence per se, and both active and passive selectivity will be included in any difference between the natural standard and the food ingested.

It was beyond the scope of the present study to measure the natural standard in terms of bank surface area coverage, vegetation surface area, or volume, and it was measured in terms of the percentage by dry mass of the various plant species and tissues. This required that the aim of this section be simplified to:

i) An estimation of the proportion of species and/or tissues occurring naturally as a percentage of their dry mass.

ii) An estimation of ingested food.

iii) A comparison of (i) and (ii) as a guide to indicate what proportion of the vegetation theoretically available is likely to be ingested by the vole population.

Unfortunately a comparison of (i) and (ii) is rendered unreliable by the fact that to measure (ii) in terms of percentage dry mass it would be necessary to examine the stomach contents of a number of killed animals and in doing so eliminate the population from precisely that section of stream that relates most directly to the proportions assessed in (i). This could be done only once after which it would be necessary to move the investigation to a neighbouring stretch of stream for the next comparison, a method which would increase non-seasonal variability and which when considered with the necessity of killing large numbers of a low frequency animal appeared undesirable.

The ingested food proportions were assessed by qualitative observation of the ingestion of different plant tissues and by the micro-analysis of faecal fragments. The latter relates principally to surface area and consequently is a poor comparison with (i) where the surface area/mass ratio changes between different species. It was considered that the investigation, though not directly comparable, would provide useful information for the evaluation of (iii).

1.) The Natural Standard

The proportions of the various plant species as a percentage of total dry weight are derived from the data reported in Section 6 and the methods employed in obtaining that data are described in that Section. The data on the relative proportion of various tissues, also derived from the alternate monthly samplings of Section 6, are confined to an evaluation of the dryweight percentages of (i) young living shoots and leaves, (ii) mature living stems and leaves, (iii) dead and decaying material. The method was as described in Section 6.

2.) Analysis of the Ingested Material

Ingested vegetable material was investigated in two ways: (i) the microscopic examination of plant epidermis remains in the faeces and, (ii) a qualitative observation of foods eaten in captivity.

(i) Examination of Faeces

The identification of plants to group or species by the structure of their epidermal cells has been a widely used technique in assessing naturally occurring herbivore food materials. Dusi (1949) used the technique in an evaluation of the food of the cotton tail rabbit, Williams (1959, 1962) for Peromyscus and a variety of microtines, Watts (1968) for Apodemus and Clethrionomys, Evans (1973) for Microtus, Storr (1961) for Australian marsupial herbivores, Martin (1964) for Blackface sheep in Argyllshire and Stewart (1967) for large grazing herbivores in Southern Africa. Hansson (1970) has reviewed the relative efficiency with which the diet of rodents may be identified by micro-analysis. In an examination of the diet of Arvicola, Holišová (1965, 1970) has used the technique successfully in a comparison of seasonal dietary changes in both fluvial and lacustrine habitats. She concluded that the principal food source was the aerial vegetative parts of monocotyledonous plants largely depending in its species composition on availability. The principal foods were grasses along the rivers, and reeds beside the shores of lakes. In the latter there appeared to be selection in favour of Phragmites communis against its co-dominants Typha angustifolia and T. latifolia

The method in all these investigations was to compile a collection of reference epidermal preparations of all the plant species available in the habitat and to compare the shape and arrangement of these cells with those observed in a preparation of the stomach contents or faeces of the animal under investigation. Usually drawings or photomicrographs were made of the reference collection to simplify the comparison.

In the present study the following method of preparation was employed:

Several examples of tissues taken from the vegetative parts of each species, (the root, stem and leaf regions) were cut into fragments and boiled in a solution of two parts water and one part Lactic acid, until most of the water had evaporated and the tissues become transparent. These were then removed from the Lactic acid and washed in water before staining in Haematoxylin alum for 20 minutes. After staining they were rinsed in water and immersed in alkaline alchohol for three minutes. They were then dehydrated in alcohol, cleared in xylene and mounted in Canada Balsam. When dry the salient features of the epidermal cells, their size, shape and stomatal configuration of abaxial and adaxial surfaces, were drawn and a soecies distinctive group of characteristics assembled. This method was employed to create a complete series of cell-distinctive features for the principal vegetative tissues of all species occurring along the stretch of stream under study.

At two monthly intervals all the faeces were collected from the 380 m. stretch of stream occupied by the Model population. They were then mixed thoroughly in a solution of Rawlins fixative and allowed to stand for approximately two days. The faeces' particles were then assembled on a series of slides, the excess fixative removed and the staining and preparation completed as for the reference tissues.

In the examination of the slide material, four, separate, continuous runs were made across each slide, the epidermis identified from the reference collection and the area of epidermis measured with a graticule in the microscope eyepiece. This was repeated for between 12 and 20 slides and the total surface area of all the fragments was summed for each species. Only epidermal tissues were identified in this way, Xylem, phloem and fibre cells were not identifiable to species.

ii) Direct Observation

The technique of watching an animal's food ingestion in the field through binoculars or telescope has been employed by Andersen (1950) on hares and Hunter (1958) on sheep but it is a method difficult to apply to small rodents which are frequently entirely obscured by the ground vegetation. An attempt was made in 1971 to watch Arvicola through binoculars and they were observed on many occasions feeding on waterside grasses, however the technique is time consuming and of limited application in the study of how the voles react to a variety of plant species as in the natural condition they will be feeding on the dominant grasses for 70 - 90% of the time even if feeding is random. In consequence a selection of grasses, reeds and dicotyledons were supplied to the animals contained in the activity enclosures described in Section 1, and their reactions to the different types of food noted during observation periods in the hide. A record was made of the species of plant eaten, the type of tissue consumed and its state of decomposition, and the age of the vole feeding on it. This observation produced valuable information on how the voles were selecting tissues from the wide variety available but are of necessity of a rather generalised nature and are poorly quantifiable.

Validity of the Method

1.) The Natural Standard

The grasses present are only identifiable from their inflorescences during the summer when a proportional occurrence was compiled from this evidence, for the remainder of the year the grazed and ungrazed grass blades and stems defied identification; in this study it is assumed that the proportional occurrence of vegetative tissues of the various species of grasses is similar to that of the inflorescence number. The estimate is one of unknown confidence but it is thought a valuable one to make in the absence of a better. It should have been possible to subsample from the two monthly quadrat cuttings, homogenise the tissues and prepare on slides as for the reference collection, and identify microscopically on a quantitative basis. Lack of time prevented the use of this method which, in any case, is open to errors from sub-sampling, differential digestive breakdown and varying surface area/mass ratio.

ii.) Lateral Feeding Range

The assumption is made here that the species composition of the voles' feeding range is similar to that of the first 60 cm. from the water's edge. No detailed investigation was conducted to test this hypothesis which must depend very largely on the parameter of the steepness of the banks. Where the banks become vertical vegetation is absent and the lateral feeding range will be nil, but there is the possibility that where the bank approaches the horizontal the range may exceed the 100 cm. suggested by Ryder (1962) because of the ease of access for the voles. Whereas this possibility must be borne in mind at no time were <u>Arvicola</u> seen to feed further from the water's edge than 100 cm and most commonly they fed at a distance of 50 cm. or less. The comparison is therefore considered the most valid that could be made. The report of Davis (1970) of <u>A. t. amphibius</u> feeding a long way from water is thought to reflect highly unusual circumstances.

iii.) Direct Observation

Direct observation of <u>Arvicola</u> feeding both in the natural condition and in captivity can only relate to aerial food sources or root tissues supplied on the ground surface. The possibility exists that the voles may burrow for roots especially during periods of severe weather in winter (Stoddart, 1965) as does A. t. scherman (Bernard and Bollaerts, 1960; Myllymäki, 1960). Roots may then become the most important food source. If the feeding became entirely fossorial then the root tissues could no longer be expected to reveal themselves in the faecal sampling as defecation may also take place underground as in the case of A. t. scherman (Bernard and Bollaerts, 1969). However in the present study Arvicola were caught throughout the winter and even under conditions of frost as severe as -10°C., minima which are rarely exceeded in the study area. It is not thought from the results of Section 1.5 that Arvicola in Co. Durham becomes fossorial for longer than a day or two at a time and then at infrequent intervals.

iv.) Differential Digestion

The adaxial surface of the tissue under investigation is frequently destroyed during in vitro digestion. This is probably true also during digestion in vivo (Stewart, 1967). If this is true for some plant species and not for others it may be a serious source of error.

