Studies into the ecological energetics of the wireworm melanotus rufipes hbst. (goleoptera : elateridae)

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Abstracts of Thesis

The study was an investigation into the ecological energetics of the Elaterid, Melanotus rufipes Hbst. Prior to this study little was known of the biology and ecology of this animal, therefore such data were presented as background material for the bioenergetic study.

Analyses of the head-width frequency distribution in relation to instar number revealed that male animals pass through fourteen instars and female animals through fifteen instars. The duration of the life cycle was found to be seven years in male and eight years in female animals, the adult stage lasting only one year.

The population ecology of M. rufipes was investigated using random and "whole log" sampling techniques. The data were expressed as the annual change in numbers and biomass.

To determine energy flow through a population of M. rufipes it was necessary to solve the bioenergetic equations:-

$C = A + F$ 1.

$A = R + Pg + Pr + U$ 2.

C = energy consumed A = energy assimilated

F = energy egested R = energy respired

Pg = energy of growth Pr = energy of reproduction

U = energy of excretion (not measured)

Preliminary feeding studies utilising simple food preference tests and

flame photometry techniques revealed that M. rufipes larvae have a carnivorous preference. Further feeding studies culminated in the calculation of ingestion, assimilation and faeces production rates. No evidence could be found for feeding in the adult stage.

A continuously recording electrolytic respirometer and Warburg apparatus were used to measure respiratory rates. This enabled the annual respiratory metabolism of larval and adult animals, to be calculated. Monthly values of oxygen consumption per unit weight of animal produced characteristic L-shaped curves. Data were presented on the respiratory loss of each instar per unit time. Further respiratory investigations were made into the effect of size upon metabolism, the effect of feeding on the respiratory rate and the release of CO_2 from the spiracles of M. rufipes. Additional data suggested that temperature acclimatization is not manifest as a change in respiratory rate.

Growth rates were calculated from laboratory and field data and expressed in the form of a growth curve.

The calorific values of whole animals, eggs, faeces and food were determined using a Phillipson microbomb calorimeter. This enabled calorific equivalents to be calculated for all parameters of the bioenergetic equations and individual energy budgets were thus prescribed for each instar and the adult stage of M. rufipes.

From these data a mean energy budget ("best estimate") was calculated thus: Mean ingestion (C):-19.35 k. cals/100 L. timber/year, assimilation (A):-17.48 k. cals/100 L. timber/year. egestion (F):- 1.86 k. cals/100 L. timber/year respiration (R):-12.74 k. cals/100 L.timber/year and growth (Pg):-4.15 k. cals/100 L. timber/year. The assimilation percentage on a calorific basis was

90.3% (cf. 86.3% by weight). The ratio of secondary production/respiration was 28.6%.

Studies into the ecological energetics of the wireworm *Melanotus rufipes* Hbst. (Coleoptera : Elateridae)

by

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GREY COLLEGE

Being a thesis presented in candidature for the degree of Doctor of Philosophy of the University of Durham

September 1968

Acknowledgments

I wish to thank Professor D. Barker for the facilities extended to me in the Zoology Department during this study, and Dr. J. Phillipson for his introduction to bioenergetics and his supervision, particularly in the writing of this thesis. My thanks also go to the Technical Staff of the Zoology Department, particularly Mr. D.V. Kelly who reproduced the diagrams in this thesis, and Mr. J. Warner who provided much technical assistance and equipment for many aspects of research. My special thanks are extended to Mrs. Ruth Reed for her careful translation and typing of my manuscripts and for co-ordinating the Department.

At the same time I would regard no acknowledgment as complete without thanking my wife, Maureen, for her constant encouragement throughout the last three years.

The study was carried out whilst I was a recipient of an S.R.C. award.

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SECTION I

Introduction

Elton (1927) indicated that ecology simply means scientific natural history, but since that time many advances have been made in ecological studies. One of the most recent advances has been the formulation and development of that branch of ecology known as "ecological energetics". From such studies a unifying theme has emerged, which is based on the unit of energy, the calorie. The use of the calorie gives rise to the possibility for quantitative comparisons to be made between all ecological units, a most difficult task, with the qualitative approach.

The energetics approach to ecology can be traced back, some considerable time, to the first quarter of this century. But it is generally accepted that Lindeman (1942) crystallized the basic energetic principles with regard to individuals, populations and trophic levels. Since 1942 a number of studies, using the energetics approach, have been made to test and modify Lindeman's hypotheses. Most notable amongst the whole ecosystem studies are those of Odum and Odum (1955), Odum (1957), and Teal (1957). However, the present trend tends towards the measurement of rates of energy flow through separate populations, with a view to eventually evaluating the energy flow through

individual trophic levels. Ultimately this could lead to the construction of energy budgets through whole ecosystems. This widely adopted approach has been used by Richman (1958), Odum and Smalley (1959), Slobodkin (1959; 1962), Golley (1960), Smalley (1960), Engelmann (1961; 1966), Kuenzler (1961), Odum, Connell and Davenport (1962), McNab (1963), Golley and Gentry (1964), Saito (1965; 1967), Wiegert (1964; 1965), Watson (1966) and Petrides and Swank (1966). Even more restricted energy flow estimates have been made by Nielsen (1961), Phillipson (1962; 1963), Berthet (1963), O'Connor (1964), Itô (1964), and Phillipson and Watson (1965), who confined their studies to the single parameter of respiratory loss. Respiration is responsible for the greatest loss of energy to the population and therefore is a good indicator of the magnitude of energy flow.

Wiegert (1968) stated that the energy budget of a population comprises the sum of energy gains and losses by each individual organism. These energy exchanges are governed by the same laws of thermodynamics that describe physical energy transfers and transformations. Basically whatever energy enters an ecological unit must ultimately be lost by it. To describe this flow of energy two basic equations have been formulated. Various forms of these have been proposed by different authors; however, the measured parameters are basically the same. In the present study the two equations will be referred to as the energetic equations. The

terminology used to describe these equations will be that proposed by the Special Committee for the International Biological Programme and published in IBP News No.10 (February 1968), p.7. Thus :-

$$C = A + F \qquad .....1.$$

$$A = R + Pg + P_r + U \qquad .....2.$$

C = energy consumed. A = energy assimilated.

F = energy egested. R = energy respiration.

Pg = energy of body growth P_r = energy of reproduction.

U = energy of excretion.

In order to solve equations 1 and 2 independent measurements are made of the various parameters and the measurements finally applied to the equations. Where one variable cannot, for some reason, be measured directly, it may be calculated from the others by difference. This approach was adopted in the present study, but U was ignored because of the difficulty of measuring excretion, as the products were egested along with faecal material.

Solving the energetic equations for a particular population realizes the quantification of energy flow through that population.

The present study concerns Melanotus rufipes Hbst., an elaterid beetle which is predatory at least in its larval stage. It has proved interesting from the point of view that productivity studies on other carnivorous invertebrates are few and have only been made by Engelmann (1961), as part of a larger energetic study on mites, and by Phillipson (1960a; 1960b; 1962) on the harvest spider Mitopus morio (F). Further, most of the earlier population energetics studies were concerned with animals having simple life histories, whereas the present study is of an animal with a very long and complex life-history. Phillipson (1967a) pointed out that the study of an animal with an overlap of generations should be no different than studying animals with only a simple life-history. In general this has proved true for M.rufipes.

Data on the life-history of M.rufipes were scarce and it was necessary to collect the relevant information, during the course of the study, to form a basis for the energetics information. Thus information was gathered regarding the general biology of the larvae and adults of M.rufipes and are presented in Chapter 1. In addition, determinations were made to ascertain the number of instars, the moulting frequency and the length of life cycle of this animal. In order to gain population biomass estimates, for use in conjunction with the energetics data, a sampling programme was followed. These general biological and population data are presented in Section II of this thesis.

Section III is devoted to the individual ecological energetic parameters of feeding, respiration and growth. Finally, data is presented in Chapter 12 concerning the flow of energy through a population of M.rufipes, together with individual energy budgets for all the life stages. Section IV forms the General Discussion. A Summary of the work is presented in Section V.

SECTION II

Chapter 1. On the biology and ecology of Melanotus rufipes Hbst.

Introduction

Joy (1932), writing in the Handbook of British Beetles, intimates the lack of knowledge regarding M.rufipes, for he wrote "a careful study of the habitat and general dissection of the genitalia is necessary". The present study deals primarily with the ecological energetics of M.rufipes, but general data are presented to provide some of the background information which was lacking.

Hyslop (1917) divided the Family Elateridae into three sub-families :-

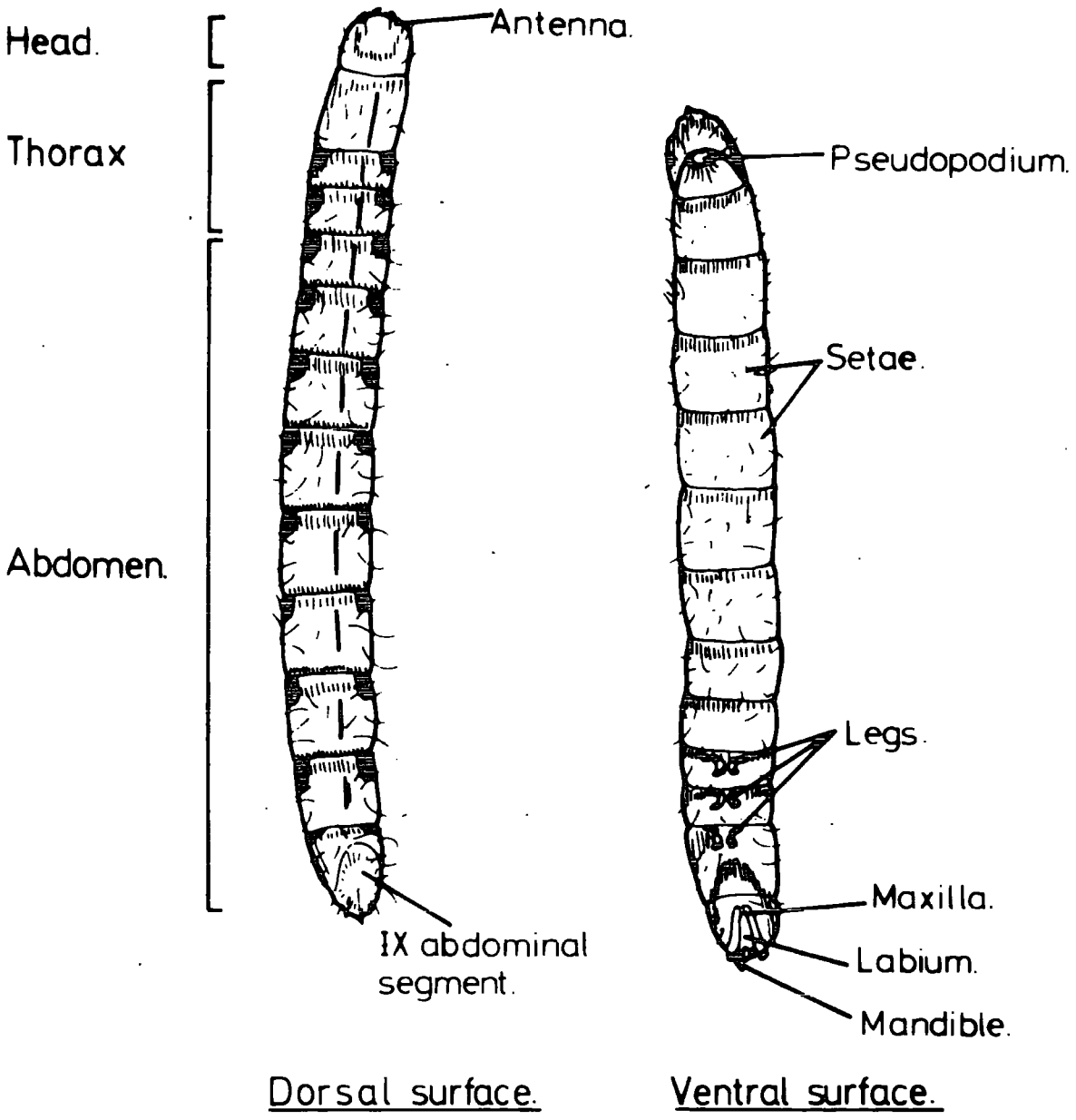
1) Sub-family Pyrophorinae
2) Sub-family Cardiophorinae
3) Sub-family Elaterinae

Further, Hyslop (1917) and Glen, King and Arnason (1943) agree that the genus Melanotus should be placed in the sub-family Elaterinae, Tribe Melanotini.

a) The larva

True wireworms are beetle larvae belonging to the Family Elateridae. Curtis (1860) listed many diverse animals as wireworms, for example, centipedes, millipedes, isopods and tenebrionid beetle larvae. Some full descriptions have been made of true wireworms but none of M.rufipes. To remedy this situation, an original

Fig.1. Diagrams of M.rufipes larvae to show external features.



Melanotus rufipes. Hbst.:-general features.

description is presented in this study.

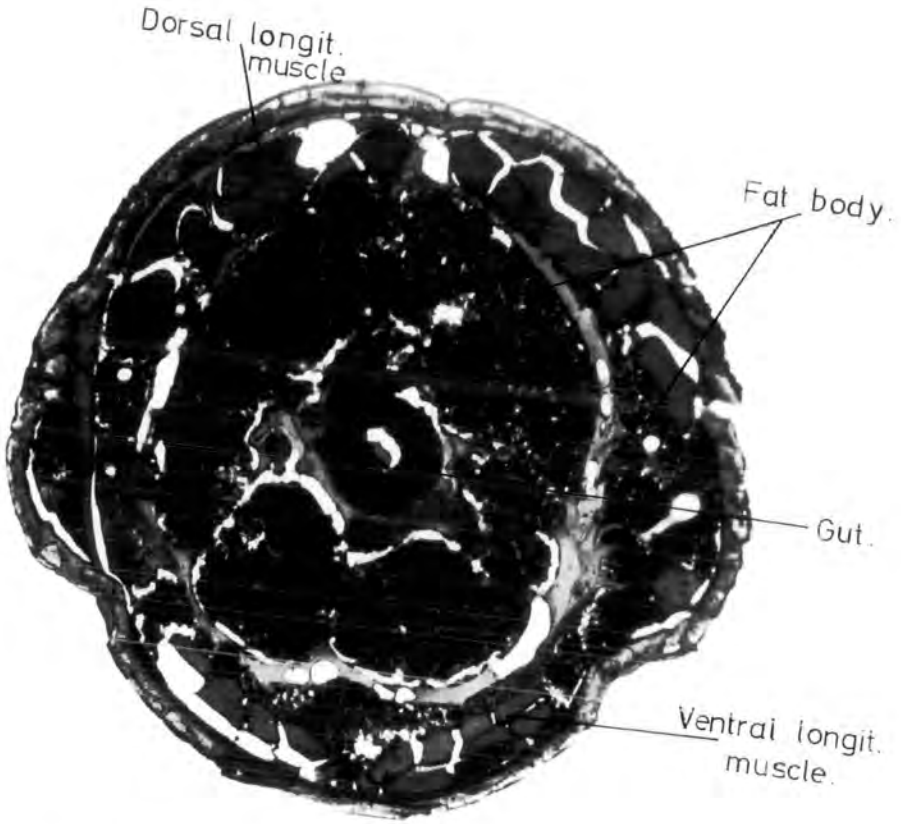
Melanotus rufipes Hbst. is typical of wireworms (Fig.1) in that its form is elongate, circular in transverse section and covered by a heavily chitinized exoskeleton. Its head is wedge-shaped, bearing antennae, labium, maxillae and a pair of powerful sickle-shaped mandibles. The thoracic segments each bear a pair of jointed legs. The elongated abdomen is formed from nine visible segments, the ninth abdominal segment being species specific in wireworms. In M.rufipes this ninth segment is flattened with a point at its apex and one or two teeth at either side. The segment has also been described by Van Emden (1945) in his useful key to the wireworms. On the underside of segment nine is a fleshy protuberance, the pseudopodium, which contains the anus. The abdominal segments 1 - 8 each bear a pair of spiracles. The body and head are sparsely covered by setae. Zacharuk (1962) believes that these are of a sensory nature.

In the present study a brief examination was made of the internal anatomy of M.rufipes larvae. The reasons for this were to provide information on possible metabolic storage organs and to add to the scant data already available on the anatomy of wireworms in general, and M.rufipes in particular. The only available work concerning wireworm anatomy is that of Eidt (1958) who studied the larvae of Ctenicera aeripennis destructor (Brown). The method used, in the present study, was to make a series of transverse sections of whole animals and to determine the anatomy from these (Figs. 2 and 3).

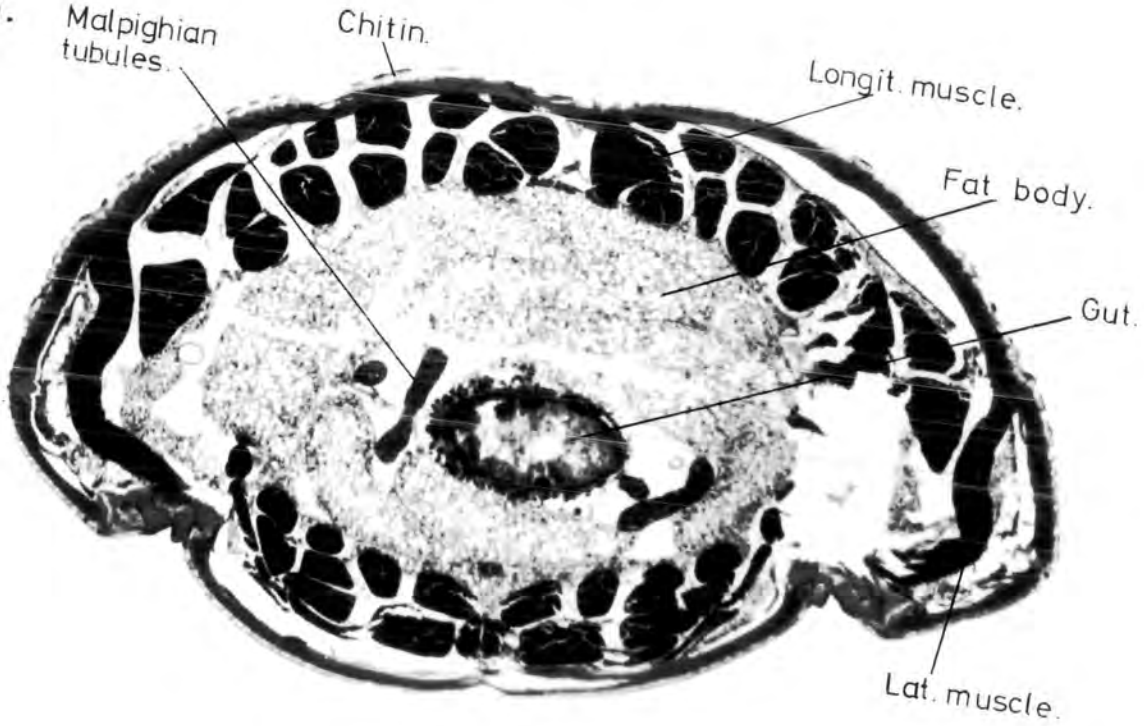
Fig.2. T.S.abdomen of M.rufipes larvae - gelatin paraffin section.

Fig.3. T.S. abdomen of M.rufipes larvae - paraffin gelatine section.

A.


Dorsal longit. muscle
Fat body.
Gut.
Ventrai longit. muscle.

B.


Malpighian tubules.
Chitin.
Longit. muscle.
Fat body.
Gut.
Lat. muscle.

Sections were made in the normal manner using standard paraffin wax techniques. It was soon evident that one of the major structures was fat body. In order to examine this fully, further sections were taken from material embedded in gelatine, and cut on a freezing microtome.

The results are shown in the photographs which are self-explanatory in their anatomical detail. The large fat bodies fill the abdominal cavity and pass between the muscle layers. In life the fat body is yellow and is comprised of connective tissue and oil globules. It is reasonable to assume that the fat bodies provide an important storage centre for metabolisable material. As will be shown in the feeding section (Chapter 7), this storage facility is of great importance.

In general the anatomy of M.rufipes is similar to that found by Eidt (1958) for C.aeripennis destructor (Brown).

b) The pupa

Pupation of M.rufipes takes place during July and lasts approximately five weeks. The last instar larva forms a hollow cell within the timber and undergoes a moult to form the white pupa, which resembles the adult apart from possessing reduced wings and elytra. The imago is formed in about five weeks. This remains in the cell over the winter period (Fig.4) and finally emerges in spring of the following year. This is in general agreement with the observations of Saalus (1923) on M.rufipes in Finland.

Fig.4. M.rufipes adult in pupal cell.

TABLE I

Size differences of male and female M.rufipes

MALES			FEMALES		
Length	Greatest Width	Area	Length	Greatest Width	Area
14.00mm	3.50mm	49.00	18.00m	4.25mm	76.50
16.00	3.00	48.00	15.00	3.20	48.00
16.00	3.00	48.00	16.00	3.75	60.00
16.50	3.50	57.75	17.00	4.00	68.00
14.50	3.00	48.50	17.00	4.00	60.80
14.00	3.00	42.00	16.00	4.00	64.00
14.00	3.20	44.80	16.00	4.00	64.00
13.00	3.50	45.50	15.50	4.00	62.00
14.00	3.00	42.00	14.45	4.00	57.80
			16.00	4.00	57.80
$\bar{x}$			16.50	4.40	72.60
14.9 ± 0.33	3.22 ± 0.081	47.30 ± 1.57	16.05 ± 0.33	3.97 ± 0.067	63.81 ± 2.11

Applying 't' test to difference between mean areas :-

$$t = \frac{M_1 - M_2}{\text{Standard Error of difference of } M_1 - M_2}$$

M_1 = Mean ♀

M_2 = Mean ♂

S.E.D. $M_1 - M_2 = 2.69$

$\therefore t = \frac{16.51}{2.69} = 6.13$

$\therefore$ 't' significant at 0.05 probability level

$\therefore$ Size differences between males and females statistically confirmed.

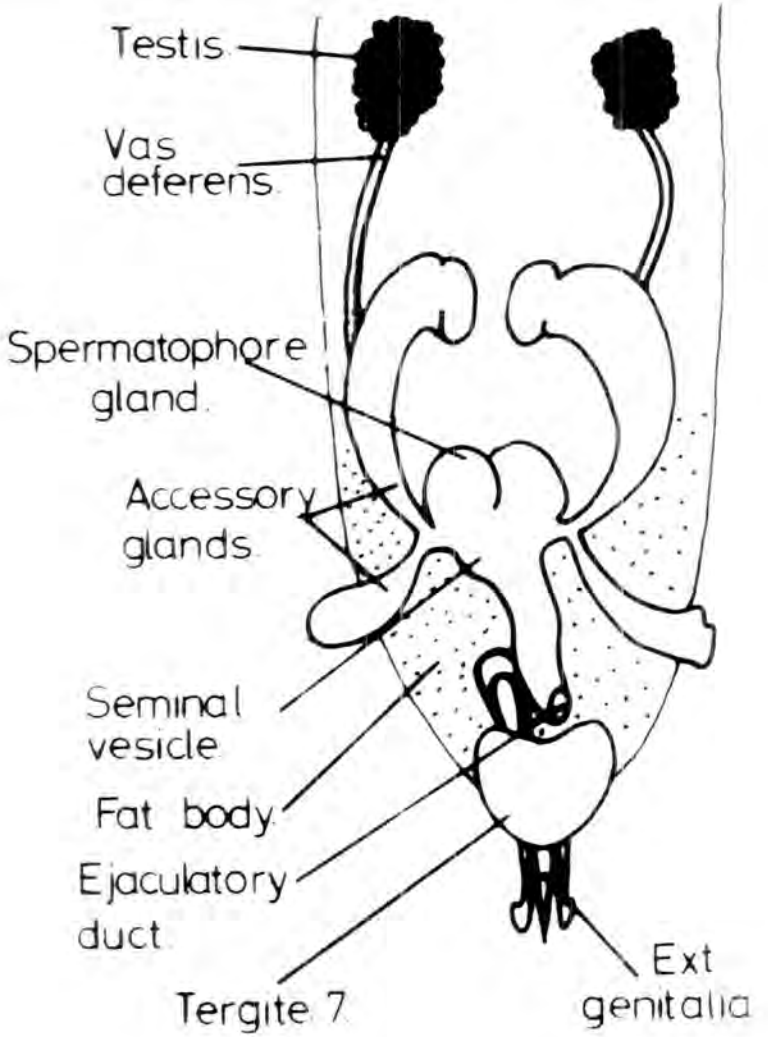
c) The Imago

A full description of the imago of M.rufipes is given by Fowler (1886). Briefly, they are black-brown beetles, approximately 14-15mm in length and have the well-known ability to jump up in the air when placed on their backs, so hence the common names of skip-jacks and click-beetles given to all Elaterid beetles.

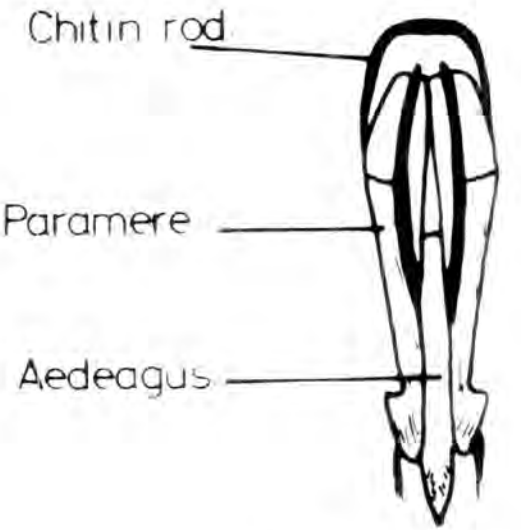
During the present study a size difference was noted between male and female adult beetles. The female appeared to be longer and wider. This was tested by finding the area of the body of each beetle and comparing the data statistically between males and females, by using a Student-t test (Table I). The average male area was found to be $47.30 \pm 1.57mm^2$ and female $63.81 \pm 2.11mm^2$. The 't' value was 6.13 and was highly significant ($p = 0.05$). The reason for the bigger female appears to be as a result of having a larger reproductive apparatus, as shown in Chapters 2 and 3; this has repercussions on the life-history.

The main functions of an imago are reproduction and dispersion. In order to determine the reproductive capacity, with a view to conversion to energetic terms, a number of dissections were made of imagos. As previous work on adult internal anatomy is very scant, some additional work is presented in this study. Some anatomical data has been presented by Van Zwaluwenberg (1922) who described the morphology, with special reference to the external genitalia, of adults of Melanotus communis Gyl. and M.fissilis and Zacharuk (1958) for Ctenicera sp. Fig.5 shows the internal

Fig.5. Diagram of male M.rufipes adult to show the reproductive apparatus.



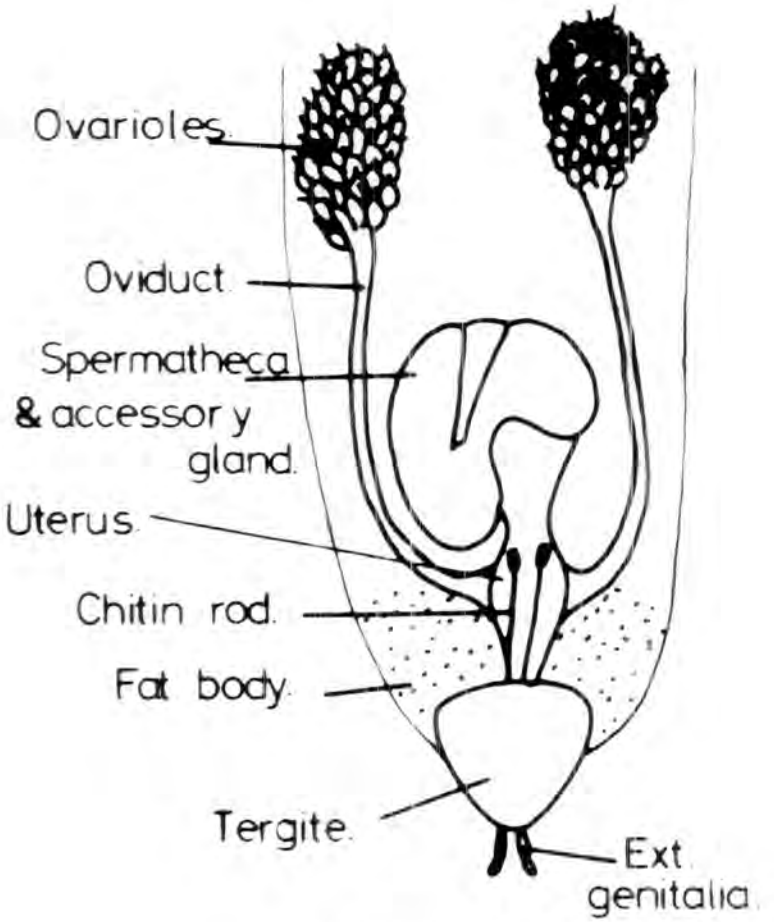
Internal genitalia



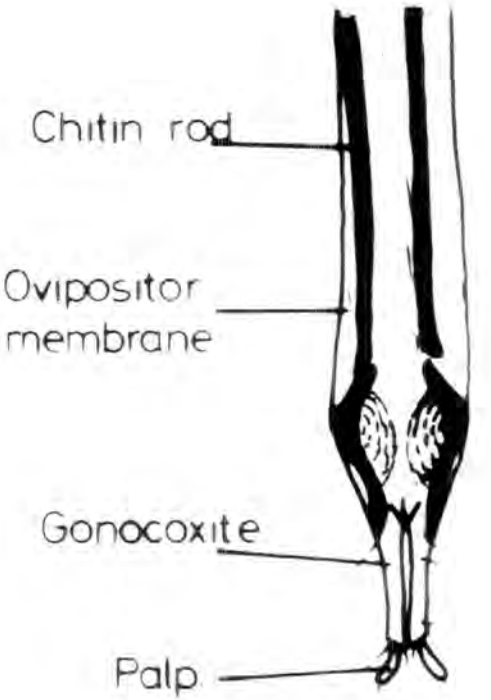
External genitalia

Melanotus rufipes. Hbst:- Male reproductive apparatus.

Fig.6. Diagram of female M.rufipes to show the reproductive apparatus.



Internal genitalia.



Ovipositor

Melanotus rufipes. Hbst:-Female reproductive apparatus.

anatomy of the male adults, with special reference to the reproductive apparatus and also the external genitalia. The latter comprise a central aedeagus containing the ejaculatory duct and a pair of hooked parameres. The internal anatomy of the females is similarly shown in Fig.6. The most conspicuous structures, apart from the fat body, are the ovaries, consisting of many ovarioles. On dissecting mature females the number of eggs in the body cavity was found to vary between 216 and 294 (Table II). The mean value was found to be 260.4. This contrasts with Fernando's (1963) paper which states that M.rufipes produces 90 eggs/female. It is possible that his counts were made from females that had part laid. In the present study counts were made from females freshly removed from the pupal cells in early summer and from females caught "on the wing" at this time. In order to ascertain the number of ovarioles per female, these were counted in an immature specimen. They were found to number 118. As each ovariole appears to be capable of producing at least two eggs, this particular animal had an egg potential of 236, which shows reasonable agreement with the egg counts. Zacharuk (1958) believes that fertile egg production is limited by the amount of fat available for metabolism. The eggs were ovoid in shape and surrounded by a tough membrane. In order to determine the size and weight of eggs produced, various measurements were made. (Tables III and IV). The mean size was found to be 0.73 x 0.48mm. The wet weight - dry weight relationship of the eggs was determined.

TABLE II

Number of egg/female

No. eggs/female
294
290
282
216
220
260.4
Mean no. produced = 260.4

TABLE III

Size of eggs

Length (mm)		Breadth
0.76	x	0.51
0.76	x	0.45
0.70	x	0.51
0.70	x	0.51
0.76	x	0.51
0.79	x	0.54
0.79	x	0.54
0.79	x	0.48
0.79	x	0.51
0.76	x	0.51
0.70	x	0.45
0.67	x	0.45
0.73	x	0.45
0.61	x	0.45
0.70	x	0.39
0.73	x	0.51
0.76	x	0.54
0.73	x	0.45
0.73	x	0.45
0.73	x	0.48
Mean egg size = 0.73	x	0.48mm

TABLE IV

Wet wt./dry wt. relationships of eggs

Wet wt. 10 eggs	Dry wt. 10 eggs	% dry wt.
0.676 mgs	0.335 mgs	49.5%
0.613	0.327	53.3
0.772	0.315	40.8
0.616	0.297	48.2
0.506	0.299	59.1
0.781	0.313	40.0
0.598	0.247	41.3
0.622	0.302	45.5
0.500	0.306	61.2
0.555	0.281	50.6
0.624 ± 0.03	0.302 ± 0.009	48.4%

$\therefore$ Mean wt. 1 egg =

Wet 0.0624 ± 0.03mgs. or 0.0302 ± 0.0009mgs. Dry

Ten groups, each consisting of 10 eggs, were placed on pre-weighed, aluminium foil, and weighed. They were dried in a vacuum oven to constant weight. The mean wet weight of one egg was found to be 0.0624mgs and the mean dry weight 0.0302mgs. The water content was 59.6% of the total weight.

In terms of weight, using mean values for the number of eggs and weight of eggs produced, a M.rufipes female produces a mean wet weight of 16.25mgs of eggs (7.86mgs dry weight).

On dissecting animals removed from the pupal cell in October the gonads were found to be immature, but by the end of the spring they were almost fully developed. As the animals cannot feed in the pupal cell this growth must depend entirely on reserves laid down by the last instar.

The external genitalia of the female M.rufipes are really part of the normally retracted ovipositor (Fig.6). Usually only the genital valves (gonocoxites) are visible, each having at its apex a terminal stylus. On extrusion the ovipositor is seen to consist of a membranous tube, strengthened by a pair of thick chitinous rods. Oviposition takes place in a suitable crevice in the bark of a log. Difficulty was found in obtaining eggs from the field, unless their oviposition sites were known. In the laboratory they proved difficult to hatch.

Little is known of flight and dispersion in M.rufipes. The author has noted a number of flights, mainly at dusk. Both

Duffy (1945) and Cooper (1945) have reported flights of M.rufipes during the crepuscular period; the former even noted an assemblage, probably for mating purposes.

d) The Habitat of M.rufipes

M.rufipes inhabits rotting logs or stumps (in this study a log is any piece of timber greater than 15cms long and 4cms in diameter). The decaying log is considered so important by Elton (1966) that he has described it as providing one of the two or three greatest resources for animal species. These resources become available to animals by decay.(Fager 1955). The flora and fauna of decayed timber is distinctly characteristic and shows a definite succession of species as decay proceeds. According to Cartwright and Findlay (1958), decay is of two main types, white and brown rot. In the former, fungi degrade ALL components of the timber; the latter is caused by Polyporus spp., which degrades most of the timber apart from lignin. It was evident, in the present study, that M.rufipes could not be found in white-rotted timber and was in agreement with Elton (1966). The reasons for the absence of M.rufipes in white-rot timber is not clear; perhaps white-rot fungus contaminates the environment with some by-product and makes it unfavourable. I believe this may be used to explain Larkin and Elbourn's (1964) failure to find M.rufipes in rotting timber from live oak trees as their timber samples contained white-rot. Wallace (1953) noted that M.rufipes in brown-rotted pine stumps was found below the soil level in winter, and above,

at the cut surface of the stump, in summer. He also found that they were abundant in clearings (20-100 individuals/stump) but sparce in forest with thick undergrowth (2-20). M.rufipes has been recorded from a variety of rotting timbers (Van Emden (1945) and Elton (1966). From personal observation, birch and alder appear to be the two most readily colonised tree species.

It is generally accepted that the first animals to colonize a piece of decaying timber are those capable of digesting wood materials, followed closely by the fungus feeders. As soon as these are established, predators, including M.rufipes, appear (Mamayev and Sokolov 1966). M.rufipes plays an important part in the mechanical destruction of the wood, through its tunneling activities, which open up the timber, hastening decay. Elton (1966) refers to M.rufipes as being one of the four main tunnellers in decaying timber at Wytham. Certainly its burrows are most conspicuous in rotting logs.

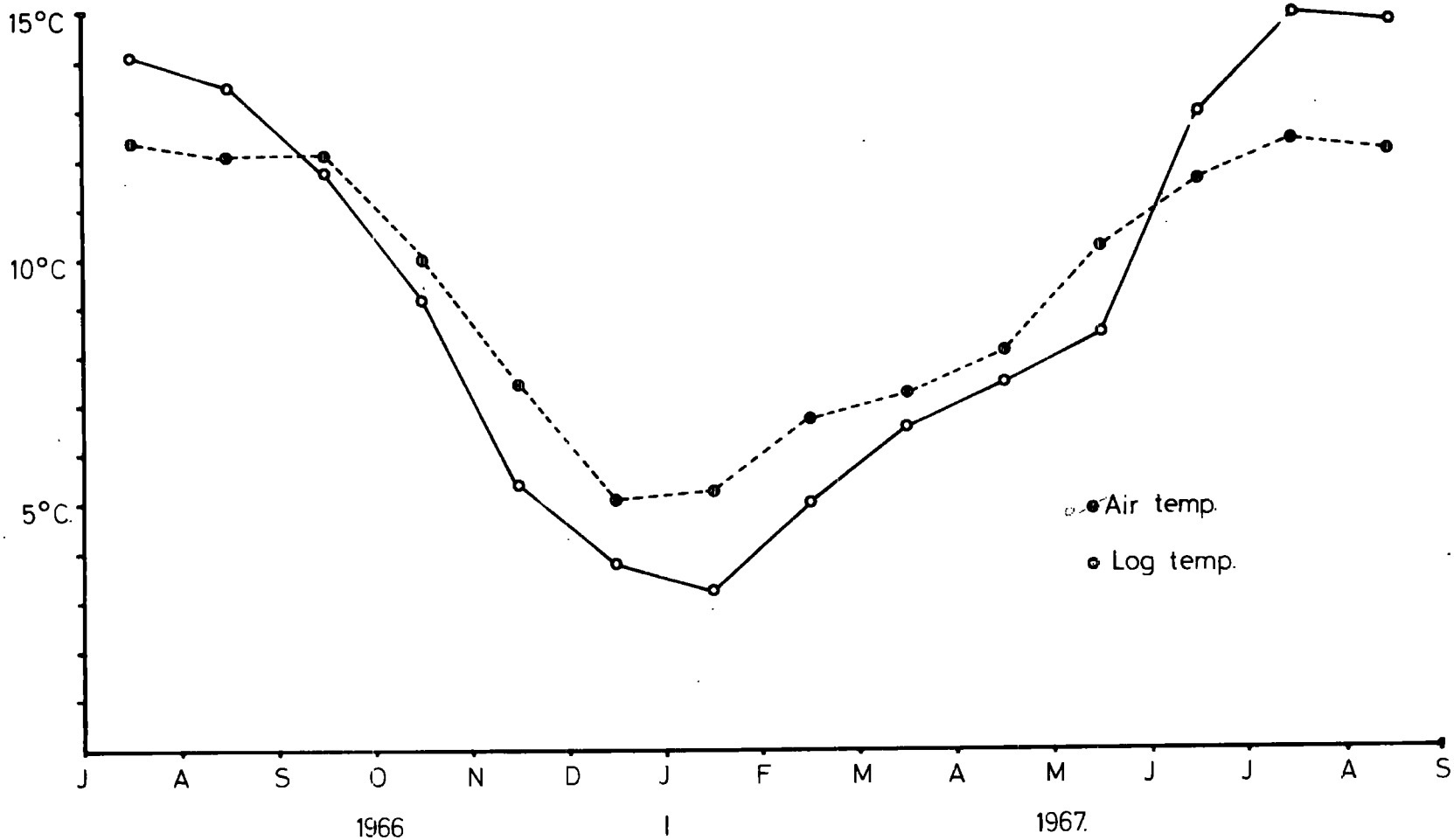
The micro-climate of the rotting log is highly specialized. According to Cartwright and Findlay (1958) rotting timber tends to an acid pH value and has a high water content (72.5% water content being found for logs in the present study). Thus a high humidity is maintained at all times and is essential to most of the inhabitants of rotting timber. According to Saveley (1939), the O_2 content in rotting timber is low and the CO_2 content high, in comparison to the outside atmosphere. Paim and Beckel (1963a) reported a cyclical change in O_2 and CO_2 content with season with O_2 reaching

TABLE V

Mean log temperature data

Air temperature figures from Durham Observatory				
1966-67	Surrounding temperature	Grade II	Grade III	Log mean temperature
July (mid-month)	14.1°C	12.26°C	12.50°C	12.38°C
August	13.5	12.13	12.07	12.10
September	11.8	12.19	12.14	12.16
October	9.1	10.00	9.96	9.98
November	5.3	7.21	7.61	7.41
December	3.8	5.12	4.96	5.04
January	3.2	5.16	5.18	5.17
February	5.0	6.67	6.66	6.66
March	6.5	7.18	7.11	7.15
April	7.3	7.10	8.24	8.16
May	8.1	10.03	9.93	9.91
June	12.9	11.40	11.52	11.46
July	14.9	12.24	12.25	12.24
August	14.7	11.89	11.83	11.80
Log figures taken from Wynyard by S. Wignarajah				

Fig.7. Comparison of mean air temperature and mean log temperature during 1966 - 67.



Temperature data, July 1966 - Aug. 1967.

a maximum and CO_2 a minimum, in winter.

In order to have estimates of the seasonal temperature changes within rotting timber in the field, log temperature measurements were made. Such data would enable conversion of energetic data obtained at a constant temperature in the laboratory to approximate field rates. The temperature measurements were carried out by S. Wignarajah at Wynyard Wood, as part of the group project (Chapter 4). The method of measurement was that described by Berthet (1960), which utilises the rate of inversion of sucrose. On the site logs were graded according to the amount of decay present as I, II, III (Chapter 6). Temperature measurements were confined to log grades II and III, partially and fully decayed timber, respectively. For each grade measurements were taken at three separate positions, a) between the bottom of the log and the surface of the ground, b) in the centre of the logs, and c) directly under the bark and on the upper surface. The same logs were measured throughout the year. Table V shows the mean log temperature for grades II and III, the mean log temperature (mean of grade II and grade III) and the surrounding air temperature. Fig.7 shows the mean log temperature compared with the surrounding temperature. Generally log temperatures follow the air temperatures, but are 'damped' so that the extremes of summer and winter are not reached. Thus a reasonable constancy of the environment is found in rotting timber.

SECTION II

Chapter 2. On the determination of instars

Introduction

Before any study could begin on the energetics of the different life stages of Melanotus sp. it was necessary to determine the number of instars involved in the life cycle. A number of methods have been used to differentiate the instars of various insects. Basden (1950), working with Agriotes sputator L., counted the number of spiracular teeth but this proved to be impracticable for M.rufipes. As each instar of Melanotus is similar in all respects apart from size it seemed obvious that the instars should be separated by measurement. In previous studies on other Coleopterous groups two parameters have been measured, the length of the body and the greatest width of the head. The former was adopted by Ford (1917) in his study on Agriotes obscurus L., Rymer-Roberts (1919, 1921, 1922 and 1930) in his work on A.sputator L., A.obscurus and Athous haemorhoidalis F., Strickland 1939 for the prairie grain wireworm Ctenicera (Ludius) aeripennis destructor, Brown and by Salt and Hollick (1944) on Agriotes spp. For many species length measurements have proved unsatisfactory, and the greatest head width has been measured. McDougall (1934), in his study of Lacon variabilis Cand. measured both the length and the greatest head width of the larva and decided that the latter was

a more accurate indicator of instar. Previously head width has been utilised by Metcalfe (1934) on the anobiid beetle Sitodrepa panicea L. and by Prebble (1933) for three species of bark beetle. More recently this approach was utilised by Van Enden (1944) in his comprehensive review of the Elateridae, and by Yoshida (1961) for Melanotus caudex Lewis. Fernando (1963) measured the head-width of a number of elaterid larvae, in particular Athous haemorhoidalis F. and analysed his measurements graphically using arithmetic probability paper. In the present study the approach of Fernando was adopted as this was thought to be the most accurate means of separating instars.

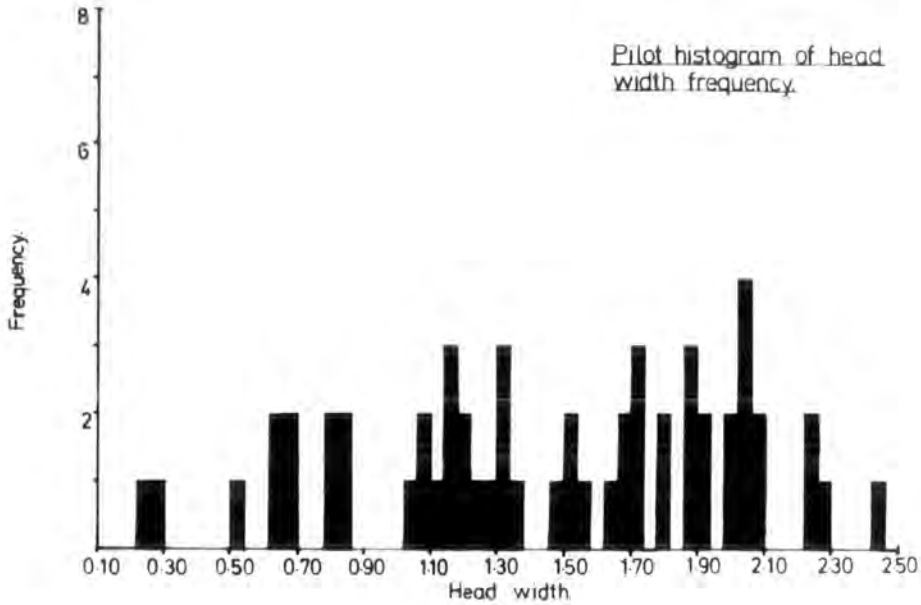
Method

The head of each larva was measured at its widest point by means of a standard eye-piece micrometer. During measurement the larva was immobilised by trapping it between a glass square and a thick pad of wet-filter paper in a Petri dish. The larva was held by the water film, aided by gentle compression of the glass square. The head width was measured under a low power microscope, easily and without damage.

In order that the tentative groupings of head widths, into instar numbers, could be made, a pilot study was made. Initially the head widths of one hundred specimens were measured and expressed as the pilot histogram (Fig.8). From Fernando's study (1963) and my own pilot study it was concluded that at least

Fig.8. Pilot histogram of head width frequency of M.rufipes.

Fig.9. Final histogram of head width frequency of M.rufipes.


Pilot histogram of head width frequency.
Frequency.
8
6
4
2
0·10
0·30
0·50
0·70
0·90
1·10
1·30
1·50
1·70
1·90
2·10
2·30
2·50
Head width

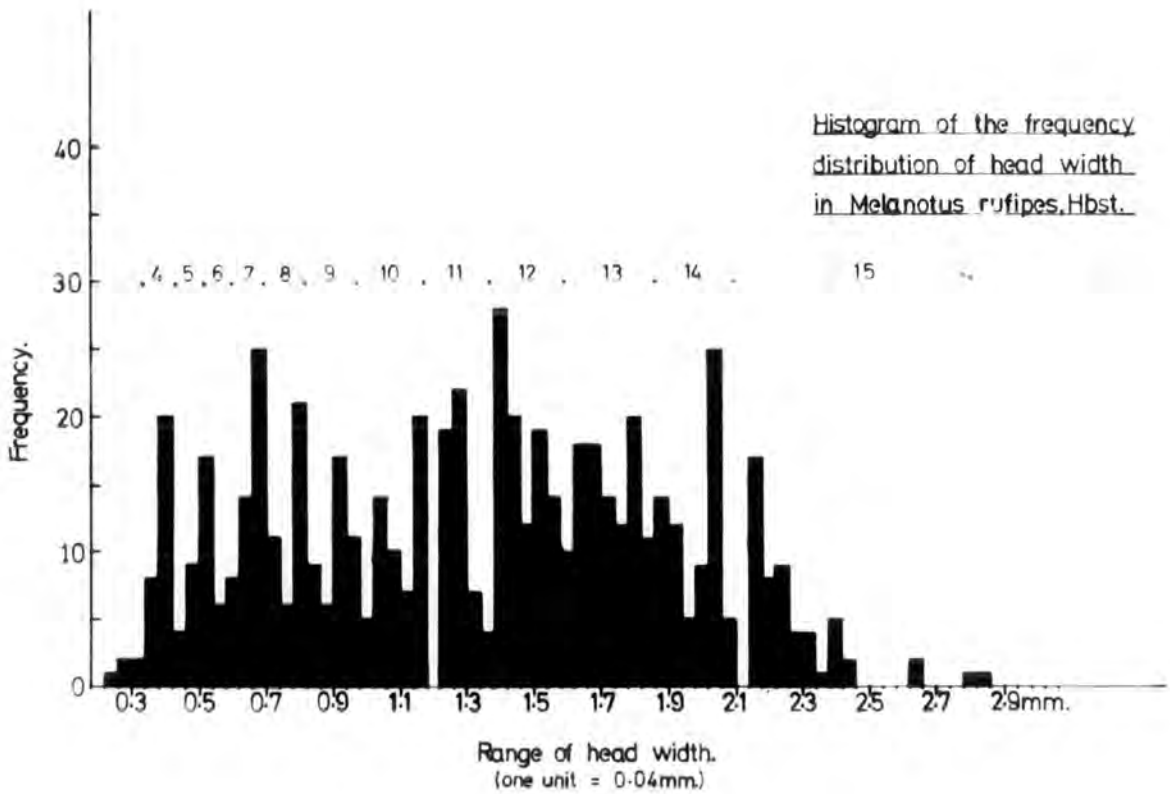

Histogram of the frequency distribution of head width in Melanotus rufipes, Hbst.
Frequency.
40
30
20
10
0
4
5
6
7
8
9
10
11
12
13
14
15
0·3
0·5
0·7
0·9
1·1
1·3
1·5
1·7
1·9
2·1
2·3
2·5
2·7
2·9mm.
Range of head width.
(one unit = 0·04mm.)

TABLE VI

Instar grouping from pilot investigation

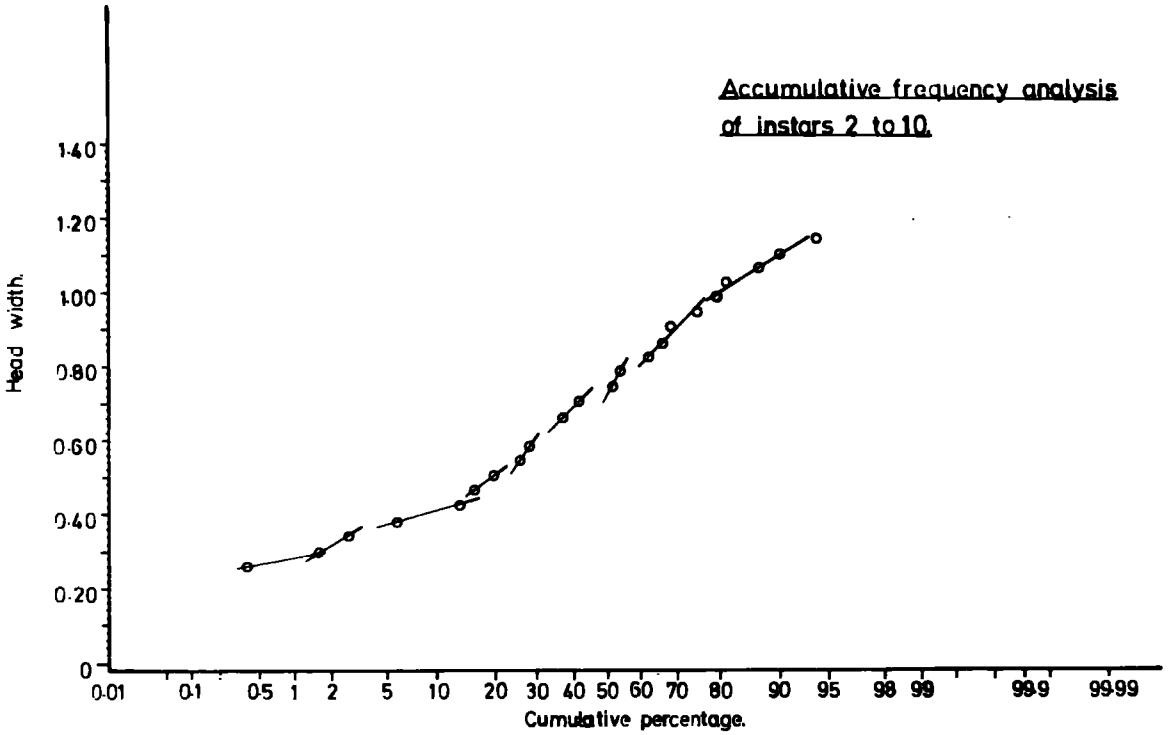
Instar	Head width range (mm)
1	0.21 - 0.25
2	0.25 - 0.30
3	0.30 - 0.35
4	0.35 - 0.42
5	0.42 - 0.50
6	0.50 - 0.59
7	0.59 - 0.69
8	0.69 - 0.81
9	0.81 - 0.98
10	0.98 - 1.15
11	1.15 - 1.38
12	1.38 - 1.62
13	1.62 - 1.90
14	1.90 - 2.23
15	< 2.23

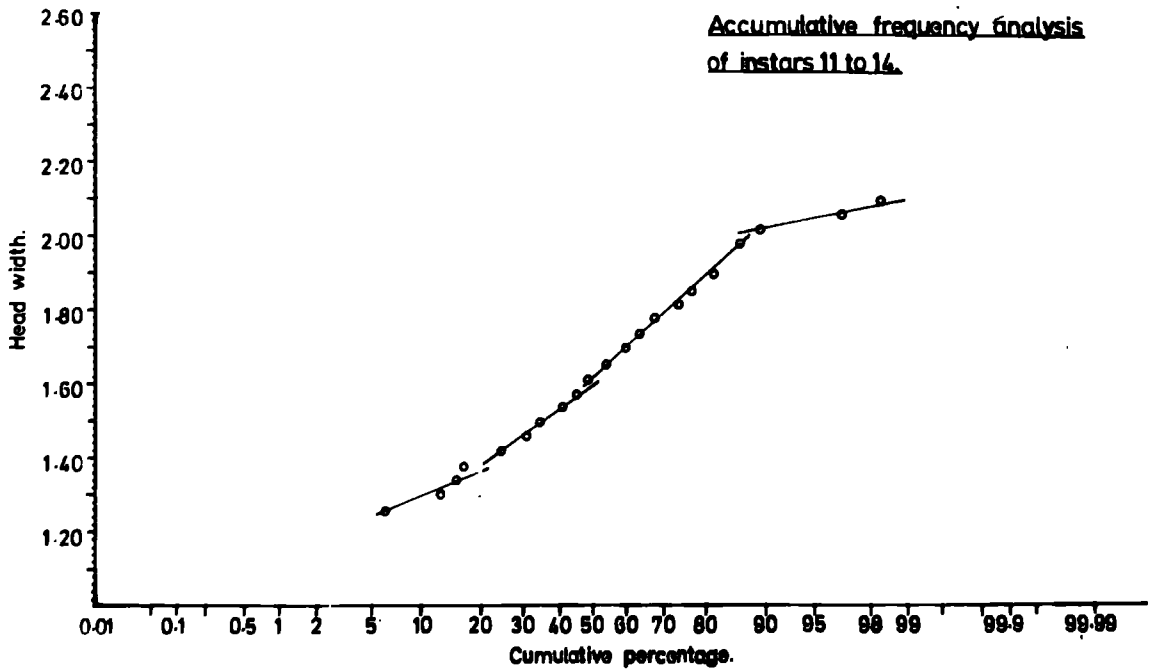
fifteen instars were present during the life-cycle of M.rufipes. Using these data it was possible to delimit the instar ranges by constructing a graph of the log. head width against the instar number; a system based on Dyars' Law. Initially the smallest head width found was plotted and assumed to be that of Instar 1. (0.23mm) which corresponds to the smallest size found by Fernando (1963). The largest head width found was also plotted and assumed to be Instar 15 (2.41mm). These are represented on the log. head width against Instar graph as black points (Fig.27). A straight line between the two points gave the approximate groupings of each Instar, whether or not they had been measured in the pilot study. The preliminary groupings for each instar are shown in Table VI which is in the form of non-overlapping groups. This work facilitated the delegation of instar numbers which were necessary for other studies.

When a large number of head widths had been measured, the data were refined to give more precise estimates. In all, the greatest head width of approximately one thousand animals were measured. All measurements were grouped and analysed to produce the final histogram of head width frequency in distribution (Fig.9). This is comparable to the histogram produced in the pilot study but includes many more measurements. The histogram shows many peaks which may be indicative of instars. The first four instars were probably not covered by enough measurements to

Fig.10. Accumulative frequency analysis of Instars 2 - 10 inc.

Fig.11. Accumulative frequency analysis of Instars 11 - 14 inc.


Accumulative frequency analysis
of instars 2 to 10.
Head width.
1·40
1·20
1·00
0·80
0·60
0·40
0·20
0
0·01
0·1
0·5
1
2
5
10
20
30
40
50
60
70
80
90
95
98
99
99·9
99·99
Cumulative percentage.


Accumulative frequency analysis
of instars 11 to 14.
Head width.
2·60
2·40
2·20
2·00
1·80
1·60
1·40
1·20
0·01
0·1
0·5
1
2
5
10
20
30
40
50
60
70
80
90
95
98
99
99·9
99·99
Cumulative percentage.

be significant on the histogram. This is due to experimental bias in which extraction and sorting of a log sample favours the larger wireworms. Further conclusions were drawn about this peaking when analysis of the frequency distribution was carried out.

The analysis of the frequency distributions of the head width in relation to instar was carried out using the method put forward by Harding (1949), for the analysis of polymodal frequency distributions. Briefly this method advocates the use of arithmetic probability paper which has, on its horizontal axis, a scale of percentages ranging from 0.01% to 99.99%. The vertical axis in this case provided the scale of head width in millimetres. The data are expressed as a cumulative percentage.

In the first instance the full range of head widths was plotted; the graph in Fig.10 extends from 0.22 - 1.18mm and that in Fig.11 from 1.18mm - 2.26mm. Individual points were joined by straight lines. Fig.10 shows that there are nine instars present which are thought to be Instars 2 - 10 inclusive (any figure below 0.24 was taken as Instar 1 but the sample measurements for this Instar were not large enough). Similarly Fig.11 shows Instars 11 - 14 inclusive, any figure greater than 2.23mm being taken as Instar 15. These graphs should only be taken as indicative of a particular instar and do not delimit any accurate parameters. To this end a more intense analysis of pairs of instars was carried out.

The head widths were plotted on arithmetic probability paper on which a straight line is indicative of a normal frequency distribution. This would be characteristic of any particular instar. Thus, if a pair of instars are analysed, a sigmoid curve should result. The line drawn through the sigmoid curve is not drawn to the points but is calculated as the resultant of two straight lines derived from percentages of the total sample. The two calculated straight lines represent the normal distribution, the mean being found where the 50% vertical intersects the line. Similarly, the standard deviation is estimated where the verticals for 15.87% and 84.13% intersect the curve. Evidently the position of the calculated line is dependent on the mean and the slope by the standard deviation of the sample.

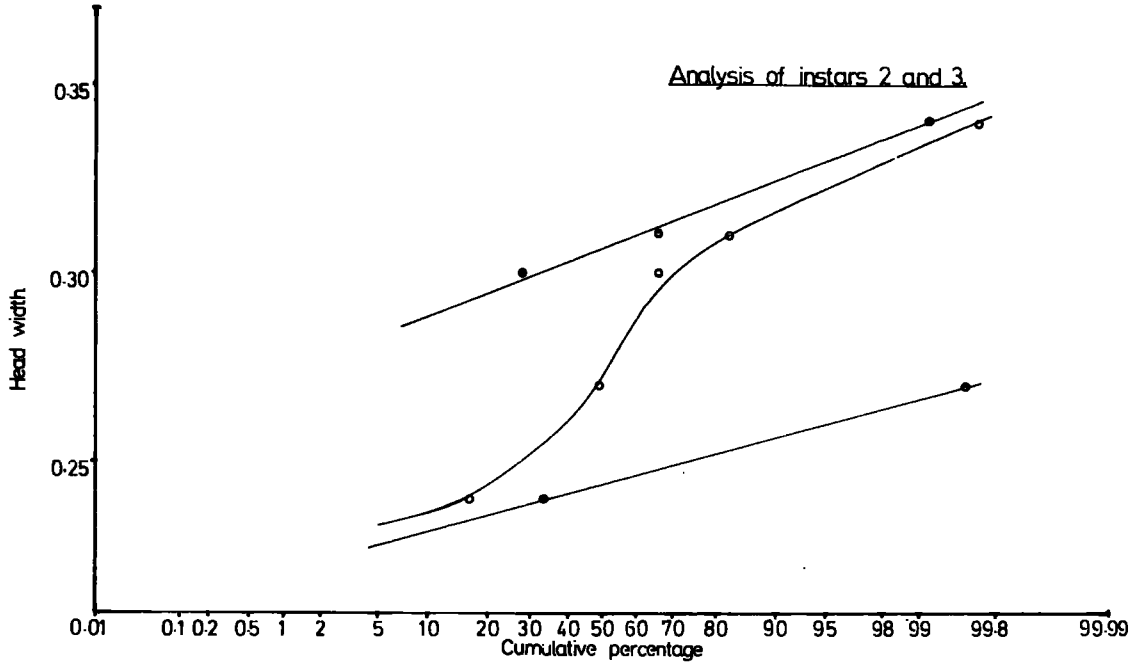
The head widths were plotted as Figs.12 to 24 in the following groups :-

Head width	Instar pairs
0.23 - 0.34 mm	2 and 3
0.28 - 0.42	3 and 4
0.35 - 0.52	4 and 5
0.43 - 0.59	5 and 6
0.53 - 0.71	6, 7 and 8 *

* Through lack of samples there appeared to be some overlap of Instars 6 and 7; to clarify this and utilise more figures it was decided to analyse the three together.

Fig.12. Head width analysis of Instars 2 and 3.

Fig.13. Head width analysis of Instars 3 and 4.


Analysis of instars 2 and 3
Head width
0·35
0·30
0·25
0·01 0·1 0·2 0·5 1 2 5 10 20 30 40 50 60 70 80 90 95 98 99 99·8 99·99
Cumulative percentage

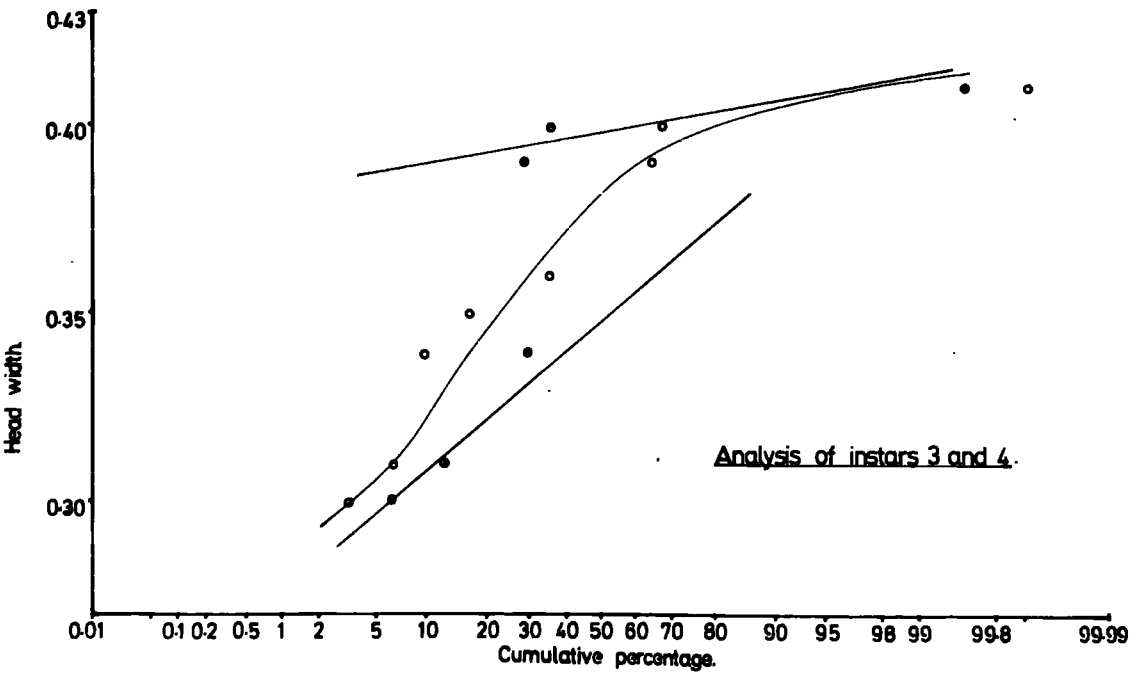
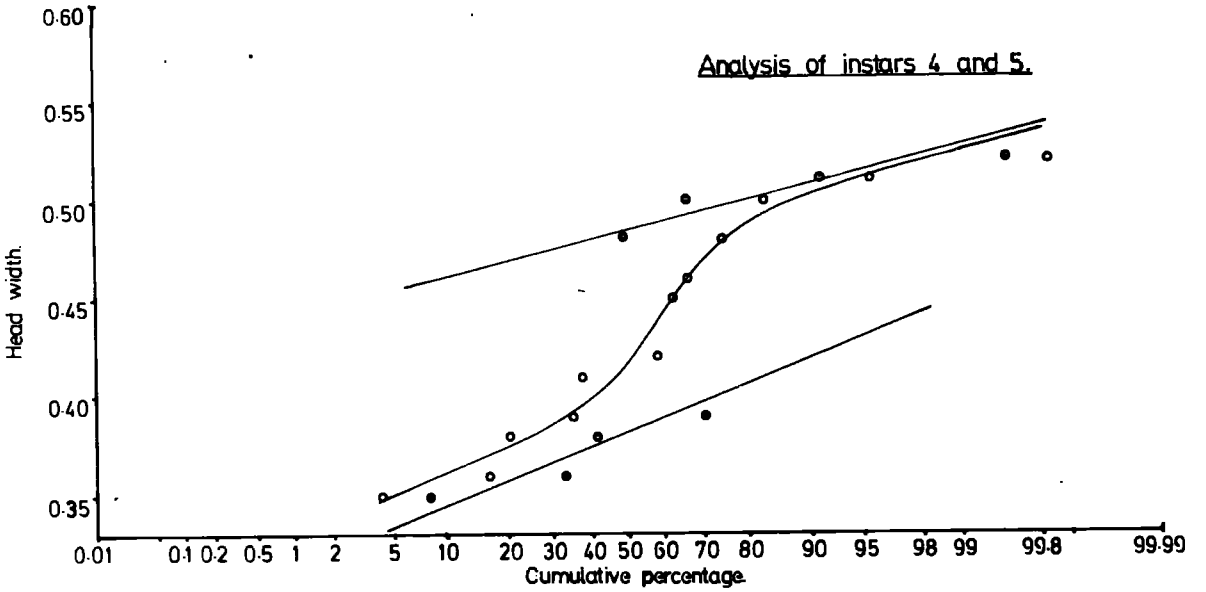

Analysis of instars 3 and 4.
Head width
0·43
0·40
0·35
0·30
0·01 0·1 0·2 0·5 1 2 5 10 20 30 40 50 60 70 80 90 95 98 99 99·8 99·99
Cumulative percentage.

Fig.14. Head width analysis of Instars 4 and 5.

Fig.15. Head width analysis of Instars 5 and 6.


Analysis of instars 4 and 5.
Head width.
0·60
0·55
0·50
0·45
0·40
0·35
0·01 0·1 0·2 0·5 1 2 5 10 20 30 40 50 60 70 80 90 95 98 99 99·8 99·99
Cumulative percentage.

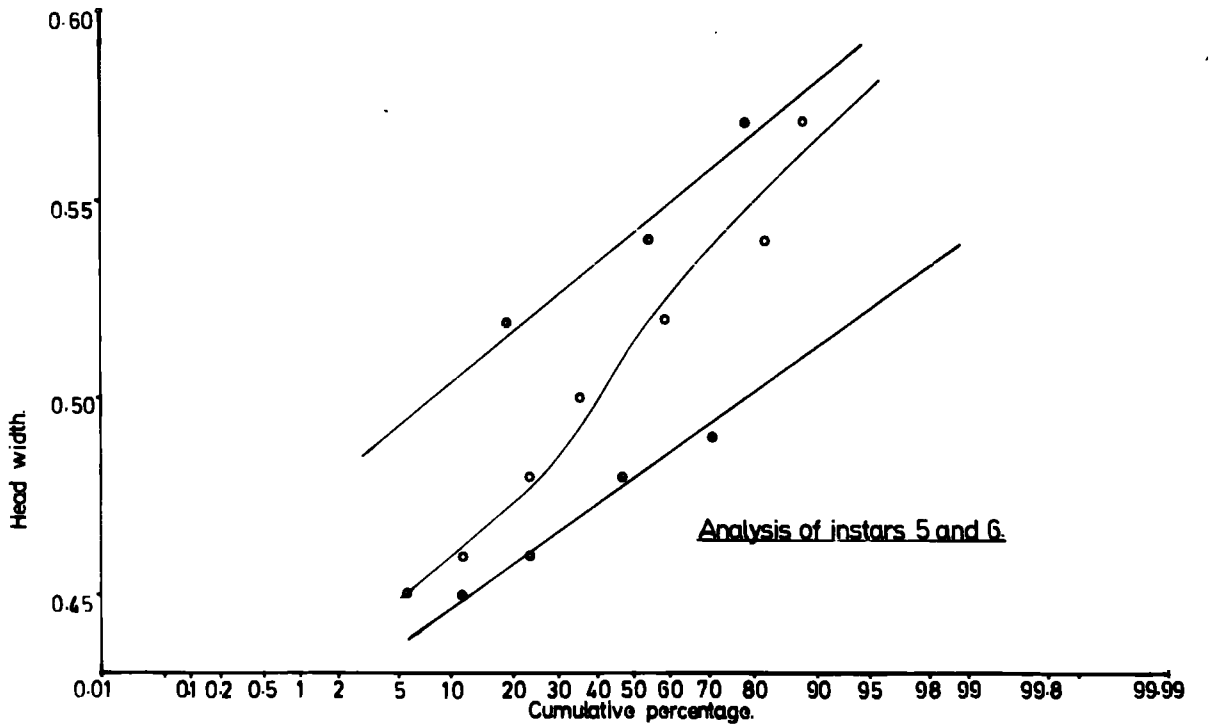
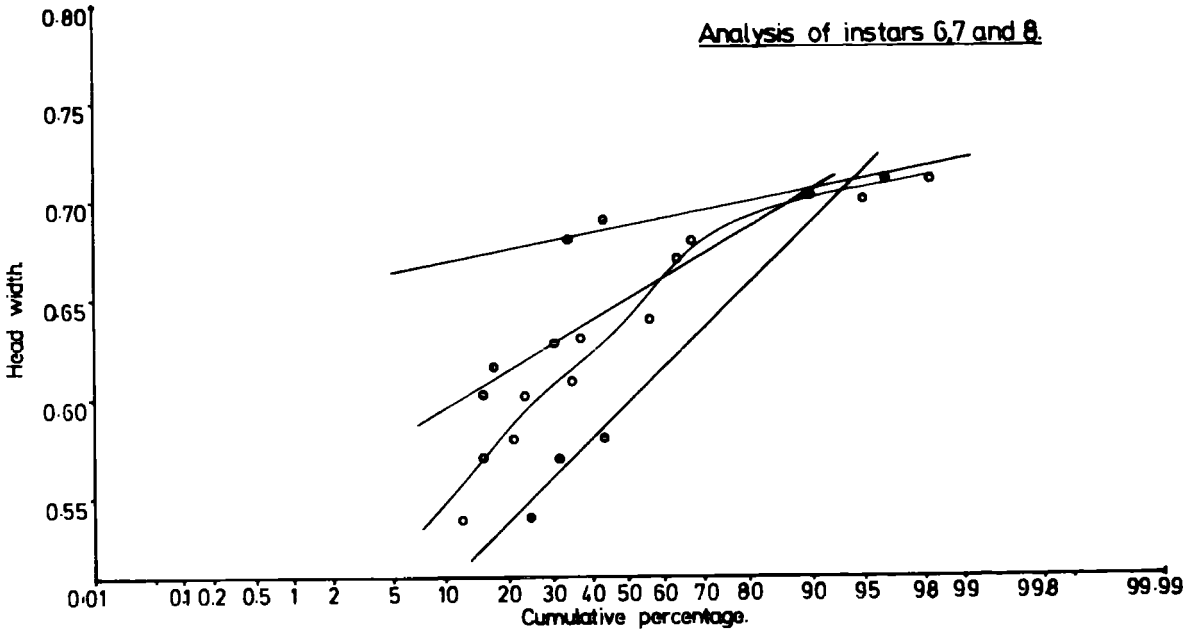

Analysis of instars 5 and 6.
Head width.
0·60
0·55
0·50
0·45
0·01 0·1 0·2 0·5 1 2 5 10 20 30 40 50 60 70 80 90 95 98 99 99·8 99·99
Cumulative percentage.

Fig.16. Head width analysis of Instars 6, 7 and 8.

Fig.17. Head width analysis of Instars 7 and 8.


Analysis of instars 6,7 and 8.
Head width.
0·80
0·75
0·70
0·65
0·60
0·55
0·01
0·1 0·2 0·5 1 2 5 10 20 30 40 50 60 70 80 90 95 98 99 99·8 99·99
Cumulative percentage.

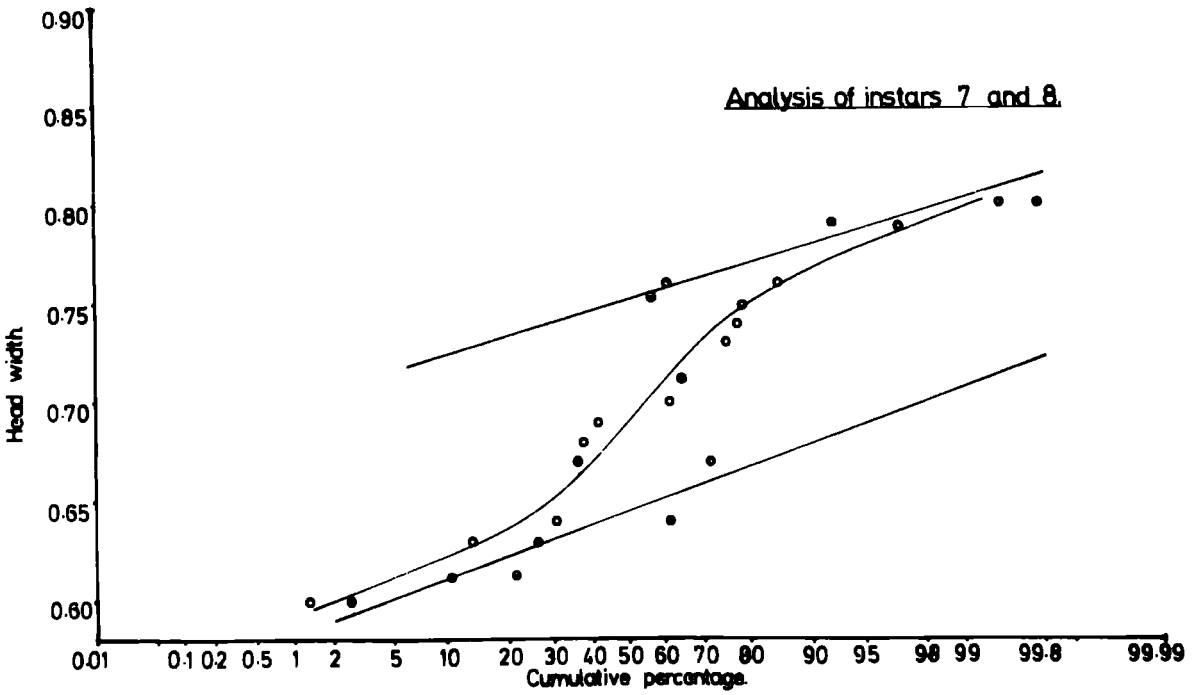
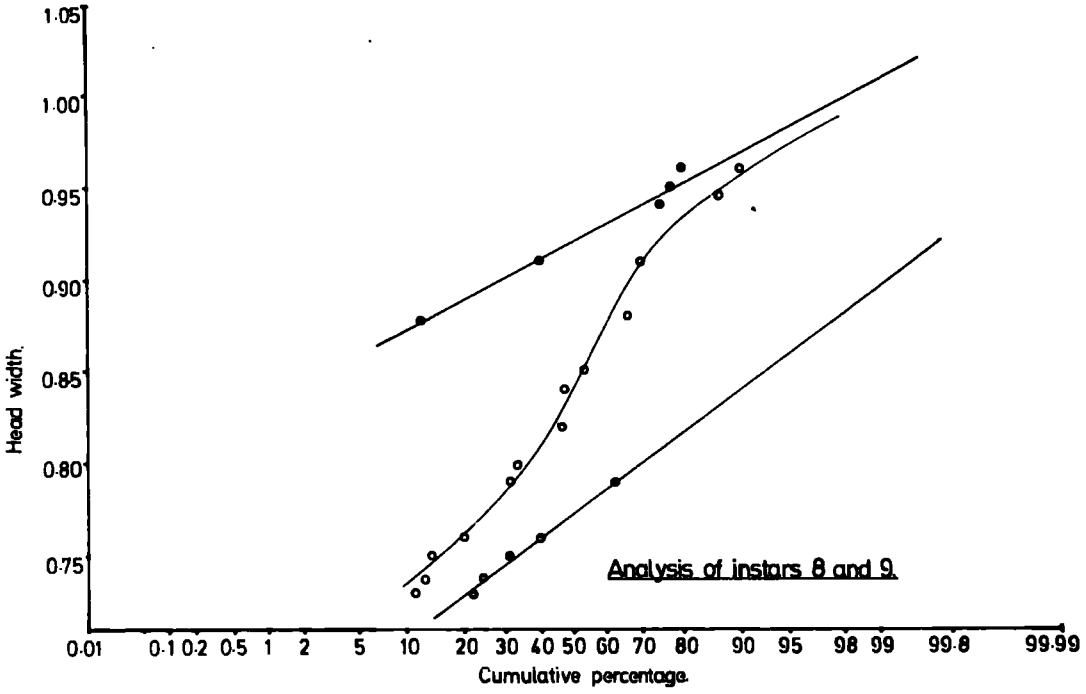

Analysis of instars 7 and 8.
Head width.
0·90
0·85
0·80
0·75
0·70
0·65
0·60
0·01
0·1 0·2 0·5 1 2 5 10 20 30 40 50 60 70 80 90 95 98 99 99·8 99·99
Cumulative percentage.

Fig.18. Head width analysis of Instars 8 and 9.

Fig.19. Head width analysis of Instars 9 and 10.


1·05
1·00
0·95
0·90
0·85
0·80
0·75
Head width.
Analysis of instars 8 and 9.
0·01
0·1 0·2 0·5 1 2 5 10 20 30 40 50 60 70 80 90 95 98 99 99·8 99·99
Cumulative percentage.

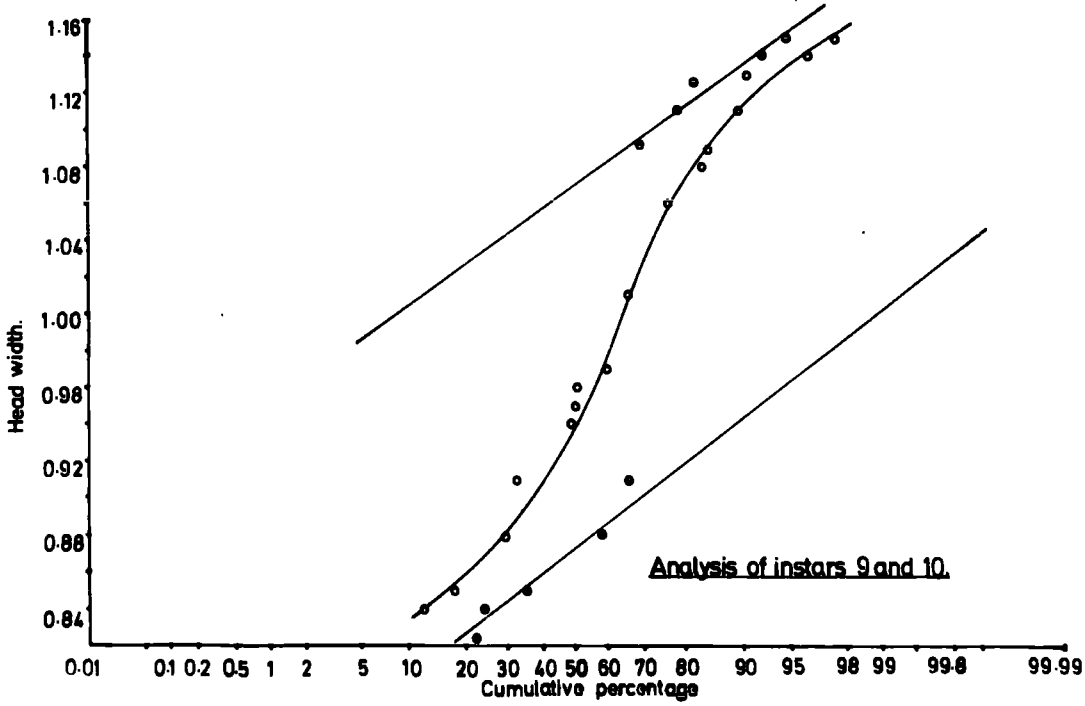
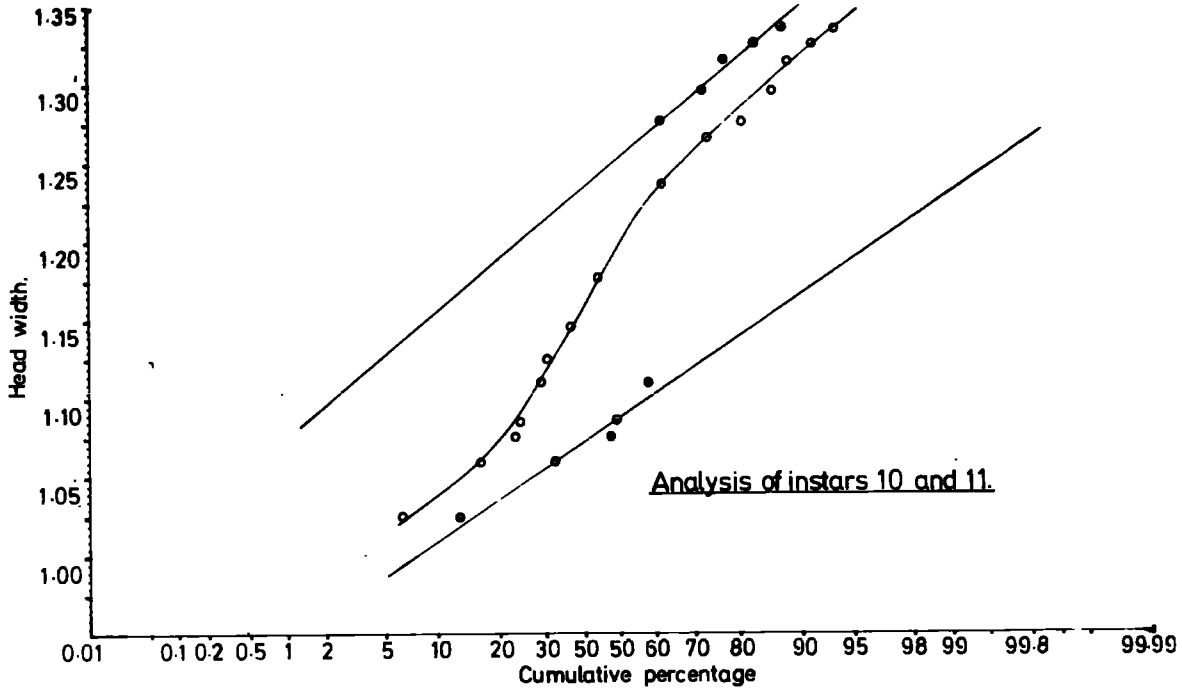

1·16
1·12
1·08
1·04
1·00
0·96
0·92
0·88
0·84
Head width.
Analysis of instars 9 and 10.
0·01
0·1 0·2 0·5 1 2 5 10 20 30 40 50 60 70 80 90 95 98 99 99·8 99·99
Cumulative percentage

Fig.20. Head width analysis of Instars 10 and 11.

Fig.21. Head width analysis of Instars 11 and 12.


1·35
1·30
1·25
1·20
1·15
1·10
1·05
1·00
Head width.
0·01 0·1 0·2 0·5 1 2 5 10 20 30 50 50 60 70 80 90 95 98 99 99·8 99·99
Cumulative percentage
Analysis of instars 10 and 11.

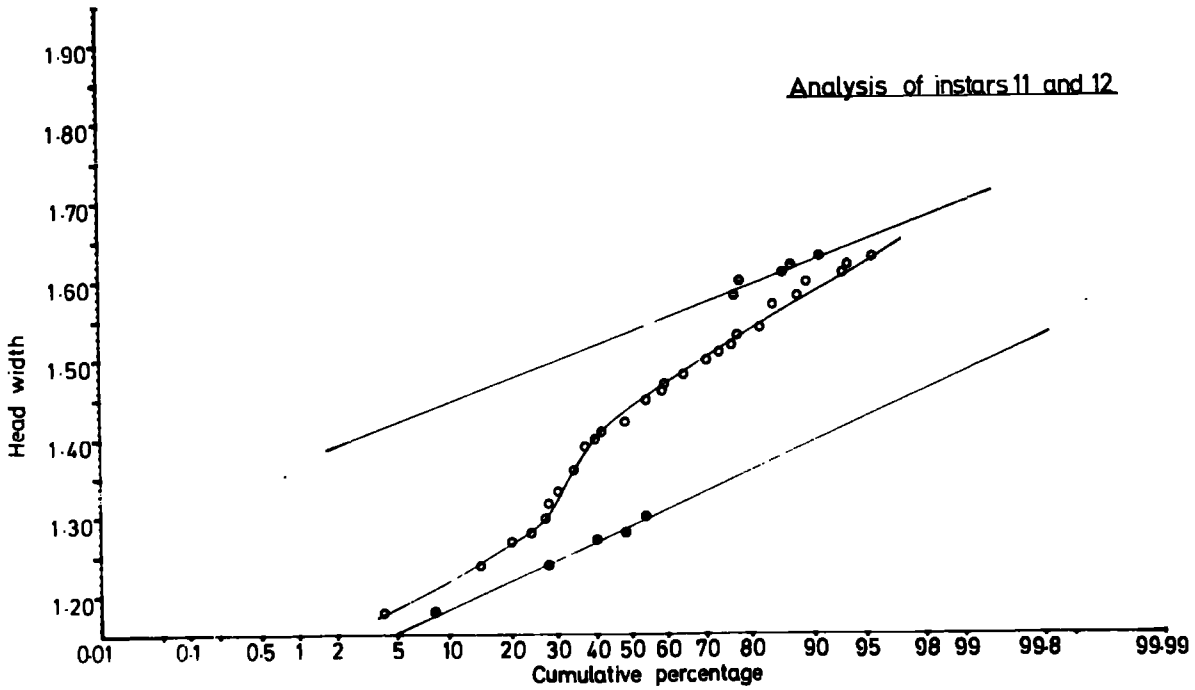
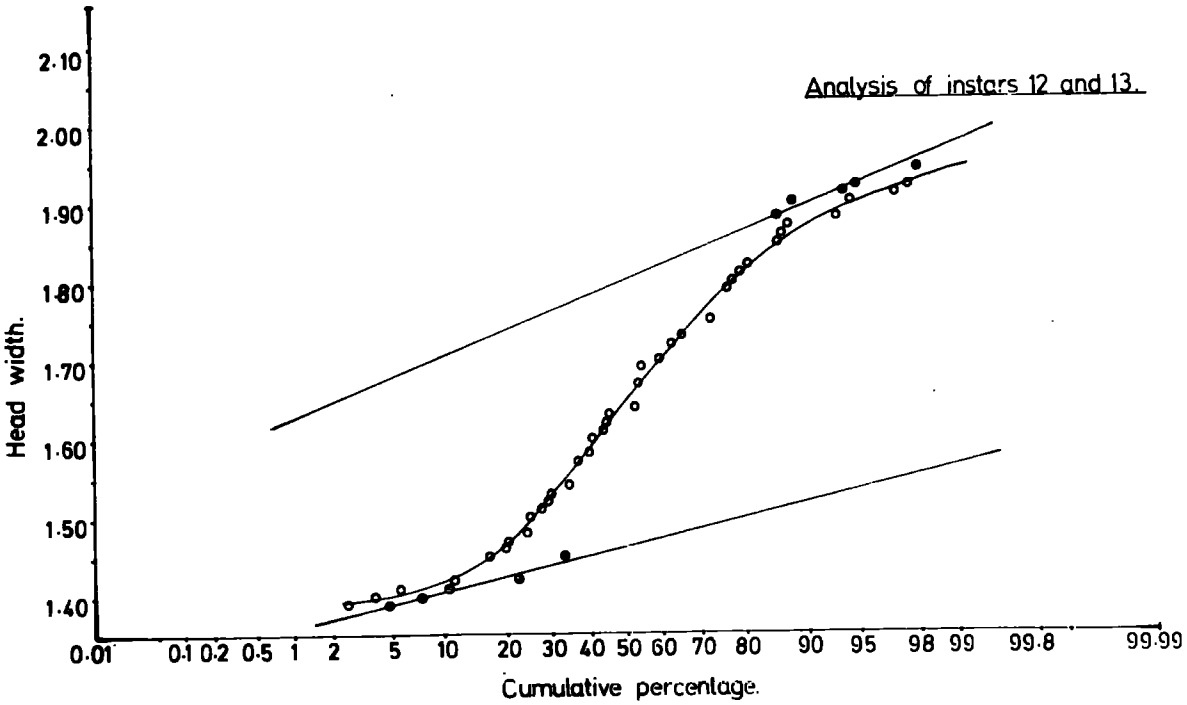

1·90
1·80
1·70
1·60
1·50
1·40
1·30
1·20
Head width
0·01 0·1 0·5 1 2 5 10 20 30 40 50 60 70 80 90 95 98 99 99·8 99·99
Cumulative percentage
Analysis of instars 11 and 12

Fig.22. Head width analysis of Instars 12 and 13.