As the process of digestion has already been completed by the time defecation occurs there is a real likelihood that species are not represented in the faeces in the same ratio as at the time of ingestion, as a result of differences of efficiency in the assimilation of different tissues. It may well be that the epidermis of some annual dicotyledonous plants does not survive the process of digestion at all. In addition the ratio of epidermis area to gross mass will vary not only between species but between different tissues in the same plant and even in a homogeneous food intake this is liable to represent a serious source of error. Stewart (1967) devised a number of correction indices which could be applied to reduce this error on application to the relevant plant species. He offered two or three foods of known weight to large African herbivores and related the proportions identified in the faeces to those actually ingested. Unfortunately no time was available for a similar investigation in the present study.

Discussion

In spite of the limitations referred to above it was considered that in a study of the energy requirement of a natural vole population some attempt should be made to relate the energy needs to the food supply. This would not have been practicable until at least the major components of the food supply were known. The direct observations of captive animals should provide a valuable insight into the original selection of food tissues from a plentiful supply as in an environment of abundant food it is these most favoured choices that will be of most importance. If some plant species are never seen to be consumed then it should be possible to remove the primary production of these species from the estimate of available food supply. Similarly if some tissues, for example, dead grass, woody stems or fibrous root material, are seen to be ignored then these too can be excluded from the available total. Faecal examination will certainly show which species are definitely being consumed in large quantities but it is doubtful whether any assumptions can be made from this technique concerning species which do not appear to occur in the food.

It was thought necessary to evaluate the relative proportions of the food ingested by the population and it is considered that a combination of the two methods employed, even allowing for the errors likely to be involved, should provide, in large measure, a realistic approximation of the true nature of ingested material.

7. Feeding Selectivity

Results

7.1 Analysis of Plant Epidermis in the Faeces

The breakdown of faeces into the component plant species expressed as a percentage of the total epidermis surface area is given in Table 19 for the principal species of grass and dicotyledons at each season of the year. An estimate of the plant species composition of the Natural Standard is also given in Table 19 expressed as a percentage of the total dry-weight biomass of the sample as calculated in Section 6.1. The figures for the plant species composition of the Natural Standard (N.S.) are shown in parenthesis.

Table 19 Composition of the Faeces

(% Epidermis surface area)

Gramineae	Winter	Spring	Summer	Autumn
Poa pratensis	39.2	19.5	37.7	37.6
Agrostis gigantea	8.5	24.7	42.1	34.0
Lolium perenne	18.5	11.8	5.7	16.8
Arrhenatherum elatius	6.0	4.4	1.3	2.4
Alopecurus pratensis	1.6	3.2	1.0	0.0
Dactylis glomerata	2.6	0.6	0.4	1.6
Holcus mollis	2.0	0.0	0.0	0.0
Total Gramineae	78.4	64.2	88.2	92.4
(N.S.)	(83.8)	(74.9)	(78.3)	(75.3)
Dicotyledons				
Urtica dioica	7.2	11.7	4.6	4.7
(N.S.)	(10.8)	(14.9)	(10.6)	(17.0)
Lamium album	6.6	21.8	2.5	0.2
(N.S.)	(0.5)	(2.5)	(0.9)	(1.1)
Unidentified dicots.	6.1	2.3	3.9	2.7
Roots	1.7	0.0	0.8	0.0

Table 19 indicates a fairly close similarity between the percentage of the diet represented by grasses (64.2 - 92.4%) and the percentage of grasses in the composition of the Natural Standard, (74.9 - 83.8%). The maximum difference between the two estimates is seen in the autumn where the percentage of grass epidermis in the diet was 92.4% while grasses formed only 75.3% of the dryweight vegetation within the feeding range. If the seasonal means are calculated for the grass percentage of the diet and for the grass percentage of the feeding range then the percentage in the faeces of 80.8% is in very close agreement with that in the feeding range of 78.1%. This suggests that over the year as a whole the voles were feeding randomly with regard to grass and dicotyledon species groups as since the percentage of root epidermis in the diet was less than 2% the dietary and feeding range percentages of dicotyledonous plants were also very similar.

Of the grasses *Poa pratensis* and *Agrostis gigantea* appeared most often in the faeces with *Lolium perenne* becoming an important component during the autumn and winter. *Agrostis gigantea* formed a greater proportion of the grass total identified from the faeces than its estimated 21.4% of the grass total (Section 6.1) would indicate from random feeding, however neither the faecal analysis data nor the estimate of grass species abundance within the feeding range is considered to be accurate enough to permit the conclusion that the voles were selecting *Agrostis* in preference to the other grass species. *Arrhenatherum elatius* was a less important component of the faeces than would have been expected from its estimated availability of 18.3% of the grass within the feeding range. *Arrhenatherum* was not common at the water's edge, being found more frequently rather higher up the bank so that should the voles have been feeding primarily fairly close to the water as they have been observed to do then this grass species may not have been taken for this reason.

Alopecurus, *Dactylis* and *Holcus* were relatively infrequent members of the feeding range flora (Section 6.1) and so it is not surprising that they formed only a relatively insignificant proportion of the grass component identified from the faeces.

The majority of the dicotyledon epidermis identified in the faeces was derived from *Urtica dioica* and *Lamium album*. Dicotyledon epidermis was found to be poorly preserved in the faeces and species identification proved to be difficult. One of the reasons why *Urtica* and *Lamium* predominated in the estimates is that these plants possess easily identifiable spines which survive digestion more successfully than the remainder of the epidermis. The percentage of dicotyledon epidermis that could not be identified may have contained an *Urtica* and *Lamium* component as well as tissues from other dicotyledonous species.

Although *Urtica* was usually the most abundant dicotyledon identified from the faeces, its percentage composition of the faeces was below that of its percentage composition within the feeding range, but except in Autumn the differences between the two are small. Lamium however was generally more abundant in the faeces than in the vegetation of the feeding range, particularly in the spring, but again the data is not regarded as being sufficiently accurate to permit the conclusion that the vole population was selecting this species in preference to others.

The data in Table 19 indicate that approximately 80% of the food eaten by the Arvicola population was composed of the aerial vegetative parts of grasses. There is no clear evidence of selection or partiality between the species of grasses growing within the feeding area. The data indicate that both Urtica dioica and Lamium album may be regarded as constituting food plants for the vole population throughout the year, but no similar conclusion is made with regard to the other dicotyledonous plants.

The percentage of root epidermis identified from the faeces was always less than 2% of the digested epidermis and it is concluded that the data suggests that the vole population was feeding almost entirely on the aerial fraction of the vegetation biomass.

Table 19 shows little selectivity in the composition of the diet, with the percentages of grass occurring in the faeces in approximate proportion to their occurrence within the feeding area. The data for autumn may suggest an unusually high dependence on the grasses for food and an avoidance of Urtica dioica which was plentiful during this season, but the data is regarded as insufficiently accurate for the conclusion to be drawn that Urtica was being deliberately excluded from the diet. The data for spring may suggest that the grasses, although still the dominant feature of the diet, were being neglected in vole feeding in favour of Lamium album, but no conclusion is drawn that this result represented a seasonal trend. It is not considered probable that seasonal differences in diet existed beyond those depending on seasonal differences in the composition of the vegetation within the study area.

Discussion on Section 7.1

The data of Table 19 refer only to that fraction of the vegetable remains within the faeces which was formed of the epidermal cells of the plant tissues. The bulk of these vegetable remains consisted of fibre and xylem cells which could not be identified to species. In the autumn faecal samples only 18.35% of the plant material present was of epidermal origin and could be identified to species and it should be emphasised that four times as much faecal material remained unidentified as was identified to species successfully. The possibility of error in the evaluation of the species composition of the food by the means of faecal analysis of plant epidermis is therefore very great and it is for this reason as well as for the limitations of the method discussed earlier that only very generalised conclusions have been drawn from the results of Table 19.

7.2 Analysis of Feeding Selectivity by direct Observation

A variety of plant species were brought from the model population study area and placed within the vole activity enclosures described in Section 1. The reactions of the voles to the plant species were observed, principally during the summer months of 1972, and the major conclusions with regard to food preferences are summarised below.

1) Grasses

The voles were not observed to show partiality in selecting their food from vegetation samples containing examples of Poa, Agrostis, Lolium and Arrenatherum; as far as could be seen no preference was demonstrated for any of these species over the others. In contrast Holcus was rarely consumed and it is possible that a selectivity existed against the ingestion of this species.