Fig.23. Head width analysis of Instars 13 and 14.


Analysis of instars 12 and 13.
Head width.
2·10
2·00
1·90
1·80
1·70
1·60
1·50
1·40
0·01
0·1 0·2 0·5 1 2 5 10 20 30 40 50 60 70 80 90 95 98 99 99·8 99·99
Cumulative percentage.

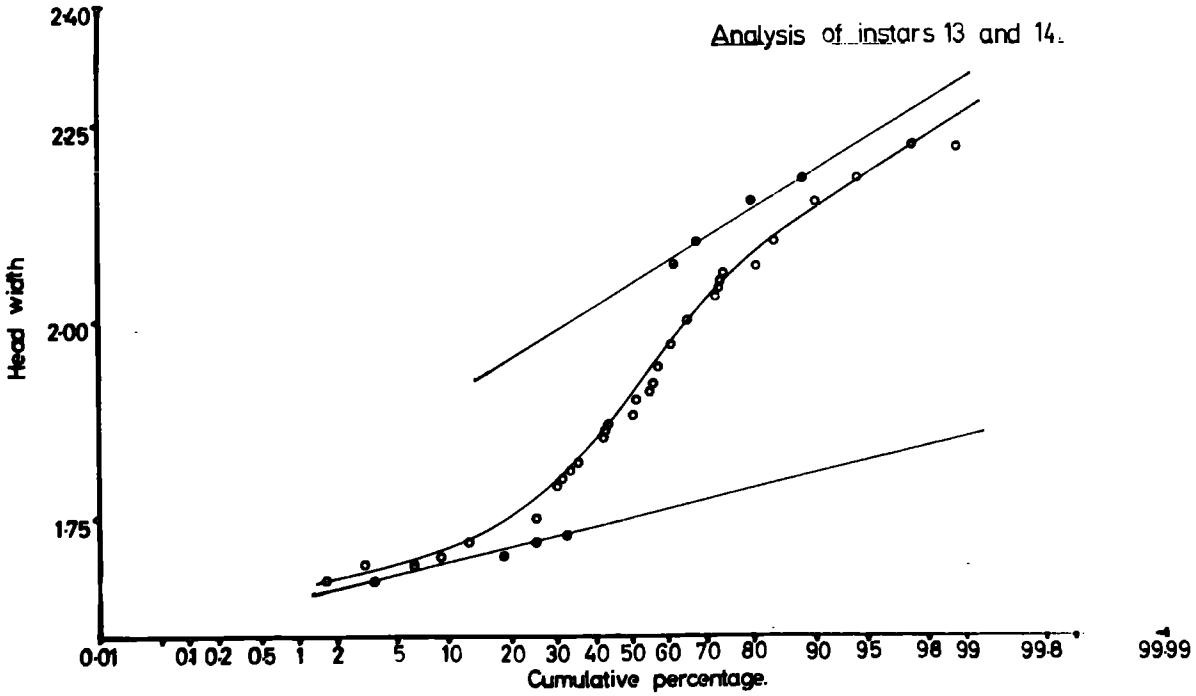
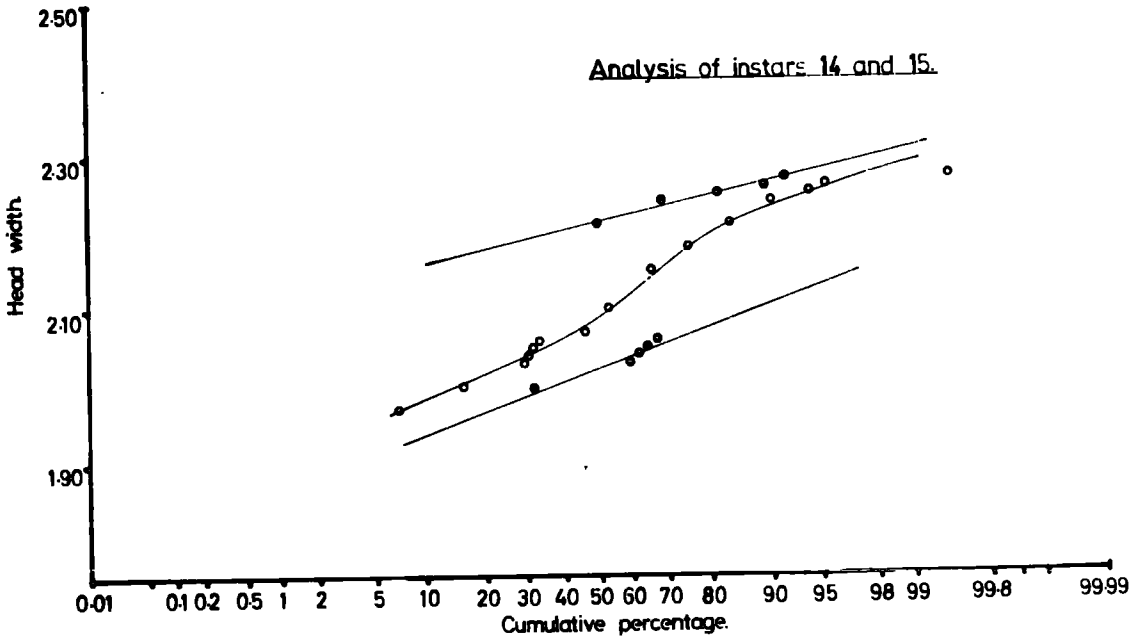

Analysis of instars 13 and 14.
Head width
2·40
2·25
2·00
1·75
0·01
0·1 0·2 0·5 1 2 5 10 20 30 40 50 60 70 80 90 95 98 99 99·8 99·99
Cumulative percentage.

Fig.24. Head width analysis of Instars 14 and 15.

Fig.25. Head width analysis of Instar 14.


Analysis of instars 14 and 15.
Head width
2·50
2·30
2·10
1·90
0·01
0·1
0·2
0·5
1
2
5
10
20
30
40
50
60
70
80
90
95
98
99
99·8
99·99
Cumulative percentage.

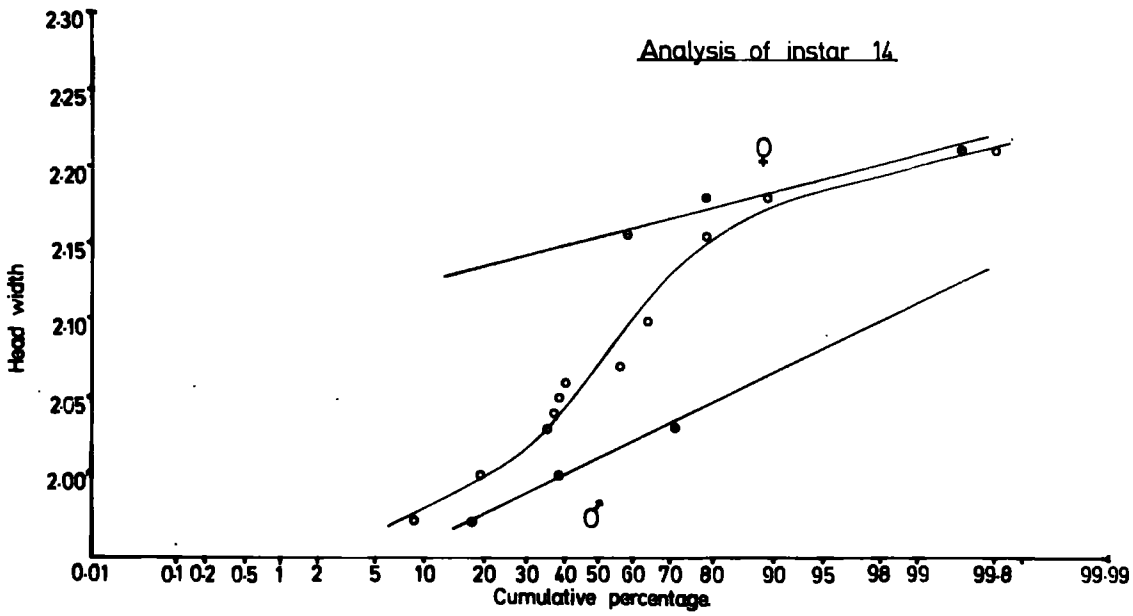

Analysis of instar 14.
Head width
2·30
2·25
2·20
2·15
2·10
2·05
2·00
♀
♂
0·01
0·1
0·2
0·5
1
2
5
10
20
30
40
50
60
70
80
90
95
98
99
99·8
99·99
Cumulative percentage.

TABLE VII

Instar	H.w. (probability paper) mm	H.w. (check) mm	Przibram's factor
1	0.23	0.24	
2	0.24 ± 0.010	0.27	1.12
3	0.31 ± 0.014	0.32 ± 0.070	1.18
4	0.41 ± 0.006	0.39 ± 0.020	1.22
5	0.49 ± 0.042	0.46 ± 0.030	1.18
6	0.54 ± 0.030	0.54 ± 0.024	1.17
7	0.65 ± 0.042	0.63 ± 0.037	1.17
8	0.76 ± 0.019	0.73 ± 0.039	1.16
9	0.92 ± 0.038	0.90 ± 0.048	1.23
10	1.07 ± 0.056	1.08 ± 0.057	1.20
11	1.26 ± 0.070	1.25 ± 0.065	1.16
12	1.54 ± 0.060	1.50 ± 0.027	1.20
13	1.80 ± 0.070	1.76 ± 0.094	1.17
14	2.05 ± 0.100	2.04 ± 0.120	1.16
15	2.47 ± 0.040	2.37 ± 0.130	1.16
			1.18 ± 0.083

Table showing mean head widths and their increases at each instar (Przibram's factor)

Head width	Instar pairs
0.60 - 0.81 mm	7 and 8
0.72 - 0.97	8 and 9
0.82 - 1.15	9 and 10
1.04 - 1.34	10 and 11
1.17 - 1.64	11 and 12
1.39 - 1.94	12 and 13
1.63 - 2.23	13 and 14
1.95 - 2.27	14 and 15
2.25 mm	15

Results

From the above data a full head width range for each instar, as well as a mean head width for each instar, was determined (Table VII). Each range was calculated by taking three standard deviations on either side of the mean. After Instar 5 there is some overlap of the ranges. This is unavoidable as each Instar range is compiled from three standard deviations. With these data most animals can be placed in an instar.

Exceptions to this are the borderline head widths which some animals exhibit prior to moulting; in certain cases animals moult and undergo a decrease in head width. Generally the final groupings agree well with the pilot studies carried out in the previous year.

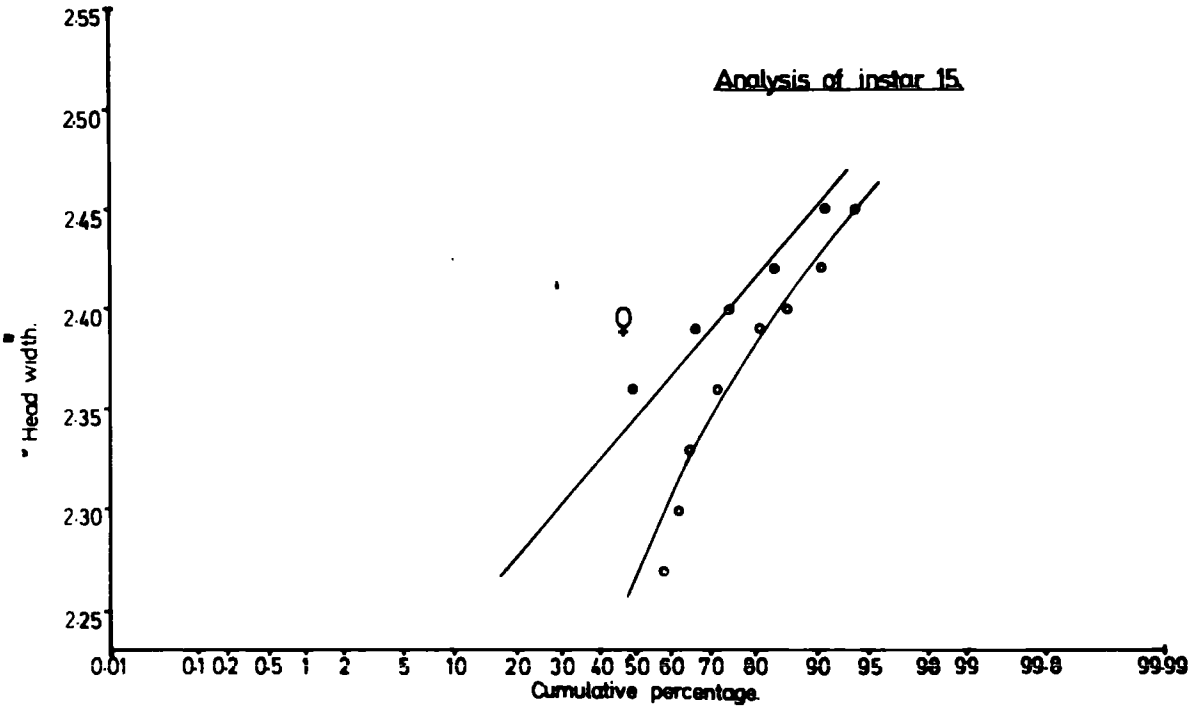
If the final Instar ranges are applied to the histogram of head width frequency, the later instars appear to have two peaks

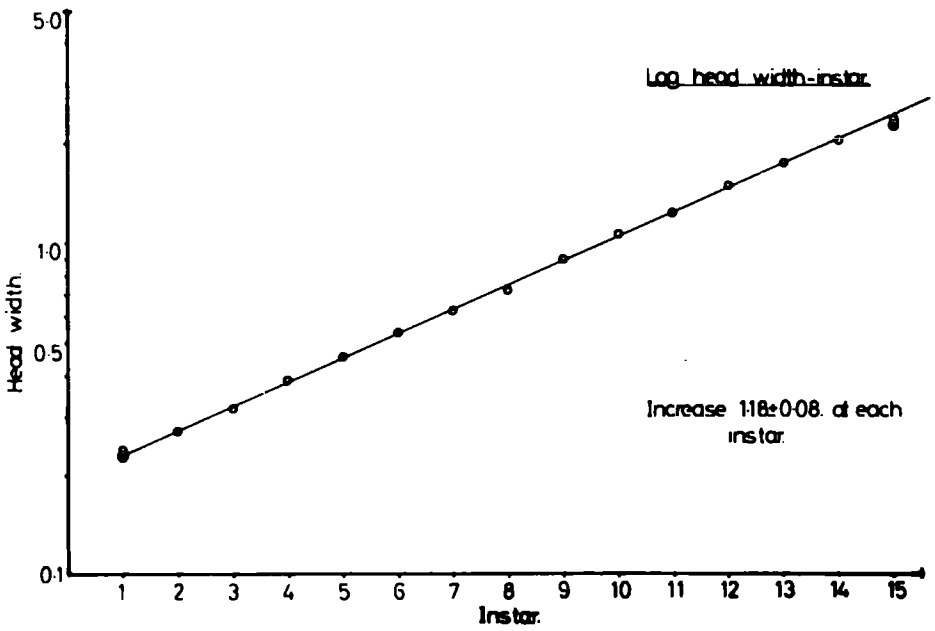
per instar, rather than the expected single peak (Fig.9). It was thought that the peaks were perhaps sex differences manifested as size differences. That the peaks are pronounced in the later instars is due to the wide head width ranges. Below Instar 8 the differences do not appear as double peaks due to the narrow head width ranges which mask the effect. If the peaks were anything other than size differences WITHIN an instar they would be in direct contradiction to Dyars' Law.

In order to test the hypothesis, a further analysis was carried out. The test was similar to the above analyses and involves the use of arithmetic probability paper, but was confined to Instar 14 only. Fig.25 clearly shows the two peaks indicated on the histogram. The male adult is known to be smaller than the female so it was assumed that the male larva is the smaller one. Thus the mean head width for a male Instar 14 larva is 2.00mm and the female larva 2.15mm. It is highly probable that the double peak per instar indicated on the histogram is a sex size difference. It was noted that Instar 15 larvae appeared to be made up of larvae destined to pupate into female adults. In the histogram this instar shows only one peak which tails off. This range was plotted on probability paper and a straight line found (Fig.26), indicating that it was made up of only one size group. As the female adults are larger, and as the Instar 15 larvae are of one sex, it must be concluded that there are fifteen instars on the female and only fourteen in the smaller male. This is

Fig.26. Head width analysis of Instar 15.

Fig.27. Graph showing the relationship of log. head width to instar numbers.


Analysis of instar 15
♀
Head width.
2·55
2·50
2·45
2·40
2·35
2·30
2·25
0·01 0·1 0·2 0·5 1 2 5 10 20 30 40 50 60 70 80 90 95 99 99·8 99·99
Cumulative percentage.


Log head width-instar.
Increase 1·18±0·08. at each instar.
Head width.
5·0
1·0
0·5
0·1
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15
Instar.

a similar state of affairs to that found in Athous haemorrhoidalis F. by Fernando (1963).

As a check on the data concerning the mean head width per instar, a further 250 measurements were taken covering all fifteen instars. These were divided into instars according to the groupings obtained in the preceding work and are presented in Table VII. The means for these check data agree well with those obtained from the probability paper.

In Table VII Przibram's factor (Wigglesworth 1965) is also shown. This is the increment in linear growth at each instar. For M.rufipes it is 1.18 ± 0.083, not 1.26 ($\sqrt[3]{2}$) in accordance with Przibram.

Discussion

It could be construed that the double peaks found on the frequency histogram (Fig.9) are instars and not sexual size differences. However, if this was so, it would be in direct contradiction to Dyars' Law and thus no straight line graph (Fig.27) could be constructed from the data. This is further verified by analysis of Instar 15 larvae (Fig.26) which consist solely of 'female' larvae and thus does not show the double peaking. Instar 14 can be analysed into two size groups, which are 'male' and 'female' (Fig.25). Thus it is unequivocally apparent that the double peaks do represent sexual size differences.

Clearly the division of M.rufipes into fifteen instars, using the criterion of head width, is valid. This also provides an easy parameter to measure. By providing two independent groups

of measurement it has been possible to check the data with good agreement. One of the most interesting facts to emerge is the variable number of instars, found in M. rufipes, fifteen in females and fourteen in males. It is probable that the phenomenon is connected with reproductive capacity.

SECTION II

Chapter 3. Studies on the life-cycle of M.rufipes

Introduction

In the present study investigations were made into the life-cycle of M.rufipes with special regard to the time of occurrence of the different instars. Such a procedure was necessary in order that some estimations of the growth rates of each instar could be made from field data, as growth studies in the laboratory proved unfruitful. Clearly a knowledge of growth rates is necessary to solve the energetics equations. Previous to this study no details were available concerning the life-history of this species. The life-cycles of other species of wireworms, especially economic pest species, have been described. The common theme of these descriptions is the variability of the life cycles of Elaterids.

The number of instars present during the life-history of M.rufipes were discussed in the previous chapter. These data were used as a basis when determining the life cycle. In order to estimate the duration of each instar it was necessary to collect data concerning the moulting activity of M.rufipes, i.e. to ascertain the number of moults undergone each year and to apply the information to the instar data. This was further supported by data obtained from general collection of experimental animals and from sampling.

TABLE VIII

Annual moulting activity of M.rufipes

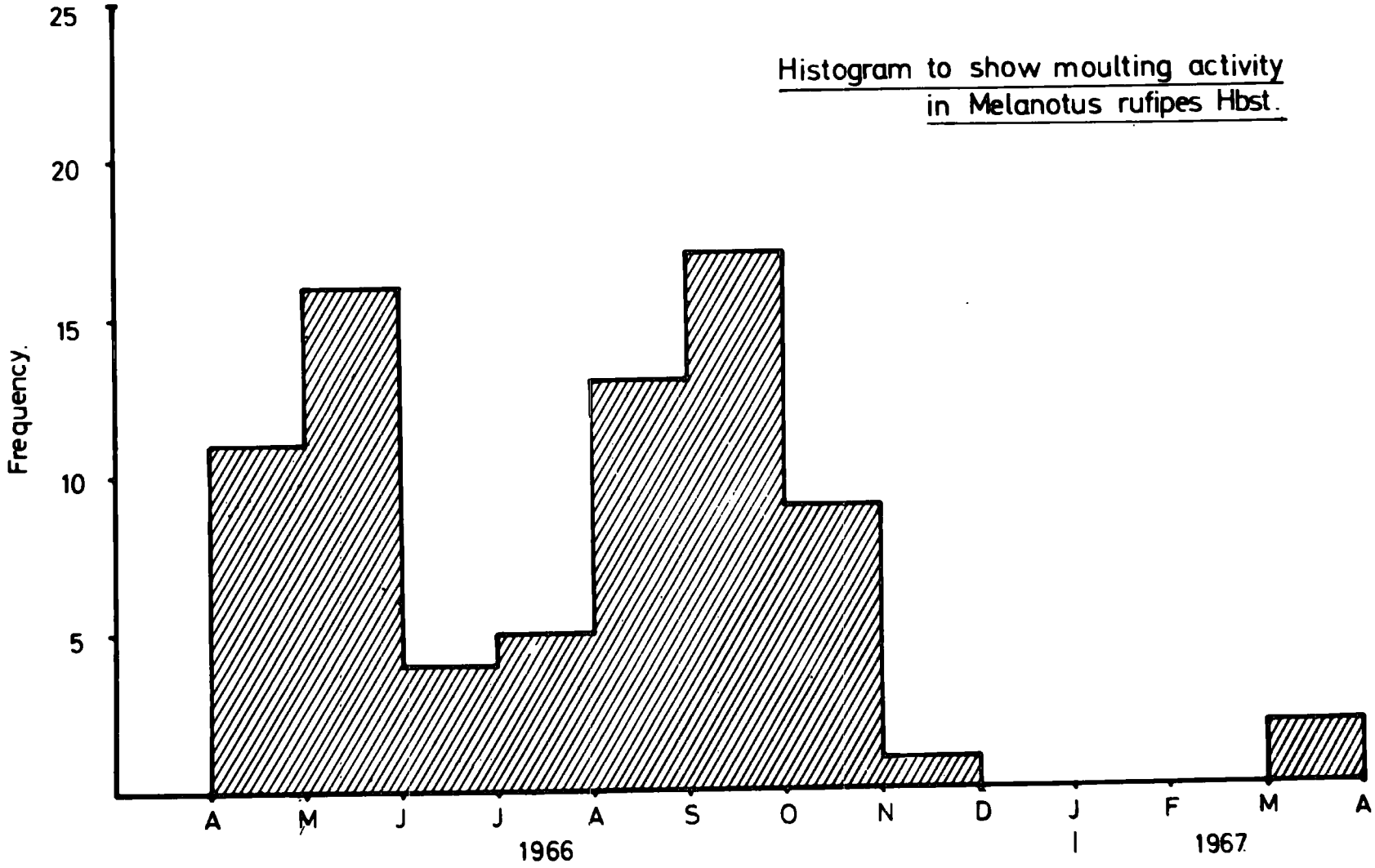
INSTAR	1966									1967		
	A	M	J	J	A	S	O	N	D	J	F	M
2												
4/5		X										
							X					
7			X		X							
7												
7												
7												
7/8				X		X						
8				X		X						
8				X								
8	X			X								
8		X			X							
8												
8					X							
8					X							
9			X			X						
9		X				X						
9		X				X						
9	X				X							
9		X			X							
9	X				X							
10					X							
10	X				X							
10				X								
10												
10/11						X						
10/11												
11		X										
11		X				X						
11	X											
11		X					X					
11		X										
11		X					X					
11							X					
11	X				X							
11		X				X						
11												X
12		X				X						
12							X					
12						X						
12						X						
12												
12							X					
12												X

TABLE VIII (Continued)

Annual moulting activity of M. rufipes

INSTAR	A	M	J	J	A	S	O	N	D	J	F	M
13	X											
13	X						X					
13					X							
13												
13	X					X						
13		X										
13			X									
13						X						
13	X											
13		X										
13		X										
13						X						
13						X						
13						X						
13/14	X				X							
14							X					
14						X						
14							X					
14			X									
14												
14		X										
14												
14												
14					X							
14					Pupa							
14								X				
14												
14												
14												
15												

Fig.28. Histogram to show the moulting activity of M.rufipes larvae.


Histogram to show moulting activity
in Melanotus rufipes Hbst.
Frequency.
25
20
15
10
5
A
M
J
J
A
S
O
N
D
J
F
M
A
1966
1967

a) The moulting activity of M.rufipes

To study the moulting activity of M.rufipes individual animals were reared in 3" x 1" glass tubes filled with damp sawdust (later granules of decaying timber) and kept in the Zoology Department Garden. The sawdust was watered each month and the animals fed on dipterous larvae at the same time. Any exuvia found at this time were removed, weighed, measured and finally stored for burning, to find their calorific content at a later date. Originally the experiment was started with one hundred animals but on its determination 27% of these had died. Due to the difficulty of finding and, more important, of successfully rearing the early instars, only animals from Instar 7 upwards were fully recorded.

The results of the moulting activity investigations are shown in the table (Table VIII) and the histogram (Fig.28). It is evident from the graph that there are two peak periods of moulting activity during the year, in the Spring from April through to May, and in Autumn from August through to October. The Autumn peak is more pronounced than the Spring peak. This is also clearly noticeable in the field as exuviae are found in great quantities during the Autumn. This is a similar situation to that found by Rymer-Roberts (1919) for Agriotes obscurus (L.).

With reference to the table of moulting activity certain conclusions may be drawn about Instars 7 to 15. It would appear from these results that an Instar 7 larva in the Spring of

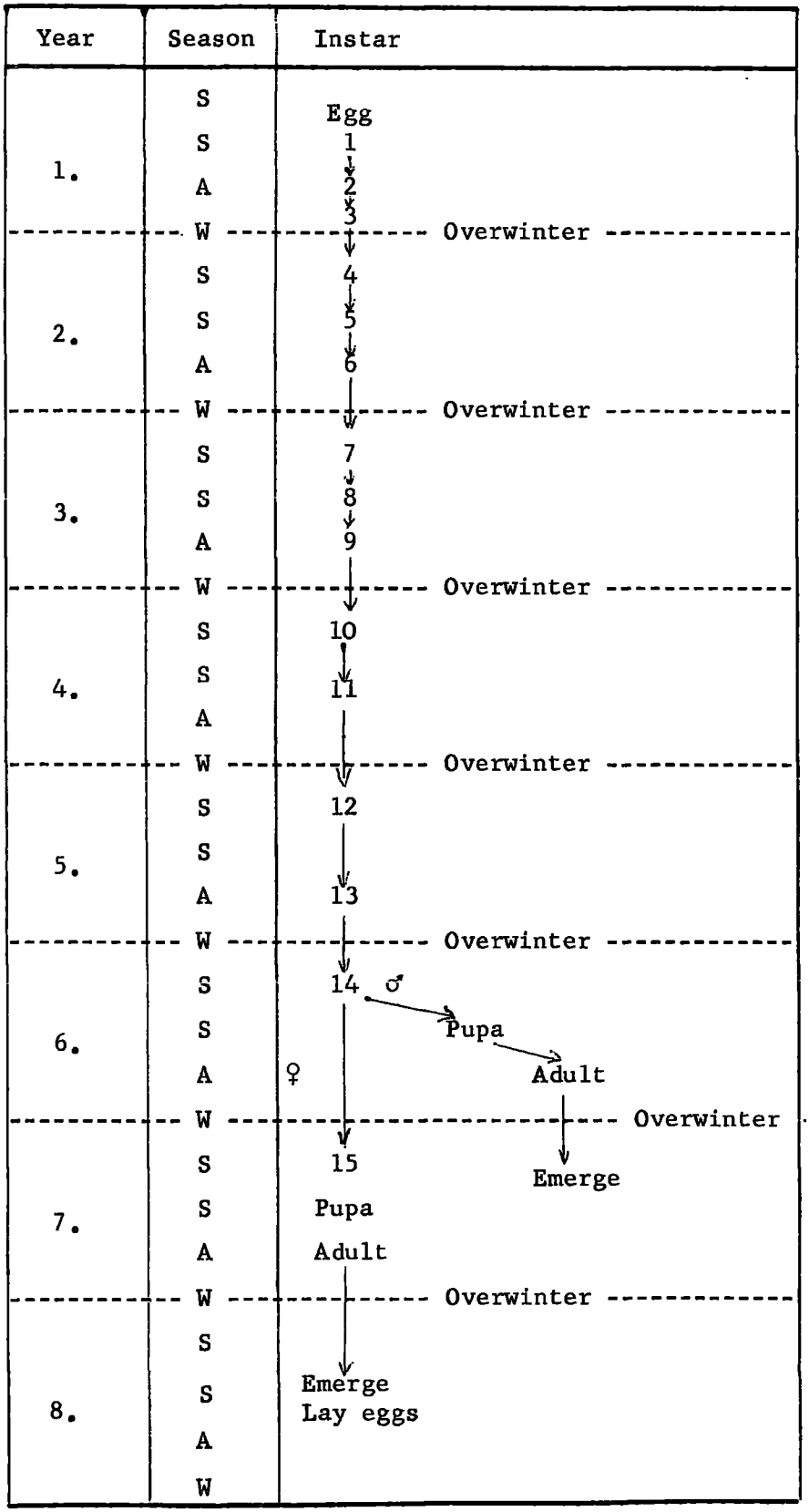
any year will, in that year, undergo two further moults and overwinter as an Instar 9 larva. An Instar 8 larva will generally undergo one moult (but under special circumstances to be discussed below, two moults) in that particular calendar year. It is very clearly demonstrated that an Instar 9 larva undergoes two moults during the calendar year, and an Instar 10 larva probably just one moult. This being so, the Instar 11 larva will overwinter and, as shown on the table, will moult in the Spring to give an Instar 12 larva which again moults in Autumn and overwinters as an Instar 13 larva. From the table it appears that in Spring Instar 13 larvae moult to Instar 14 larvae which can either moult to Instar 15 larvae or pupate, depending on sex (Chapter 2).

b) On the life-cycle of M.rufipes

Using the above data for Instars 7 to 15 and further data obtained by general observation during the collection of experimental animals it was possible to elucidate the life-cycle of M.rufipes. It was noticed during the collection of animals for respiratory purposes that Instar 1 and 2 animals had vanished by September and only Instar 3 animals remained. Furthermore, eggs were observed to be laid at the end of June to hatch in July. Thus three instars are passed through before the Spring of the following year. From the moulting data it was found that Instar 7 larvae are found in Spring and undergo two further moults, therefore it must be concluded, by elimination, that Instars 4, 5 and 6 are passed through in the second year of life.

TABLE IX

Life cycle of Melanotus rufipes Hbst.



The life cycle may now be described (see Table IX). Eggs are laid in July and hatch after approximately 2 weeks. Instars 1 and 2 are passed through very quickly, lasting a total of some six to seven weeks. Instar 3 larvae are found in the field, particularly in late Autumn and all through the Winter. Occasionally some Instar 4 animals were found during the Winter, therefore some overlapping of instar times occurs.

During the second year of life it appears that three more instars are passed through so that M.rufipes overwinters in its second year as an Instar 6 larva. This moults in Spring to an Instar 7 larva.

As seen from the moulting data, Instar 7 larvae undergo two further moults in that year (3rd year of life) and the larva overwinters as an Instar 9 larva.

In the fourth year only two moults are undergone, thus, as shown in the moulting data, the animal reaches, and overwinters, as an Instar 11 larva.

Similarly, in the fifth year, two further moults and instars are passed through. In the Spring of the sixth year the wireworm moults to give an Instar 14 larva.

At this stage a dichotomy occurs according to the sex of the larva. As demonstrated in the previous section on the determination of the instars, Instar 14 larvae will pupate and become a male adult beetle. However, if the larvae is female it overwinters as an Instar 14 larva only to moult to give an

Instar 15 larva in the Spring. Consequently the Instar 15 larva pupates in the Summer and forms a female adult beetle.

From field and laboratory observations it is known that both male and female pupae take 4 - 5 weeks to fully form the adult. The adults overwinter in the pupal cells and emerge the following Spring to mate in May - June. The eggs are laid in late June - early July.

Female animals take 7 years to complete their larval stages and male larvae 6 years. Thus the total length of life cycle for females is 8 years and males 7 years.

Discussion

It is evident from the above data that the moulting pattern of M.rufipes changes with age. During the first three years of life there are three moults per year. In the fourth and fifth years there are only two moults per year and in the final years only one moult. Thus there is a basic 3 - 2 - 1 pattern. This may be true for all wireworms as similar moulting patterns have been found by Evans and Gough (1942) for Agriotes spp. and Fernando (1963) for Athous haemorrhoidalis (Fab.). On the graph of moulting activity only the 2 - 1 parts of this pattern are shown as intermediate and late instars are shown, although Instars 7, 8 and 9 represent the last year of the 3 moults per year pattern.

It is apparent from Table VIII, which shows moulting activity, that moulting is not fully synchronised, but occurs throughout the Spring, Summer and Autumn, but with two main periods

in Spring and Autumn. It is probable that some overlapping of instars occurs.

In this study it is stated that the minimum length of life cycle of M.rufipes is 7 years in males and 8 years in females. Fenton (1926) found that the larval period of M.communis and M.pilosis, two American species, was 6 years, i.e. the complete life cycle takes 7 years. He also stated that this may be extended. Thus the results of the investigations in the present study tend to be in agreement with Fenton. Various other wireworm species have been investigated. The shortest recorded life cycle is one year, found by Dobrovsky (1954) for Conoderus vagus Cand. Wireworms of Agriotes spp. appear to complete their life cycles in five years (Ford 1917; Miles 1941). The longest life cycle recorded is in Ctenicera aeripennis destructor Brown, which takes up to 9 years to complete its life cycle (Strickland 1939). All these authors stress that the life cycles may vary in length. This appears to be an inherent characteristic of the group and can give rise to difficulties in studying their life histories which are already long and complex. Thus a life cycle of 7 - 8 years for M.rufipes appears to be quite reasonable.

SECTION II

Chapter 4. Descriptions of the major study areas

Introduction

It was necessary, as an integral part of the population energetics study, to gain information concerning the distribution and numbers of M.rufipes. Such data could be used as a basis on which to apply the energetic data. In order to do this, and to collect animals for experimental material, a number of woodlands were investigated. The three most important areas were Wynyard Wood (map.ref.NZ.420280), High Wood (map.ref.NZ.275405) and Park End Wood (map.ref.NY.923260).

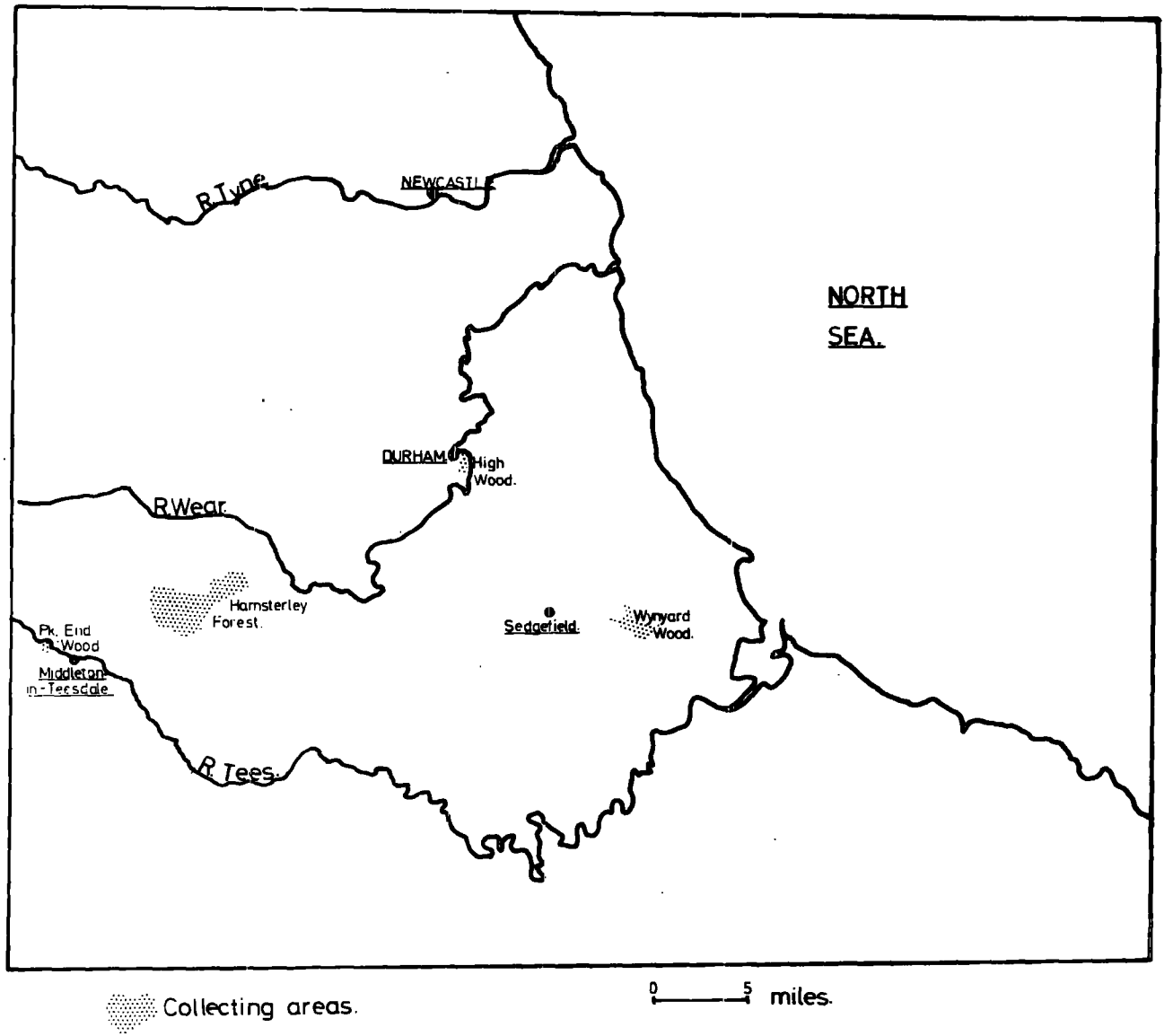
a) Wynyard Wood

This woodland is situated approximately five miles east of Sedgefield, County Durham (Fig.29). It is part of an estate belonging to Lord Londonderry and is now under Forestry Commission management.

In order to gain as much information in this woodland as possible, energetic studies were initiated on a group basis. Thus my colleagues and I started investigations on M.rufipes, earthworms, centipedes and primary productivity. It was hoped by adopting this approach to provide comprehensive data concerning this woodland ecosystem. Certainly this was an ideal study area because of its general lack of outside interference.

As one of the first group tasks my colleagues and I marked out and mapped a research site (Fig.30). This area will

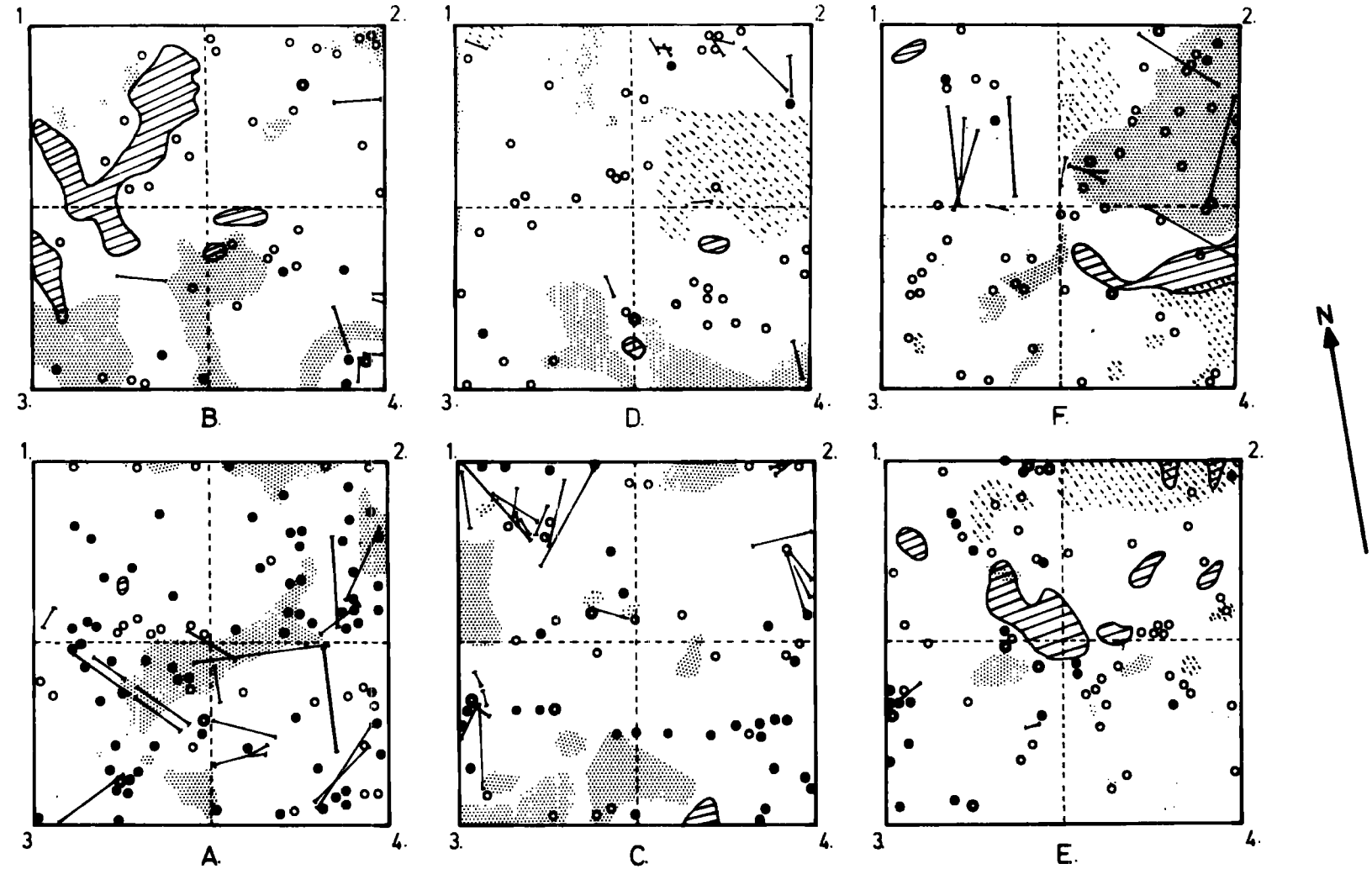
Fig.29. Map showing the major sampling and collecting areas.