The parts of the grasses ingested were almost totally confined to the living stems, stolons and leaves. Grasses placed in the enclosure with their rootlet bundles still attached to the stolons were eaten down to the rootlet bundles which were then discarded. Only once was a vole observed to feed on a grass sample that consisted principally of root material. Yellowing and dead stems and leaf blades invariably remained uneaten and on only one occasion was an inflorescence seen to be consumed, inflorescences were normally bitten off and ignored.

2) Sparganium erectum

The green blades and stems of the Bur-reed were eaten on several occasions, although the voles rarely continued feeding for long on this species, frequently moving off to feed on another vegetation type after only a few seconds of feeding upon the reeds. No dead or dying blades or stems were seen to be ingested.

3) Urtica dioica

This species was observed to be eaten on a number of occasions with the ingested material being confined to the young shoots and leaves at the top of the plant, only occasionally were older leaves seen to be eaten and these were invariably green. On no occasion was a vole seen to feed on a dead or dying leaf or upon a mature stem whether living or dead. The nettles appear to be consumed without the voles demonstrating any discomforture from the effect of nettle stings.

4) Lamium album

This species was observed to be eaten on a number of occasions with the ingested material being confined to the young growing shoots and to the younger green leaves of the plant. No dead or dying leaf or stem and no mature stem was seen to be eaten.

5) Impatiens glandulifera

The growing shoots of this species were seen to be eaten on two occasions, once by a young vole and once by an adult, but on no occasion was the mature stem or any dead or dying stem or leaf seen to be ingested.

6) Conium maculatum

This species, the poisonous Hemlock, was not observed to be eaten by an adult vole but was eaten by a juvenile on one occasion. The young vole nibbled at the green leaves of the plant for approximately half a minute.

7) Brassica rapa, Alliaria petiolata, Cirsium arvense.

These dicotyledonous species, which were common in the study area, seem to be distasteful to voles. Each was fed to the enclosure animals on a number of occasions and also to laboratory voles without an alternative food supply but were never seen to be ingested. This is not surprising in the case of the thistle Cirsium which is protected by its prickles and was the only plant to grow ungrazed inside the vole enclosures, nor possibly in that of the garlic mustard Alliaria which may have an unpleasantly strong taste. The avoidance of the wild turnip Brassica is more surprising as it appears a succulent herb with no obvious distasteful characteristics. It has been noted in the laboratory, however, that carrots and grass are usually selected as food in preference to cabbage. This was eaten in large quantities only in the absence of other foods, although the strength of this trait varies with individual animals. It is possible therefore that brassicas in general are not an attractive food to Arvicola.

Discussion on Section 7.

The possibility of the avoidance of the grass Holcus mollis in feeding is not very important in the context of Arvicola feeding within the study area where this species was relatively infrequent. It may be concluded with some confidence that Arvicola feeds upon the green stems and leaves of all the major grass species within its feeding range while dying and dead grass tissue and to some extent grass roots and inflorescences remain uneaten.

It is concluded that Urtica dioica and Lamium album were eaten frequently and that Sparganium and Impatiens were also consumed during their growing season. In Urtica, Lamium and Impatiens there is evidence to suggest that it was principally the new shoots and youngest leaves which were eaten and that old leaves, mature stems and dead and dying vegetation were avoided. As far as could be determined the roots of these species did not form part of the diet.

Cirsium, Alliaria and Brassica are not considered to form part of the Arvicola diet and this may also be true of Conium maculatum.

There was some indication that juvenile voles sample more species of plants than do adults, becoming progressively more conservative in their diet as they grew older. Such a behavioural change in food choice would account for the observation of a juvenile feeding on the poisonous Conium, a plant avoided by adult voles.

No evidence was found to suggest that animal food formed a part of the diet of *Arvicola*.

Seasonal differences in food composition appear to be determined by changes in food availability. In the study area there were no marked seasonal differences in the species composition of the plants ingested.

Holišová (1965) investigated the feeding selectivity of a population of *A. t. terrestris* inhabiting the banks of a canal in southern Moravia. The species composition of the vegetation along the canal banks was similar to that in the present study, this being dominated by grasses with *Urtica dioica* common among the dicotyledons which also included such plants as the dock *Rumex aquaticus*, Comfrey *Symphytum officinale* L., and the dead nettles *Lamium album* and *L. maculatum* L. The canal banks were scythed in late June, about a month before they were cut in the present study area, were lined with the fruit tree *Prunus domesticus* L. and flanked by fields containing crops of maize, wheat and barley. In the present study *Prunus* was absent and the fields adjoining the stream were given over to pasture grassland.

Holišová (1965) found that in early June, prior to scything, approximately half the food consumed by the voles consisted of grasses and the remainder of various species of dicotyledons. Nearly all the food was derived from the aerial fraction of the plant biomass. The component of the food derived from the vegetative parts of dicotyledons declined after the canal banks were scythed and the vole stomachs were found to contain the remains of the unripe fruits of Prunus domesticus. The unripe fruits of Prunus were also found in the vole stomachs in July together with quantities of cereal grains, by this time the grass component had declined to some 20% of the total food consumed.

Since neither Prunus nor cereals were present in the present study area it is the composition of the voles' diet prior to the scything of the canal banks in Holišová's (1965) study that is the more relevant for comparison with the present results. Holišová (1965) found that among the dicotyledons, Rumex, Urtica, Lamium and Ranunculus were all fairly frequent components of the diet, particularly Rumex which she suggests was selected in preference to the other species.

The Comfrey Symphytum officinale was considered by Holišová (1965) to be avoided as a food source as it was abundant within the study area but never identified in the food remains. Underground vegetative tissues formed little part of the diet of Arvicola, in the riverine habitat a conclusion similar to that of the present study. In contrast Holišová's (1970) investigation of a population of A. t. terrestris on a lake in southern Moravia indicated that here roots and rhizomes formed some 20% of the total food ingested while in the populations of A. t. terrestris and A. t. scherman in other habitats root material has been found to constitute very much higher proportions of the diet than this (Bernard and Bollaerts, 1960; Tahon, 1970; Meylan and Morel, 1970; Myllymäki, 1969).

The results of the present study agree with those of Holišová (1965, 1970) suggesting that animal food does not normally form a component of *Arvicola* diet. However Ryder (1962) has demonstrated that *Arvicola* may occasionally feed from the flesh of dead fish under certain circumstances and some authors (Barrett-Hamilton and Hinton, 1911; Southern, 1964) have maintained that *Arvicola* feeds regularly upon freshwater molluscs. The stream in the present study was floored with sand and mud, and lacked substantial submerged vegetation, conditions representing an unfavourable habitat for freshwater molluscs which were consequently uncommon and were never identified in the faeces.

Holišová (1970) found that the stomachs of young individuals of *A. t. terrestris* contained a greater variety of plant species than did those of the adults. This conclusion agrees with the writer's suggestion that young voles sample a larger variety of plant foods than do adults, becoming progressively more conservative in their diet as they grow older. This would necessitate an increase in selectivity with advancing age.

It is concluded that the *Arvicola* of the present study area feed upon the entire green, above-ground vegetation of the majority of the grass species within their feeding range, upon the young shoots and leaves of *Urtica*, *Lamium*, *Impatiens* and the green stems of the bur-reed Sparganium. The dicotyledons Cirsium, Alliaria, Brassica and Conium are considered to be selected against as a food source. No conclusion is made concerning the remainder of the plant species within the study area.

Those plant tissues which have been concluded to form part of the natural diet of Arvicola formed up to 95% of the primary production within the feeding range of the study area, at the time of its production by the existing standing crop of vegetation.

CHAPTER 8

ENERGY FLOW THROUGH THE MODEL POPULATION

8. Energy Flow through the Model Population

In the calculation of the energy flow through the model population the components of net primary production and of energy ingested, assimilated and converted into tissue (secondary production) by the Arvicola population have been evaluated for each calendar month.

Energy converted into tissue (p) has been calculated in section 4.2 and was estimated as 7.9 (8.1) kcals/m^2/yr. (Here and in the description following the initial figure represents that for the observed 1971 population and the figure in parenthesis that for the predicted 1973 population).