Map of North-east England to show sampling and collecting areas.

Fig.30. Map showing details of the Wynyard site.

Wynyard Site



be referred to in this thesis as 'the site'. It consisted of six, twenty metre squares, laid out in a three by two formation. Each twenty metre square was identified by a letter A, B, C, D, E or F, and each of these was further subdivided into four quarters of ten by ten metres and bearing a number 1, 2, 3 or 4. Thus any ten metre square could be described, e.g. A_4 or B_3. In order to pinpoint sampling areas, each ten metre square could be further sub-divided into one metre squares. However, this was not necessary for the present study.

In the Spring of 1966 the group workers undertook to plot the positions of all the trees on the site and measure the boundaries of the ground vegetation. The results are shown on the map of the site.

For the study of M.rufipes it was also necessary to measure the length and diameter of all the rotting timber, both stumps and logs, to be found on the site. From this it was possible to calculate the volume of wood available on the site for the colonization by M.rufipes.

A species list of the flora of the site has been prepared by M.K. Hughes (see Appendix 1).

Wynyard Wood is a birch-alder woodland (Fig.31). The woodland floor supports a dense undergrowth of Dryopteris felix-mas (L) and Polystichum setiferum (Forsk). The large areas of these ferns are interspersed with dense areas of bramble, Rubus fruticosus agg. and rosebay willow-herb Chamaenerion angustifolium (L). Where the tree canopy is thin there are

Fig.31. Wynyard site in summer.


B3
A1


E3

extensive grass patches consisting of three main species, Deschampsia caespitosa (L) Beauv, creeping soft grass Holcus mollis(L) and the common bent grass Agrostis tenuis Sibth.

The two main tree species are birch Betula spp. and alder Alnus glutinosa (L) Graertn. The canopy provided by these is patchy; where it is thinner, grass predominates; where it is thicker, ferns predominate. In certain cases where little or no light reaches the forest floor, bare patches are found.

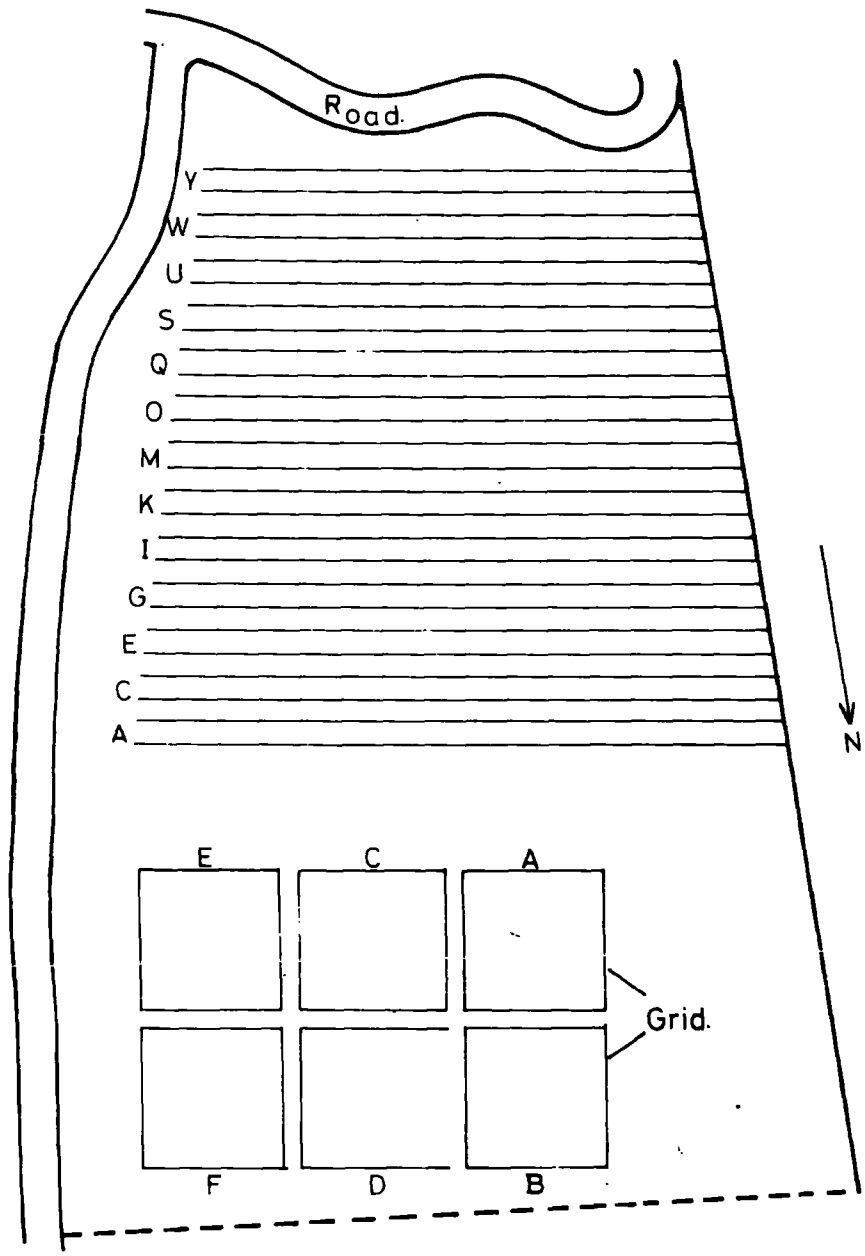
The soil is boulder clay and retains much water. The water table appears to fluctuate rapidly, especially after heavy rain when much of the water remains behind on the surface. Thus most of the rotting timber which is lying on the ground is waterlogged, especially during the winter months. Such conditions are conducive to the growth of white rot fungi, but not brown rot fungi (Cartwright & Findlay 1958). As brown rot influences the distribution of M.rufipes, thus indirectly rainfall also affects its distribution.

In winter the woodland floor has a thick layer of birch and alder leaves as well as die back from the ferns and rosebay-willow herb. The litter layer serves to protect the logs from frosts and snows. As litter removal is slow, much timber is covered throughout the year thus reducing the number of sites available for oviposition.

During the present study on M.rufipes it was necessary to provide an additional log sampling area at Wynyard. This was

Fig.32. Wynyard - additional sampling site.

Wynyard:- additional sampling areas.



A-Z = log sampling transects.

Fig.33. Great High Wood in Summer.

done in order that the timber on the site was not depleted by sampling. An area adjacent to the site was marked off A - Z. Each line was parallel to its neighbour and spaced six feet apart. Thus transect lines extended from the roadway to the fence (Fig.32). Any log on or near a particular line was tagged, numbered and graded for rotteness for future reference (Chapter 6). As population numbers proved to be low at Wynyard it was necessary to find additional sampling sites.

b) High Wood

This woodland is situated approximately one mile south of Durham City. It is an area of large mixed woodland. The particular area of interest was a small valley of birch-alder trees a number of which had been felled some years ago. No formal mapping was carried out in this area. The tree canopy is high but very thick allowing only a little light to reach the forest floor; because of this the undergrowth is poor, consisting of some ferns and grasses. In parts the woodland floor has a thick covering of leaf litter which appears to be present all the year round (Fig.33). The soil is dark and rich in organic matter and appears porous. As the 'valley' is on a hillside the drainage is good, therefore waterlogging of timber does not occur. Thus brown rot is prevalent in the rotting timber, leading to a high density of M.rufipes. This woodland was particularly suitable as a collecting area owing to its close proximity to the laboratory.

Fig.34. Park End Wood in Summer.

c) Park End Wood

Further sampling was carried out at Park End Wood. This is situated in the Tees valley, one mile west of Middleton-in-Teesdale. It is a practically pure stand of birch with no alder at all (Fig.34). The soil layer is very thinly spread over limestone; because of this the trees have shallow roots and are soon uprooted and supplies of rotting timber are abundant for colonization by M.rufipes. The tree canopy is not thick and so light easily reaches the woodland floor; this encourages the growth of long grass. In the more shaded areas there are patches of bracken. The small logs and stumps are protected from heat and dessication by the tall grass. However, some of the larger trees were dessicated in their upper surface and yielded no animals at all. As this woodland was situated on a limestone hillside no waterlogging of the timber occurred and thus most of the ground timber was infected by brown rot. Infestation by M.rufipes was widespread in this woodland which proved to be a very productive sampling and collecting area.

Other woodlands in County Durham were visited but none proved to be as profitable as the above areas. One of the main difficulties was finding any sizeable birch-alder woodlands. All too often where these were found they were very well tended by the Forestry Commission with very little suitable decaying timber to be found. The main additional woodlands visited were Hamsterley Forest (map ref.NZ.042218), Chopwell wood (map ref.NZ.132584) and Tunstall wood (map ref.NZ.068410).

SECTION II

Chapter 5. Extraction and Culture Methods Used in the study of M.rufipes

a) Extraction technique

To extract M.rufipes larvae from the monthly samples of timber (Chapter 6) an extraction procedure was devised. Each month timber was collected and in the laboratory the length and diameter of the sample was measured and the species of timber noted (this was either birch or alder). In the random samples (Chapter 6) the rot type and degree of rotteness was also noted. Samples were then broken up over a large, white-enamelled tray and examined. Any animals found were removed. The remaining timber 'chips' were extracted in a modified Tullgren funnel apparatus. The animals were collected live by lining the bottom of the collecting vessel with a pad of damp filter paper, kept moist by an inverted 3" x 1" tube of water. The extractions were checked each day, all animals removed, and the water reservoirs topped up.

The chips were extracted on an increasing heat regime for 11 days. The length of extraction time was determined in a preliminary study in which a known number of animals were allowed to bore into wood chips. The chips were extracted and the time taken for the maximum number of animals to re-appear noted. The average maximum re-appearance time proved to be 9 days. Two extra

days were added as an insurance to make a total extraction time of 11 days. By using this method the efficiency of the funnels was estimated to be 70% - 78%.

After the extraction period the samples were re-sorted by hand to establish that all or practically all animals had been removed. The extraction was probably biased in favour of the larger specimens of M.rufipes. By this the larger animals were extracted more easily than the smaller ones. Many of the larger specimens were disturbed on the manual destruction of the sample, whilst smaller animals often remained inside the chips, only to move immediately prior to desiccation. It is more than probable that some of these were desiccated.

b) Collection

Collecting experimental M.rufipes wireworms for general use other than for population estimates was done by hand. Animals were collected by finding suitable logs, peeling off the bark carefully and examining the soft, decayed wood and the underside of the bark. If the log was suitably rotted it was broken up over a tray or polythene sheet, so that animals dropping from it could be seen easily. The specimens obtained were placed in jars with chips of wood or damp cotton wool. The latter proved to be more convenient as the animals could then be found more easily. Such animals were used immediately for experimental work or else placed in culture.

c) Culture Methods

As a precaution against the lack of sufficient experimental animals at any time, cultures of M.rufipes larvae were set up. A number of methods have been suggested for keeping soil-dwelling wireworms but none for wood dwelling forms. Most commonly they have been kept in large earthenware plant pots, full of soil (Fernando 1963) or some derivation of this method such as soil-filled earthenware drain-pipes (Bryson 1929). Dobrovsky (1954) used soil-filled test-tubes, whilst Evans and Gough (1942) kept wireworms in soil-filled 3" x 1" tubes for growth studies. LaFrance (1963) has suggested a method of rearing wireworms in a glass apparatus consisting of an animal chamber and a reservoir of water, the two being connected by a wick. Yoshida (1959) used 500cc vials filled with damp sawdust to rear individuals of Melanotus caudex Lewis.

Depending on the experimental work being carried out, the animals were kept in one of two types of culture. The first type of culture consisted of 3" x 1" glass tubes, filled with damp sawdust and plugged with a loosely fitting cork. Such tubes were kept either in a constant temperature cabinet at 15^{o}C or outside in the Zoology Garden.

The second type of culture consisted of a number of sawdust-filled, 3" diameter plant pots, in which the drainage holes had been corked. These were embedded in sawdust-filled earthenware sinks and again kept in the Zoology Garden. The

sinks were provided with closely fitting lids to keep out the rain and to prevent flooding. The sawdust in the sinks was watered daily in the summer, but only twice weekly in the winter. By using this method it was possible to maintain a high relative humidity, therefore it was only necessary to dampen the sawdust in the pots very occasionally. The method was designed to alleviate the effects of overwatering, which proved to be fatal to M.rufipes larvae and enhanced the chances of fungal attack. Death by overwatering is characteristic in that the animal dramatically increases in weight as water is taken in. Hydrostatic pressure causes the animal to become completely rigid. A further refinement was to replace the sawdust in the tubes and pots with granules of rotting timber produced by milling decayed wood chips. The use of granules cut down the mortality rate, most probably through the addition of vitamins and trace elements (Fager 1953).

All cultures were fed weekly using either blowfly or Drosophila larvae. Any excess food was quickly removed as this was liable to set up fungal attack in the culture. The medium was replaced monthly and inspected for exuviae which were weighed, measured and stored for future use.

Animals only being kept for a short while were placed in jars containing pads of damp cotton wool or paper tissues. These materials kept the animals clean and easily accessible as they cannot readily form long burrows in it.

Adult animals were kept in large ventilated screw-topped jars containing damp paper tissues. Moisture was not allowed to collect on the sides of the jar as it trapped animals by their clytra. A number of foods were offered to the adults but were never taken.

SECTION II

Chapter 6. Population Studies on M.rufipes

Introduction

The investigation of energy flow through a given population requires that some estimates of population density, distribution and biomass be attempted. Melanotus rufipes Hbst. is confined to decaying timber and quantitative sampling of such a specialized habitat poses many problems. In order to overcome these problems a method of sampling was evolved with a statistical basis. Initially samples were taken at Wynyard Wood.

a) Method of sampling at Wynyard Wood

The rotting timber was found to be in a number of stages of decay. Therefore it was necessary, in order to make results comparable, to grade these decay stages. Thus three arbitrary grades of rotteness were allotted to the samples :-

Grade 1 - Sample solid but with flaking bark and surface rotteness to a depth of 2cms.

Grade 2 - Sample rotten to a depth of 10cms but with a hard core.

Grade 3 - Completely rotted throughout.

At the Wynyard site all the logs and stumps on the grid were mapped, measured and their volumes calculated from these data. In all 66 logs and 22 stumps with a volume of 0.46 litres of

wood/m^2 were dealt with in this way. The preliminary mapping, carried out when the vegetation cover was negligible (Fig.30), suggested that the grid, although adequate for the needs of the other workers, did not carry enough timber for a monthly sampling programme. Therefore it was necessary to extend the sampling site for timber into the adjacent woodland. To do this an area was marked off in parallel transect lines lettered A-Z, as described in the study area section (Fig.32). During the spring when the ground vegetation was sparse, all the timber on this additional site was tagged, numbered and graded for future reference. In all, some 306 logs and stumps were dealt with, in this way, on the additional grid. It was decided that 18 samples per month could be economically removed from this area. The samples were chosen randomly from a table of random numbers (Snedecor 1949, new ed. 1967). The data collected from this additional site could be applied to the logs available for colonization in the one grid.

Samples were taken by sawing a piece of timber out of the log. The approximate sample length was 20cms although the diameters of the logs differed. As M.rufipes is fairly slow moving it was assumed that the animals would not escape from the samples during sawing. Before the sample was taken the bark was carefully removed and any M.rufipes collected. The samples were also used in estimating the numbers of centipedes for a research colleague, as part of the group project. The position, from which

the sample was taken, was determined by dividing the log into 10 arbitrary units and choosing a number 1-10 from a bag of numbers. It was hoped this would offset any 'end-effects' (Beaver 1966). 'End effects' appear at the cut ends of the logs, which become the primary centres of decay and colonization, as they are in close contact with the external environment.

The samples thus collected were taken to the laboratory and extracted, according to the procedure outlined in the methods section, for wireworms and associated animals. The samples taken from the site at Wynyard were 'random samples'. The aim of the random samples was to determine the numbers and distribution of M.rufipes in that wood.

b) Results

The random samples taken at Wynyard were only successful in showing that M.rufipes was not important in this woodland. Infestation was very low, approximately 2.2 animals/100L of timber. However the samples served to collect data concerning other timber-dwelling animals (Appendix 2). After the study commenced it became apparent that M.rufipes was not to be found in white rotted timber. This was later confirmed by Elton (1966). As 45.8% of the samples taken from Wynyard contained white rot, these had to be immediately precluded. Clearly this is one cause of the low distribution of M.rufipes.

Another factor which could account for the low density of M.rufipes was the thick undergrowth of brambles, ferns and grasses and the large amounts of decaying leaves which covered the logs.

Wallace (1953) found many more M.rufipes in logs situated in woodland clearings than in logs covered with thick undergrowth. The density of the undergrowth probably governs the number of oviposition sites and therefore is an important factor in governing the distribution of M.rufipes. Further, distribution is probably governed by the position of logs in relation to sunlight and flooding by heavy rain.

Fernando (1963) reported that the larvae of Denticollis Linearis (L) (Elateridae) would attack and overwhelm M.rufipes especially in the early instars. This was noted in a laboratory culture but probably holds true in the field. In the present study if D.Linearis and M.rufipes were put in the same jar during collection from the field, the latter was still attacked by the former. This suggests that the attack is not merely a manifestation of starvation. As much of the timber at Wynyard contained D.Linearis this would further contribute to the low population of M.rufipes. As these two species have similar diets and habitat requirements, it appears this is an example of interspecific competition.

As the Wynyard site proved insufficient for sampling of M.rufipes, additional sampling sites and procedures had to be sought, in order to give a meaningful population estimate.

c) Additional population studies in High Wood and Park End Wood

The additional sampling was carried out at High Wood and Park End Wood (see descriptions of study areas). The method adopted was to take a 'whole log' sample each month. The change of site and

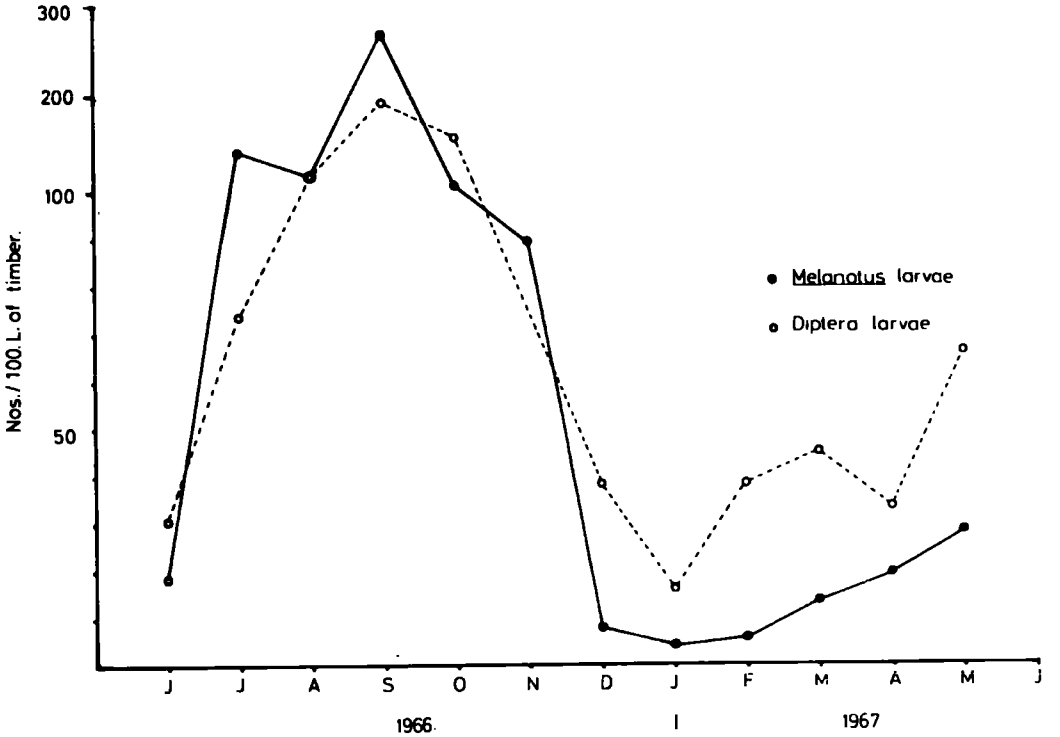
TABLE X

Whole log extraction data 1966 - 67

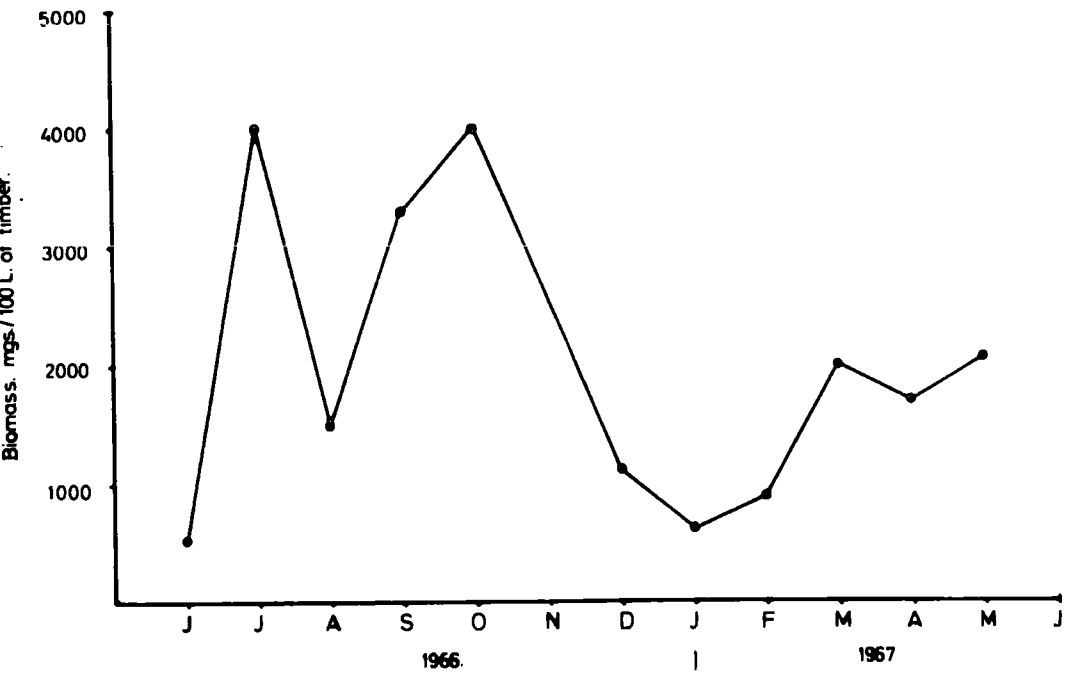
Date	Site	Sample Size	No. Melanotus/100L	Biomass M.rufipes /100L mgs.	No. Dipt./100L
June	High Wood	70,695 ccs.	30.8	552.4 mgs	18.0
July	High Wood	31,420	73.6	3,928.8	147.2
Aug.	High Wood	22,783	119.0	1,465.2	119.0
Sept.	High Wood	15,288	195.0	3,314.4	247.0
Oct.	High Wood	28,930	156.4	4,013.5	105.4
Nov.	High Wood	14,472	-	-	89.7
Dec.	High Wood	62,868	38.4	1,124.7	8.0
Jan.	High Wood	137,700	16.1	625.8	4.2
Feb.	High Wood	83,995	38.4	877.7	6.0
Mar.	Park End Wood	67,500	45.0	1,983.4	13.5
Apr.	Park End Wood	96,080	33.0	1,692.2	19.0
May	Park End Wood	52,920	66.0	2,050.8	28.0

Fig.35. Comparison of the numbers of M.rufipes larvae and dipterous larvae obtained from timber.

Fig.36. Monthly biomass of M.rufipes larvae.



Monthly nos. of M. rufipes larvae compared with Dipterous larvae.



Monthly biomass data for M. rufipes larvae.

method was initiated when it was realized that the 'random samples' would not yield as much information as was hoped for. The procedure adopted for taking a whole log sample was first of all to examine a Grade 3, brown-rotted log, for M.rufipes . If present, the log was removed to the laboratory where it was measured, broken up and extracted, using the Tullgren apparatus described in the methods section. The M.rufipes found were counted and removed daily. Similarly the numbers of Diptera were noted as it was thought, by this time, that they were a possible food source. The aim of the 'whole log' samples was to determine the degree of infestation and the population numbers and biomass per volume of Grade III, brown-rotted timber, of M.rufipes.

d) Results

Table X and Fig.35 show that logs attacked by M.rufipes support a high infestation. The mean sample size per log for the year was 57,074ml, the mean number of M.rufipes being found was 68.4/100L of timber or 39.0/mean sample size. The only previous population figure for M.rufipes is 0.3 - 0.4 animals/m^2 obtained by Schaerffenberg (1941). The data expressed in the present study are numbers per unit volume of timber, as this is more salient to the problem. This also follows the practice of other authors working on the fauna of timber.

The only other animals counted in these samples were the numbers of dipterous larvae. Preliminary feeding experiments had suggested that Diptera are the predominant prey of M.rufipes. An attempt was made to correlate the numbers of Diptera with the

number of M.rufipes in the samples (Table X and Fig.35). Stone (1954) and Lipa (1958) both report that, after application of insecticides to certain crops in an attempt to control wireworms, the number of wireworms decreased, followed by an increase in the number of dipterous pests. They both concluded that wireworms were a major predator of Diptera.

In the present study (Fig.35) the Dipterous larvae populations are seen to build up in spring to a summer maximum. This is closely followed by an increase in the number of M.rufipes larvae. This increase of M.rufipes occurs partly through the hatching of eggs, and partly through migration into the timber from the litter layer. Conversely in winter there is a decline in the numbers of Diptera and a corresponding decline in the numbers of M.rufipes mainly through mortality and migration. The summer maxima and winter minima of Diptera and M.rufipes are very evident, with a slight lag in the response of the latter. This suggests that M.rufipes is predating these larvae.

The numerical data may be converted to biomass estimates by multiplying by the mean weight per instar data (see Table X and Fig.36); this was only done for the wireworms. In the months of June and July 1966 there was an increase in biomass of M.rufipes with a corresponding increase in numbers as migration and hatching got under way. In August 1966 there was a decline in biomass even though numbers still increased. The decrease in biomass was probably due to the Instar 14 and 15 larvae pupating, whilst the increase in numbers was due to the hatching of eggs. As these

gain in weight so the biomass increases, reaching a maximum in October. After October there was a decline in biomass with a corresponding decline in numbers, probably through migration to the soil. This was maintained over winter, until the following spring. In spring numbers and biomass of M.rufipes increase once more. The mean biomass per month was found to be 1,966.2mgs/ 100L of timber.

Discussion

Data from Wynyard, although indicating a low infestation of M.rufipes, may be used in conjunction with other data, compiled as part of the group project for the site.

It appears from the whole log samples that migration in the autumn and spring months, between the litter layer, soil and decayed timber, is more important than was formerly thought. Migration in M.rufipes has been reported by Wallace (1953) who found M.rufipes below the surface of the soil in winter and at the surface of cut stumps in the summer. Rubzova (1967) found M.rufipes in the soil from October, throughout the winter. In the present study M.rufipes has been found in the soil only twice, both times in winter. However, no information is available regarding the depth to which M.rufipes will burrow in the soil. It is apparent that migration is an integral part of the behaviour of M.rufipes. The consequences of migration are shown in the variation of numbers and biomass with season, which will also be

enhanced by mortality, especially during the winter months.

The Diptera - M. rufipes relationship is interesting. Its close fit is probably a further indication that the data presented is a workable guide.

SECTION III

Chapter 7. Investigations into the feeding Biology of M.rufipes

Introduction

As already indicated in the Introduction, in any energy flow study it is necessary to solve the following equations :-

$$C = A + F \quad \ldots\ldots 1$$

$$A = R + Pg + Pr + U \quad \ldots\ldots 2$$

Feeding investigations were carried out to solve equation 1. Many authors have attempted to solve this equation, for example, Teal (1957), Richman (1958), Odum and Smalley (1959), Smalley (1960), Phillipson (1960a : 1960b), Golley (1960), Kuenzler (1961), Engelmann (1961), Odum, Connell and Davenport (1962), Slobodkin (1962, 1963), Golley and Gentry (1964), Wiegert (1964, 1965), Saito (1965), Hubbell, Sikora and Paris (1965), Petrides and Swank (1966) and Watson (1966). Most of these authors have concentrated their attentions upon herbivores and decomposers in the ecosystem. The exceptions are Phillipson (1960a : b), who worked on the carnivore Mitopus morio L. (Opiliones) and Engelmann (1961) who dealt with some carnivorous mites, as part of a larger study. Thus few studies have been made of the energetics of carnivores and fewer comparisons made between the energetics of herbivores and carnivores.

Initially, for M.rufipes, a supposed carnivore, it was necessary to fully determine its diet and mode of feeding. Studies into the former were aided by flame photometry in addition to normal food preference tests.

a) Food preference studies

It is commonly thought that wireworms are solely herbivorous, a misunderstanding that has arisen through the widespread investigation of those species which constitute serious economic pests. Certain other elaterid species have been recognised as carnivores for some time (Thomas 1940).

Zacharuk (1963b) made some food preference investigations on a number of soil-, sand- and wood-inhabiting wireworms, including M.rufipes, and found this species to have a definite carnivorous preference. In the present study the true food preference of M.rufipes was determined by experiment.

Method

The experimental procedures were derivatives of the methods used by Phillipson (1960a : b), Zacharuk (1963b) and Watson (1966). Firstly, as a preliminary experiment, a simple screening process was carried out by offering to individuals of M.rufipes potential plant and animal food and noting what was eaten. During the screening, twenty petri-dishes were lined with moistened filter paper and two M.rufipes larvae placed in each. The plant material offered was carrot, potato, germinating wheat, cabbage and grass roots, all of which were reported foods

TABLE XI. Preliminary food preference trials

Aim - to find whether M.rufipes is a herbivore or carnivore.

Dish	1	2	3	4	5	6	7	8	9	10
Carrot			N.E.		N.E.	N.E.				N.E.
Potato										
Wheat										
Cabbage										
Grass Root										
Enchytraeids									√	
Blowfly larvae	√	√					√	√	√	
Mealworms		√		√			√		√	
Mites										

Dish	10	12	13	14	15	16	17	18	19	20
Carrot					N.E.	N.E.		N.E.		
Potato										
Wheat		√								
Cabbage										
Grass Root										
Enchytraeids										
Blowfly larvae	√		√	√			√		√	√
Mealworms	√		√				√			
Mites										

N.E. = not eaten.

Each dish contained 2 M.rufipes larvae, kept at 15°C for 24 hours.

of other wireworm species. The animal foods offered were enchytraeid worms, blowfly larvae, mealworm larvae and additionally mites obtained from rotting timber. The dishes were kept at 15°C for 48 hours and then scored.

The results are expressed in Table XI. In 40% of the replicates no feeding was recorded at all. Of the remaining 60%, only in one case (No.12) was plant material taken, this being a wheat grain in which the endosperm was eaten away. In the rest the food eaten was animal, either blow-fly larvae or meal-worm larvae, although enchytraeids appear to have been attacked but not ingested.

The results of these preliminary experiments support Zacharuk (1963b), in which 70% of the animal food was eaten by M.rufipes. Thus a definite carnivorous preference was established for M.rufipes.

Further food preference tests were carried out using animal foods only. These were set up as before but were kept for a period of four days before being examined and scored. As dipterous larvae from the field were in short supply at this time (February 1967), laboratory bred blowfly larvae were substituted.

Two separate sets of experiments, each of ten replicates, were made on the 8th and 20th February respectively. The choice of foods offered in any single replicate were blowfly larvae and pupae, meal-worm larvae and enchytraeid worms.

Tables XII and XIII show the results obtained. In the first series (8/2/67) animals in nine out of the ten replicates fed,

Table XII. Food preference tests. Series 1.

Aim - to determine the food preference of M.rufipes larvae.

Dish

1		2		3		4		5	
Offered	Eaten	O	E	O	E	O	E	O	E
2 B.p. 2 B.l. 2 T. 2 E.	 2	2 B.p. 2 B.l. 1 T. -	 1 	2 B.p. 2 B.l. 1 T. 2 E.	1 2 2	2 B.p. 2 B.l. 2 E. -	1 2 	2 B.p. 2 B.l. 2 E. -	N.E.

6		7		8		9		10	
O	E	O	E	O	E	O	E	O	E
1 B.p. 1 B.l. 4 E.	. . . 1	1 B.p. 1 B.l. 4 E.	1 3	1 B.p. 1 B.l. 4 E.	1 2	1 B.p. 1 B.l. 4 E.	1 2	1 B.p. 1 B.l. 4 E.	1 2

B.p. = Blowfly pupa.

B.l. = " larva.

T. = Mealworm larva.

E. = Enchytraeid.

2 M.rufipes larvae per dish. Dishes kept at 15°C for 4 days.

Feeding recorded in 90% of the replicates.

Table XIII. Food preference tests. Series 2.

1		2		3		4		5	
O	E	O	E	O	E	O	E	O	E
2 B.p. 2 B.l. 4 E.	N.E.	2 B.p. 2 B.l. 4 E.	1 2	2 B.p. 2 B.l. 4 E.	1	2 B.p. 2 B.l. 4 E.	N.E.	2 B.p. 2 B.l. 4 E.	1

6		7		8		9		10	
O	E	O	E	O	E	O	E	O	E
2 B.p. 2 B.l. 4 E.	1	2 B.p. 2 B.l. 4 E.	3	2 B.p. 2 B.l. 4 E.	1 2	2 B.p. 2 B.l. 4 E.	1 1	2 B.p. 2 B.l. 4 E.	NE.

B.p. = Blowfly pupa.

B.l. = Blowfly larva.

E. = Enchytraeid worms.

2 M.rufipes larvae per dish. Dishes kept at 15°C for 4 days.

Feeding recorded in 70% of the replicates.

in the second series (20/2/67) animals in only seven out of the ten replicates fed. In the first series blowfly larvae and pupae were attacked in seven of the nine replicates in which feeding was recorded, and in the second series in six out of the seven replicates. Thus both sets of experiments indicate a food preference for Diptera. In both series enchytraeid worms were attacked but apparently not ingested; the M.rufipes larvae were seen to bite the enchytraeids into pieces but never seen to devour them. Possibly M.rufipes finds their mucus repellent.

In addition to these experiments further observations were made on feeding in M.rufipes. In a set of experiments not previously reported, both Collembola and mites were offered as potential foods but none were ever taken. In the field M.rufipes has been found eating centipedes and dead earthworms, by the author. In the laboratory the author has observed cannibalism although Fernando (1963) states that it does not occur in M.rufipes.

b) Flame photometry

Complementary studies to the standard food preference procedure were made using flame photometry techniques. It has been known for some time that the relative amounts of sodium and potassium present in insect body fluids may be used to differentiate between herbivores and carnivores (Boné 1944, 1946 and 1947), Du Chateau, Florkin and Le Clerq (1953) and Buck (1953). Kfing (1959) used a modified technique to determine whether or not the wireworm Limonius agonus Say, was a predator. This technique involved the

use of whole animals rather than insect blood alone.

Method

The sodium-potassium ratio of M.rufipes was determined for comparison with the ratios of other insects of known food régime. Pre-weighed samples of whole animals were ashed in a muffle furnace at 500°C, until complete combustion, as indicated by a light grey deposit. (Dark particles in the ash indicated incomplete combustion). On removal from the muffle furnace the ash of each individual was allowed to cool in a desiccator. After cooling each sample was dissolved completely in a known volume of distilled water to which a little hydrochloric acid had been added (one ml. of concentrated acid added to one litre of distilled water). One millilitre of this 'acidified' distilled water was added for every ten mgs wet weight of the sample before ashing.

Determinations of the amounts of sodium and potassium were made using a standard EEL flame photometer which was calibrated by standard solutions of sodium and potassium, after zeroing with 'acidified' distilled water.

The experimental animals had varied diets and comprised M.rufipes larvae, Denticollis linearis L. (known carnivore), Calliphora erythrocephala (Meigen) (known carnivore), Tenebrio molitor L. larvae (herbivore) and Pieris brassicae L. caterpillars (known herbivore).

Table XIV. Flame Photometry Data

All ionic quantities expressed as mgs. Na(K)/100mls.distilled water.

Pieris brassicae L.

wt.	Na.	K.	Na : K.	wt.	Na.	K.	Na : K.
207.6mgs	0.10	0.81	1 : 8.10	205.7mgs	0.09	0.65	1 : 7.00
130.9	0.10	0.75	1 : 7.50	238.3	0.10	0.31	1 : 3.10
227.1	0.19	0.42	1 : 2.21	178.2	0.11	0.65	1 : 5.91
91.3	0.43	0.81	1 : 1.88	248.2	0.01	0.44	1 : 6.28
230.6	0.22	0.45	1 : 2.04	237.0	0.08	0.24	1 : 3.00
196.9	0.08	0.81	1 :10.12	185.5	0.14	0.31	1 : 2.21
223.6	0.21	0.46	1 : 2.19	137.2	0.17	0.76	1 : 4.47
207.4	0.22	0.47	1 : 2.14	242.6	0.08	0.42	1 : 5.20
189.8	0.22	0.44	1 : 2.00	145.9	0.18	0.43	1 : 2.39
141.5	0.12	0.86	1 : 7.17	124.6	0.25	0.34	1 : 1.36
257.2	0.17	0.35	1 : 2.06				

Mean ratio Na : K. = 1 : 4.12. Range (1 : 1.88 - 1 : 10.12)

Table XV.

Tenebrio molitor L.

wt.	Na.	K.	Na : K.	wt.	Na.	K.	Na : K.
144.8mgs	0.24	0.30	1 : 1.25	36.1mgs	0.18	0.26	1 : 1.44
122.1	0.22	0.32	1 : 1.45	30.8	0.19	0.23	1 : 1.21
117.2	0.21	0.36	1 : 1.71	52.6	0.19	0.18	1 : 0.95
139.6	0.23	0.32	1 : 1.39	43.8	0.17	0.21	1 : 1.23
111.9	0.18	0.41	1 : 2.28	44.7	0.12	0.20	1 : 1.67
133.3	0.20	0.36	1 : 1.80	45.5	0.11	0.28	1 : 2.54
115.7	0.18	0.33	1 : 1.83	38.9	0.13	0.29	1 : 2.23
14.98	0.27	0.36	1 : 1.33	39.6	0.18	0.31	1 : 1.72
15.46	0.32	0.50	1 : 1.56	66.4	0.12	0.24	1 : 2.00
13.10	0.30	0.44	1 : 1.47	79.6	0.09	0.20	1 : 2.22
7.32	0.31	0.39	1 : 1.26	61.2	0.15	0.31	1 : 2.07
9.62	0.33	0.52	1 : 1.56	57.0	0.12	0.24	1 : 2.00
11.68	0.35	0.38	1 : 1.09	53.4	0.10	0.31	1 : 3.10
5.62	0.30	0.44	1 : 1.47	77.9	0.12	0.26	1 : 2.17
11.36	0.22	0.47	1 : 2.14	75.7	0.12	0.29	1 : 2.42
22.0	0.12	0.37	1 : 3.08	71.2	0.17	0.28	1 : 1.65
31.7	0.12	0.26	1 : 2.17	53.7	0.15	0.29	1 : 2.23
33.4	0.14	0.31	1 : 2.21				

Mean ratio Na : K. = 1 : 1.81. Range (1 : 0.95 - 1 : 3.10)

Table XVI. Flame Photometry Data

All ionic quantities are expressed as mgs.Na(K)/100mls.distilled water.

Melanotus rufipes Hbst.

Wt.	Na.	K.	Na : K.	Wt.	Na.	K.	Na : K.
145.5mgs	0.13	0.18	1:1.33	41.6mgs	0.15	0.32	1:2.13
38.2	0.18	0.36	1:2.00	11.6	0.13	0.26	1:2.00
25.1	0.16	0.50	1:3.10	14.6	0.09	0.29	1:3.22
34.3	0.14	0.22	1:1.56	25.9	0.14	0.19	1:1.36
31.2	0.17	0.14	1:0.83	7.2	0.20	0.30	1:1.50
8.0	0.20	0.30	1:1.50	22.4	0.12	0.31	1:2.58
10.0	0.23	0.20	1:0.87	19.7	0.12	0.29	1:2.42
20.5	0.18	0.27	1:1.50	89.7	0.09	0.16	1:1.78
3.9	0.23	0.22	1:0.95				

Mean ratio of Na : K. = 1 : 1.77. Range (1 : 0.83 - 1 : 3.22)

Table XVII

Denticollus linearis L.

Wt.	Na.	K.	Na : K.
53.2	0.19	0.25	1 : 1.32
53.4	0.09	0.21	1 : 2.33
47.4	0.11	0.13	1 : 1.18
43.1	0.10	0.12	1 : 1.20
34.6	0.16	0.10	1 : 0.62

Mean ratio of Na : K. = 1 : 1.33. Range (1 : 0.62 - 1 : 2.33)

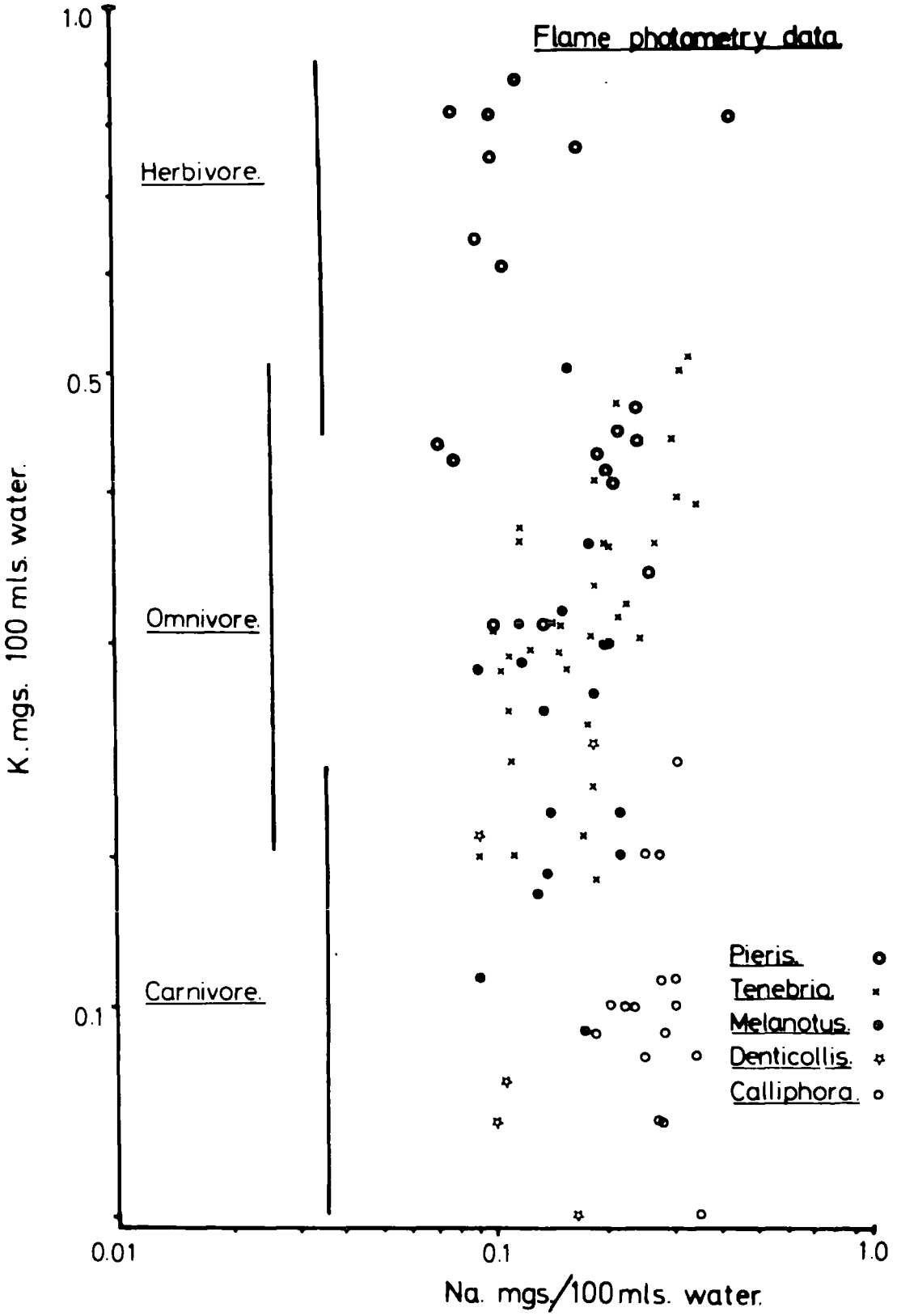
Table XVIII

Calliphora erythrocephala (Meigen)

Wt.	Na.	K.	Na : K.	Wt.	Na.	K.	Na : K.
49.3	0.34	0.14	1 : 0.41	31.3	0.29	0.14	1 : 0.48
58.1	0.35	0.10	1 : 0.29	48.5	0.28	0.20	1 : 0.71
52.3	0.31	0.16	1 : 0.52	34.8	0.28	0.16	1 : 0.57
47.4	0.25	0.14	1 : 0.56	55.4	0.25	0.20	1 : 0.80
46.6	0.23	0.15	1 : 0.65	56.2	0.30	0.15	1 : 0.50
49.5	0.28	0.12	1 : 0.43	56.2	0.19	0.14	1 : 0.74
56.5	0.28	0.12	1 : 0.43	42.4	0.31	0.24	1 : 0.77
61.1	0.24	0.15	1 : 0.62	55.9	0.21	0.15	1 : 0.71

Mean ratio of Na : K. = 1 : 0.57. Range (1 : 0.29 - 1 : 0.80)

Fig.37. Flame photometry data.