Energy assimilated by the vole population (A) is considered to be equal to the sum of the total energy respired (r), which has been calculated in section 5.5, plus the energy converted into tissue.

$$A = r + p$$

The assimilated energy was estimated as 199.2 (214.2) kcals/m^2/yr. Energy ingested by the vole population (I) is considered to be equal to the assimilated energy ÷ 0.477

$$I = \frac{A}{0.477}$$

where 0.477 represents the assimilation efficiency of Arvicola feeding upon a grass diet reported by Drożdż et al. (1971). This figure is similar to that reported by Erdakov (1972) of 0.503 for Arvicola which were fed on a mixed diet. Since the Arvicola in the present study have been shown to feed primarily on grass (Section 7) the figure of Drożdż et al. (1971) is preferred. The ingested energy was estimated as 417.7 (449.1) kcals/m^2/yr.

The net primary production (P) was calculated as the sum of the residual primary production (p^1) estimated in section 6.3, plus the energy ingested by the vole population.

$$P = p^1 + I$$

The net primary production is considered to be the closest possible estimate of that part of the primary production available to the voles as food within their feeding range, and represents the remainder of the total primary production after losses from flooding and the feeding activities of other herbivores. The net primary production was estimated as 2,047.7 (2,079.1) kcals/m^2/yr.

The components of net primary production, and of energy ingested, assimilated and converted into tissue by the Arvicola population are shown for each calendar month in Figure 40, expressed as kcals/m^2/month. The data for the estimate of each component in Fig. 40 were calculated twice during the months from January to May inclusive, firstly in relation to the population as determined in 1971, and secondly for the population as predicted for the first half of 1973.

In Figure 40 the histogram has been drawn showing the mean of these two calculations.

It may be seen from Fig. 40 that the residual primary production occurring from November until February was nil, the net primary production during these months consisting of the energy ingested by the vole population only. Such a situation would demand that the primary production of the feeding range during these months was exactly equal to the feeding requirement of the vole population. This is not likely to have been true. Particularly during the coldest months of winter it is probable that the primary productivity of the feeding range was less than the feeding requirements of the vole population. The voles must therefore either extend their feeding range or over-exploit* the vegetation biomass of their original feeding range so that the standing crop of vegetation is reduced during this period to a lower level than would have resulted from death and decay by other means.

Where the estimate for net primary production exceeded the energy ingested by the vole population a residual primary production is shown in Fig. 40. A residual primary production was estimated to occur during all the months from March until October inclusive, when it may be concluded that the biomass of vegetation was being under-exploited and was therefore increasing when allowances have been made for the death and decay of vegetation by other means.

Figure 40 shows that by March the residual primary production had become the major component of the net primary production, the ingested energy requirement of the vole

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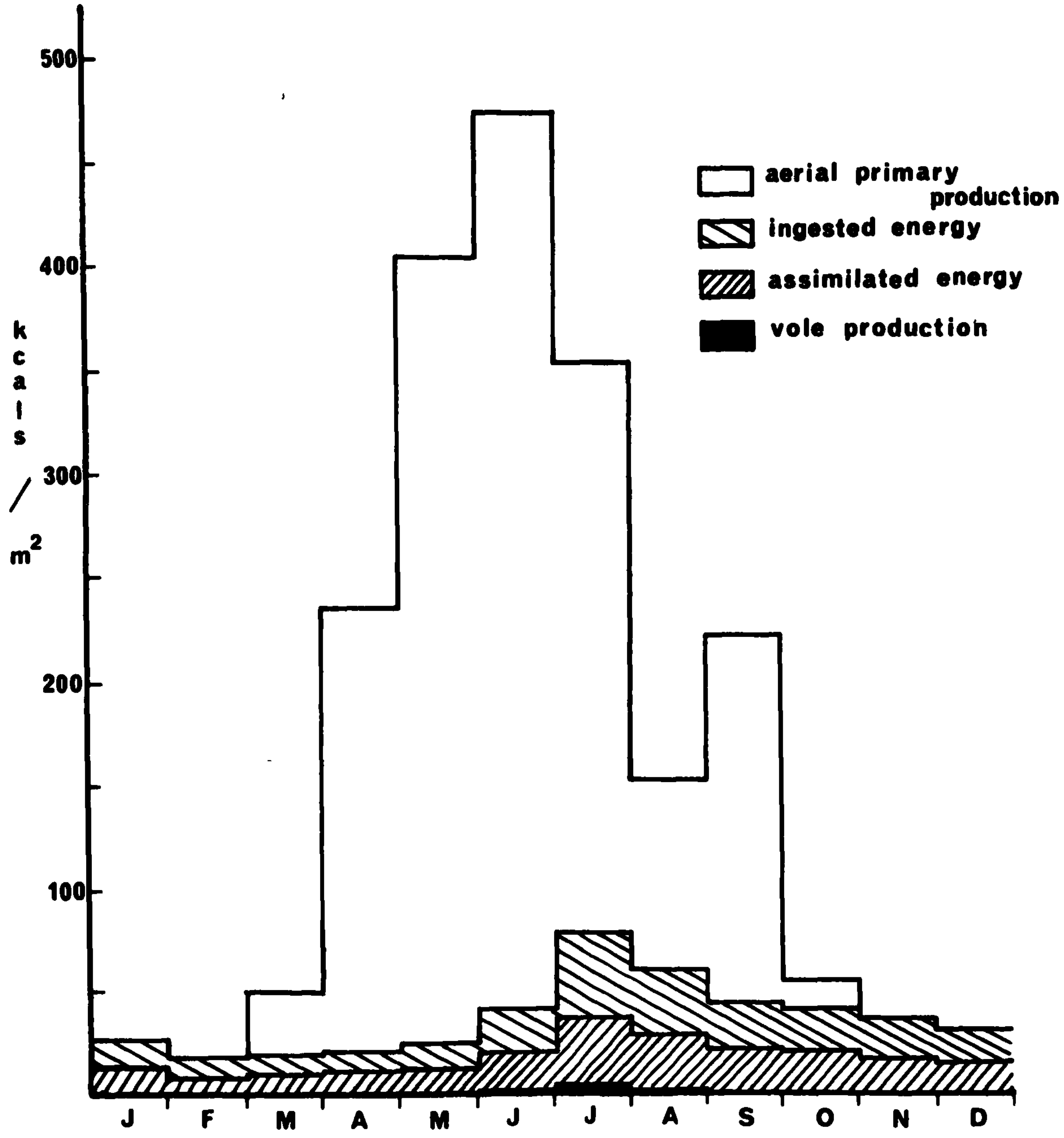
* where "exploitation" implies that the rate of food production/m^2 is equal to the rate of ingestion/m^2.

Figure 40

Energy flow through the model population

The net primary production (as defined in the text), the figures for ingested and assimilated energy, and for energy converted into secondary production, expressed as kcals/m^2, have been calculated for consecutive periods of approximately 30 days. The data refer to a 380m stretch of stream assuming a population feeding range of 760 m^2. From January until May 31 the estimate for all four energy categories are based on an average of the figures calculated firstly for the observed 1971 population and secondly for the predicted population for 1973.


500
400
300
200
100
kcals / m²
aerial primary production
ingested energy
assimilated energy
vole production
J
F
M
A
M
J
J
A
S
O
N
D

population remaining at a fairly low level. The residual primary production increased rapidly during April and May, reaching a maximum in June where the net primary production at 476.8 kcals/m^2/ month was more than nine times the March level of 48.5 kcals/m^2/month. The residual primary production fell in July as a result of the reduction in the biomass of vegetation after the scything of the banks and underwent a further fall in August from the same cause. These falls coincided with a marked rise in the ingested energy requirement of the vole population which was at a level over four times greater in July than it had been in March. Even in August, however, where the net primary production was at a much lower level, the ingested energy component constituted only 39.5% of the net primary production so that although the vegetation biomass had been reduced by scything the rate of vegetation production still exceeded by a large margin the rate of energy consumption of the vole population.

The residual primary production rose in September as the vegetation made new growth after the summer scything but by October it had fallen to a level where it formed a minority component of the net primary production.

The ingested energy requirement of the vole population fell during the late winter from 25.3 kcals/m^2 in January to 17.5 kcals/m^2 in March as a result of the reduction in abundance of the population as a result of winter mortality. Increases in the bodyweight of adult voles of both sexes together with a numerical increase of the population due to immigration resulted in a rise in the ingested energy requirement of the population between March and May.