Flame photometry data
1.0
0.5
0.1
K. mgs. 100 mls. water.
Herbivore.
Omnivore.
Carnivore.
Pieris.
Tenebria.
Melanotus.
Denticollis.
Calliphora.
0.01
0.1
1.0
Na. mgs./100 mls. water.

Results

Tables XIV to XVIII inclusive and Fig.37 show the results of the sodium/potassium analyses. It is clear that the ratios of sodium : potassium show a graded series of 1 :4.12 in the herbivore P. brassicae to 1 :0.57 in the carnivore C. erythrocephala. The intermediate values of 1 :1.81, 1 :1.77 and 1 :1.33 were shown by T.molitor, M.rufipes and D.linearis respectively.

D.linearis is a known carnivorous wireworm and cannot be reared successfully on plant food.(Zacharuk 1963b). Although chosen as representing a herbivore, the sodium : potassium ratio of T.molitor suggests a omnivorous habit, a finding supported by the work of Cotton and St. George (1929). Thus the graded series of ionic relationships can be correlated with diet. As Du Chateau, Fiorkin and Le Clerq (1953) state "en general, le potassium prédomine dans le liquide coelomique des Insectes végétariens, tandis que la concentration en sodium dépasse celle du potassium chez les carnassiers".

In the field it is likely that M.rufipes will mainly feed on soft bodied prey such as dipterous larvae, as indicated in the food preference studies. A conclusion supported by the work of Stone (1954) and Lipa (1958), who found that the number of Diptera increased after various crops had been treated for wireworm attack, and deduced that wireworms are probable predators on dipterous larvae. In rotting timber Tipulid larvae are often the most

commonly occurring, sizeable Diptera, although other Diptera are present. Probably these constitute the main item of diet of M.rufipes although beetle larvae and pupae as well as moribund earthworms and centipedes are possible additions.

c) Mode of feeding

Observations on feeding by wireworms have been made by Langenbuch (1932), Subklew (1934), Dobrovsky (1954) and Eidt (1959). Although all the wireworm species described by these authors were herbivores, observations on M.rufipes showed that the mode of feeding of this species is similar. Dobrovsky (1954) noted that when the herbivorous Conoderus vagus Cand. fed on potato, lumps of pulp were discarded, and suggested three reasons for this :- 1) that only the liquid portions were extracted, 2) that pre-digestion occurred, 3) that some solids were broken up into minute fragments and ingested, the rest being discarded. Langenbuch (1932) described a dense oral filter of hairs in the herbivore Agriotes spp. Eidt (1959) believes that the oral filter is characteristic of all wireworm species. In order to test the efficiency of this filter mechanism he fed particles of known size to Ctenicera aeripennis destructor Brown., another herbivore. He found that particles above 3 microns diameter were rejected by the filter. Eidt (1959) also found that feeding wireworms, or those disturbed, regurgitated a dark brown liquid. Fernando (1963) also noted this in Athous haemorrhoidalis L., as did the author in M.rufipes. Eidt (1959) believes that this same fluid has a pre-

digestive function. It is secreted, not by the salivary glands, which are absent in wireworms, but by the ventricular epithelium. Thus predigestion would allow food to be ingested in fluid form, any indigestible large particles being filtered out by the oral mechanism.

Ingestion of fluids was noted in M.rufipes which, after attacking its prey, proceeded to suck the body juices, leaving the outer covering. Wireworms, including M.rufipes, have a modified pharynx forming a sucking pump which would clearly aid fluid ingestion. The body fluids of most animals consist of suspensions of minute particles which may be either reduced to a liquid by predigestion or else rejected by the oral filter, before being ingested.

In M.rufipes, as in other wireworms, the faeces are fluid and light brown in colour. When viewed under a microscope, no particles or crystals can be defined, supporting the view that large particles ($> 3\mu$) are filtered off and small ones ($< 3\mu$) digested.

d) Feeding rate studies

Feeding rates of single species populations have been studied by Phillipson (1960a : b), Hubbell, Sikora and Paris (1965), Saito (1965), Wiegert (1964, 1965), and Watson (1966). In the present study it was hoped that the 'marker food' technique developed by Phillipson (1960a : b) and used by Watson (1966) could be used to delimit the food intake and faeces production of an individual for any one particular meal. Unfortunately no suitable marker food was found as the faeces remained the same colour whatever food was ingested. Food marked with dyestuff was

also tried, but this proved unsatisfactory as only the outer portion of the prey was stained, but the internal fluids, the food source of M.rufipes, were unaffected.

During the feeding studies animals were starved for at least 48 hours prior to being fed. After being fed they were left a further 48 hours. It was hoped this procedure would allow a) the gut to empty after its previous meal, b) the faeces produced from the given food to be isolated. It was further noted that faeces were only produced during or shortly after feeding.

A major problem was the collection of the fluid faecal matter; thus a method had to be devised for the collection of the fluid droplets. At first faeces were collected on oven-dried, pre-weighed filter paper. This was rolled, re-wetted and placed as a lining in a 2" x 1/4" glass specimen tube. The prey and wireworm were left for 48 hours before the filter paper was removed, dried and re-weighed. Theoretically this should have allowed the calculation of the dry weight of faeces produced. However, the results were so variable, due to the hygroscopic nature of the filter paper during weighing, that another method was sought.

Methods

The method finally adopted was a modification of the above technique. Experiments were carried out in 2" x 1/4" glass specimen tubes containing cylinders of damp filter paper, lined internally with perforated aluminium foil. The perforations allowed the passage of water vapour into the experimental chamber,

Fig.38. Diagram showing the chamber used in the quantitative feeding studies.

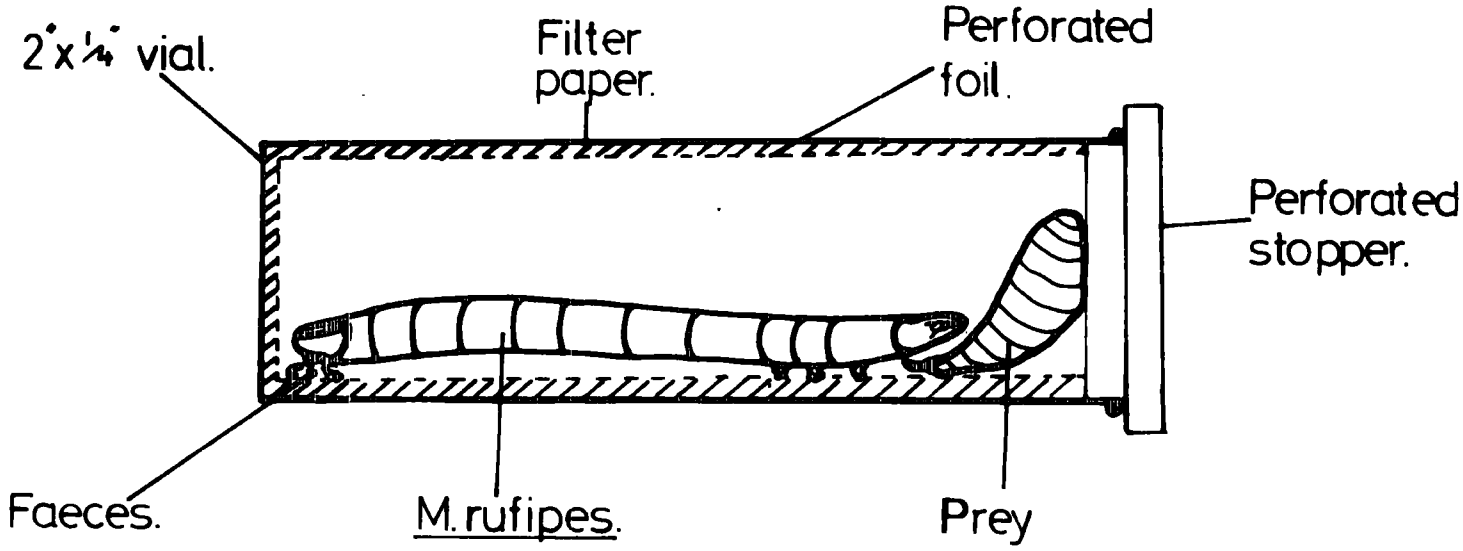


Diagram to show a feeding tube.

but still enabled the faeces to be retained (Fig.38). The experimental animals were contained in the chambers by a perforated stopper.

As dipterous larvae, which form the probable normal food of M.rufipes, were not found in sufficient quantities to be used experimentally throughout the year, laboratory bred blowfly were substituted, and used as the food source. Fortunately blowfly larvae have a period during their life history, prior to pupation, when they clear their guts of food and faecal matter. Thus it was convenient to use these prepupal animals as prey animals as they did not defecate, and thus allowed only M.rufipes faeces to be collected.

In any particular experiment the foil was pre-weighed and placed in the tubes. The weights of the predator, M.rufipes and the prey C.erythrocephala were determined and the animals placed in the experimental chamber. Each experiment was terminated after 48 hours and the weights of M.rufipes and the food remains determined. The foil plus faeces was dried in a vacuum oven at 60^{o}C for 48 hours. On removal they were cooled in a desiccator and finally weighed to give the dry weight of faeces produced during 48 hours. This proved to be a most successful technique for the quantitative estimation of fluid faeces.

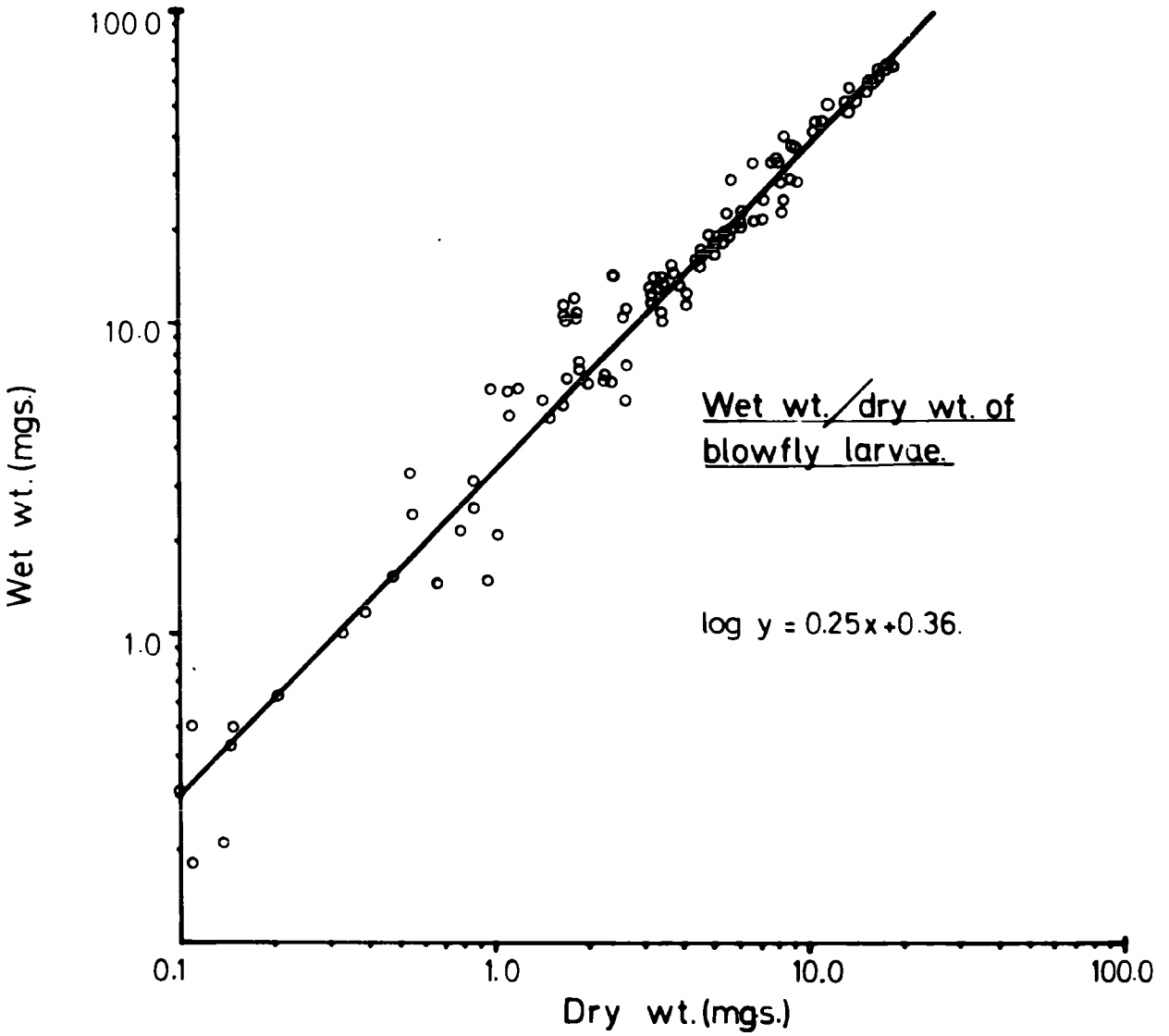
Because of the intention to convert all weights to calories, it was necessary in the first instance to express the

Table XIX. Wet weight - dry weight data of Calliphora erythrocephala (Meigen)

Wet wt.	Dry wt.	Wet wt.	Dry wt.	Wet wt.	Dry wt.	Wet wt.	Dry wt.
64.58	16.84	64.50	16.74	19.77	5.40	0.31	0.10
52.20	13.41	52.12	14.95	19.01	4.83	0.21	0.14
5.12	1.10	13.02	3.14	15.79	4.46	1.18	0.39
58.88	15.60	61.42	17.45	18.63	5.18	1.02	0.32
52.83	12.85	53.58	13.90	21.34	6.65	0.18	0.11
61.60	16.39	64.35	15.82	15.12	4.54	1.61	0.47
53.78	15.35	57.45	15.44	21.22	6.13	15.82	3.10
61.38	16.57	56.44	17.05	28.24	8.03	1.09	0.38
65.81	17.60	60.90	16.35	21.82	7.08	0.12	0.06
12.42	1.80	54.41	14.95	13.25	3.31	2.46	0.55
59.02	16.21	67.49	18.88	19.47	5.50	2.31	0.79
63.15	17.00	44.88	11.35	11.01	2.61	3.12	0.86
1.50	0.95	25.27	7.60	19.24	5.70	6.40	2.00
10.38	1.81	28.40	9.13	14.28	3.72	2.56	0.86
56.62	15.10	17.82	5.03	15.16	3.70	5.52	1.70
47.82	13.62	21.66	6.66	16.49	4.39	7.49	1.90
10.68	1.68	50.55	12.94	6.35	0.97	7.21	1.90
14.31	2.40	53.28	11.89	21.14	6.20	0.50	0.15
2.10	1.02	11.64	1.69	29.85	8.90	6.77	1.73
10.16	1.70	60.20	16.56	3.73	0.53	5.68	1.42
67.75	17.91	58.04	16.54	10.15	2.65	6.33	2.09
40.65	8.40	42.46	10.56	12.99	3.38	4.37	1.49
65.60	16.88	34.72	7.85	19.80	5.52	10.76	3.42
54.66	15.06	34.18	7.68	12.94	3.40	6.62	2.22
61.50	15.49	38.32	8.84	23.73	7.49	10.20	2.75
44.29	10.23	45.30	11.00	13.32	3.37	16.47	5.04
56.40	15.10	44.70	10.02	13.36	3.36	6.87	2.26
62.10	16.15	34.52	8.00	23.56	7.59	5.66	2.67
62.05	15.55	38.28	9.00	13.34	3.65	6.53	2.32
6.16	1.10	34.20	6.75	16.45	4.65	1.43	3.90
6.19	1.20	53.40	11.22	21.50	6.20	7.37	2.66
10.82	1.85	50.92	11.15	11.47	3.20	12.89	4.18
58.30	13.41	29.64	5.64	0.50	0.11	11.68	4.11

All weights expressed as milligrams.

Fig.39. Wet weight - dry weight relationship of blowfly larvae (*Calliphora erythrocephala*(Meigen))


100.0
10.0
1.0
Wet wt. (mgs.)
0.1
1.0
10.0
100.0
Dry wt. (mgs.)
Wet wt./dry wt. of blowfly larvae.
log y = 0.25x + 0.36.

results as dry weights. This was already done for faeces production. To estimate the dry weight of blowfly larvae, a series of wet weight - dry weight determinations were made. The results are expressed in Table XIX and Figure 39. The correlation coefficient of r = 0.94 indicates a highly significant relationship where :-

$$y = 0.25x + 0.36$$

y = dry weight
x = wet weight

The wet weights of food and food remains were converted to dry weights using this formula. The dry weight of faeces produced was measured directly. After weighing the faeces were scraped off the foil and collected for bomb calorimetry.

From the information produced by these experiments the following parameters were measured

1) wt. of food ingested (C) = wt. of food offered - wt. of food remains

2) Wt. of food assimilated (A) = food ingested (C) - faeces produced (F).

The percentage assimilation was calculated as :-

$$\frac{\text{dry wt. assimilated (A)}}{\text{dry wt. ingested (C)}} \times 100$$

Results

Raw data was calculated as mgs. dry wt. of food/mgs. live wt. M.rufipes/24 hours. Table XX and Figure 40 show results for ingestion/mgs. live wt./24 hours as well as the assimilation percentage. Data for faeces production is not expressed as it can be calculated from these parameters.

Table XX. Feeding data for M.rufipes larvae

Wt. Animal	% Assim.	Ingestion mgs/mg. Animals/24 hrs	Wt. Animal	% Assim.	Ingestion mgs/mg. Animals/24 hrs.
40.9	90.3	0.09	38.6	78.4	0.06
55.1	91.4	0.06	29.1	89.5	0.06
85.5	98.5	0.04	29.4	85.0	0.10
91.2	95.3	0.03	83.7	95.3	0.04
81.0	95.2	0.04	120.0	86.8	0.01
54.5	94.1	0.06	50.0	91.1	0.04
10.6	89.7	0.20	69.6	90.8	0.04
44.3	96.8	0.11	71.2	88.9	0.06
141.7	75.5	0.01	117.5	69.4	0.02
46.5	76.7	0.04	18.0	92.6	0.03
36.9	77.2	0.06	82.8	97.2	0.04
82.0	80.4	0.03	81.4	84.1	0.04
37.2	82.0	0.04	5.4	50.0	0.09
49.3	80.9	0 06	5.0	80.0	0.10
76.8	78.6	0.03	109.9	80.0	0.03
148.5	85.4	0.02	114.9	90 0	0.02
98.9	94.3	0.04	97.5	89.3	0.02
60.9	91.7	0.06	42.6	82.9	0.05
61.9	94.4	0.06	52.3	88.8	0.08
28.1	68.3	0.07	55.6	85.5	0.06
118.7	90.9	0.02	60.4	90.2	0.07
69.7	95.6	0.06	40.2	88.7	0.15
103.2	95.3	0.05	47.3	82.0	0.10
86.7	74.5	0.02	73.0	84.2	0.01
65.7	74.2	0.03	91.1	89.4	0.05
52.4	88.4	0.06	80.0	92.4	0.03
111.6	96.1	0.06	74.8	85.5	0.05
138.3	78.1	0.02			
85.8	89.7	0.04			
117.3	90.2	0.04	70.1	86.5	0.05 Mean figs.
74.5	97.0	0.04			
20.1	75.0	0.04			
34.0	95.4	0.06			
52.1	90.5	0.09			
28.2	83.8	0.11			
76.0	75.6	0.02			
81.1	93.2	0.06			
71.5	94.2	0.07			

n.b. Assimilation percentage of 86.5% $\pm$ 0.34%

Table XXI. Feeding rates/mg/24hrs

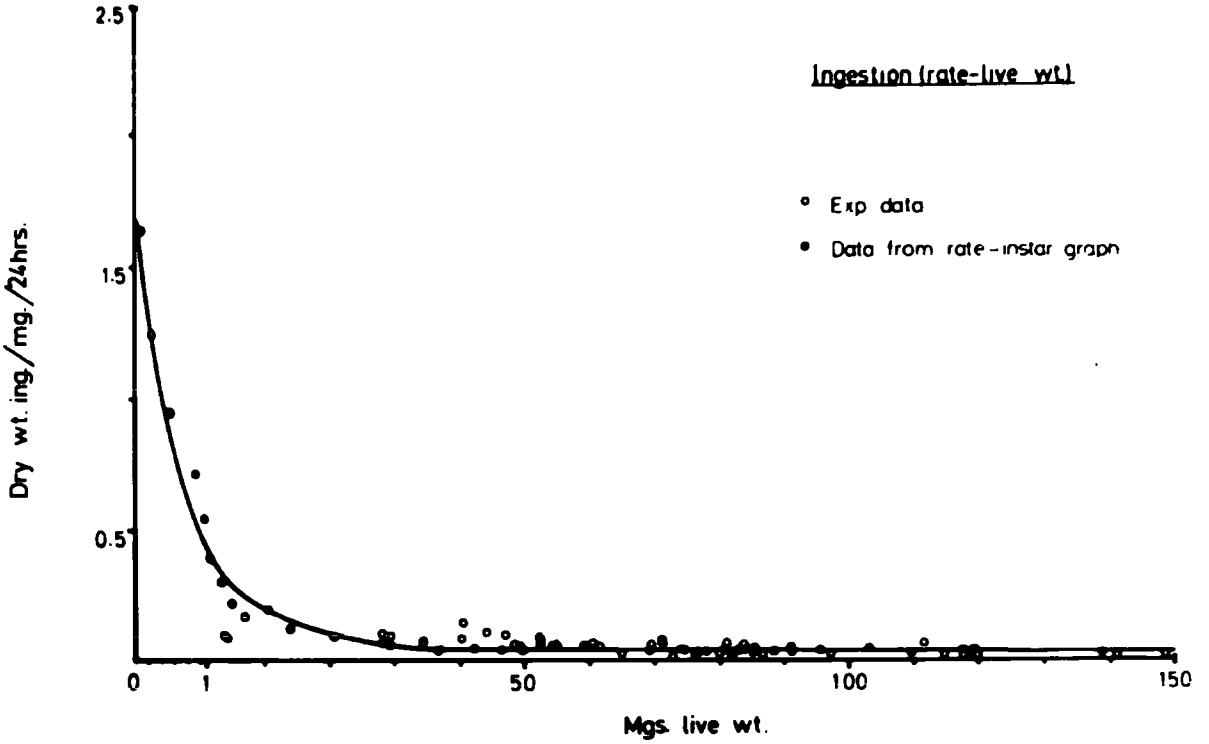
All measurements in mgs day wt./mg of animal/24 hours

Mean figures per instar. See graphs

INSTAR	Ingestion	Assimilation	Faeces prodn.
9	0.190	0.165	0.019
10	0.04	-	-
11	0.04	-	-
12	0.080	0.070	0.012
13	0.060	0.055	0.007
14	0.040	0.037	0.004
15	0.030	0.024	0.0035

Fig.40. Rate of ingestion per mg. per 24 hours.

Fig.41. Rate of ingestion per instar per 24 hours.


Ingestion (rate-live wt.)
Exp data
Data from rate-instar graph
Dry wt. ing./mg./24hrs.
2.5
1.5
0.5
0
1
50
100
150
Mgs. live wt.

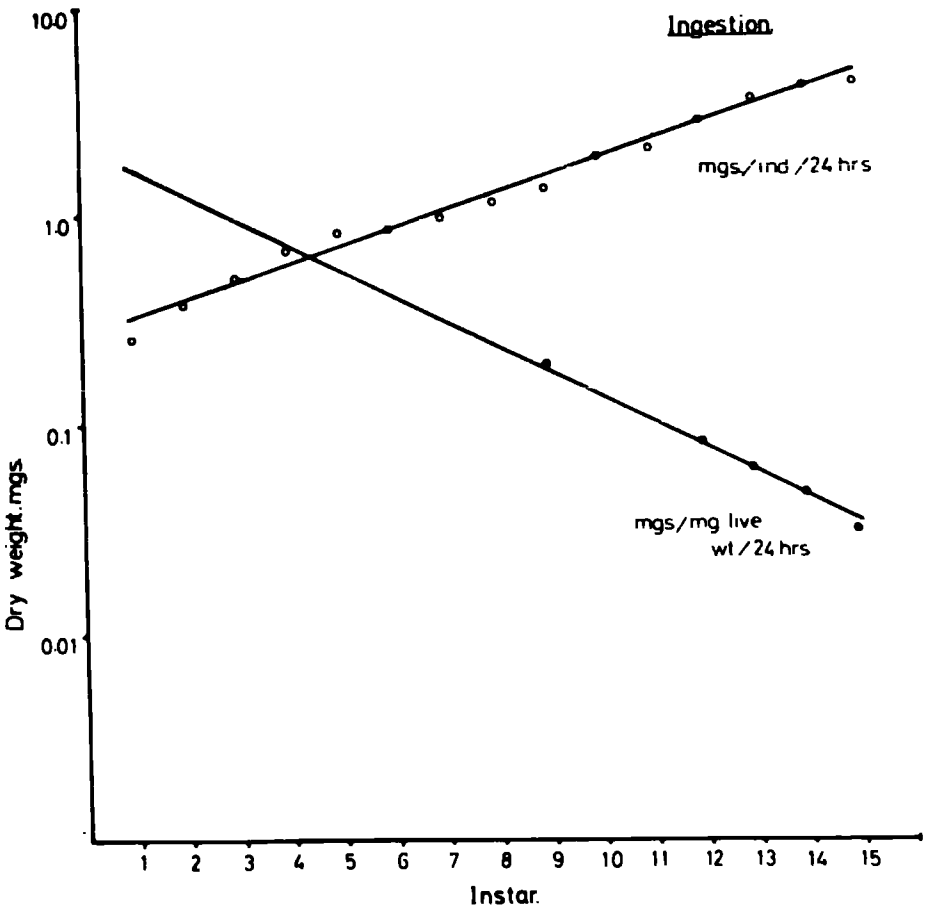
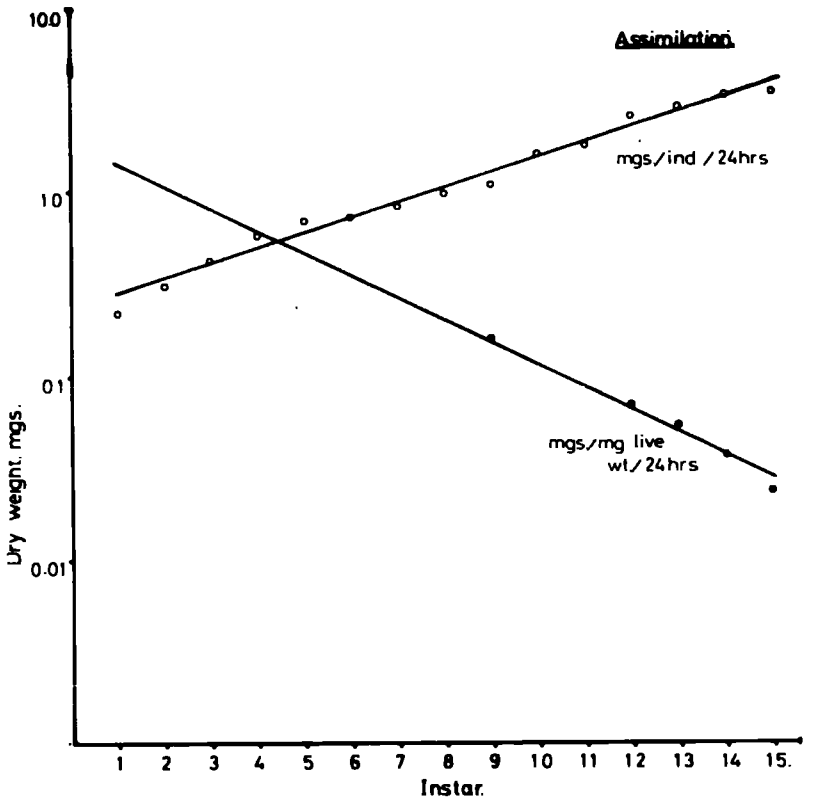

Ingestion
mgs./ind./24 hrs
mgs/mg live wt/24 hrs
Dry weight. mgs.
100
1.0
0.1
0.01
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
Instar.

Fig.42. Rate of assimilation per instar per 24 hours.

Fig.43. Rate of faeces production per instar per 24 hours.


Assimilation
100
10
01
0.01
Dry weight. mgs.
mgs/ind / 24hrs
mgs/mg live wt/ 24hrs
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15.
Instar.

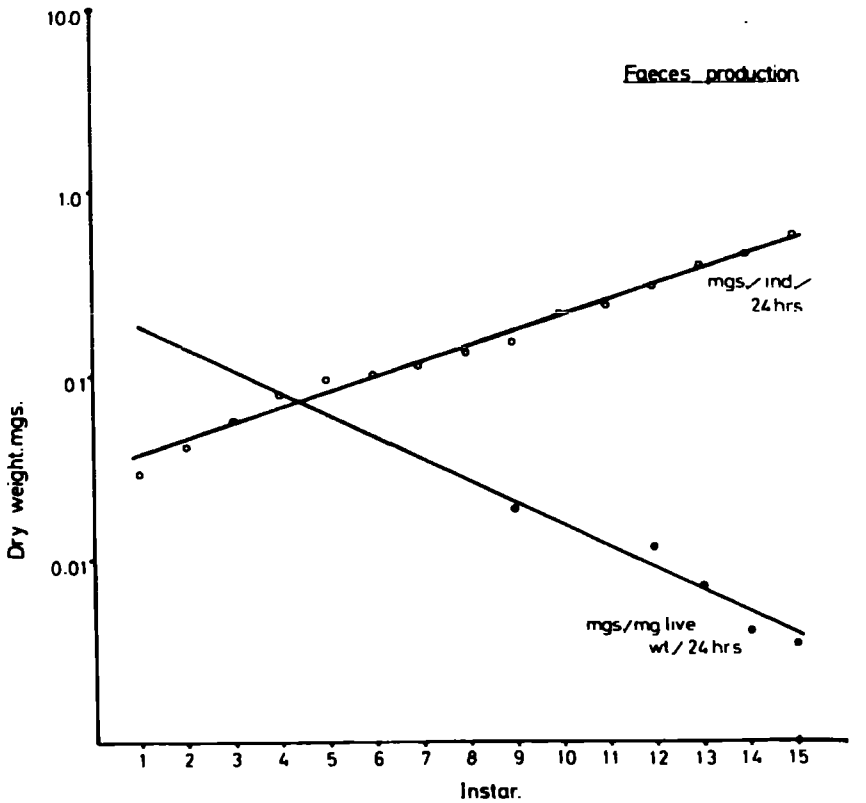

Faeces production
10.0
1.0
01
0.01
Dry weight.mgs.
mgs./ ind./ 24hrs
mgs/mg live wt/ 24hrs
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15
Instar.

Table XXII. Feeding rates per instar per 24 hours

Feeding rates from extrapolated data. All measurements mgs day wt./ instar/24 hours

Instar	Ingestion	Assimilation	Faeces prodn. 24 hours
1.	0.260	0.220	0.030
2.	0.380	0.310	0.042
3.	0.500	0.430	0.058
4.	0.690	0.590	0.080
5.	0.820	0.700	0.096
6.	0.840	0.740	0.101
7.	0.960	0.830	0.115
8.	1.150	0.980	0.137
9.	1.310	1.100	0.156
10.	1.810	1.640	0.224
11.	2.050	1.800	0.246
12.	2.760	2.620	0.310
13.	3.550	2.960	0.402
14.	4.000	3.360	0.460
15.	4.190	3.470	0.581

Above data calculated by extrapolating from graph depicting mgs feeding activity/mgs live wt./instar/24 and converting by multiplying by mean wt/instar to give mgs feeding activity/ instar/24 hours. i.e. for one single animal of that particular instar.

Table XXI and Figs. 41, 42 and 43 show the raw data expressed as mgs. dry wt./mgs. live wt./instar/24 hours for stages above Instar 8. Great difficulty was experienced in getting larvae below Instar 8 to feed. It was thought that the size of prey offered to these early instars was too large. Experiments were repeated with these animals, using Drosophila sp. larvae as prey, but no feeding could be induced. As the feeding data for animals above Instar 8 took the form of a straight line (Figs. 41, 42 and 43) it was possible to extrapolate the feeding data for the early instars. As no direct measurements could be made, extrapolition proved the only method possible of estimating feeding data for the early instars.

Mean ingestion, defaecation and assimilation were obtained from the above data and expressed as mgs. dry wt./instar/24 hours. This was accomplished by multiplying the data by the known mean weight of an individual per instar. Tables XXII and Figures 41, 42 and 43 show the results in this form.

It is clear from these tables and figures that the estimated rates of ingestion varied from 0.26mgs. dry weight of food/24 hours for Instar 1 animals to 4.19mgs. dry weight/24 hours for Instar 15 animals. Similarly the rates of assimilation varied from 0.22mgs. dry weight/24 hours for Instar 1 to 3.47mgs./24 hours for Instar 15 larvae. Of special note is the very high mean assimilation percentage of 86.5% $\pm$ 0.34% by weight. The rates of faeces production varied from 0.030mgs. dry weight/24 hours for Instar 1 to 0.587mgs. dry weight/24 hours for Instar 15 onwards.

Discussion

During each series of experiments many animals did not feed at all. Evans and Gough (1942) and Zacharuk (1963) both reported that wireworms undergo fasting periods, generally prior to moulting. It is probable that the non-feeders were undergoing fasting phases. It is unfortunate that the early instars could not be induced to feed at all, but some measure of food intake can be gained from extrapolation. The actual magnitude of food intake per instar was very high, but it should be noted that the above experiments assumed that M.rufipes feeds daily when later investigations suggested that this was not so.

Few bioenergetic studies have been made on carnivorous invertebrates. Phillipson (1960a : b) obtained a 75% assimilation percentage for juvenile Mitopus morio L with a mean value of 47% for adults. It is notable that the high percentage in juveniles can be correlated with the fact that they only eat the soft parts of their prey. Engelmann (1961) obtained a variable assimilation percentage of 14 - 32% for certain carnivorous mite. In addition a value of 80% assimilation has been found for Pyrrhusoma nymphula (Sulz) (Lawton pers.comm.). Therefore a mean assimilation percentage of 86.5% (by weight) for M.rufipes appears to be reasonable especially considering its fluid diet.

Adults were offered many varied foods, including pollen, roots, honey and germinating seeds, as well as crushed dipterous larvae and enchytraeid worms. At no time could they be induced

to eat. Fernando (1963) stated that adults do not feed and these data reinforce his supposition. However, it is surprising that the adults can undergo pupation, overwintering and egg production on food accumulated during the larval life.

SECTION III.

Chapter 8. Respiratory metabolism of M.rufipes

Introduction

In any bioenergetic study it is necessary to obtain estimates of the respiratory loss (R_r). Bioenergetic studies, in which respiratory metabolism was estimated, were carried out by Richman (1958), Odum and Smalley (1959), Smalley (1960), Kuenzler (1961), Nielsen (1961), Engelmann (1961), O'Connor (1963 : 1964), Berthet (1963), Phillipson (1962 : 1963), Ito (1964), Saito (1965 : 1968), Wiegert (1964 : 1965), Phillipson and Watson (1965).

Although the respiratory rates of certain wireworm species have been determined, such measurements were not directed towards the evaluation of energy flow. Edwards (1946) reported on the oxygen consumption of adults of Melanotus communis. Yashida (1961) studied the short-term oxygen metabolism of Melanotus caudex Lewis.

In the present study two independent methods of measuring respiratory metabolism was used. The annual respiratory metabolism was measured in a continuously recording, electrolytic respirometer, of the type described by Phillipson (1962). Studies on certain aspects of respiration, which emerges from the above measurements, were investigated using standard Warburg apparatus and techniques (Umbreit et al 1964).

a) Determination of the respiratory loss

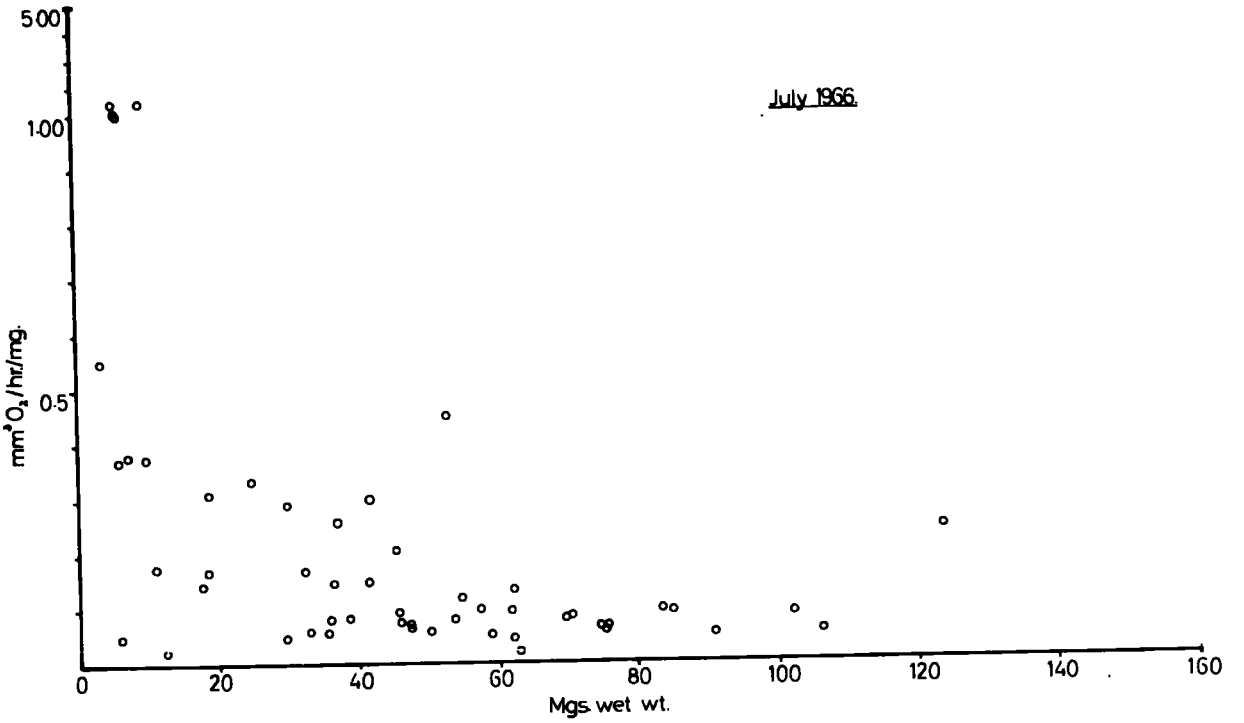
Methods

To estimate annual respiratory loss by M.rufipes the oxygen consumption of approximately 600 individuals was measured from June 1966 to June 1967. This total included larvae, and adults when available. All respiratory measurements were made at a constant temperature of $15^{o}C \pm 0.1^{o}C$. A standard procedure was adhered to throughout. The animals were collected from the field and confined in respirometer chambers as soon as possible. Any one experiment lasted for 48 hours, but only measurements recorded AFTER the first 24 hours were used to calculate the oxygen consumption of M.rufipes. The first 24 hours was ignored as the animal settled down in the respirometer, after handling. Animals were not fed during the experimental period.

In addition to the oxygen uptake, the live weight, head-width, instar and date of capture of the animal concerned, were recorded. Metabolic rates were expressed both as mm^3 oxygen consumed/mg.live weight/hour and mm^3 oxygen consumed/individual of known weight/24 hours. No diurnal respiratory rhythm was detected in the 24 hour experiments.

Results

Fig.44. Respiratory data for July and August 1966.


5·00
1·00
0·5
mm³O₂/hr/mg.
July 1966.
0
20
40
60
80
100
120
140
160
Mgs. wet wt.

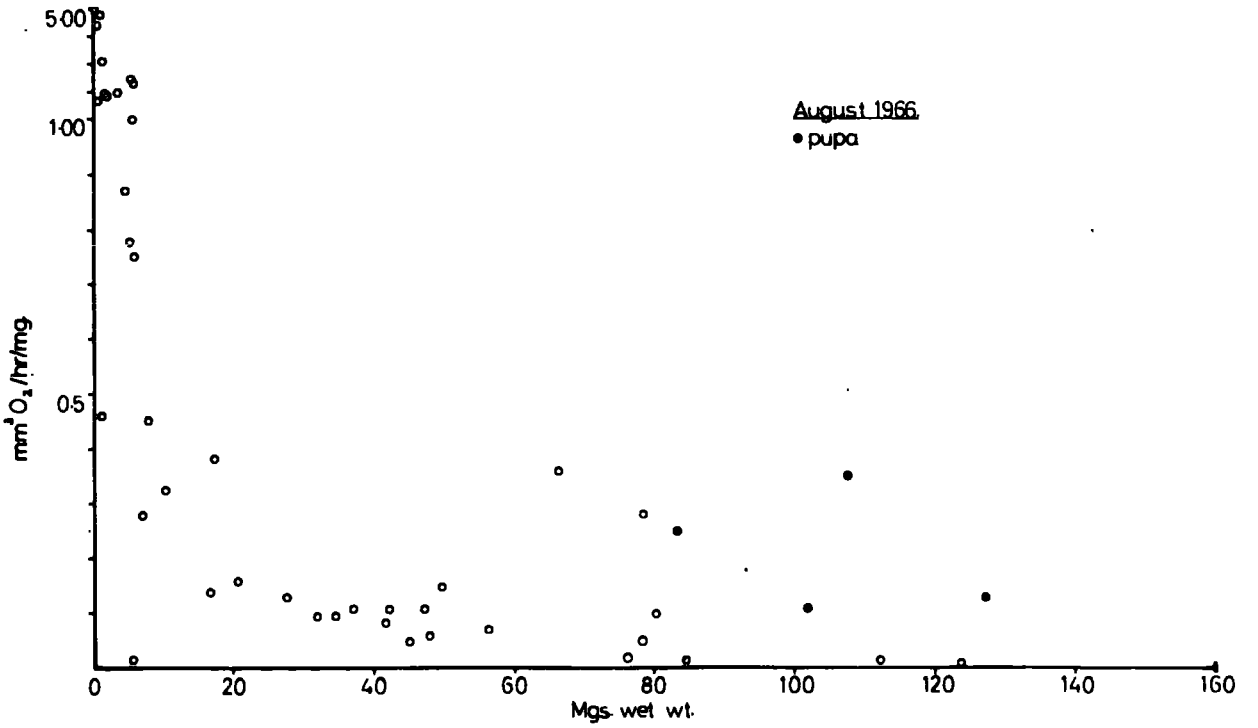
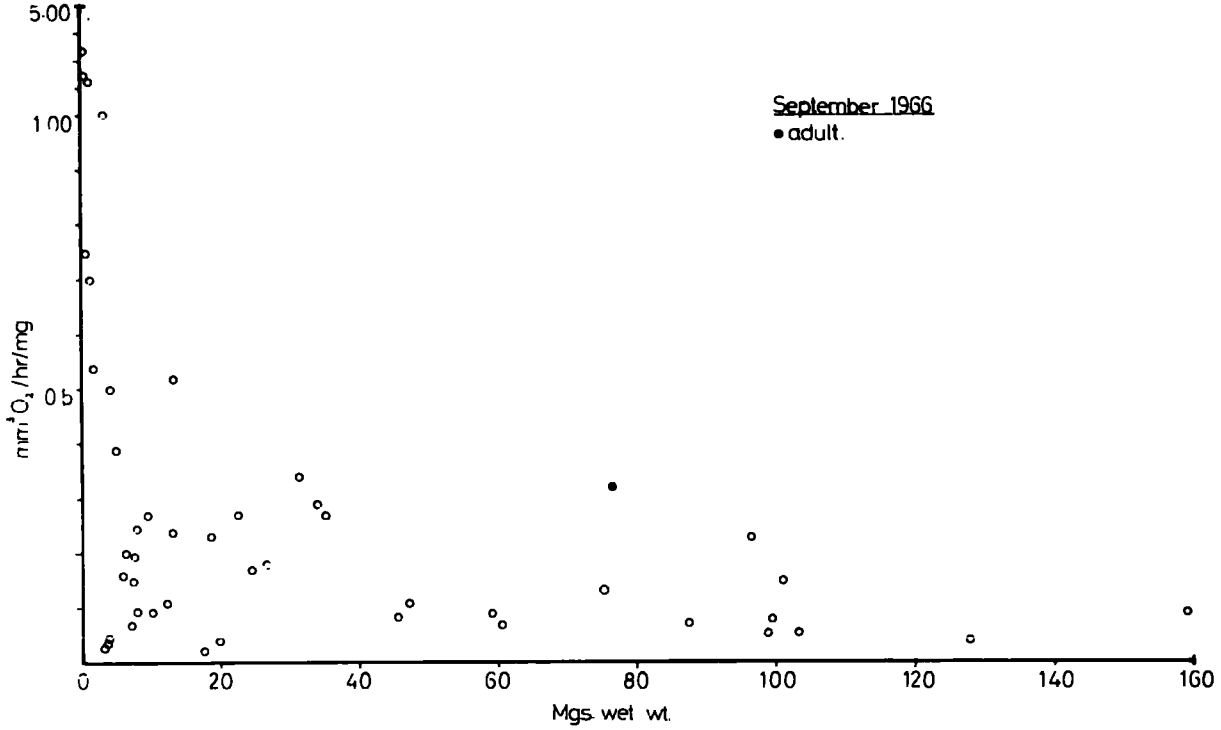

5·00
1·00
0·5
mm³O₂/hr/mg.
August 1966.
• pupa
0
20
40
60
80
100
120
140
160
Mgs. wet wt.

Fig.45. Respiratory data for September - October 1966.


5·00
1·00
0·5
mm³O₂/hr/mg
September 1966
• adult.
0
20
40
60
80
100
120
140
160
Mgs. wet wt.

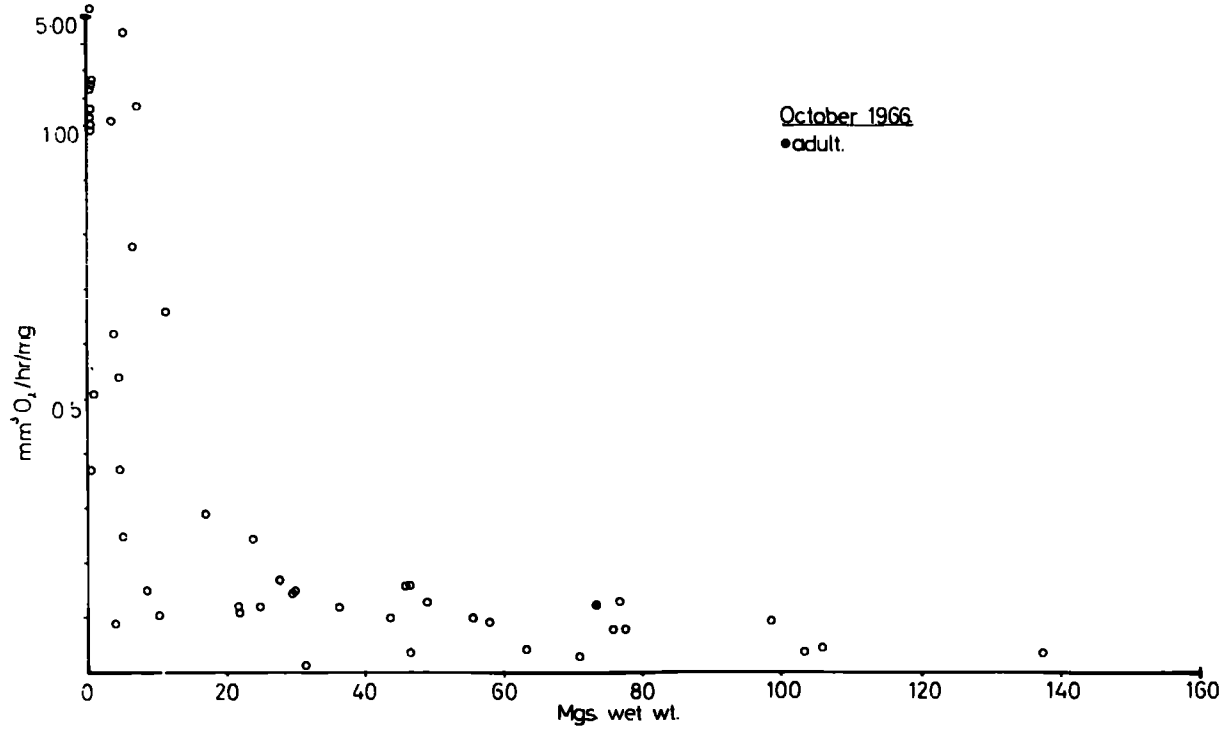
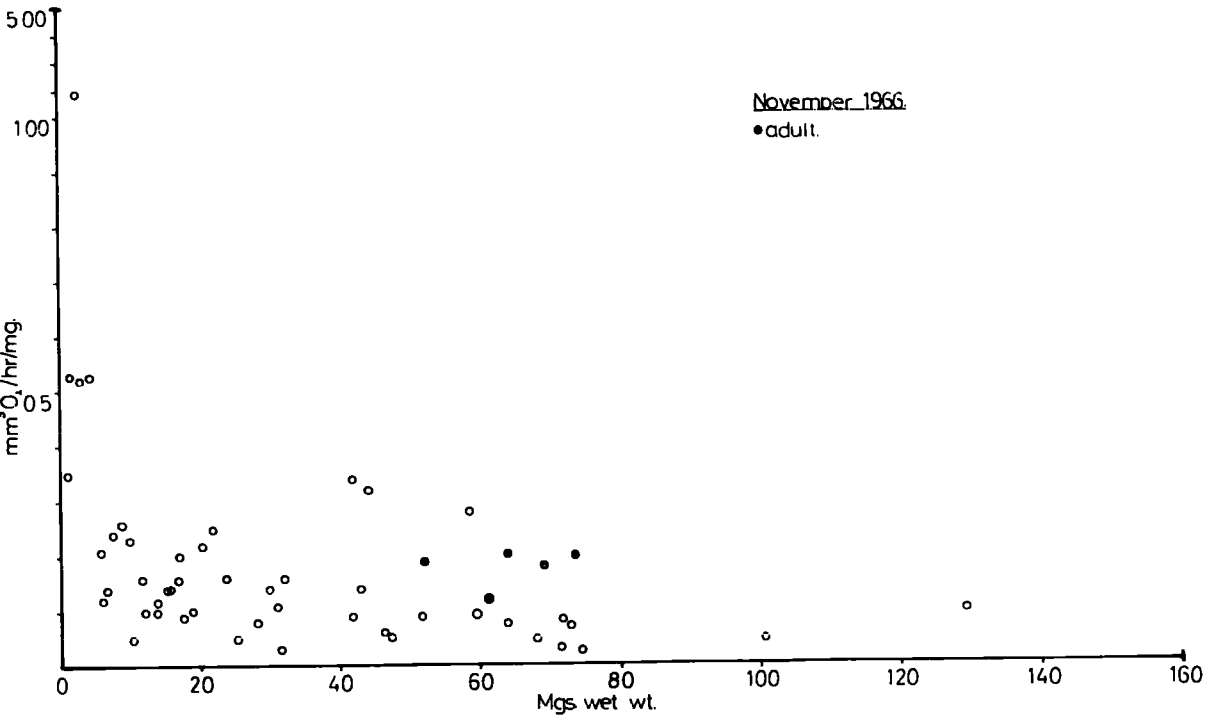

5·00
1·00
0·5
mm³O₂/hr/mg
October 1966
• adult.
0
20
40
60
80
100
120
140
160
Mgs. wet wt.

Fig.46. Respiratory data for November - December 1966.


5·00
1·00
0·5
mm³O₂/hr/mg.
November 1966.
• adult.
0
20
40
60
80
100
120
140
160
Mgs. wet wt.

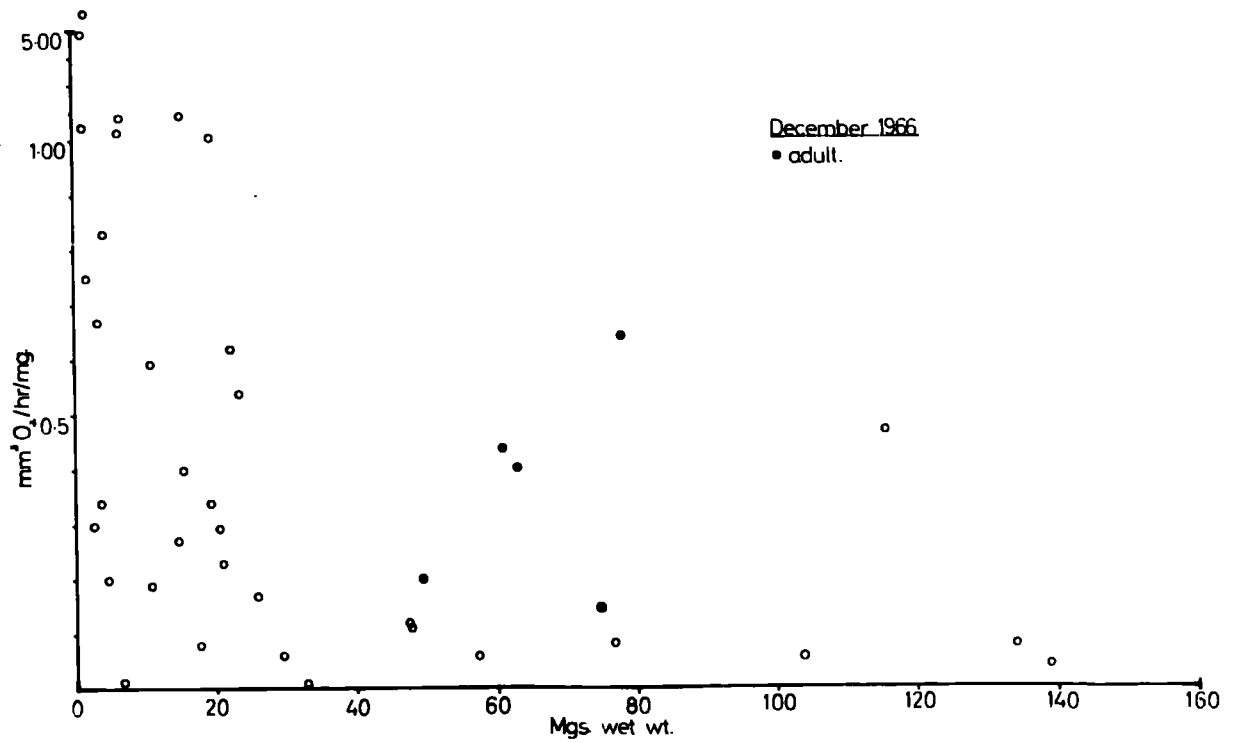
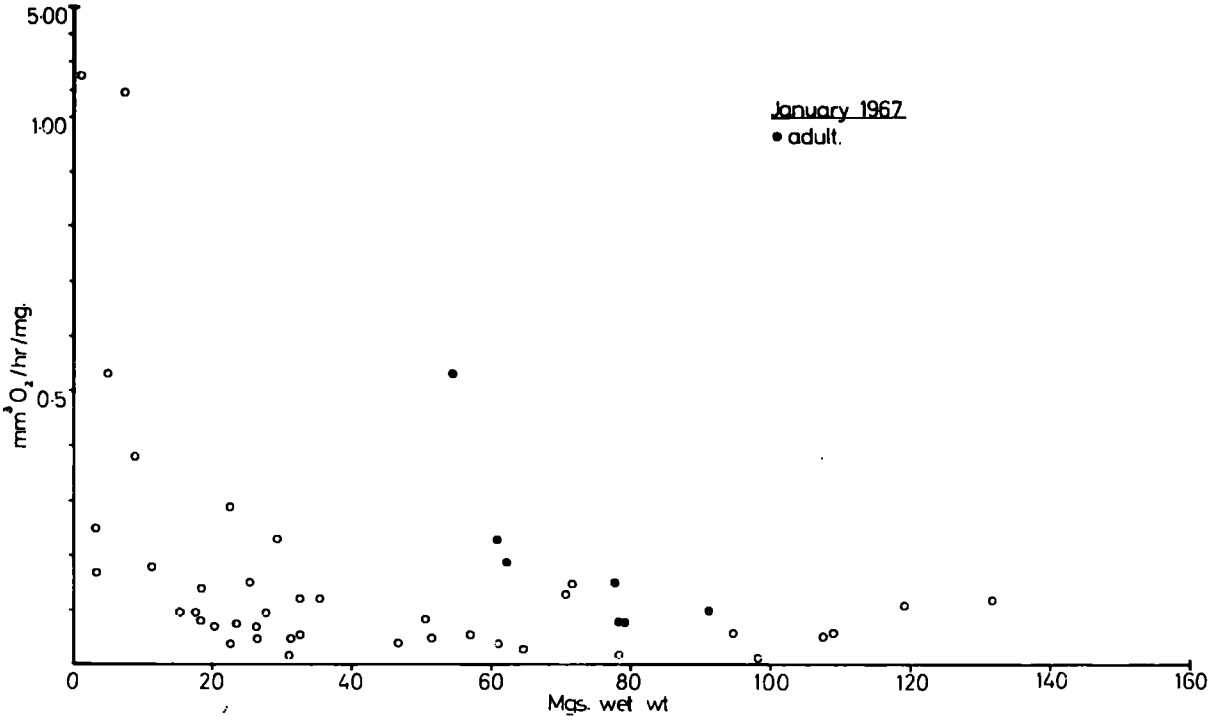

5·00
1·00
0·5
mm³O₂/hr/mg.
December 1966.
• adult.
0
20
40
60
80
100
120
140
160
Mgs. wet wt.

Fig.47. Respiratory data for January - February 1967.


5·00
1·00
0·5
mm³ O₂ /hr /mg.
January 1967
• adult.
0
20
40
60
80
100
120
140
160
Mgs. wet wt

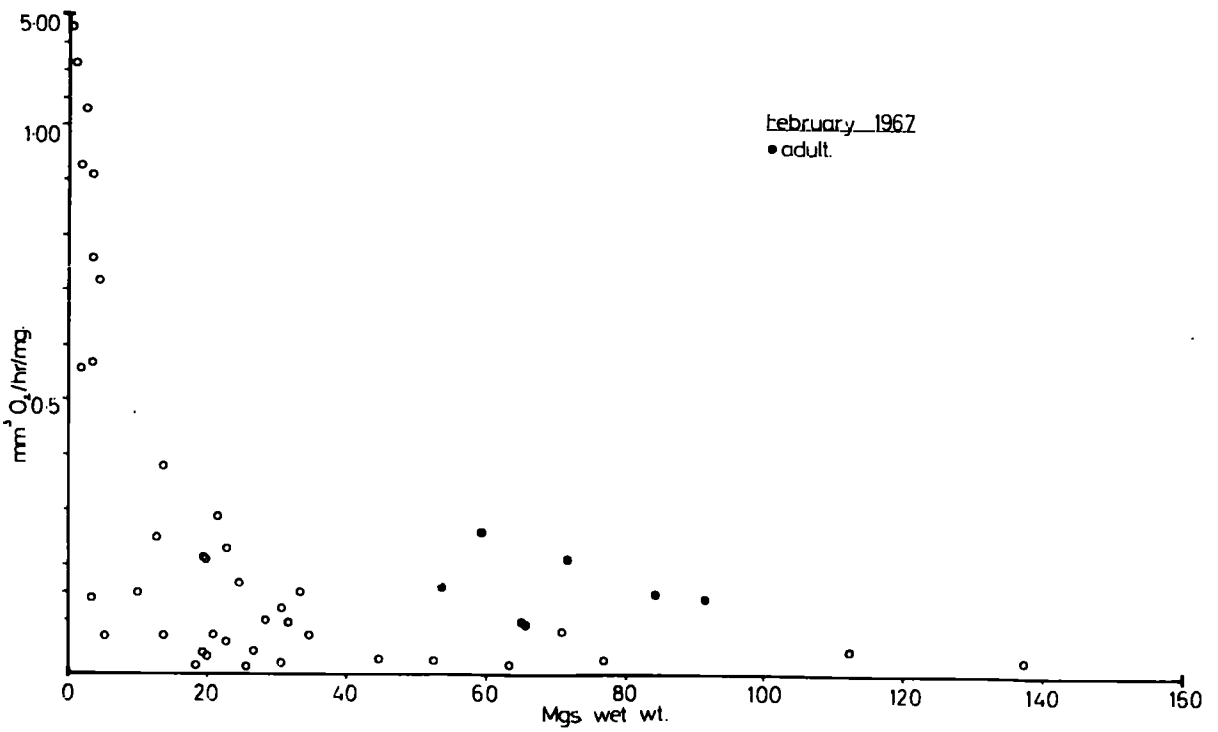
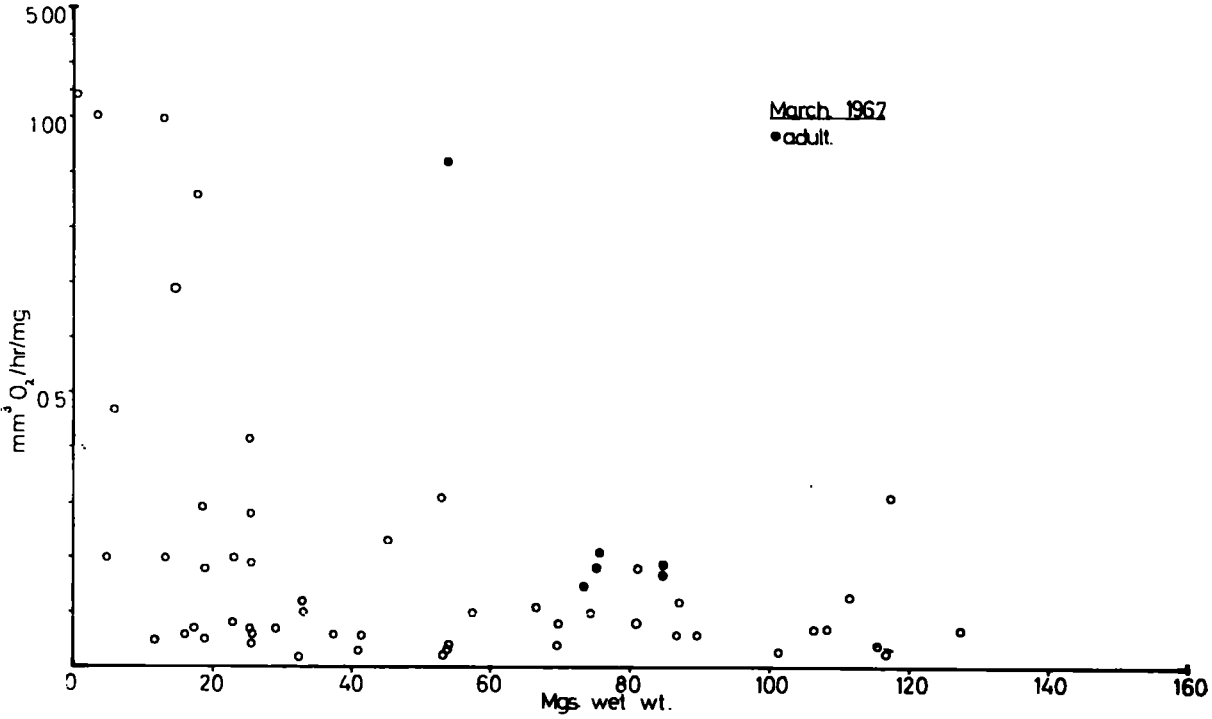

5·00
1·00
0·5
mm³ O₂/hr/mg.
February 1967
• adult.
0
20
40
60
80
100
120
140
150
Mgs. wet wt.

Fig.48. Respiratory data for March - April 1967.


5·00
1·00
0·5
mm³ O₂/hr/mg
March 1967
•adult.
0
20
40
60
80
100
120
140
160
Mgs wet wt.

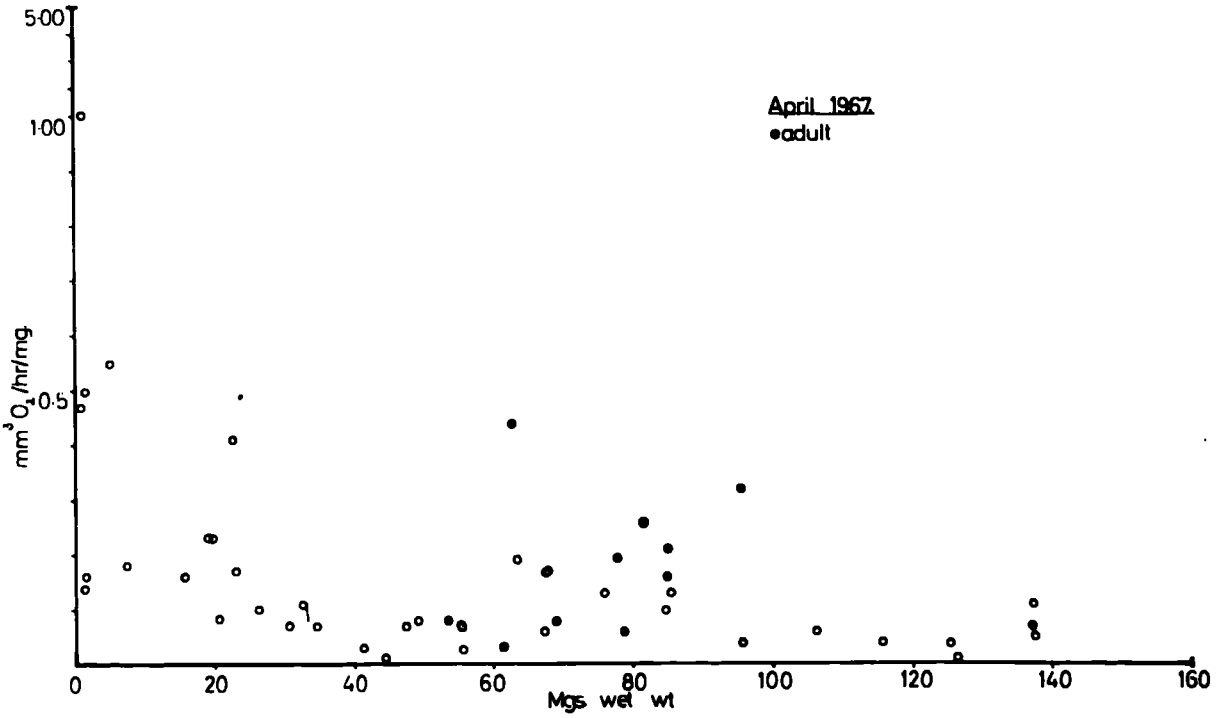
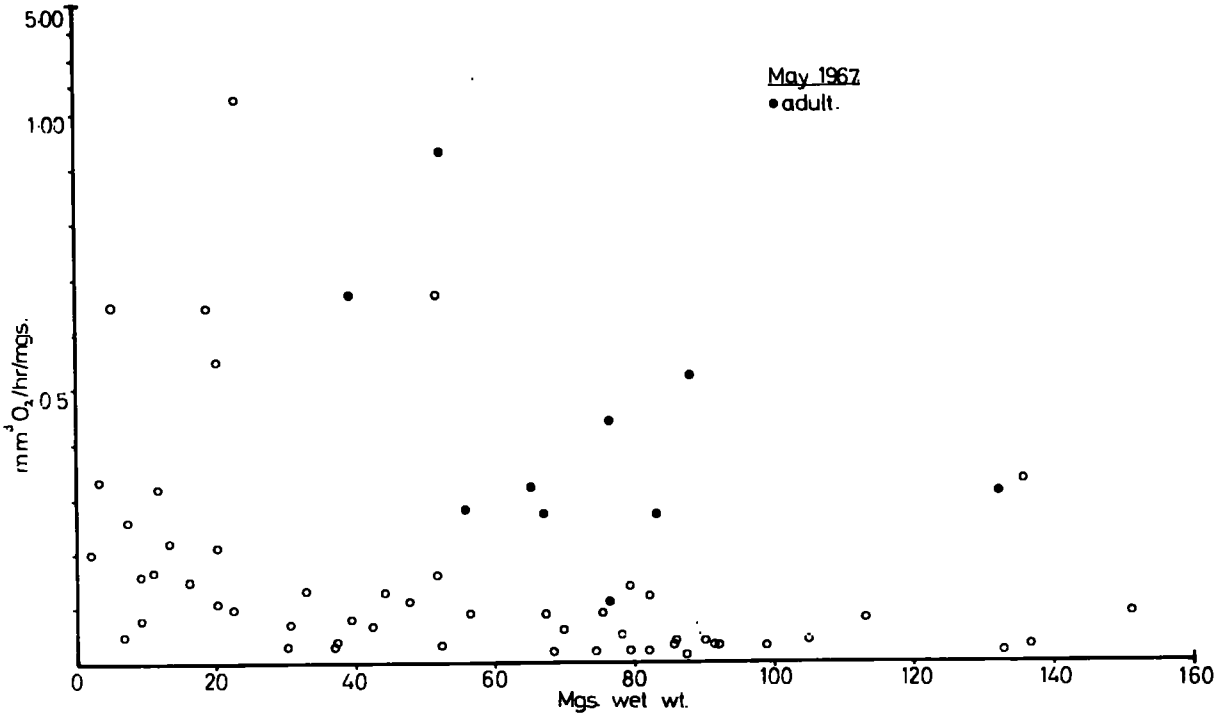
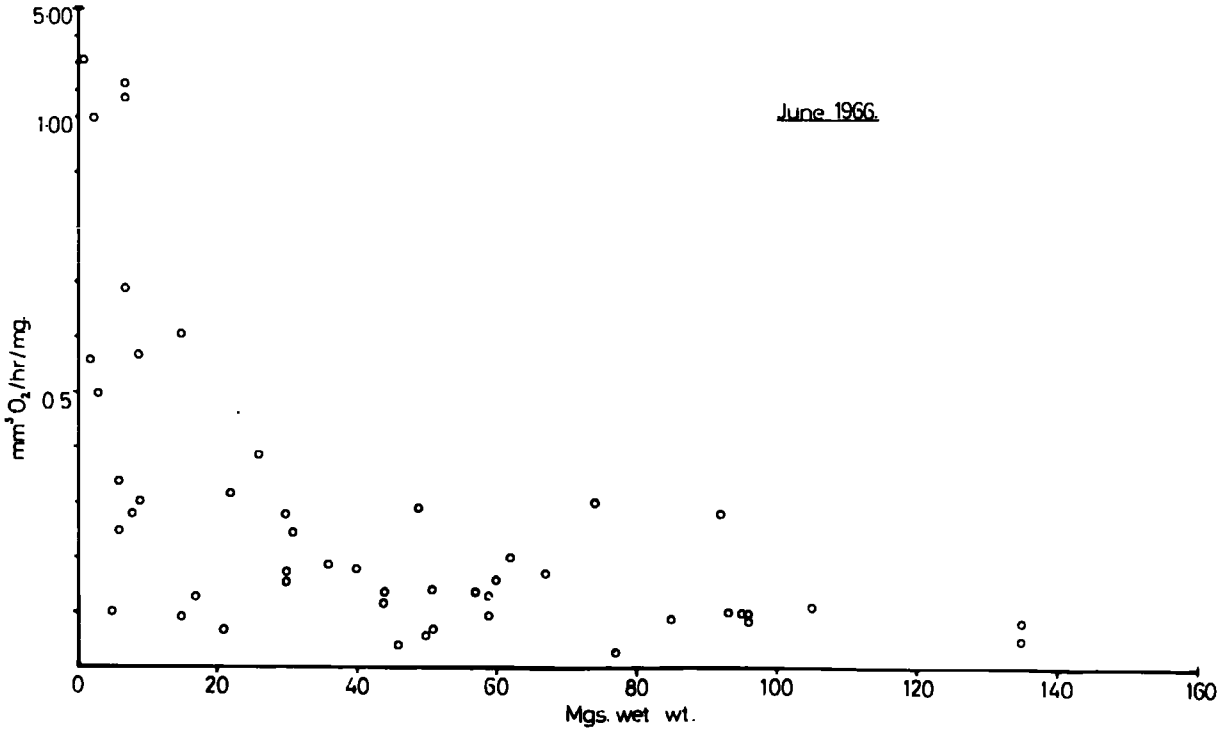

5·00
1·00
0·5
mm³ O₂/hr/mg
April 1967
•adult
0
20
40
60
80
100
120
140
160
Mgs wet wt

Fig.49. Respiratory data for May 1967 - June 1966.


5·00
1·00
0·5
mm³ O₂/hr/mgs.
May 1967
• adult.
0
20
40
60
80
100
120
140
160
Mgs. wet wt.


5·00
1·00
0·5
mm³ O₂/hr/mg.
June 1966.
0
20
40
60
80
100
120
140
160
Mgs. wet wt.

i) Larvae

Figs. 44-49 show the oxygen consumption per unit weight, per hour, expressed graphically for each month. Each monthly figure depicts an L-shaped curve. As might be expected, the smallest animals showed a very high respiratory rate (the highest recorded was 7.62 mm^3/mg/hour, for an individual in August 1966). As size increases, the respiratory rate/mg decreased. The inflexions of all the monthly curves are at approximately 15-20mgs. Live weight, above this weight range only a shallow decline, in the rate of oxygen uptake, is noticeable. Phillipson and Watson (1965) reported that in some months, notably May, June and July, certain individuals of O.asellus L. exhibited a far higher respiratory rate than is normal for their size. It was suggested that this was due to breeding phenomenon, most probably gonad development. Clearly similar increases were not found in M.rufipes larvae, nor would they be expected in the non-reproductive larval form.

Table XXIII and Fig.50 show the mean respiratory rate of larvae per month over a 12 month period. Seasonal effects are obvious, showing a low winter-spring respiratory rate and a higher summer-autumn rate. The August-October peak is probably due to a number of factors, the main ones being, the additional metabolism of new, young animals, temperature, and general increased activity due to moulting, which is at its peak at this time.

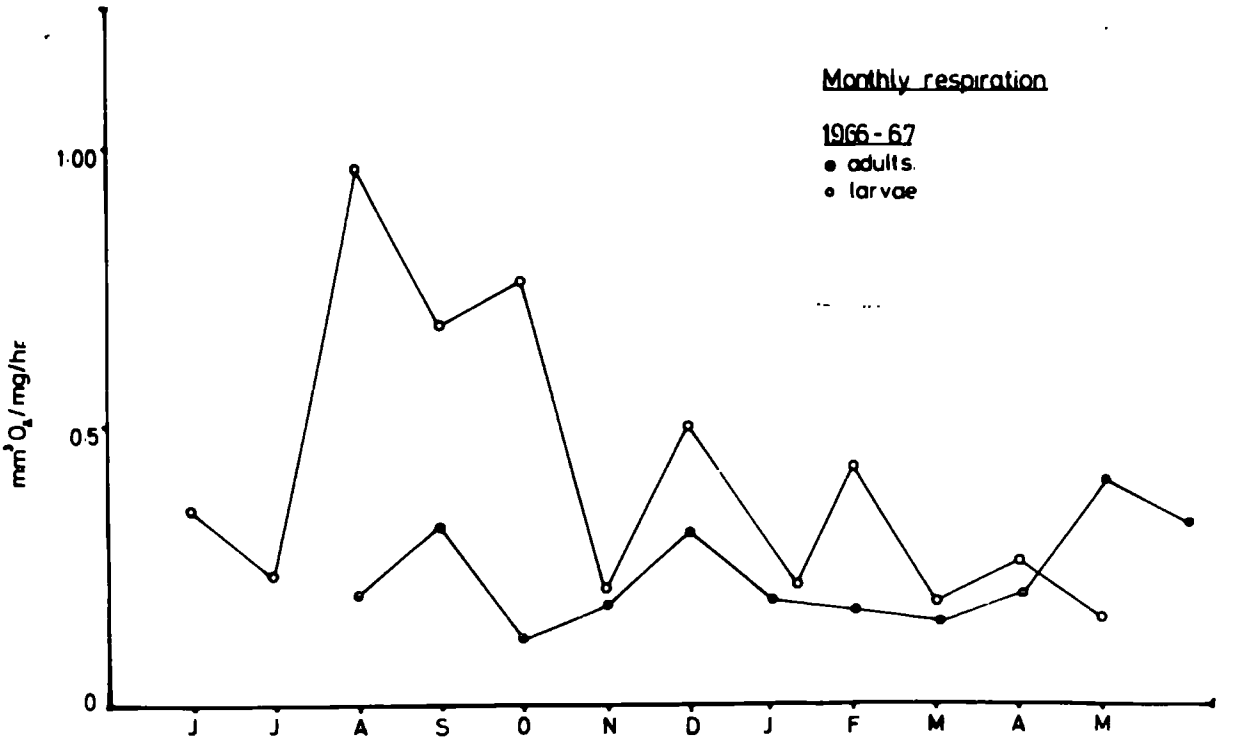
Table XXIII. Mean Monthly Respiratory Data

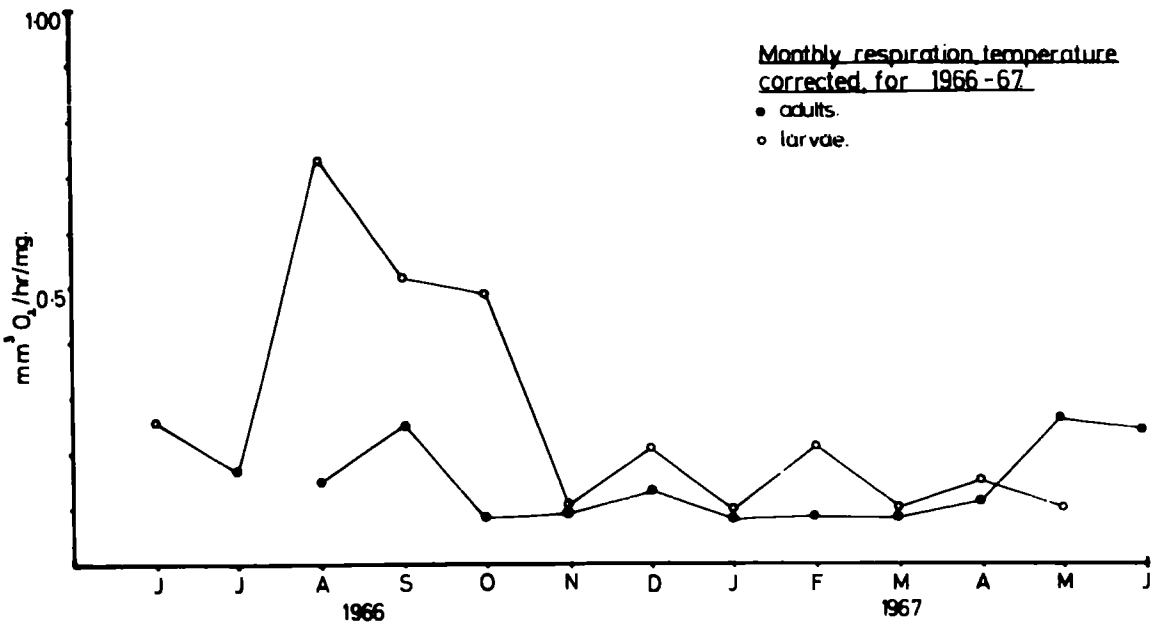
	LARVAE Mean O_2	Temp. Corrected	ADULTS Mean O_2	Temp. Corrected
June (1966)	0.35 ± 0.078	0.26	-	-
July	0.23 ± 0.044	0.17	-	-
August	0.96 ± 0.220	0.73	0.20 ± 0.076	0.15
September	0.68 ± 0.220	0.52	0.32	0.25
October	0.76 ± 0.180	0.49	0.12	0.08
November	0.21 ± 0.044	0.11	0.18 ± 0.010	0.09
December	0.50 ± 0.160	0.21	0.31 ± 0.090	0.13
January (1967)	0.22 ± 0.070	0.10	0.19 ± 0.060	0.08
February	0.43 ± 0.134	0.21	0.17 ± 0.071	0.08
March	0.19 ± 0.043	0.10	0.25 ± 0.054	0.08
April	0.26 ± 0.105	0.15	0.20 ± 0.042	0.10
May	0.16 ± 0.014	0.10	0.40 ± 0.070	0.10
June	-	-	0.32 ± 0.024	0.23

All quantities expressed as $O_2 mm^3/mg/hr$.

Fig.50. Mean monthly respiratory data (1966-67) for larvae and adults of M.rufipes.

Fig.51. Mean monthly respiratory data (1966-67), corrected for temperature, for larvae and adults of M.rufipes.


Monthly respiration
1966 - 67
● adults.
o larvae
1·00
0·5
0
mm³ O₂ / mg/hr
J J A S O N D J F M A M


Monthly respiration temperature corrected, for 1966 - 67
● adults.
o larvae.
1·00
0·5
mm³ O₂ /hr/mg.
J J A S O N D J F M A M J
1966
1967

ii) Adults

Pupae and adults were studied using the same procedure and apparatus as the larvae. The results are depicted in Figs. 44-49 for individual animals. In general the respiratory rates of both pupae and adults were higher than larvae of similar weights, probably due to the developmental processes affecting these stages.

Table XXIII and Fig.50 show the effect of season on pupal and adult respiration. The pattern of respiratory activity can be related to the developmental history of these life stages. During the formative pupal period the oxygen consumption is high as organs are broken down and re-developed. However, as soon as the adult is formed, this rate drops by almost half, and remains at this level throughout the winter period. At the onset of emergence, in spring, the oxygen consumption again rises, probably initiated by the increased temperatures. This high rate continues as long as the animal lives, and is probably associated with gonad development. No difference in the rates of oxygen uptake could be detected between males and females.

iii) Temperature effects

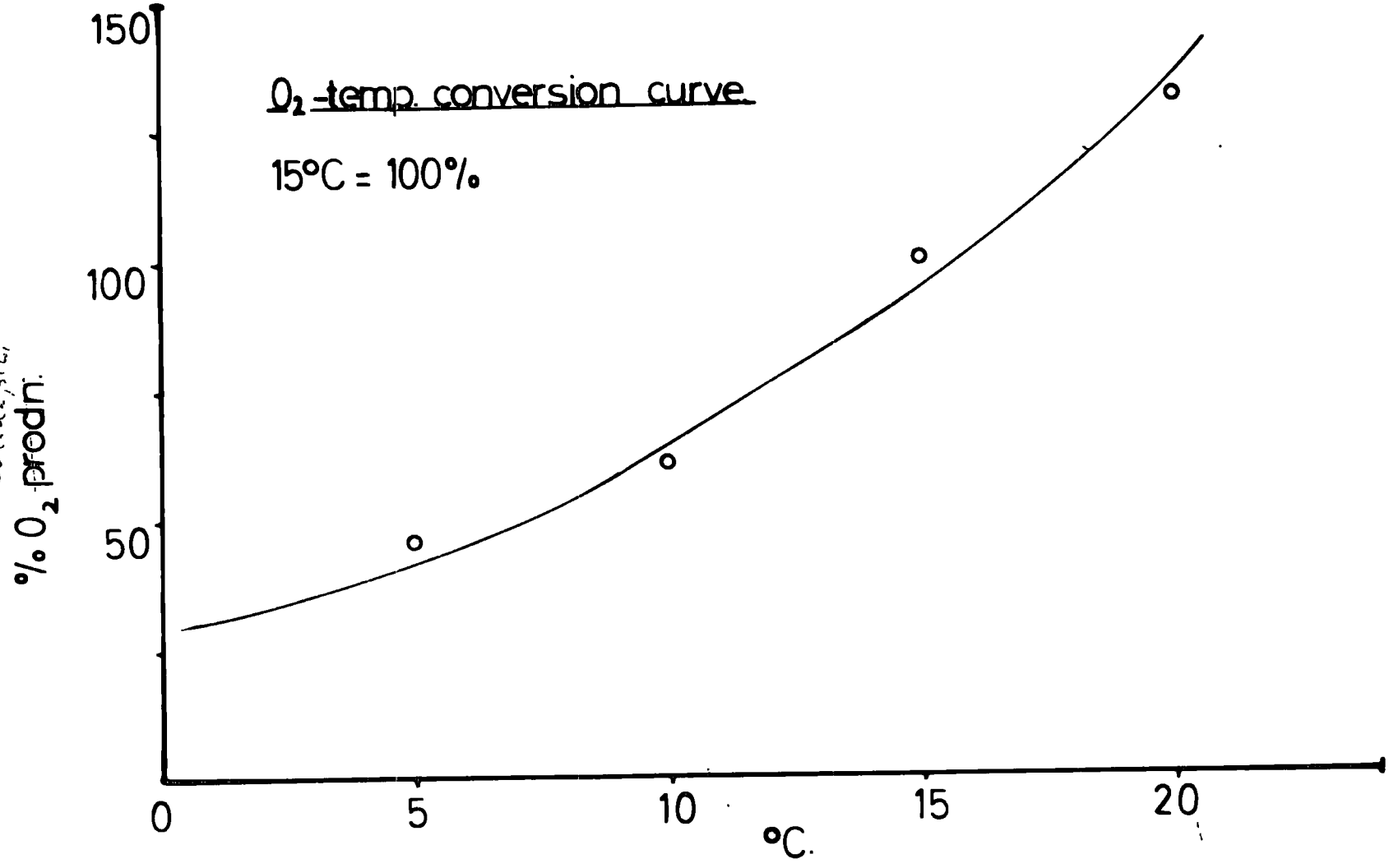
As all the above respiratory measurements were made at the constant temperature of 15^{o}C, it was considered necessary to derive a temperature compensation factor in order to convert the laboratory rates to field rates by using the field temperature data, previously described. The compensation factor was derived

Table XXIV. O_2 uptake - temperature conversion data

100% = O_2 uptake at 15°C. 29 samples at each temperature.

Temp.	5°C.	10°C.	15°C.	20°C.
O_2 uptake $mm^3/mg/hr.$	0.06	0.08	0.13	0.20
Percentage	46%	61%	100%	131%

Fig.52. Relationship between oxygen uptake and temperature.


O_2 -temp. conversion curve
15°C = 100%
150
100
50
% O_2 prodn.
0
5
10
15
20
°C.

from animals subjected to Warburg respirometry at 5^{o}, 10^{o}, 15^{o} and $20^{o}C$. During any one experiment the same animal was exposed to all four temperatures, in ascending order. The period of exposure at each temperature was 1.1/4 hours during which the oxygen uptake was noted. After an exposure at a single temperature, the Warburg water bath was heated to the next temperature and the experimental animal allowed 30 minutes to settle down before readings were commenced at that temperature.

Table XXIV shows the mean oxygen uptake expressed as $mm^3/mg/hour$, at each of the four experimental temperatures. Fig.52 shows the same data expressed as a percentage, in which the oxygen consumption at $15^{o}C$ ($0.13mm^3/mg/hr$) is 100%. Thus for any given field temperature a conversion percentage is available to apply to the laboratory data. This is similar to the procedure adopted by O'Connor (1963 : 1964), for enchytraeid worms.

Compensation factors, using the known field temperatures, were applied to the seasonal respiratory data of both larvae and adults; Table XXIII and Fig.51 show that irregularities were reduced and major peaks extended. The seasonal peaks are still very evident and it is probable that they indicate a higher respiratory metabolism due to increased activity with increased field temperatures. This would also include moulting activity which is at a maximum at this time of the year.

Table XXV. Daily respiratory metabolism of M.rufipes. No.1.