By June the young of the first litters had entered the population causing a more pronounced rise in the ingested energy requirement, a rise which continued in July where it reached an annual maximum of 77.3 kcals/m^2 as the young of the second litters entered the population. The growth of the young voles during August and subsequent months was insufficient to compensate fully for the losses in population biomass caused by the deaths of adult and juvenile animals and possibly also by their emigration, with the result that the ingested energy requirement of the population showed a decrease during autumn and early winter to a level of 31.2 kcals/m^2 in December.

Energy assimilated by the population is regarded here as an unvarying proportion of the energy ingested, and no correction is made for possible seasonal changes in the efficiency of assimilation of the food. Assimilated energy therefore is assumed to fluctuate seasonally as a proportion of the ingested energy.

The energy converted into tissue exceeded 1 kcal/m^2/ month during three months of the year. These were June (1.4 kcals/m^2/month) where the production was entirely due to the embryonic and post-natal development of the young of the first litters, July (3.7 kcals/m^2/month) and August (1.6 kcals/m^2/month). The production in July was due to the embryonic development of the young of the second litters and in both July and August to the post-natal development of both cohorts of litters.

Table 20 shows the percentage of assimilated energy which was converted into tissue by the vole population for each calendar month and for the year as a whole. Figures in parenthesis refer to the population structure which was predicted for 1973.

Table 20. Secondary production as a percentage of Assimilated Energy

Month	%	
Jan	0	(0)
Feb	1.43	(1.16)
Mar	2.93	(2.36)
Apr	2.42	(2.27)
May	2.60	(2.59)
Jun	7.09	
Jul	9.96	
Aug	5.41	
Sep	1.35	
Oct	1.29	
Nov	0.09	
Dec	0	
Year	3.98	(3.80)

Secondary production as a percentage of assimilated energy increased from nil in January to a level of 2 - 3% during the months from March until May. During February, March and April this increase was due to the spring increase in bodyweight of the adult voles of both sexes but by May this source of production was declining and was partially replaced by the embryonic development of the early litters.

Secondary production as a percentage of assimilated energy increased markedly in June when the first litters were born and began to grow rapidly, and in July reached an annual maximum of 9.96% as a result of the birth and post-natal development of the second litters in addition to the continued growth of the first litter juveniles. Both the numbers of juveniles and their rate of growth fell in August where a consequent decline occurred in secondary production to a level of 5.41% of assimilated energy, a decline that continued in September and October by which time the rate of development of juveniles was greatly reduced. There was little secondary production in November, and by December it had ceased.

Over the year as a whole 3.80 - 3.98% of the energy assimilated by the vole population was converted into tissue.

Table 21 shows the percentage of the net primary production utilized as ingested energy, assimilated energy and energy converted into tissue (secondary production), for each calendar month and for the year as a whole. The figures in parenthesis refer to the population structure predicted for 1973.

Table 21. The Percentage utilization of the net primary production.

Month	Ingested Energy %		Assimilated Energy %		Secondary Production %	
Jan	100	(100)	47.7	(47.7)	0	(0)
Feb	100	(100)	47.7	(47.7)	0.7	(0.6)
Mar	30.8	(40.8)	14.7	(19.5)	0.4	(0.5)
Apr	7.3	(10.1)	3.5	(4.8)	0.1	(0.1)
May	5.4	(6.6)	2.6	(3.1)	0.1	(0.1)
Jun	8.7		4.2		0.3	
Jul	21.7		10.3		1.0	
Aug	39.5		18.8		1.0	
Sep	19.3		9.2		0.1	
Oct	74.1		35.3		0.5	
Nov	100		47.7		0	
Dec	100		47.7		0	
Year	20.4	(21.6)	9.7	(10.3)	0.39	(0.39)

Table 21 shows that the ingested energy requirements of the vole population equalled or exceeded the net primary production of the feeding range from November until February. The ingested energy expressed as a percentage of the net primary production fell from 100% in February to 30.8 - 40.8% in March and by May had reached an annual minimum of 5.4 - 6.6%, a result primarily of the rapid increase in primary production at a time when the ingested energy requirements of the vole population were increasing only slowly.

By June the percentage of the net primary production ingested by the vole population had risen slightly as a result of the increased energy requirement of the population due to reproductive costs. In July and August this requirement reached its maximum with the rapid growth of the juveniles, and as this increased demand occurred at a time when primary production had been reduced as a result of scything, particularly in August, the percentage utilization of net primary production rose to a summer maximum of 39.5% in the latter month.

The percentage of primary production ingested by the voles fell in September where declining population demand due to a reduction in population number co-incided with a post-scything rise in primary production. In October however the percentage ingested rose to a high level once more as a result of the great reduction in primary production in mid and late autumn.

The assimilated energy requirement of the vole population is regarded as a proportion of the ingested energy requirement and alters as a percentage of the net primary production during the year for the same reasons.

The percentage of net primary production converted to tissue was nil in January but rose to the relatively high level of 0.6 - 0.7% in February as the population increased in bodyweight at the end of winter at a time when primary production was at a very low level. From March until May the spring increase in adult bodyweight co-incided with a sharp rise in primary production and the percentage of net primary production converted into tissue therefore fell.

The modest increase in June in the percentage of primary production converted into tissue was a result of the embryonic and post-natal development of the young of the first litters occurring at a time of rapidly increasing primary production. This primary production fell slightly in July and more appreciably in August, and at the same time the maximum secondary production occurred in the former month as the embryonic and post-natal development of the young reached its peak. As a result the secondary production in July and August attained an annual maximum of 1.0% of the net primary production.

In September this percentage was reduced to 0.1% as a result of the reduction in juvenile growth rate, the fall in population density and the increase in primary production in early autumn. There was a rise in secondary production to 0.5% of net primary production in October due largely to the marked reduction in primary production but by November secondary production had almost ceased and it represented less than 0.05% of net primary production in this month. No secondary production was observed in December.

Of the annual net primary production it was estimated that in the order of 20.4 (21.6)% was ingested by the vole population, 9.7 (10.3)% was assimilated, and 0.39% was converted into tissue. If it assumed that 95% of the net primary production is available to be selected by the vole population as food, as concluded in section 7, then the ingested, assimilated and converted energy may be expressed as a percentage of the net edible primary production. Of the 1,945.3 (1,975.1) kcals/m^2/yr of the net edible primary production an estimated 21.5 (22.7)% was ingested, 10.2 (10.8)% assimilated, and 0.41% converted into tissue.

From March until October the primary production of the feeding range exceeded the ingested energy requirement of the vole population and it is concluded that the food supply was more than adequate to sustain the population throughout this period. Even in August when the primary production was curtailed by the reduction in biomass after scything the rate of production was still sufficient to supply more than twice the ingested energy requirements of the vole population without over-exploitation of the standing crop of vegetation. It is concluded therefore that lack of food was not likely to have exerted a limiting effect on the population during the period from March until October.

It has been concluded that from November until February the net primary production within the feeding range may have fallen below the ingested energy requirement of the vole population. It was during this winter period that a food shortage is most likely to have occurred. Some appreciation of the food reserve remaining in the standing crop of vegetation during this period may be gained by estimating the mean standing crop of vegetation/m^2 for any month, calculating the energy available as food and comparing this with the ingested energy requirement of the vole population, although variability in food quality and digestibility remains an unknown factor.

It was estimated from samples of the biomass of aerial vegetation taken during the period from September until April that an average of 86.3% of the living component of the aerial biomass within the feeding range constituted food material available for vole consumption. This figure included only the green shoots and young leaves of plants known to be eaten by the *Arvicola* of the model population.

An approximate mean figure for living ash-free, dry weight biomass for the month of January was calculated as 52.5 gms/m^2. This figure was multiplied by 4.5 to give its calorific equivalent and by 0.863 to give the calories available for vole ingestion.

$$52.5 \times 4.5 \times 0.863 = 203.9 \text{ kcals/m}^2\text{/ month.}$$

The maximum estimate of energy ingested by the vole population for January, the 1973 figure, was 27.74 kcals/m^2/ month. By dividing 203.9 by 27.74 it may be calculated that there was sufficient food available within the feeding range to supply the vole population for 7.3 months during January at the current rate of energy ingestion.

Even in mid-March where the standing crop was at an annual minimum there would still have been an estimated 7.1 months supply of food for the March vole population, however by March the net primary production was itself sufficient to satisfy the population's food requirement. The March figure of 7.1 months supply of food available in the standing crop is an annual minimum.