INSTAR	$O_2 mm^3/mg/hr.$ Actual	Theoretical	$O_2 mm^3/mg/day$ Theoretical
1	-	5.94	142.50
2	-	4.25	102.00
3	3.30	3.02	72.48
4	1.92	2.19	52.56
5	1.83	1.58	37.92
6	0.99	1.12	26.88
7	0.72	0.70	16.80
8	0.60	0.58	13.92
9	0.54	0.42	10.08
10	0.21	0.29	6.96
11	0.23	0.21	5.04
12	0.14	0.15	3.60
13	0.11	0.11	2.64
14	0.09	0.08	1.92
15	0.07	0.06	1.44

Theoretical values taken from the regression line of the 'actual' figures.

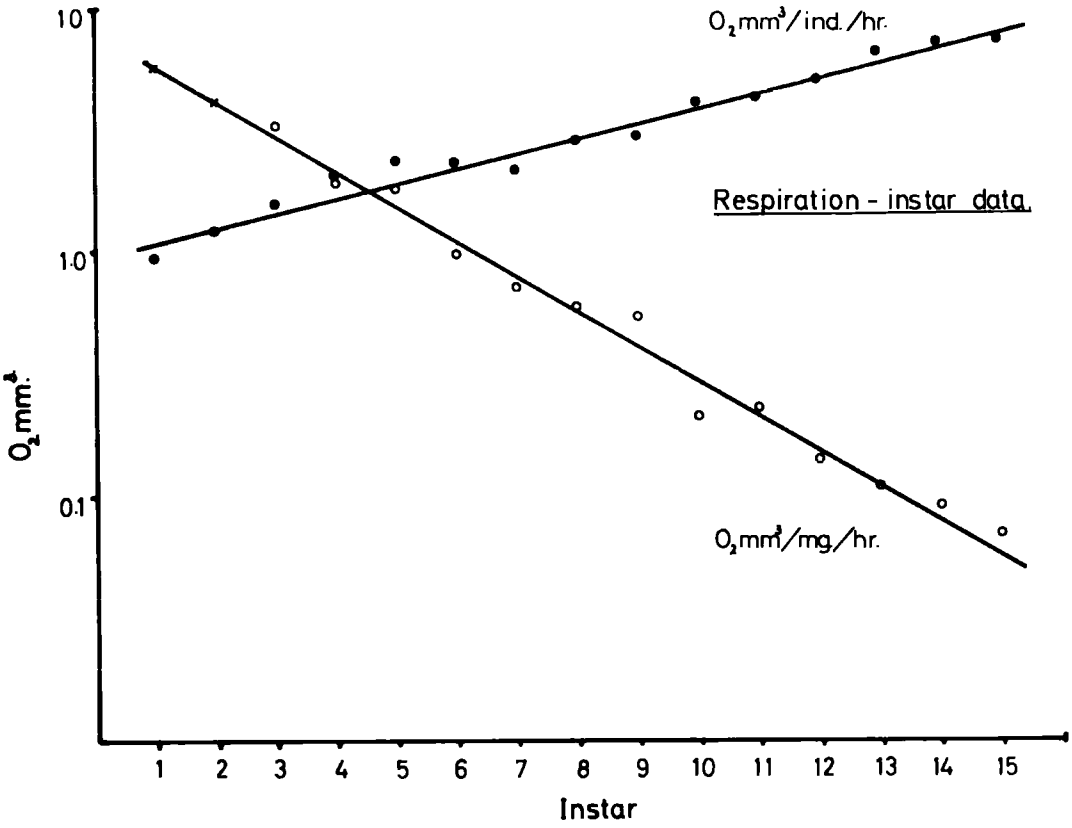
Table XXVI. Daily respiratory metabolism of M.rufipes. No.2.

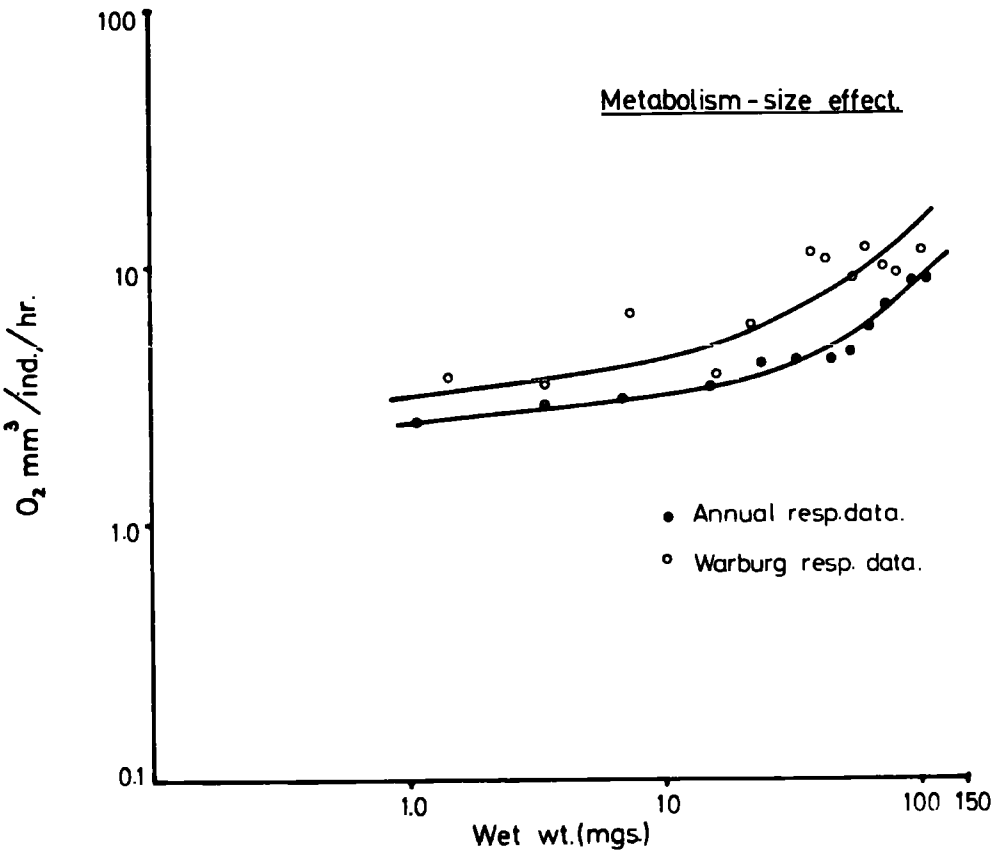
INSTAR	Mean wt/instar (mgs)	$O_2 mm^3$/ind./hr.	$O_2 mm^3$/ind./day
1	0.16	0.95	22.80
2	0.29	1.23	29.52
3	0.53	1.60	38.40
4	0.95	2.08	49.92
5	1.50	2.37	56.88
6	2.10	2.35	56.40
7	3.10	2.17	52.08
8	4.90	2.84	68.16
9	7.10	2.98	71.52
10	14.00	4.06	97.44
11	20.50	4.31	103.44
12	34.30	5.17	124.08
13	59.20	6.51	156.24
14	88.50	7.08	169.92
15	119.80	7.19	172.56

All calculations based on values from regression line.

Fig.53. Respiratory metabolism per instar.

Fig.54. Relationship between metabolism and size.


$O_2 mm^3$/ind./hr.
Respiration - instar data.
$O_2 mm^3$/mg./hr.
$O_2 mm^3$.
10
1.0
0.1
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15
Instar


Metabolism - size effect.
O_2 mm^3/ind./hr.
100
10
1.0
0.1
• Annual resp.data.
° Warburg resp. data.
1.0
10
100 150
Wet wt.(mgs.)

iv) Daily respiratory metabolism

As the instar composition of M.rufipes was known the respiratory rate/unit weight/instar/hour (day) was calculated. The results are expressed in Table XXV and Fig.53. which show a clear linear relationship. As data was not available for Instars 1 and 2 the oxygen consumption was estimated by extrapolation. Further calculations were based on this regression ($r = -0.92$).

In order to standardize the measurements of oxygen uptake with the other bioenergetic parameters measured, certain conversions were necessary. The above rates/unit weight/instar/hour (day) were converted to rate/instar/hour (day) by multiplying the former by the known mean weight/instar. Table XXVI and Fig.53 show the converted data. This gives an estimate of the oxygen consumption of a 'mean' individual for each instar per unit time. The data again has a linear relationship.

The data can be converted to a calorific basis by the use of an oxy-calor equivalent. The equivalent used was 4.7cals/mlO_2 as used by Phillipson (1963), O'Connor (1963 : 1964), Phillipson and Watson (1965). This particular value assumes that fat is being metabolized.

As the instar composition of M.rufipes was known it was possible to calculate the respiratory data as rate/instar/unit time rather than rate/unit weight per se. This technique was used in preference to the 'best estimate' technique of Phillipson (1962 : 1963), Phillipson and Watson (1965) as instar determination was possible. Phillipson (1967) has pointed out that 'the best

Table XXVII. Metabolism - size data

Size group (mgs)	Annual resp. data Mean wt.	$O_2 mm^3$/ind/hr	Warburg data Mean wt.	$O_2 mm^3$/ind/hr
0-2	1.1(41)	2.50	1.49(2)	3.68
3-5	3.5(37)	2.90	3.50(6)	3.50
6-10	7.0(43)	3.04	7.46(6)	6.74
11-20	15.3(64)	3.40	16.18(2)	3.80
21-30	24.3(57)	4.15	22.83(3)	5.83
31-40	33.2(46)	4.30	38.22(2)	11.42
41-50	45.4(43)	4.24	43.35(3)	10.50
51-60	54.9(33)	4.60	56.14(5)	8.85
61-70	65.1(28)	5.75	62.78(5)	11.75
71-80	74.7(31)	6.87	74.83(4)	10.87
81-100	90.5(33)	8.41	84.22(3)	9.50
100+	110.5(39)	8.77	127.27(2)	11.25

Figures in parentheses indicate the number of samples used in determining the mean figure.

estimate' is a possible means of calculating respiratory losses from population data, when the age structure is not available.

b) Metabolism versus size

According to Bertalanffy (1957), the rate of metabolism in insects is dependent on weight and not on surface area. Hemmingsen (1950 : 1960), Zeuthen (1953) and Bertalanffy (1957) agree that the ratios of metabolism : size are in the order of 1 : 0.75 - 1.00, thus if the data are drawn as a double log plot, a regression line approximating 45^{o} should be obtained. Respiratory data with regard to bioenergetic studies have been treated in this way by Smalley (1960), Engelmann (1961) and Wiegert (1964 : 1965), therefore it seems reasonable to discuss this aspect in relation to M.rufipes larvae.

The data obtained for M.rufipes by electrolytic respirometry was grouped into size categories and expressed in Table XXVII. Fig.54 shows the same data drawn as a double log plot.

Clearly the expected straight line is not apparent but instead an upward sloping curve was obtained. Only above a body weight of 40mgs does metabolism : size approach 1:0.75 - 1, with a value of 1:0.80. It was thought that the electrolytic respirometer may contain some error, therefore in order to test this hypothesis a further range of estimations of metabolism were made in a Warburg apparatus.

The results of the Warburg experiments are shown in Table XXVII. Fig.54 shows the data drawn on a double log plot.

The points obtained are more variable than those obtained by electrolytic respirometry. However, the shape of the curve is similar indicating that the electrolytic respirometer is not in error. Variability of the Warburg data was attributable to two things :- 1) fewer animals being used in the Warburg determinations than in the electrolytic determinations; 2) by measuring the oxygen uptake of animals left only 30mins to settle down, therefore measuring more active animals. It is reasonable to suppose that such animals had a higher metabolic rate, a fact supported by the Warburg data trend line being higher than that produced from the electrolytic data.

A non-linear relationship was found by Wiegert (1964) for the metabolism : size ratio of the meadow spittle bug. The curve he obtained had a downward slope. He found that the metabolism : size relationship of the 1st and 2nd instars was in the expected order of 1:1.0, but that change occurred with increasing size, so that the relationship of late instars and adults was 1: 0.2. His explanation is that the change is caused by an increasing proportion of non-metabolic chitin in the bodies of older nymphs and adults. This explanation was found not to hold in the present study, but it is not possible to propose any definite explanation for the shape of the curve. The phenomenon may be connected with the high assimilation rate, possibly the early instars are more efficient in producing somatic tissue. Certainly it would appear from Fig.54 that they are able to gain rapidly in weight without excessive increase in

respiratory metabolism/individual. It is obvious, especially from a bioenergetic viewpoint, that a linear metabolism : size relationship should not be automatically assumed, for, as shown, this would lead to an underestimate in the respiratory metabolism in the case of the early instars of M.rufipes.

c) Acclimatization data

In order to test the effects of bringing animals from the field at various temperatures and subjecting them to constant temperature respirometry, a minor acclimatization investigation was carried out.

Method

Animals were kept at $5^{o}C$ for a period of 3 weeks in order to 'acclimatize' at that temperature. After this time the animals were transferred to a temperature of $16.5^{o}C \pm 0.1^{o}C$ and Warburg investigations made daily for three days at this temperature. A final Warburg investigation was made after 6 days, at $16.5^{o}C$.

Results

Table XXVIII and Fig.56 show that no significant differences were found between the mean respiratory rates during the six day period at $16.5^{o}C$. From this it must be concluded that respiratory compensation, as a function of acclimatization, does not occur within the experimental period of 6 days. This further supports the use of the temperature conversion factor described earlier in this section.

Table XVIII Acclimatization data

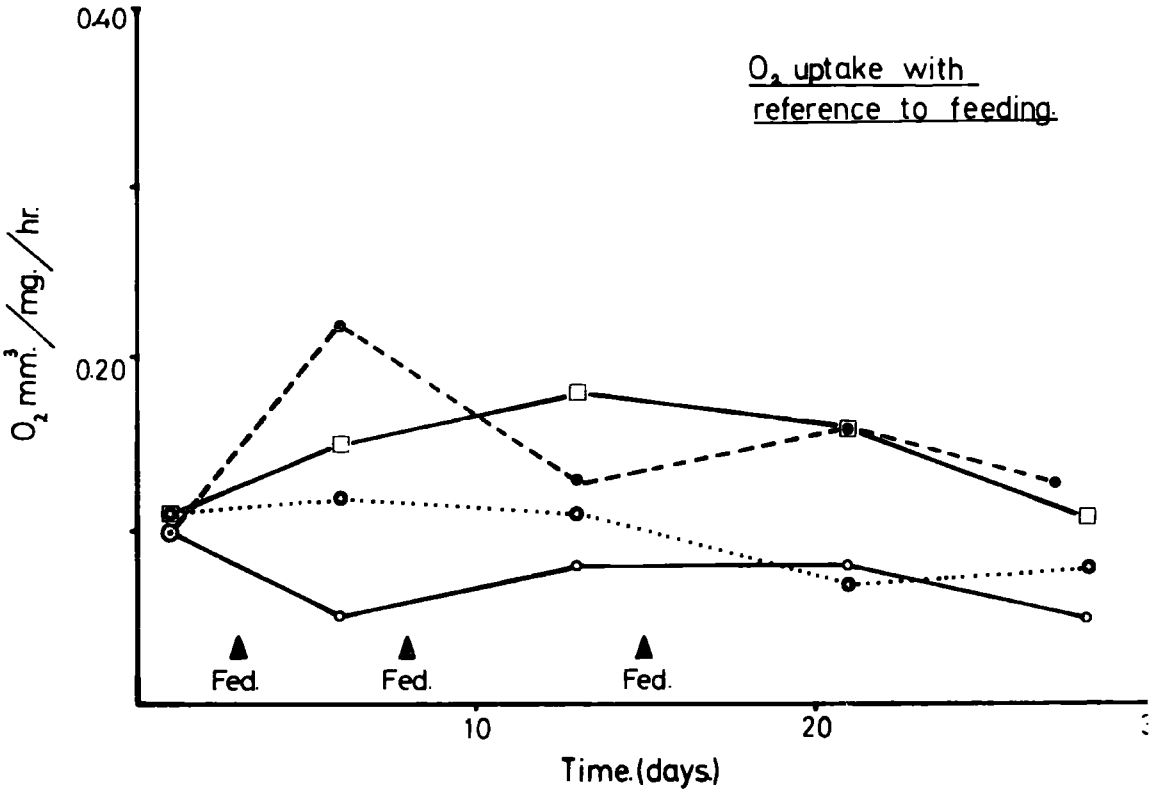
All animals were acclimatized at 5°C for a period of 3 weeks before being tested in a Warburg apparatus at 10.5°C.

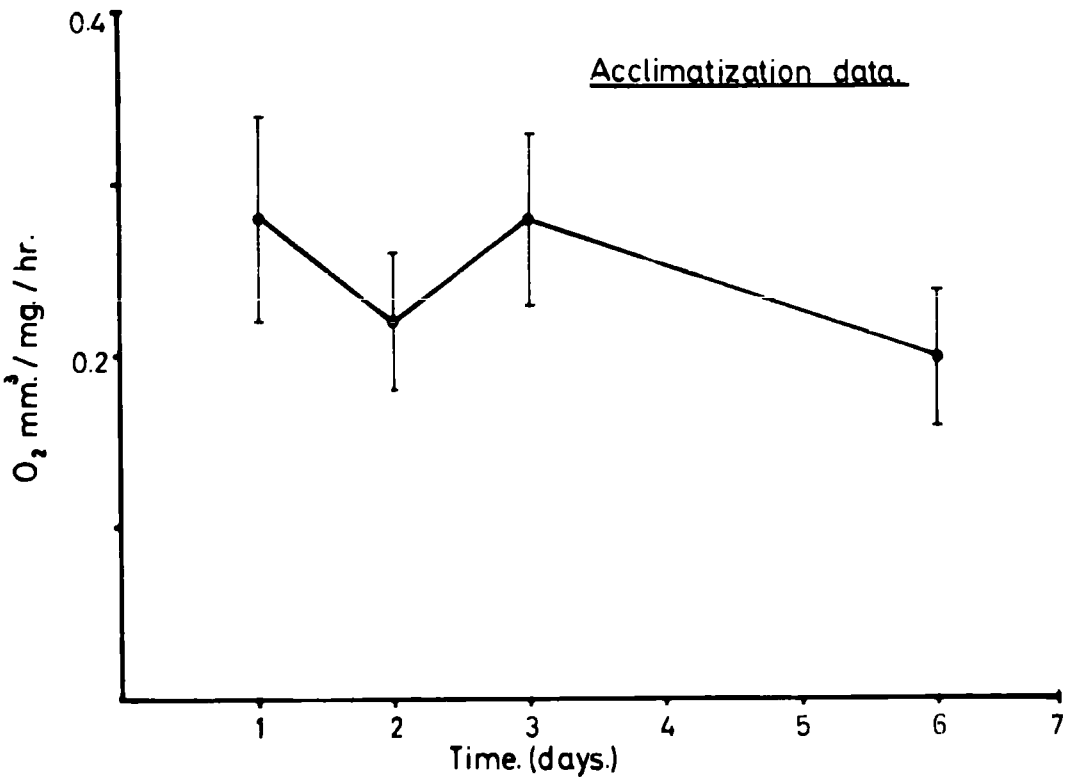
FLASK	Expt.1. 11/10/67	Expt.2. 12/10/67	Expt.3. 13/10/67	Expt.4. 16/10/67
3	0.28	0.22	0.26	0.21
4	0.33	0.21	0.25	0.20
6	0.34	0.30	0.37	0.28
7	0.31	0.23	0.27	0.22
8	0.22	0.19	0.29	0.13
10	0.14	0.17	0.24	0.17
Mean Totals	± 0.28 0.001	± 0.22 0.045	± 0.28 0.055	± 0.20 0.040

All O_2 consumption expressed as $O_2 mm^3/mg/hr$.

Fig.55. Rate of metabolism with regard to feeding.

Fig.56. Acclimatization data.


0.40
0.20
O_2 mm.^{3}/mg./hr.
O_2 uptake with reference to feeding.
Fed.
Fed.
Fed.
10
20
Time.(days.)


0.4
0.2
O_2 mm.^{3} / mg. / hr.
Acclimatization data.
1
2
3
4
5
6
7
Time. (days.)

That no respiratory compensation could be detected in this study of M.rufipes does not mean that acclimatization does not take place. Edwards, D.K. (1958) found that acclimatization was only detectable in Tenebrio sp. as an increased survival at -3°C. A similar mechanism may exist in M.rufipes

d) Additional respiratory data

As previously explained, Warburg apparatus and techniques were employed to check the electrolytic respirometer. Additional information accrued from its use which is of general physiological interest, and it is presented here. Warburg experiments were continued in order to determine the spiracular activity with regard to CO_2 release, and the effect of feeding on the respiratory rate.

Animals for the additional Warburg experiments were used either directly from the field or from culture stocks. For oxygen determinations the CO_2 was absorbed from the flasks by the addition of 10% KOH to the centre well. This also maintained a high humidity.

i) Spiracular mechanism

During previous Warburg investigations it was noted that carbon dioxide was released in abrupt bursts and the question arose as to whether this discontinuity affected the measurements of oxygen and carbon dioxide production.

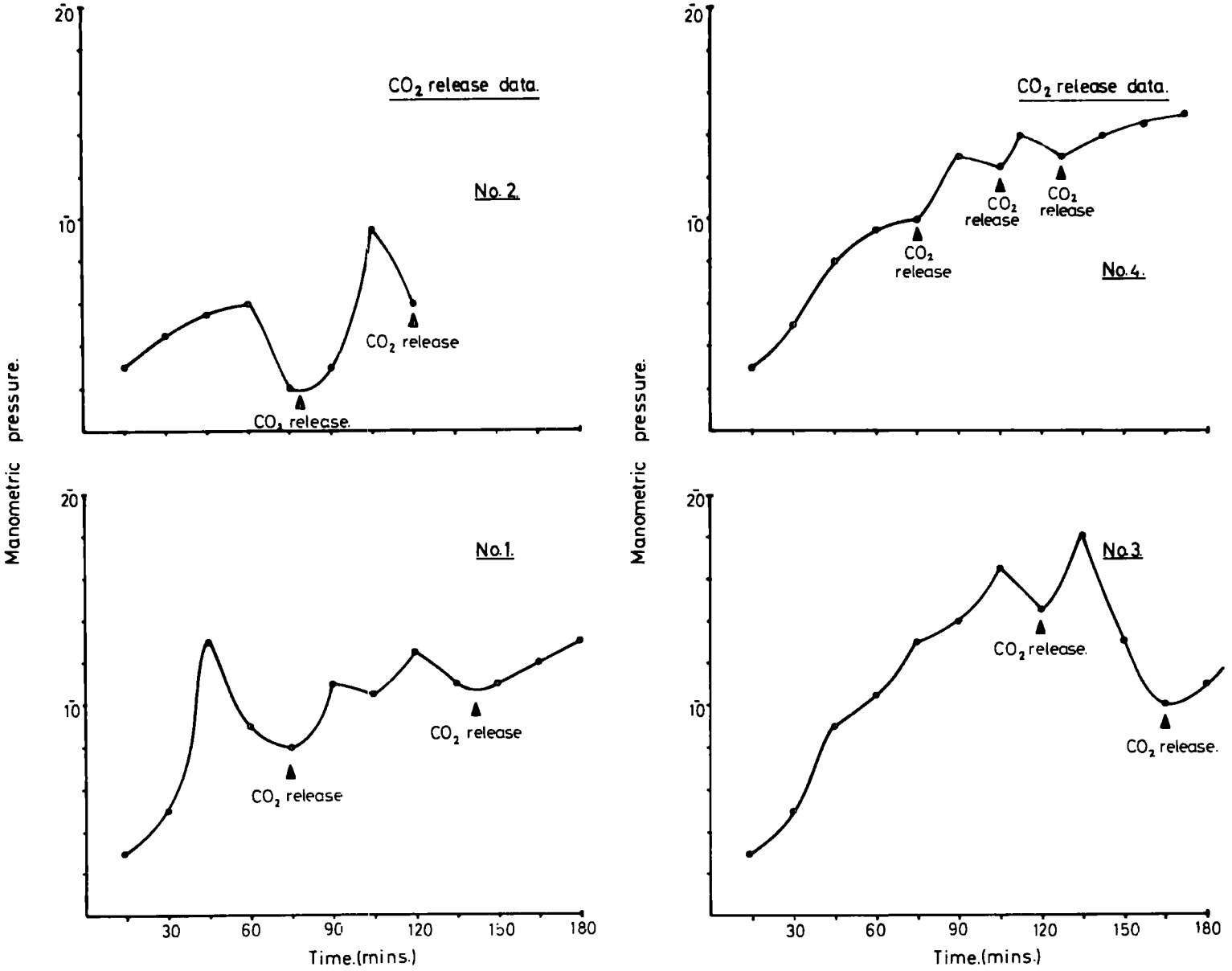
In order to study this further animals were run in the Warburg apparatus/and the results noted. without 10% KOH

Table XXIX. Carbon Dioxide Release Data

Time	No.1.	No.2.	No.3.	No.4.
	-	-	-	-
15	3	3	3	3
	-	-	-	-
30	5	4.5	5	5
	-	-	-	-
45	13	5.3	9	8
	-	-	-	-
60	9	6	10.5	9.5
	-	-	-	-
75	8	2	13	10
	-	-	-	-
90	11	3	14	13
	-	-	-	-
105	10.5	9.5	16.5	12.5
	-	-	-	-
120	12.5	6	14.5	14
	-		-	-
135	11	-	18	13
	-		-	-
150	11	-	13	14
	-		-	-
165	12	-	10	14.5
	-		-	-
180	12.5	-	11	15

All CO_2 readings expressed as the cumulative decrease of monometric pressure in the Warburg apparatus.

Fig.57. Data concerning the release of carbon dioxide.


CO_2 release data.
No. 2.
CO_2 release.
CO_2 release
CO_2 release data.
No. 4.
CO_2 release
CO_2 release
CO_2 release
No. 1.
CO_2 release
CO_2 release
No. 3.
CO_2 release.
CO_2 release.
Manometric pressure.
Manometric pressure.
20
10
20
10
20
10
20
10
30
60
90
120
150
180
30
60
90
120
150
180
Time.(mins.)
Time.(mins.)

Results

Table XXIX and Fig.57 show the changes in monometric pressure, against time, for individual animals. Most evident are the abrupt changes in monometric pressure. During oxygen determinations, in which the CO_2 is absorbed by KOH, a constant uptake was recorded. Thus abrupt changes in the monometric pressure, in the absence of KOH, must be caused by CO_2 release.

The changes were found to be similar to those obtained by Paim and Beckel (1963b); the same authors also state that the spiracles of many insects are not continuously open, in atmospheric air, but fluctuate. They managed to correlate the opening of the spiracles with the output of bursts of CO_2 in Orthosama brunneum (Carambycidae). The present work suggests that this may also be true of CO_2 release in M.rufipes. Saveley (1939) stated that the ambient concentration of gases in wood might keep the spiracles of wood-boring insects open, leading to excessive water loss. This might be an important factor in restricting such insects to moist parts of the wood.

ii) Effect of feeding

Ito (1964) noted a 20% decrease in the respiratory rate of starved spiders Lycasa pseudsonnulata. In comparison he measured the oxygen consumption of fed and unfed houseflies. There was no difference. From this data he concluded that spiders might reduce their metabolic rate during starvation to a degree not found in primary consumers. Other authors, including

Table XXX. O_2 uptake with reference to feeding

4 sets of experiments run at $15^{o}C$.

DAY	No.1.	No.2.	No.3.	No.4.
1.	0.11	0.1	0.1	0.10
6.	0.15	0.12	0.05	0.22
13.	0.18	0.11	0.08	0.13
21.	0.16	0.07	0.08	0.16
28.	0.11	0.08	0.05	0.13

All oxygen consumption figures expressed as $O_2 mm^3/mg/hr$.

Animals fed on days 3, 8 and 15.

Marshall, Nicholls and Orr (1935) and Richman (1958) found no difference in the oxygen consumption of various fed and unfed Crustacea.

To test the effect of feeding on the oxygen consumption of M.rufipes, a series of experimental animals was kept for 28 days. They were fed three times (Day 3, 8 and 15) during this period and the oxygen consumption was measured on five separate occasions (Day 1, 6, 13, 21 and 28).

Results

Table XXX and Fig.55 suggest that there is little or no change between the oxygen consumption, of M.rufipes, of fed and unfed animals. In Chapter One, histological investigations revealed a pair of large fat bodies, which are probably sufficient to carry the animal through a period of starvation, without any immediate alteration in the oxygen consumption.

Discussion

M.rufipes has fifteen instars and lives for eight years. Therefore this study of respiratory metabolism is on an animal with a most complex life history. The apparent complexity did not present insuperable difficulties, in that it was possible to investigate a wide range of instars on a monthly basis. A similar method was used by Phillipson and Watson (1965) in the study of O.asellus L. (Isopoda), which also has a relatively complex life-history, but where the physiological life expectancy is only 3 - 4 years as compared with 7 - 8 years for M.rufipes. The present

study was not complicated by pre-adults maturing gonad material as this process was completely restricted to the adult stage. Neither was the study complicated by diurnal respiratory rhythms, even so, respirometry was carried out for a 24 hour period.

By using Warburg techniques it was possible to investigate certain subsidiary aspects of respiratory metabolism with some direct bearing on the energetic studies. This is further discussed in Section VII of this thesis.

SECTION III.

Chapter 9. Weight Data

Introduction

The collection of weight data was orientated to the need for conversion factors for use in computing energy budgets, where wet weight - dry weight conversions are essential. As Engelmann (1966) pointed out, "dry weight measurements are directly comparable and eliminate any variability due to water content of the animal, which may be a possible source of error". Clearly wet weight (live weight) measurements are often the only direct measurements possible, e.g. in growth and feeding experiments, but it is necessary to convert such data to dry weights for calorific determinations. Hence these give meaningful comparative studies from an energy viewpoint.

All weighings above ten milligrams were made on an electric Mettler, Type H - 16 balance. All measurements below ten milligrams were made on a portable Cahn, M - 10 Electrobalance, and weighed to two decimal places of a milligram.

To obtain dry weight measurements the material was treated as follows. First, the wet weight of the sample was determined, following which the sample was placed in a vacuum oven at 60^{o}C, with a vacuum of 30 in. Mg, and left for a period varying between 48 and 72 hours. On

Table XXXI. Wet weight - head width data - M.rufipes

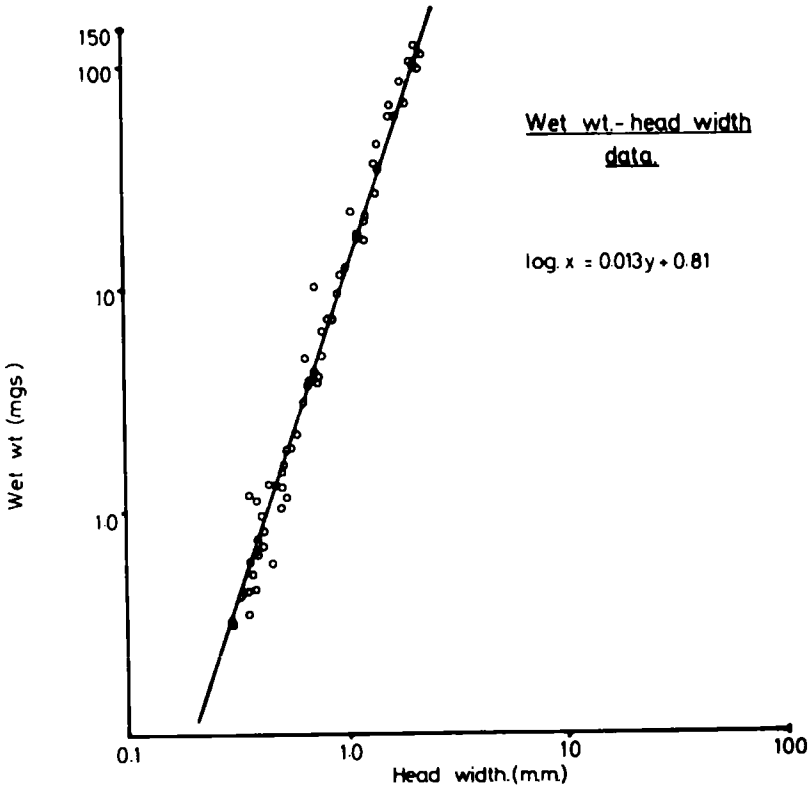
Head width (mm)	Weight (mgs)	Head width (mm)	Weight (mgs)
0.30	0.31	0.74	4.24
0.30	0.32	0.66	4.92
0.36	0.34	0.78	5.00
0.33	0.42	0.79	6.40
0.36	0.44	0.84	7.25
0.38	0.45	0.83	7.25
0.38	0.52	0.94	9.60
0.46	0.58	0.74	10.30
0.36	0.60	0.96	11.80
0.39	0.64	1.02	12.40
0.39	0.66	1.15	16.80
0.42	0.70	1.18	18.50
0.39	0.76	1.25	16.50
0.42	0.82	1.25	20.00
0.41	0.96	1.28	21.40
0.51	1.04	1.10	22.00
0.39	1.12	1.41	26.50
0.54	1.16	1.48	34.00
0.36	1.20	1.40	36.50
0.52	1.30	1.45	45.00
0.48	1.31	1.75	60.00
0.45	1.35	1.65	59.00
0.51	1.50	1.95	69.00
0.52	1.64	1.65	67.00
0.54	1.90	1.85	84.00
0.56	1.95	2.25	98.00
0.60	2.21	2.05	105.00
0.64	3.10	2.35	114.00
0.67	3.64	2.20	125.00
0.76	3.75		
0.68	3.90		
0.76	4.00		

Correlation coefficient $r = 0.91$

$x = 0.031\ y + 0.81$

Fig.58. Relationship between wet weight and head width of M.rufipes.

Fig.59. Relationship between wet weight and instar number of M.rufipes.


150
100
10
1.0
Wet wt (mgs)
0.1
1.0
10
100
Head width.(m.m)
Wet wt.- head width data.
log. x = 0.013y + 0.81

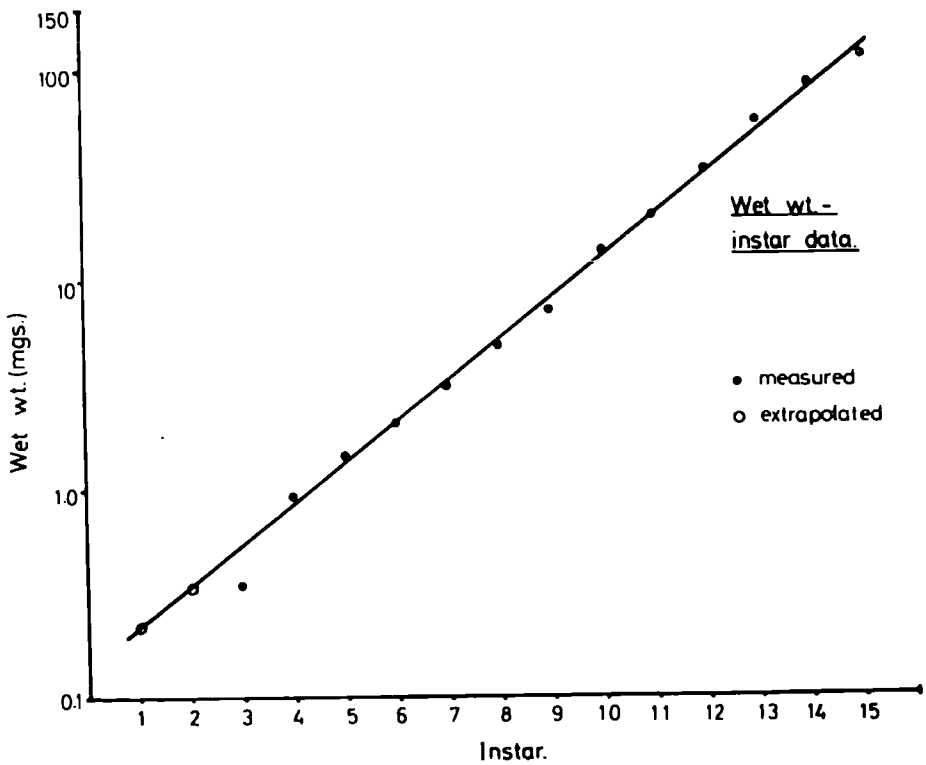

150
100
10
1.0
0.1
Wet wt.(mgs.)
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
Instar.
Wet wt.- instar data.
measured
extrapolated

Table XXXII. Wet weight - instar data - M.rufipes

INSTAR	WEIGHT
1.	-
2.	0.10
3.	0.35 ± 0.02
4.	0.95 ± 0.18
5.	1.50 ± 0.20
6.	2.10 ± 0.38
7.	3.10 ± 0.28
8.	4.90 ± 0.49
9.	7.10 ± 0.30
10.	13.90 ± 1.17
11.	20.50 ± 0.60
12.	34.50 ± 1.09
13.	59.20 ± 2.07
14.	88.50 ± 2.90
15.	119.80 ± 4.70

Mean increase/instar = 1.57 ± 0.2

removal from the vacuum oven the samples were immediately placed in a standard desiccator containing calcium chloride, and left for 24 hours, during which time they cooled down to room temperature. On cooling the samples were weighed and their dry weights obtained.

All data were expressed graphically and following the least squares analysis, a regression line was calculated.

a) Wet weight - head width data

Before the determination of the head width ranges had begun, some relationship between the wet weight and the head width was considered probable. Head width and weight measurements were made and are shown in Table XXXI. Fig.58 shows the data expressed as a double log plot. A direct relationship was indicated by the plot, the straight line having a correlation coefficient (r) = 0.91. This indicates a highly significant relationship between head width and wet weight, which may be expressed as :-

$$x = 0.13\ y + 0.81$$

x = head width, y = wet weight

This formula was later proved useful in estimating the live weights of the early instars, with special reference to the compilation of growth data for these animals.

b) Wet weight - instar data

Once the instar ranges were determined (as described in Chapter 2), an investigation was made to determine the relationship,

Table XXXIII. Wet weight - dry weight data of M.rufipes

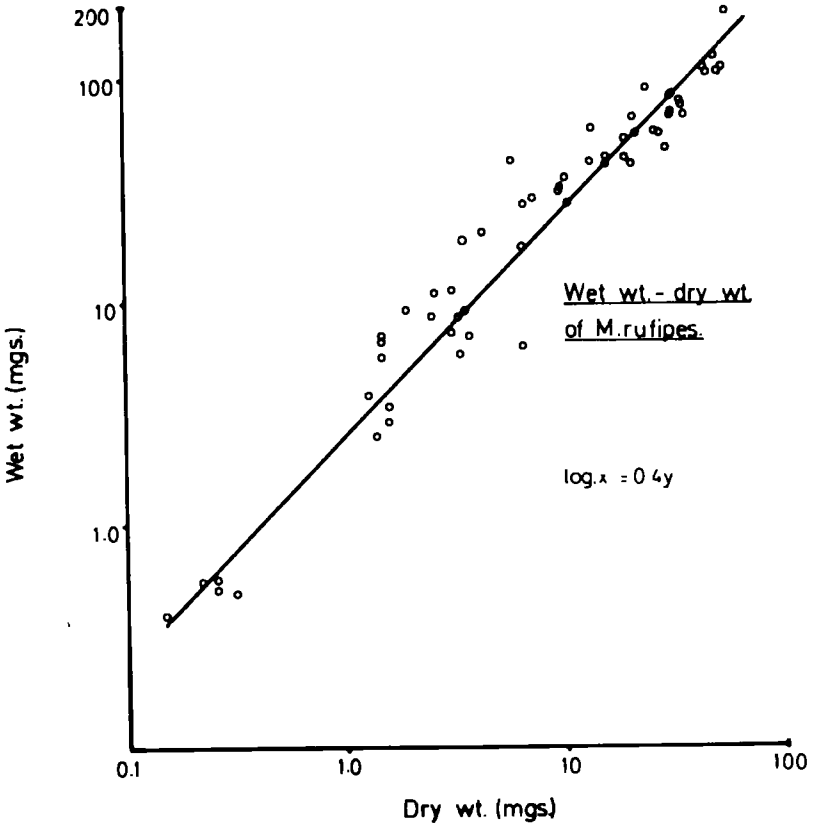
Wet weight(mgs)	Dry weight	Wet weight	Dry weight
11.1	3.1	7.0	3.8
9.3	1.9	17.2	6.6
11.0	2.6	3.4	1.6
93.1	34.0	2.5	1.4
27.5	6.8	2.9	1.6
20.3	4.3	5.4	3.8
44.3	15.9	42.0	15.7
56.2	21.3	47.4	29.6
7.1	1.5	46.2	15.6
19.0	3.5	68.0	26.9
35.9	10.2	43.0	15.1
0.4	0.1	105.0	52.6
6.6	1.5	57.9	27.6
42.1	13.4	41.6	20.6
8.6	3.4	44.0	15.2
8.7	2.5	86.4	31.1
44.0	19.6	27.8	10.2
79.1	34.5	0.49	0.32
33.0	19.7	19.0	3.5
29.5	16.3	16.3	6.5
198.2	55.0	0.32	0.26
62.5	33.5	3.8	1.3
110.9	44.4	0.56	0.22
105.0	52.2	86.4	31.5
31.0	9.7	5.8	1.5
57.4	27.2	54.2	24.3
121.5	49.8	60.7	13.2
69.6	36.2		
70.0	31.3		
75.9	35.0		
106.0	46.5		

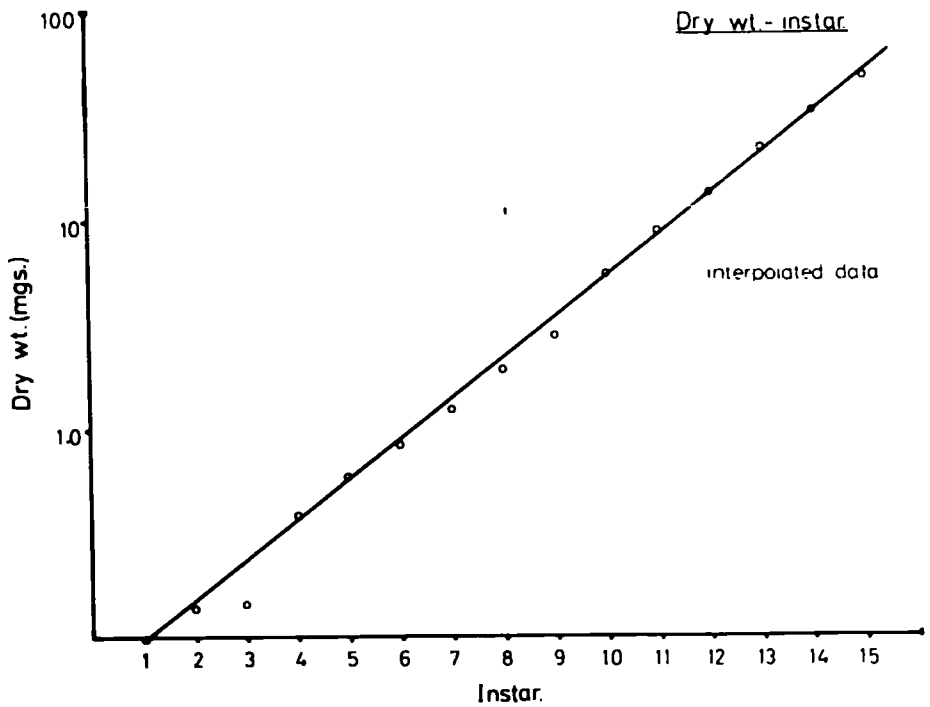
Correlation coefficient r = 0.89

x = 0.4y

Fig.60. Relationship between wet weight and dry weight of *M.rufipes*.

Fig.61. Relationship between dry weight and instar number of *M.rufipes*.


200
100
10
1.0
Wet wt. (mgs.)
Wet wt. - dry wt.
of M. rufipes.
log.x = 0.4y
0.1
1.0
10
100
Dry wt. (mgs.)


100
10
1.0
Dry wt. (mgs.)
Dry wt. - instar
interpolated data
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
Instar.

if any, between the wet weight of individual animals and its particular instar number.

Table XXXII and Fig.59 show the mean weight of individuals at each instar, expressed as a single log plot. There is a regular geometrical increase in weight at each instar, as shown by the straight line relationship. The increased weight at each instar was 1.57 times the weight of the previous instar. The points for Instars 1 and 2 were obtained from the wet weight - head width equation above, and are seen to fall on the existing regression line, and provide a check on the data. This information was also used in the compilation of growth data.

c) Wet weight - dry weight data

Samples of M.rufipes larvae were vacuum dried as outlined above, and their dry weights obtained. The results are expressed in Table XXXIII. Fig.60 shows the data expressed as a double log plot. The regression was calculated and had a correlation coefficient (r) = 0.89, indicating a significant relationship. This can be expressed as :

$$x = 0.4y$$

x = dry weight, y = wet weight

OR Dry weight = 40% of the wet weight.