It is concluded from these figures that even towards the end of the winter there was sufficient food within the original feeding range to supply the ingested energy requirement of the vole population without necessitating an extension of that range either laterally away from the water's edge or to other food sources, for example in the consumption of root material.

The wide margin by which food supply exceeded demand, even when the former was at its minimum in mid-March, suggests that food was not sufficiently scarce to require an increase in foraging intensity on the part of the vole population. It is considered therefore that lack of food was not likely to have exerted a limiting effect on the population in winter. Even in severe winters it seems probable that food supply will comfortably exceed demand, however if food were to exert a limiting effect on the population in occasional years, then the effect could be expected to be most pronounced during late February when both the standing crop of aerial vegetation and the net primary production are at a low level. It is admitted, however, that the requirements of breeding voles for particular elements in the food, for example calcium, may represent a cause for limitation in population growth which has not been considered here.

Discussion on Section 8

The efficiency with which assimilated energy is converted into tissue has been investigated in a number of rodent populations. Golley (1960) estimated that the rodent population of an old field grassland in Michigan where the rodent community is dominated by Microtus pennsylvanicus, converted 2.8% of the energy assimilated annually into secondary production, while Odum et al. (1962) reported a figure of 1.8% for a population of Peromyscus polionotus Wagner from an old field grassland in Georgia. Grodziński (1966) reported values of 1.2 - 1.8% for a variety of rodent species living in the taiga forests of Alaska, and Grodziński et al. (1969) found an average value of 2.65% in populations of Clethrionomys glareolus and Apodemus flavicollis in Polish beechwoods. Trojan (1969) reported that a population of Microtus arvalis from an agricultural ecosystem in Poland converted as much as 10.1% of assimilated energy into secondary production.

In the present study it has been concluded that the Arvicola population converted 3.80 - 3.98% of assimilated energy into secondary production. This figure is high when compared with the usual range of 1.2 - 2.8% for small rodents reported above, although markedly lower than the figure of 10.1% suggested by Trojan (1969) for Microtus arvalis, and may be due partially to the greater size of Arvicola effecting a relative reduction in the vole's daily maintenance costs with a consequent increase in production efficiency.

However when it is considered that other factors, for example the supply and nutritional quality of food, the duration and intensity of daily activity, and the size and frequency of litters, will all affect the production/assimilation ratio it is reasonable to conclude that inter-specific differences in production efficiency between rodents are inevitable and that the figures presented here for Arvicola are substantially similar to those reported for other small rodents.

The efficiency with which rodent populations utilize the primary production of their feeding area will depend primarily upon the proportion of that production which is available to them as food. Such a proportion will inevitably be much higher for a grazing species inhabiting a grassland than for a forest animal feeding largely upon seeds. When comparing the degree of utilization of the food supplies of the rodent populations of differing habitats the annual consumption of the population may be related more relevantly to the annual primary production actually available to the rodents as food than to the total primary production, part of which may be inaccessible to the population and part unpalatable or inedible.

Golley (1960) estimated that the rodent community of the old field grassland in Michigan dominated by Microtus pennsylvanicus consumed 1.6% of the annual edible primary production while Odum et al. (1962) reported a much higher utilization figure, 13.0%, for a population of the seed-eating Peromyscus polionotus in a herb-stage, old field habitat in Georgia. Grodziński et al. (1969) reported that the rodents Clethrionomys glareolus and Apodemus flavicollis together consumed 2.4 - 6.8% of the food available annually in a beech forest in Poland, the proportions depending upon population density, while Trojan (1969) found that the more strictly herbage-feeding Microtus arvalis consumed a lower percentage, 0.5 - 1.3%, of the food available in a Polish agricultural habitat.

Chew and Chew (1970) who investigated the mammal population of a desert scrub grassland in Arizona found that the dominant Dipodomys rodents consumed 3.5% of the available primary production and that when all the herbivorous mammals were considered together this figure was 5.5%.

The figures for the utilization of the annual primary production which is available as food as reported above range from 0.5 - 13.0% depending largely on the feeding competition of other species, the ease with which the food source can be exploited, and upon the density of small rodents within the habitat.

The value estimated for the utilization of the net edible primary production by the Arvicola population in the present study is, at 21.5 - 22.7%, appreciably higher than the usual consumption efficiencies reported for small rodents. This is very largely a result of the far greater densities of rodents in the present study where an average biomass of some 25,000 g/ha represents a figure 13.2 times greater than the average biomass of Microtus pennsylvanicus (1,900 g/ha) reported by Golley (1960). Golley (1960) found that Microtus consumed approximately 1.6% of the available primary production; if the biomass of Microtus had been as high as 25,000 g/ha this consumption would have been 21%, a figure very close to that of the present study.

The high densities achieved by Arvicola in the present study are considered to be due largely to the very favourable environment in which this species lives. The vegetation within the feeding range grows on rich alluvial soils which are kept moist throughout the year by the close proximity of the stream. Primary production is limited principally by the low temperatures in winter and early spring and although annual production at approximately 2,060 kcal/m^2 is less than that of an old field grassland in South Carolina where it attains 2,730 kcal/m^2 (Golley, 1965)* it exceeds the 1,610 kcal/m^2 produced by a similar grassland in Michigan (Golley, 1960). Of the standing crop of vegetation in the present study it is estimated that between 40 and 80% was available to the voles as food at the various seasons (minimum in late winter, maximum in mid summer) and that this figure of food availability was as high as 95% of the net primary production.

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*This estimate of primary production includes a figure for root growth.

The degree of utilization of the primary production by the other vertebrate herbivores within the study area is not known but there is no visual evidence to suggest that their feeding has any marked impact upon the streambank vegetation, and although rats have been known to attack adult *Arvicola* and to devour their young (Ryder, 1962) it is considered that one reason for the high density of Arvicola in this habitat lies in the lack of vertebrate competitors.

Apart from rats, predators on water voles in the study area are probably confined to stoats *Mustela erminea* L., tawny owls *Strix aluco* Shaw, and domestic cats and dogs, although weasels *Mustela nivalis*, Kestrels *Falco tinnunculus* L. and other predators may take young or sickly animals. *Arvicola* may be more susceptible to predation during the winter when the protection afforded by the tall vegetation present in summer is removed, and when the stream may be frozen over, this preventing diving as a means of escape. Kraft (1960) has reported that the cutting of the bank vegetation in summer has the effect of increasing predation on water voles by hawks and owls as it exposes the voles to view from above. Such an increase in predation may be a factor in reducing the numbers of juvenile voles in late summer after the banks have been scythed in the present study area.

Although the flooding of a nest chamber shortly after a female vole has given birth may have resulted in the destruction of the litter, it is not thought that the intermittent stream flooding of the study area resulted in significant vole mortality as it was observed that the stream flowing into the experimental enclosures frequently rose above the level of the nest chamber without resulting in the death of a single experimental animal, adult or juvenile.

It is considered therefore that the high density of *Arvicola* in the study area and the high efficiency of utilization of the food supply which results from this is due to a combination of factors which include the high primary productivity of the feeding range, the high percentage of that primary production which is available to *Arvicola* as food, the lack of vertebrate herbivore competition, and the protection afforded against the restricted number of predators present in the ecosystem by the close proximity of the stream as a refuge.

The utilization of the food supply is increased by the low assimilation efficiency of the voles when fed on a grass diet. The assimilation efficiency of 47.7% found by Drożdż et al. (1971) for *Arvicola* fed on grass is far lower than the assimilation efficiencies found for species of *Microtus*, *Clethrionomys* and *Apodemus*, when fed on diets which ranged from woodland herbs to acorns and beechmast, of from 65 - 91% (Drożdż, 1968) but is close to the assimilation efficiency for *Arvicola* fed on a mixed vegetarian diet of 50.3% reported by Erdakov (1972). Because of this low assimilation efficiency *Arvicola* has to ingest approximately 50% more food in order to satisfy a given requirement of assimilated energy when feeding on grass than does *Clethrionomys* feeding on a mixed diet of herbaceous plants and seed.

This combination of high biomass density and the low assimilation efficiency of the grass diet results in the high utilization of edible primary production of 21.5 - 22.7%.

However this figure has been calculated assuming that the lateral feeding range of the Arvicola population was restricted to the first metre from the water's edge. This restriction of the lateral feeding range was proposed by Ryder (1962) and is supported by the reports of Dean (1946) and Stoddart (1970), and although the veracity of this assumption was not investigated the writer considers that the estimate is a reasonable one, although it is clear that to some extent the lateral range must depend upon the gradient of the bank. If however the average lateral range were 2 m. and not 1 m. then all the percentage utilization figures of the net primary production would have to be halved. However in the writer's experience the assumption of 1 m. is likely to be an overestimate rather than an underestimate as not only are the banks along certain sections of the stream sheer from the water's edge to 1 - 2 m. in height and are barren of any vegetation but also the voles showed a strong preference to feed within the first ½ m. from the water's edge. This first ½ m. is the most accessible part of the range to be reached by a swimming vole and it also has the advantage of being that part of the feeding range nearest to the refuge represented by the stream. That the feeding range was not grazed uniformly by the voles was testified by the prevalence of preferred areas adjacent to the water's edge where the grass was almost grazed to the level of the soil.

Such areas were particularly noticeable in winter when a great part of the standing crop of vegetation was removed from these preferred sites.

It is emphasised that the figures for the utilization of the net primary production and for edible primary production are presented assuming a lateral feeding range which extends an average of 1 m. from the water's edge and are subject to this assumption.

The extent of the feeding range and the intensity of its utilization requires further investigation. The range is almost certain to vary with the bank configuration and may also vary with population density and in relation to the height of emergent and bank vegetation.

The assimilation efficiency of water voles feeding upon a natural diet also requires further investigation. It may be that the assimilation efficiency of 0.477 assumed here is rather low bearing in mind that 20 - 25% of the ingested food will be of dicotyledon origin and will contain a lower fibre content and higher digestibility than that of grasses. Even so it is not thought that the assimilation efficiency is likely to have exceeded 0.55 and the error involved will be small and easy to correct. The assimilation efficiency may also change with season, environmental temperature, age and the digestibility of the various food sources themselves. An association of the techniques of Drożdż (1968) of assimilation trials, and of those used by Evans (1973) in assessing the pepsin digestibility of grasses, might well produce valuable information concerning the changes in the value of food sources to Arvicola from season to season and aid the understanding of the population pressures which may be present in this species and in the utilization of the stream bank ecosystem.

General Summary

1. Histograms of daily activity suggested that from October until April the level of activity remained fairly uniform throughout the diel period, while from May until September activity levels were higher during the night and early morning than during the early afternoon. (1.1)[*]

2. The location of peaks and depressions of activity during the diel period showed closer agreement between adjacent months than non-adjacent months. (1.1).

3. No strong alteration in the presence or absence of above-ground activity was observed in response to the timing of dawn or dusk. (1.1)

4. The duration of daily external activity varied seasonally. From September until March there was a fairly stable level of activity of approximately 6 hrs/day, whereas from April until August the duration of daily activity changed, firstly rising to a maximum of 9.1 hours in July and then decreasing to the winter level of September. (1.2)

5. No difference was observed in the duration of daily activity between the two sexes. (1.3)

6. The duration of daily activity was greater for voles which were permitted contact with each other than for isolated individuals. (1.3)

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[*] refers to the section number

7. The duration of daily activity of the experimental voles showed significant differences from one year to the next. (1.3)

8. The duration of above-ground activity taking place during the day exceeded that during the night for seven months of the year, from March until August, and also during October.
The duration of above-ground activity taking place during the night exceeded that during the day for five months of the year, from November until February, and also in September.(1.4)

9. There was a slight tendency during winter for the voles to counteract the shortened photoperiod by increasing the relative proportion of activity taking place during the day. In summer the voles showed a stronger tendency to counteract the shortened period of darkness by increasing the relative proportion of activity taking place during the night. (1.4)

10. The duration of daily activity was positively correlated with temperature during the coldest months of winter, at which time some evidence suggested an additional negative correlation with the duration of sunshine and a positive correlation with the degree of cloudiness. No correlations between activity and weather conditions were found during the summer months. (1.5)

11. No correlation was found between the duration of daily activity and either rainfall or windspeed at any time of the year.(1.5)

12. Over the year as a whole there was a positive correlation between the duration of daily activity and the diel photoperiod and also between the duration of daily activity and

mean temperature. It was not possible to conclude which of photoperiod or temperature was the more important as a possible regulating influence on the duration of activity. (1.6)

13. The number of periods of activity, interrupted by periods of rest of longer than 1 hour's duration, per day was fairly stable throughout the year, with no clear seasonal pattern. There was a maximum of 6.2 periods of activity/day in April and a minimum of 5.3 in September. The mean for the year of 5.74 represented an average duration of each cycle of activity and rest of 4.18 hours. (1.7)

14 The mean monthly duration of activity within each short-term cycle ranged from a minimum of 0.97 hours in October to a maximum of 1.54 hours in July. The mean duration of the rest period within each short-term cycle ranged from 2.52 hours in July to 3.52 hours in October. The duration of activity/cycle was longer in summer than in winter. (1.7)

15. Changes in the duration of daily activity were effected principally by increasing or decreasing the duration of activity within each activity cycle rather than by changing the frequency of these cycles. (1.7)

16. There was no difference in the number of activity cycles/24 hours between voles which were permitted contact with each other and those maintained in solitary confinement. (1.7)

17. The timing of the onset of the various periods of activity showed closer agreement between the activity patterns of consecutive days than between days more than 4 days apart. (1.8)

18. Synchronisation in the timing of the onset of periods of activity from one day to the next was more likely to be shown by voles kept in solitary confinement than by voles permitted contact with a neighbour. Solitary voles showed such synchrony of activity on a majority of consecutive days while with accompanied voles it was only on a minority of consecutive days. (1.8)

19. There was no difference between the sexes in the probability of voles showing synchronisation in the timing of the onset of periods of activity on consecutive days. (1.8)

20. The behaviour of the voles outside the nest was observed and classified into six principal groups, Swimming, Grooming, Exploration, Rest, Digging and Feeding. The duration of each item of a given behaviour type was timed. The median and mean duration of an item of each behaviour group, with confidence limits, was calculated on a seasonal basis. (2.1)

21. There was no difference in the average duration of an item of any behaviour group between male and female voles, nor was there a difference between the sexes in the amount of time devoted to the various types of behaviour. (2.1)

22. The average duration of a period of Rest and of Swimming was greater in juvenile voles than in adults. These two types of behaviour also formed a greater proportion of the total activity of juvenile than of adult voles. Juveniles showed a corresponding reduction in time spent Feeding as a percentage of the total activity. (2.1)

23. The average median duration of an item of Swimming behaviour over the year as a whole was 3.5 secs. The figure for Grooming was 4.5 secs., for Exploration 5.6 secs., for Rest 8.25 secs., for Digging 13.0 secs., and for Feeding 21.25 secs. (2.1)

24. The types of behaviour observed were allocated to three categories on the basis of the amount of energy expended per unit time. The first two groups requiring a low or moderate consumption of energy combined formed 84.8% of the total activity, over the year as a whole. The percentage did not vary seasonally. The third group of behaviour, requiring a high expenditure of energy, formed 15.2% of the total activity. (2.1)

25. When two voles were active outside the nest at the same time and could see each other, it was observed that their behaviour became less excitable and timid, apparently as a result of the other's presence, and both voles were likely to stay outside the burrow for a longer period than if they had been alone. (2.2)

26. Voles of different sexes and sometimes of the same sex were observed to share nests at all times of the year. (2.2)

27. In winter the mean external (above-ground) temperature experienced by the voles exceeded the actual external (above-ground) mean temperature by 0.62°C. over the aggregate periods when the latter was below 4°C. and by 0.17°C. during those periods when the external mean temperature exceeded 4°C. In

Summer the external mean temperature experienced was 0.97°C. below the actual external mean temperature during the aggregate periods when the latter exceeded 12°C., and by 0.36°C. during those when the external mean temperature was below 12°C. (3.1)

28. The mean temperature experienced by voles while inside the nest chamber was on average 6.58°C. higher than the mean external temperature. The mean temperature of the nest chamber while the vole was absent was up to 1.27°C. lower than the mean temperature when the vole was present. (3.1)

29. The mean temperature of the soil at a depth of 30 cm. was on average 5°C. below the mean nest temperature experienced by the voles at a similar depth in the winter and spring and 4°C. below it in the summer and autumn (3.1)

30. The hours of the year are assigned to a temperature and activity level with regard to what the average vole is likely to experience. The hours of each of the 18 "20 day" periods were divided into those of rest and of activity. The hours of activity were further divided into the proportion for behaviour types requiring low or moderate energy consumption and the proportion for behaviour types requiring a high energy consumption. An ambient temperature was ascribed to each hour. (3.2)

31. The weight of adult voles increased from approximately 180 g. during the winter to 250 g. in late May by which time all the females were pregnant. Each female had two litters during the year. The average bodyweight of the adults declined somewhat

during late summer and autumn to approximately 215 g. in December. Some adults survived a second winter and even increased in bodyweight the following spring but failed to survive into a second breeding season. (4.1)

32. The first pregnancy of each female resulted in births from 5-20 June. The juveniles of the first litters grew very rapidly, reaching 140 g. at 30 days of age, 170 g. at 60 days and 184 g. at 90 days. They maintained a bodyweight of approximately 195 g. throughout the winter. (4.1)

33. The second pregnancy of each female resulted in births from 9 - 21 July. The juveniles from the second litters grew less rapidly than those of the first litters reaching 110 g. at 30 days of age, 145 g. at 60 days, 160 g. at 90 days and 170 g. at 5 months. Individuals from the second litters remained significantly lighter than those from the first litters at least until January and at a given age the individuals from the second cohort were lighter than those from the first for at least 5 months after birth.

34. The bodyweight of first litter juveniles was less than that of the adults born the previous year at least until October and the bodyweight of second litter juveniles was less than that of the adults at least until December. (4.1)

35. Although male voles were generally heavier than non-pregnant females the difference in bodyweight was not significant. (4.1)

36. The population tissue production due to adult growth began in mid-February and reached a maximum of 102 kcals/10 day period

in early May. Adult bodygrowth then ceased and was replaced by the growth of the embryos from mid-May until the end of July when all tissue production by adults ceased. (4.2)

37. The tissue production of the first cohort of juveniles began in June and by mid-June exceeded the tissue production of the adults, having risen to 287 kcals/10 day period. By early July it formed the great majority of the population production, which had reached a maximum for the year of 1,640 kcals/10 day period, but by late July and early August the production of the first litter juveniles had become reduced. (4.2)

38. The tissue production of the second cohort of juveniles began in mid-July and was dominating the population production by late July. It continued to do so during August and September. All production had virtually ceased by November. (4.2)

39. The total annual production of the population was estimated at approximately 8 kcals/m^2 or 6,100 kcals per 380 m. of stream. Adult production formed 10 - 15% of the total population production, that of the first cohort of juveniles 50 - 55%, and that of the second cohort of juveniles 32 - 37%. (4.2)

40. Of the adult tissue production 78.9% was calculated to result from individual growth and 21.1% from the production of embryos and placental membranes. (4.2)

41. It is considered that the resting metabolic rate measured in the laboratory at the temperature of the nest chamber observed from the activity enclosures provided a reliable indication

of the rate of metabolism while in the nest and is referred to as Nest Metabolic Rate (N.M.R.).

The nest metabolic rate was calculated for the individuals of the population im summer ranging in weight from 55 to 320 g. at temperatures between 3° - 28°C. (5.1)

42. Small voles not only consumed a greater volume of oxygen/g. bodyweight than large voles but also showed a greater relative increase in N.M.R. at low temperatures. The percentage increase of oxygen consumption of nesting metabolism over the range of 28° - 3° C. was 2.18% per 1°C. fall in temperature for voles of 320 g. compared with 3.35% per 1°C. fall in temperature for voles of 60 g. (5.1)

43. Nest metabolic rate was calculated during the winter for voles between 170 - 190 g. bodyweight at temperatures from 3° - 15°C. Oxygen consumption increased by 2.9% per 1°C. fall in temperature within the experimental range. At a given temperature over this range the N.M.R. in winter was in the order of 12% lower than in the summer. (5.1)

44. Constants were deduced for converting nest metabolic rate to the metabolic rate during activity requiring a low expenditure of energy. (5.2)

45. Constants were assumed for converting nest metabolic rates to the metabolic rate during activity requiring a high expenditure of energy. (5.2)

46. The daily respiration demand of a non-breeding vole of 180 g. was estimated to range from 41.15 to 43.3 kcals during the year.

The variability was a result of fluctuations in activity levels, ambient temperature and pelage thickness. The daily respiration demand was considered to be slightly higher in summer than during the winter. (5.4)

47. The daily respiration demand was calculated for a non-breeding vole at intervals of 20 days from weaning until death. (5.4)

48. The respiration cost of the model population was calculated for each 20 day period during the year. The annual respiration cost was estimated to be in the order of 150,000 kcals. (5.5)

49. Throughout the year the bank vegetation was dominated by grasses which formed between 74.9 and 83.8% of the total vegetation depending upon season. The nettle <u>Urtica dioica</u> was the most important dicotyledon forming from 10.6 to 17.0% of the vegetation biomass depending upon season. (6.1)

50. The biomass of the bank vegetation reached a minimum in early spring of approximately 76 gms ash-free, dry weight/m^2 as a result of mortality, removal by floodwater and decomposition during the winter. The biomass increased rapidly during late spring and early summer to reach an estimated peak of 327 g/m^2 in late July. At this time the vegetation was cut by scything, following which the biomass fell to 222 g/m^2 by mid-August. Growth in the late summer resulted in a second increase in biomass to 270 g/m^2 in early October after which the biomass of vegetation declined rapidly as a result of mortality to 188 g/m^2 in early December. (6.2)

51. The biomass of bank vegetation contained a component of dead

vegetation which varied as a proportion of total biomass from a maximum of approximately 62% in late winter to a minimum of 10% in mid-summer. (6.2)

52. The biomass of vegetation appeared to be greatly affected by rises in stream water level which would smother, destroy, and remove vegetation on the banks. This resulted in unusually low biomass estimates shortly after the occurrence of floods. (6.2)

53. The rate of decomposition of dead vegetation estimated over periods of two months, was found to reflect environmental temperature being least in mid-winter when 0.3% of the sample was lost per day, and greatest in mid-summer, when 1.3% of the sample was lost per day. Lack of moisture was also thought to be an important factor in reducing the rate of decomposition of dead vegetation during periods of dry weather. (6.3)

54. The rate of residual primary production ranged from nil during the winter to a maximum of 96.7g/m^2/month in June. Residual primary production commenced in March at a rate of 6.9 g/m^2/month and continued until October, when the rate was 3.1g/m^2/month. The annual residual primary production was estimated as 1,630 kcals/m^2. (6.3)

55. The *Arvicola* diet was dominated by grasses, which accounted for between 64.2 and 92.4% of the total epidermis identified in the faeces depending upon season. The frequency of the various grasses in the diet was approximately proportional to their abundance within the feeding range. *Urtica dioica* and *Lamium album* were often eaten by voles, but roots did not form a substantial component of the diet. (7.1)

56. Voles were observed to feed most frequently upon the living stems, stolons and leaves of grasses and upon the young shoots and leaves of dicotyledonous plants. Dead and dying material was avoided. Apart from Urtica, Lamium and the grasses, Sparganium was eaten frequently, Impatiens occasionally, and Conium, Brassica, Alliaria and Cirsium were rarely or never consumed. The plant tissues normally selected by the voles as food formed up to 95% of the primary production within the feeding range. Young voles were thought to be less conservative in their selection of plant species for food than older animals. (7.2)

57. The energy ingested annually by the vole population was estimated to be approximately 430 kcals/m^2. Of this approximately 205 kcals/m^2 was assimilated and 8.0 kcals/m^2 converted into secondary production. The net primary production (the residual primary production plus the energy ingested by the voles) of the area used for feeding was estimated as being in the order of 2,060 kcals/m^2/yr. (8)

58. Secondary production was estimated as constituting approximately 3.9% of the energy assimilated. It ranged on a monthly basis from 0% in December and January to 9.96% In July. (8)

59. Of the annual net primary production it was estimated that in the order of 21% was ingested by the vole population, 10.0% was assimilated and 0.39% was converted into tissue. It is estimated that 95% of the net primary production was available to the voles as food. (8)

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'I confess I am not charmed with the ideal of life held out by those who think that the normal state of human beings is that of struggling to get on; that the trampling, crushing, elbowing, and treading on each other's heels which forms the existing type of social life, are the most desirable lot of human kind.'

John Stuart Mill.