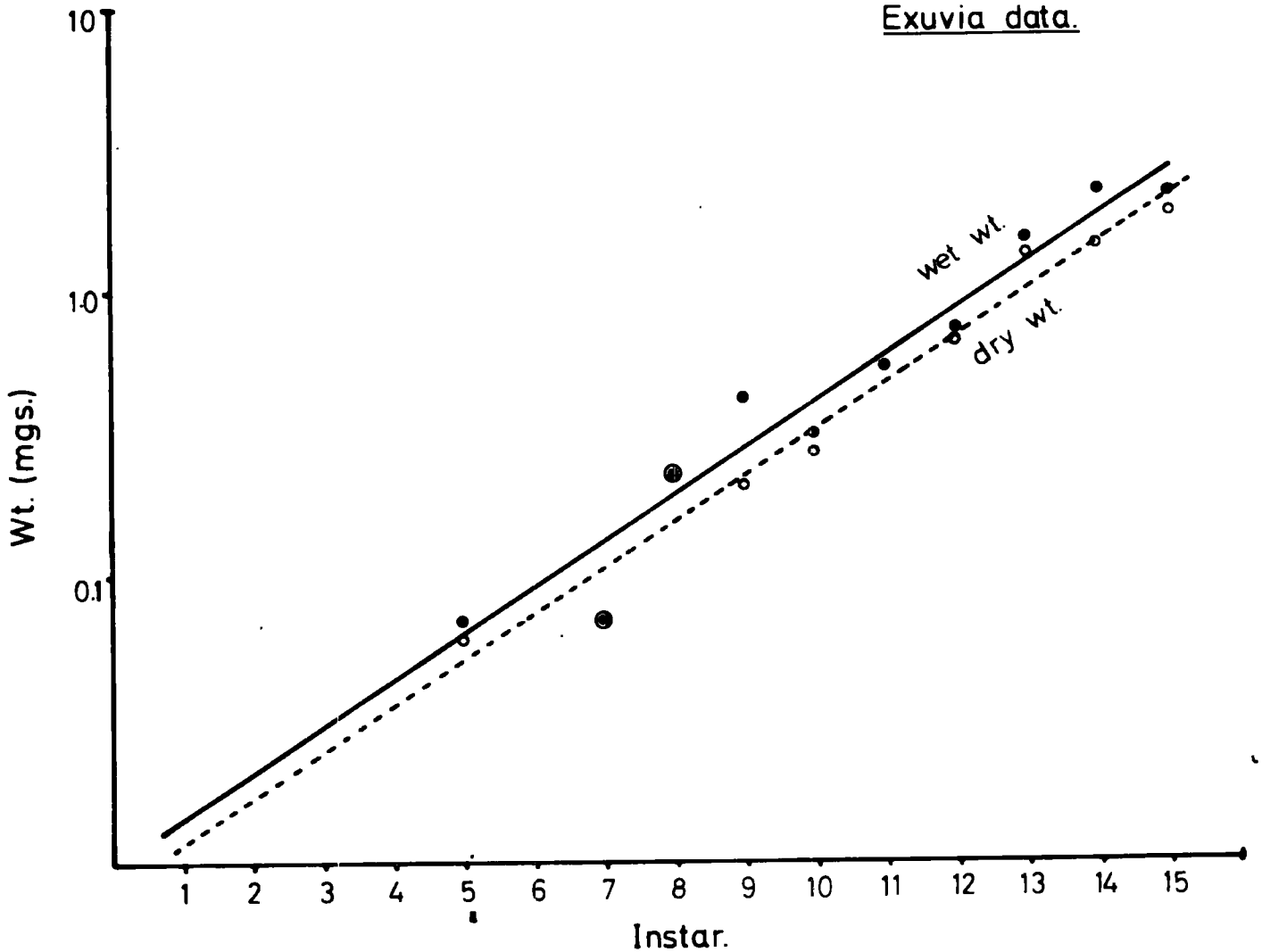
This formula was used as a basis for converting all wet weight data to dry weight equivalents in M.rufipes. Therefore it was vital in drawing up the final energy budgets of this animal, especially with reference to growth data.

Table XXXIV. Exuvium weights - M. rufipes

INSTAR	Wet weight	Dry weight
1	-	-
2	-	-
3	-	-
4	-	-
5	0.07mgs	0.07mgs
6	-	-
7	0.07	0.07
8	0.23	0.23
9	0.42	0.21
10	0.31	0.27
11	0.54	0.52
12	0.73	0.67
13	1.51	1.36
14	2.22	1.43
15	2.14	1.81

Mean water content = 19.4% of total wet weight.

Fig.62. Exuvia weight data with regard to instar number of M.rufipes.


Exuvia data.
10
1·0
0·1
Wt. (mgs.)
wet wt.
dry wt.
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
Instar.

d) Dry weight - instar data

Fig.59 showing the wet weight - instar relationship and Fig.60 showing the wet weight - dry weight relationship of M.rufipes, were combined to produce Fig.61 depicting the dry weight relationship - instar. The regression was fitted by eye as the data was from two separate sources. The information was useful for conversion of data to calorific equivalents.

e) Exuvia weight data

Table XXXIV and Fig.62 show both the mean wet weight of exuvia per instar and the mean dry weight of exuvia per instar. The regressions were again fitted by eye. The increase in the weight of the excuvium at each instar appears to be of the same order as the increase in weight of individual animals at each instar, i.e. 1.57 times. Exuvia constitute approximately 3.1% of the total wet weight of the animal or 4.9% of the total dry weight. The data was necessary in order to calculate the energy loss, by moult, at each instar.

SECTION III.

Chapter 10. Growth rates

Introduction

In any study of population energy flow it is desirable to make estimations of growth to quantify Pg in the equation :-

$$A = R + Pg + pr + U$$

Pg may be calculated in terms of weight and converted to calories.

For the purpose of energy flow investigations, growth studies have been made by Odum and Smalley (1959), Smalley (1960), Kinne (1960), Kuenzler (1961), Engelmann (1961), Odum, Connell and Davenport (1962), Golley and Gentry (1964), Wiegert (1964 : 1965), Mann (1965), Saito (1965 : 1967), Petrides and Swank (1966), and Watson (1966). Certain aspects of growth have been discussed by Brody (1945) and so-called laws governing growth with regard to metabolism have been published by Bertalanffy (1957).

Although no growth investigations have been made on M.rufipes, growth data for Agriotes obscurus L. was published by Evans and Gough (1942), but not for bioenergetic purposes. Further growth data has been presented by Yoshida (1961) for M.caudex.

Three basic methods have been widely adopted for estimating growth :-

1) Mean growth rates may be measured in the field, as the increase in the mean weight of each size class between successive sampling periods. Such an approach is only valid where the animal concerned can be placed in a definite size class, as can M.rufipes.

2) This is the measurement of growth parameters, over a unit period of time, of known individuals. Such an approach was adopted by Evans and Gough (1942) for A.obscurus and by Watson (1966) for the measurement of growth in O.asellus.

3) A method which may be used when growth data is lacking is to calculate Pg by difference from the bioenergetic parameters, when assimilation and respiration are known.

In the present study two approaches were adopted in order to obtain two independent measures of growth.

Growth Study A

This was measurement of growth per unit time, carried out with laboratory animals, i.e. approach 2.

Method

Individual wireworms were confined in 3" x 1" glass vials containing moist sawdust. The tubes were plugged with cotton wool and kept upright at a temperature of 15°C. The substrate was moistened and the animals fed once a week, any excess food being removed. Food consisted of dipterous larvae obtained from the log samples or cultures in the laboratory. The animals were removed and weighed once per month and the substrate renewed.

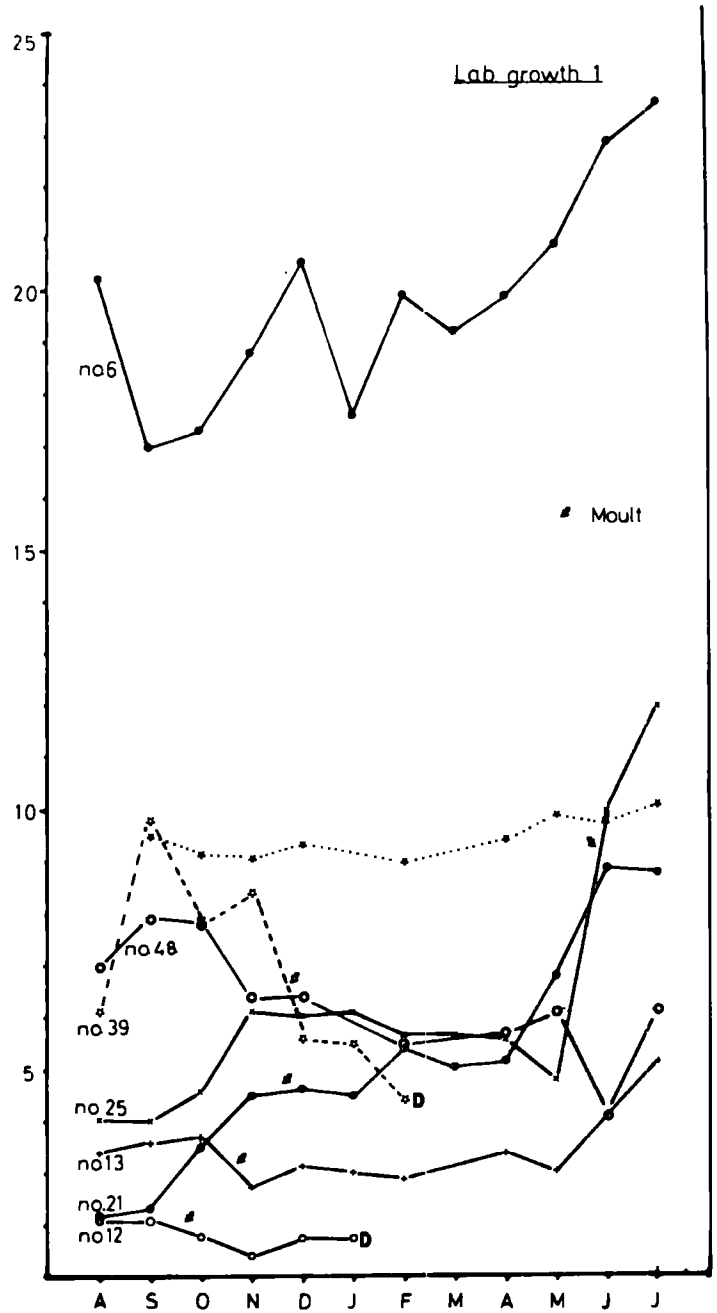
Table XXXV. Laboratory growth data

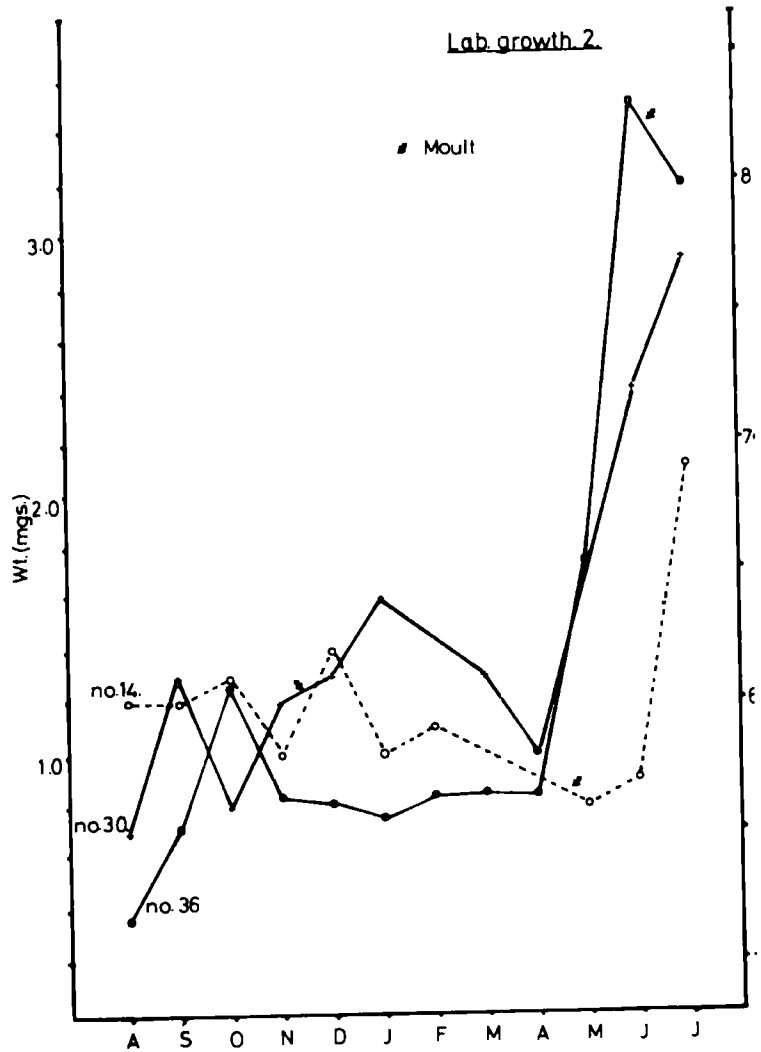
Expt. No.	6.	12.	13.	14.	21.	25.	30.	36.	39.	48.*	56.
Instar	11.	5.	7.	5.	7.	8.	5.	13.	8.	9.	9.
Aug.	20.2mg	2.1mg	3.4mg	1.2mg	2.2mg	4.1mg	0.7mg	51.7mg	6.2mg	7.0mg	-
Sept.	17.0	2.1 Moult	3.6	1.2	2.3	4.1	1.3	55.2	9.8	7.9	9.5
Oct.	17.3	1.7	3.7	1.3	3.5	4.6	0.8	60.6	7.9	7.8	9.2
Nov.	18.8	1.4	2.7	1.0	4.5 Moult	6.2	1.2 Moult	56.4	8.4 Moult	6.4	9.1
Dec.	20.6	1.7	3.2	1.4	4.7	6.1	1.3	56.2	8.6	6.4	9.3
Jan.	17.6	1.7	3.1	1.0	4.5	6.2	1.6	55.6	5.5	5.5	-
Feb.	19.9	-	2.9	1.1	5.4	5.7	-	50.4	4.4	5.9	9.0
Mar.	19.2	-	-	-	5.1	5.7	1.3	56.5	-	-	-
Apr.	19.9	-	3.4	1.0 Moult	5.2	5.6	1.0	56.4	-	5.7	9.4
May	20.9	-	3.1	0.8	6.8	4.8 Moult	-	65.3	-	6.1 Moult	9.9
June	22.9	-	?	1.0	8.9	10.0	2.4	83.0 Moult	-	4.0	9.7
July	23.7	-	5.2	2.1	8.5	12.0	2.9	79.9	-	6.2	10.1

* This animal moulted but did not increase its head width

Fig.63. Laboratory growth data 1, for M.rufipes

Fig.64. Laboratory growth data 2, for M.rufipes


Lab. growth 1
25
20
15
10
5
no.6
Moult
no.48
no.39
no.25
no13
no.21
no12
D
D
A S O N D J F M A M J J


Lab. growth 2.
Moult
3.0
2.0
1.0
Wt. (mgs)
no.14.
no.30.
no. 36
A S O N D J F M A M J J

Initially 150 animals were dealt with in this way. Mortality was high in the first few months, mainly through overwatering and fungal attack. It became apparent that M.rufipes did not lend itself as well, to laboratory culture, as did A.obscurus used by Evans and Gough (1942).

Results

Some of the experiments were successful in that the animals did gain weight. Table XXXV and Figs. 63 and 64 show the results. It is clear that individual animals varied in weight from month to month, with a general increase in weight over a long period. Often, prior to moulting, there was an increase in weight. However, during moulting the weight dropped. In apparently 'normal' animals this was regained within a very short period. Evans and Gough (1942) showed that in A.obscurus variability in weights over the short term and prior to moulting was due to the variability of their water content. This is probably true of M.rufipes.

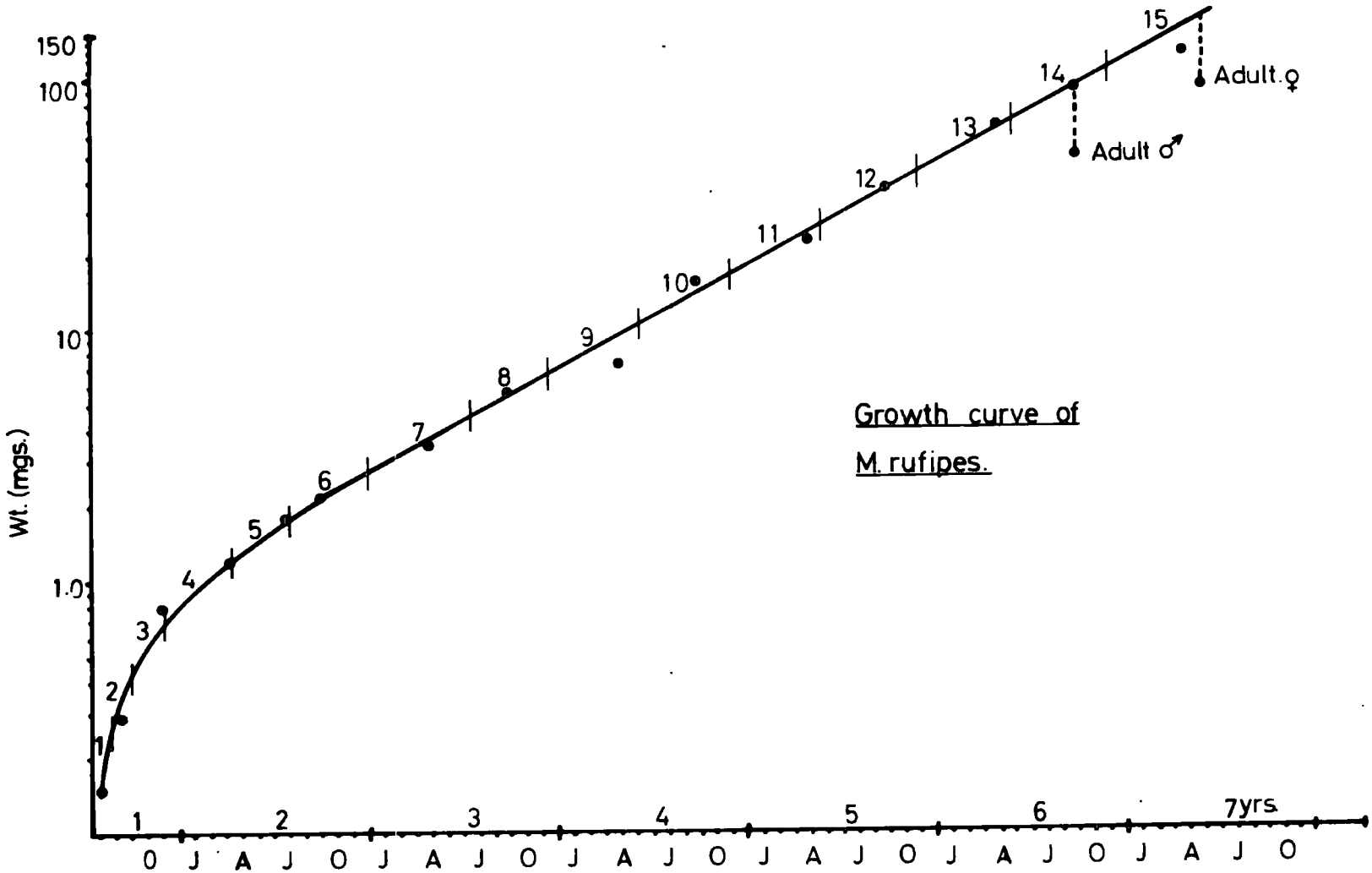
In the laboratory experiments the time of moulting did not coincide with that shown by individuals kept under field conditions for moulting data (see Chapter 3). Further, a number of animals moulted but did not increase in weight. In fact some specimens decreased in weight (see Fig.63); it was noticeable that such specimens died. Obviously such aberrances are not normal, therefore doubt must be cast on the reliability of such data for bioenergetic purposes. Thus it was necessary to place

Table XXXVI. Growth curve data

Instars	Time	Mean Weight (mgs)
1.	July	- Interpolated
2.	August	"
3.	October	0.8mgs
4.	March	1.2
5.	June	1.8
6.	September	2.2
7.	April	3.5
8.	September	5.6
9.	April	7.2
10.	September	15.7
11.	April	22.7
12.	September	36.7
13.	April	64.1
14.	September	90.9
15.	April	126.5

Time expressed to nearest month

Fig.65. Growth curve for M.rufipes


150
100
10
1.0
Wt. (mgs.)
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
Adult ♀
Adult ♂
Growth curve of
M. rufipes.
1
2
3
4
5
6
7yrs
O J A J O J A J O J A J O J A J O J A J O J A J O

greater reliance on growth data obtained partly from the field and partly from laboratory data accrued for other purposes.

Growth study B

Chapter 9 demonstrated how the mean weight per instar could be calculated from field data. This information was used in conjunction with the information on the life-history, moulting activity, and hence the duration of the life cycle presented in Chapter 1.

Method

The procedure consisted of expressing in graphical form the mean weight/individual instar, against duration of that instar. The duration of each instar, obtained from the above collective data, is also shown. The data does not include overlapping instars as it is considered that these are abnormal types.

Results

Table XXXVI and Fig.65 show the growth data and the growth curve constructed from the above data. The points representing Instars 1 and 2 were obtained from the wet weight - head width data, as information on these was lacking. The line through the points was fitted by eye.

The resulting curve is typical of many growth curves. The first three instars have a higher growth rate than the later ones, which reach a steady rate of increase. The growth curve exhibits a typical pattern.

Also shown on Fig.65 are the mean weights of male and female adults. During and after pupation a large weight decrease

Table XXXVII. Growth rates estimates from graph $\frac{\Delta w}{\Delta t}$

Instar	Wet weight increase/24 hours.	Dry weight increase/24 hours.
1.	0.008mgs	0.0032mgs
2.	0.003	0.0013
3.	0.005	0.0020
4.	0.004	0.0016
5.	0.004	0.0016
6.	0.006	0.0024
7.	0.007	0.0028
8.	0.014	0.0066
9.	0.020	0.0080
10.	0.040	0.0160
11.	0.040	0.0160
12.	0.090	0.0360
13.	0.130	0.0520
14.	0.230	0.0920
15.	0.330	0.1320

takes place. The final result is that the imago is only approximately 55% of the wet weight of the final instar.

The growth rates for the individual instars of M.rufipes were calculated directly from the growth curve, Fig.65 :-

$$\text{Growth (Pg)} = \frac{\Delta W.}{\Delta t} \qquad \begin{matrix} W = \text{growth increase} \\ t = \text{time} \end{matrix}$$

Table XXXVII shows this data expressed both as wet weight and dry weight. The conversion to dry weight was made using the wet weight/dry weight regression formula. (Chapter 9). Thus for bioenergetic purpose the data may be converted to a calorific basis, using the known calorific values for M.rufipes.

Discussion

Growth study A was carried out in the laboratory at $15^{o}C$, as were measurements of the other bioenergetic parameters. The temperature represented by the growth rates in Growth Study B was unknown, as the data was compiled from various sources. Clearly some error will arise from this; however, the data is the best yet available for M.rufipes and is used in this study.

It was noted in Chapter 2 that the increase in linear dimensions of M.rufipes was 1.18 ± 0.08 times, at each instar. According to Przibom's rule (Wigglesworth 1965), this should have been 1.26 times ($\sqrt[3]{2}$). He also stated that a linear increase of 1.26 times is equivalent to the weight doubling. It is possible to calculate the theoretical growth increase at each instar :-

$$\frac{1.18}{1.26} \times 2 = \underline{\underline{1.88}}$$

The actual increase found was 1.57 ± 0.033 Table XXXII and Fig.59). The theoretical increase is therefore an overestimate, the major discrepancy appearing in the first three instars which have a higher growth rate per unit time.

The advantage of compiling growth from various pertinent data is that complications due to variability in weight and the effect of sporadic feeding are not manifest.

SECTION III.

Chapter 11. Calorific data

Introduction

To convert the estimated dry weights of food consumption (C), assimilation (A), egesta or faeces (F), and growth (Pg), to calories, micro-bomb calirometry was employed.

The calorific values of various animal species have been determined by Slobodkin and Richman (1961), Golley (1961), Comita and Schindler (1961), Paine (1964), Phillipson (1964), Weigert (1964 : 1965) and Watson (1966). By far the most useful and comprehensive data is found in the booklet by Cummins (1967), which collates the calorific values of many plant and animal species, from various sources. Generally the average calorific value for animal material obtained by these authors is of the order of 5.0 K.cals/gm.

Method

The apparatus used to make the calorific determinations in the present study was a micro-bomb calorimeter of the type described by Phillipson (1964) and now produced commercially by Gentry-Wiegert Instruments Incorporated. The material to be burnt was dried in a vacuum oven at 60^{o}C and ground to a powder in an agate mortar and pestle. The powder was pelleted, and the pellets stored in a desiccator until needed. All pellets made in

Fig.66. Specimen calorific data sheet.

RIAL D. rufipes. Instar II. (whole animals) | CALIBRATION = 0.5689 Mv/Cal^{100}

LE NO. 38 DATE 5.3.68 Mv SCALE USED 1

SCALE READING (2) 0.624

(1) 0.361

0.263

Wt. of Pan + Pellet = 37.760 mg

Wt. of Pan = 29.485 mg

∴ Wt. of Pellet = 8.275 mg

But 0.005659 MV = 1 CAL

263 MV = 263/5.659 = 46.4746 Cals.

Thus 8.275 mg = 46.4746 Cals

1000 mg = 46.4746/8.2750 x 1000 = 5.6163 Cals.

1g + _____ Cals. i.e. 5.6163 Kcals/gram

Wt. of Pan + Ash = 29.550 mg

Wt. of Pan = 29.485 mg

∴ Wt. of Ash = 0.065 mg

Wt. of Pellet = 8.275 mg

Wt. of Ash = 0.065 mg

∴ Ash Free Wt. = 8.210 mg

ABOVE 1 GRAM ASH FREE WT. = $\frac{\text{Cals Produced x 1000}}{\text{Ash Free Wt.}} = \frac{46.4746}{8.210} \times \frac{1000}{1}$

= 5.6607 Kcal/gram

ENTS:

this way approximated 10mgs in weight.

The operation of the bomb has been described by Phillipson (1964). Prior to burning the sample pellets, the bomb was calibrated by burning benzoic acid pellets, which were of known calorific value. The mean value of twenty consecutive benzoic acid pellet burnings was 0.005659 $\pm$ 0.000450 millivolts $\equiv$ one calorie. This was taken as the calibration factor. Further checks were made periodically to test the calibration factor, but it was found to remain constant throughout the experimental period.

All results were recorded on the data sheets and converted using the above calibration factor. Fig.66 shows a specimen data sheet. The ash-free values were not calculated from the burnings, as preliminary work indicated that such data was variable.

Results

Table XXXVIII shows the material, number of samples and calorific data of the pellets burnt; where possible standard errors were calculated.

It was not possible to obtain sufficient material, below Instar 8, to make pellets without the use of a filler substance. The disadvantages of using filler substances is discussed by Phillipson (1964). On burning pellets of whole animal material from individual instars, 8 - 15, it was clear that a calorific difference existed between each instar. Fig.67 shows

Table XXXVIII. Table of calorific data

Material	Kcals/gm	S.E.	No.samples
In. 8. Larva	4.3232	-	2.
In.9. "	5.0141	± 0.1277	3.
In.10. "	5.6356	± 0.0843	3.
In.11. "	5.7152	± 0.0600	3.
In.12. "	5.0869	± 0.1587	3.
In.13. "	5.8738	± 0.1766	3.
In.14. "	6.2805	± 0.2081	3.
In.15. "	6.5238	± 0.0933	3.
In.1-11 Exuvia	5.4534	± 0.2610	3.
In.12. "	4.7625	-	1.
In.13 "	4.9370	-	2.
In.14. "	4.7795	-	1.
In.15. "	4.7595	-	2.
Food Blowfly	5.7681	± 0.0620	4.
Faeces	4.7296	-	1.
Adult ♀s	5.9320	± 0.0680	4.
Adult ♂	4.8463	± 0.1790	3.
Eggs	5.3039	-	2.

Data includes ash content.

Data calculated using the calorific calibration factor of

0.005659 ± 0.000450 mV ≡ 1 calorie.

Fig.67. Calorific value per instar of M.rufipes.

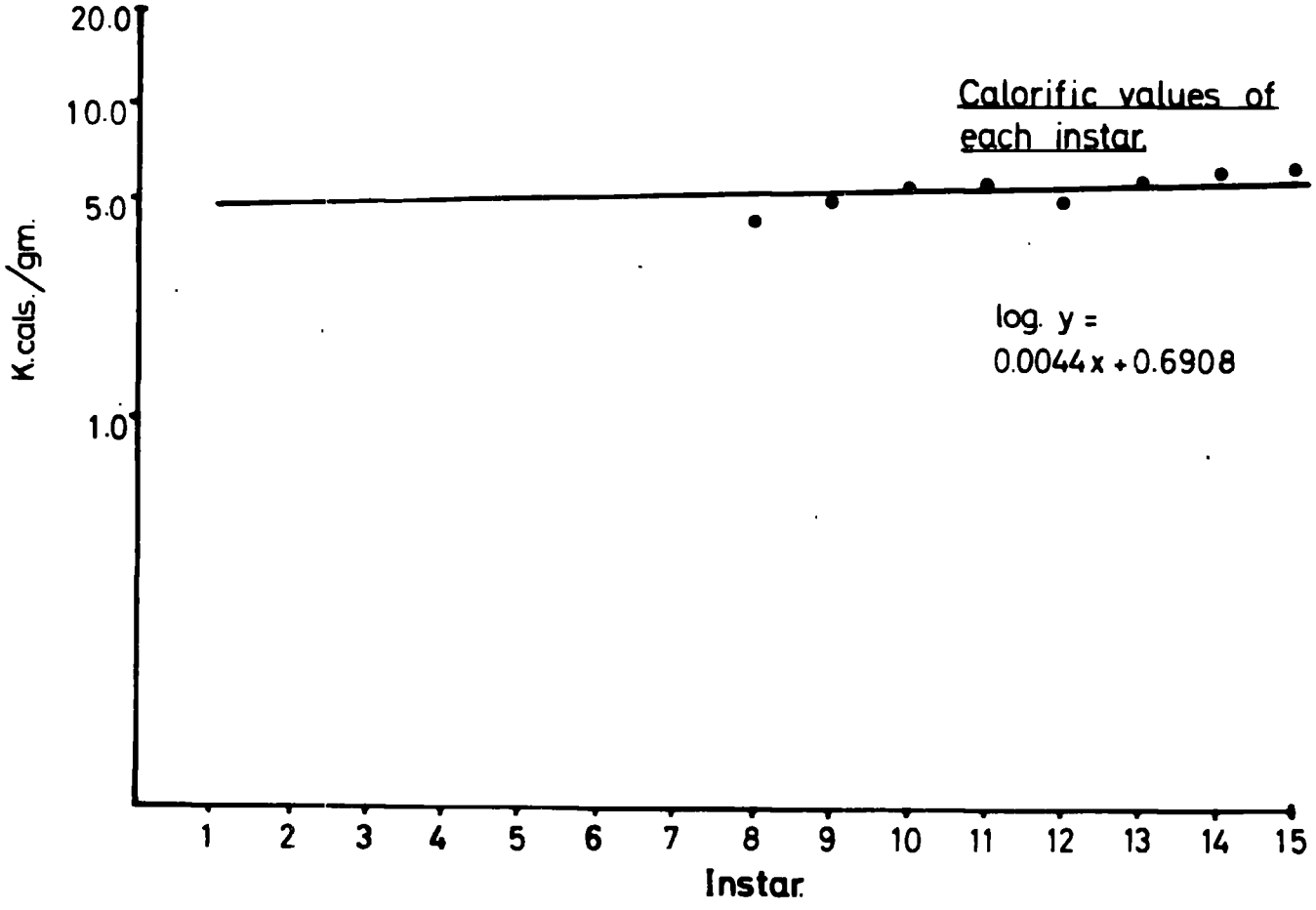

20.0
10.0
5.0
1.0
K.cals./gm.
Calorific values of each instar
log. y =
0.0044x + 0.6908
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15
Instar

Table XXXIX. Calorific data - larvae at each instar

Calculated from Log y = 0.0044x + 0.6908

Instar	Kcals/gm
1.	4.957
2.	5.007
3.	5.058
4.	5.110
5.	5.162
6.	5.214
7.	5.267
8.	5.446
9.	5.375
10.	5.430
11.	5.486
12.	5.542
13.	5.598
14.	5.654
15.	5.712

the data expressed as a single log plot. The regression line was calculated and can be expressed as :-

$$\log y = 0.0044x + 0.6908$$

y = calorific value. x = instar number

Table XXXIX shows the calorific value of each instar, calculated from this formula. Values vary from 4.957 Kcals/gm for Instar 1 larvae to 5.712 Kcals/gm in Instar 15 larvae, a difference of 0.755 Kcals/gm. The amount of faecal matter available for burning was small, therefore only one pellet was made and burnt.

The above calorific values were applied to the quantitative data and are expressed in Chapter 12.

SECTION III.

Chapter 12. On the energetics of M.rufipes

Tables XL - XLV show the energy budget parameters, C, F, A, R and Pg, converted to calories, as used to derive the energy budgets for M.rufipes. All data are expressed as calories/instar of known mean weight/24 hours. All the calorific conversions, apart from R, were made using the calorific equivalents obtained by bomb calorimetry, and applied to the dry weight data. The calorific value of R. was determined using the oxycaloric equivalent of 4.7 cals/ml of O_2 (Chapter 8).

a) Ingestion (C)

Table XL shows the ingestion rates. The data was obtained from the laboratory feeding experiments described in Chapter 7.

b) Egestion (Faeces) (F)

Table XLI shows the egestion rates. These data were also obtained in the experiments described in Chapter 7.

c) Assimilation (A)

This data is expressed in Table XLII. All assimilation data were calculated from the difference between calories ingested - calories egested. On a calorific basis the mean assimilation percentage increased from 86.5% by dry weight to 90.3% by calories,

Table XL. i) Calorific value of larval ingestion

Instar	Mean Live Weight (Mgs)	Mgs.Dry Wt. Ingestion/24hrs.	Cals. Ingestion/24hrs.
1.	0.16	0.260	1.5000
2.	0.29	0.380	2.1919
3.	0.53	0.500	2.8840
4.	0.95	0.690	3.9800
5.	1.50	0.820	4.7298
6.	2.10	0.840	4.8452
7.	3.10	0.960	5.5374
8.	4.90	1.150	6.6333
9.	7.10	1.310	7.5562
10.	14.00	1.890	10.9017
11.	20.50	2.050	11.8246
12.	34.50	2.760	15.9199
13.	59.20	3.550	20.4767
14.	88.50	4.000	23.0724
15.	119.80	4.190	24.1680

Table XLI. ii) Calorific value of faeces production

Instar	Mean Live Weight (Mgs)	Mgs.Dry Wt. Faeces/24hrs.	Cals. Faeces/24hrs.
1.	0.16	0.030	0.1420
2.	0.29	0.042	0.1986
3.	0.53	0.058	0.2743
4.	0.95	0.080	0.3784
5.	1.50	0.096	0.4540
6.	2.10	0.101	0.4870
7.	3.10	0.115	0.5439
8.	4.90	0.137	0.6479
9.	7.10	0.156	0.7378
10.	14.00	0.224	1.0594
11.	20.50	0.246	1.1635
12.	34.50	0.310	1.4612
13.	59.20	0.402	1.9013
14.	88.50	0.460	2.1756
15.	119.80	0.587	2.7763

Table XLII. iii) Calorific values of assimilation

Instar	Mean Live Weight (Mgs)	Dry Wt. Assim./ 24hrs	Cals. Assim./ 24hrs
1.	0.16	0.220	1.3580
2.	0.29	0.310	1.9933
3.	0.53	0.430	2.6097
4.	0.95	0.590	3.6016
5.	1.50	0.700	4.2758
6.	2.10	0.740	4.3582
7.	3.10	0.830	4.9935
8.	4.90	0.980	3.9854
9.	7.10	1.100	6.8184
10.	14.00	1.640	9.8423
11.	20.50	1.800	10.6011
12.	34.50	2.620	14.4537
13.	59.20	2.960	18.5754
14.	88.50	3.360	20.0153
15.	119.80	3.470	21.2917

Table XLIII. iv) Calorific values of respiration

Instar	Mean Live Weight (Mgs)	$O_2 mm^3/hrs.$	Cals.Resp./ 24hrs.
1.	0.16	22.80	0.114
2.	0.29	29.52	0.148
3.	0.53	38.40	0.192
4.	0.95	49.92	0.250
5.	1.50	56.88	0.284
6.	2.10	56.40	0.282
7.	3.10	52.08	0.260
8.	4.90	68.16	0.341
9.	7.10	71.52	0.358
10.	14.00	97.44	0.487
11.	20.50	103.44	0.517
12.	34.50	124.08	0.620
13.	59.20	156.24	0.781
14.	88.50	169.92	0.846
15.	119.80	172.56	0.863

Table XLIV. v) Calorific values of growth

Instar	Mean Live Weight (Mgs)	Mgs.Dry Wt. Growth/24hrs.	Cals. Growth/ 24hrs.
1.	0.16	0.0032	0.016
2.	0.29	0.0012	0.006
3.	0.53	0.0020	0.010
4.	0.95	0.0016	0.008
5.	1.50	0.0016	0.008
6.	2.10	0.0024	0.012
7.	3.10	0.0028	0.015
8.	4.90	0.0060	0.033
9.	7.10	0.0080	0.043
10.	14.00	0.0160	0.087
11.	20.50	0.0160	0.088
12.	34.50	0.0360	0.199
13.	59.20	0.0520	0.291
14.	88.50	0.0920	0.520
15.	119.80	0.1320	0.753

Table XLV. vi) Calorific values of exuvia

Instar	Mean Live Weight (Mgs)	Wt.Ex./Instar	Cal.val.Exuvium/ 24hrs.
1.	0.16	0.010	0.0024
2.	0.29	0.017	0.0030
3.	0.53	0.025	0.0006
4.	0.95	0.036	0.0030
5.	1.50	0.052	0.0043
6.	2.10	0.072	0.0017
7.	3.10	0.110	0.0090
8.	4.90	0.160	0.0132
9.	7.10	0.230	0.0064
10.	14.00	0.330	0.0130
11.	20.50	0.480	0.0130
12.	34.50	0.700	0.0276
13.	59.20	1.000	0.0235
14.	88.50	1.460	0.0197♀ (0.1201♂)
15.	119.80	2.100	0.0284

owing to faeces having a lower calorific value per unit weight, than the food material.

d) Respiration (R)

This data is expressed in Table XLIII from the respiration data described in Chapter 8, and converted by the oxy-caloric equivalent.

e) Growth (Pg)

Table XLIV shows the calorific growth data obtained from the growth curve presented in Chapter 10.

f) Exuvia

The mean dry weight of exuvia produced/day was calculated from the mean weight of exuvium/instar (Chapter 9), and growth data (Chapter 10). Table XLV shows the calorific equivalents found. A difference in the daily production of exuvium was found between males and females during Instar 14. Males pupate in the same year that they reach Instar 14 (Chapter 3), whereas females overwinter at this stage, therefore exuvium production/day in males is higher than females who produce the same amount of exuvium over a longer period.

g) Adults

The calorific values of adult respiration and growth of reproduction are tabulated below :-

	Mean weight	Respiration	Reproduction
Male	59.4mgs	1.640 cals/ins./24hrs	-
Female	90.9mgs	2.310 cals/ins./24hrs	0.14 cals/24hrs.

h) Energy budgets of each instar

Figs. 68 - 82 show the individual energy budgets for each instar/day. Most noticeable is the discrepancy in the measured feeding rates obtained from the laboratory experiments (Chapter 10) which are shown in parenthesis, and those calculated by summation of the laboratory measurements of respiration, growth and moult. For the calculations by summation, the assimilation percentage of 90.3% obtained in the present study was assumed correct. Considerations of the reasons for these discrepancies have been left to the Discussion.

The data as presented in Figs. 68 - 82 can be applied to a population, where the instar composition is known.

i) Mean energy budgets as applied to the biomass data

Biomass data was presented in Chapter 6; however, the instar composition of the population was not known and therefore the data above could not be used, in that form, to calculate the energy budget. It was possible to calculate a 'best estimate' (Phillipson 1964) of the annual energy budget by use of the biomass data in conjunction with the mean values, over the whole life history of C, A, F, R and Pg. Fig.83 shows the results.

Fig.68

Energy budget for Instar 1 Larva

All values expressed as calories/individual of 0.16mgs/24 hours. Feeding rate figures in brackets denote amounts found in lab. experiments, figures outside brackets are calculated from the other parameters of respiration + growth + moult.

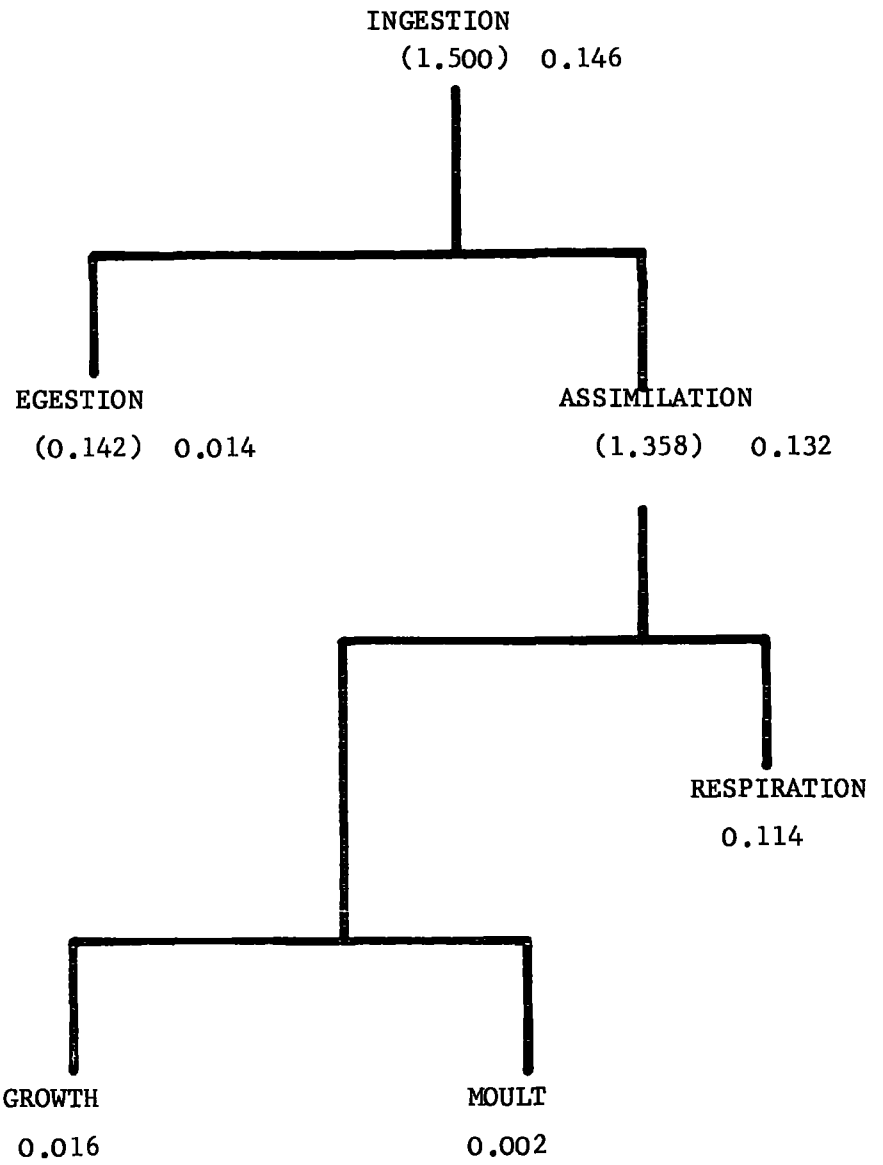


Fig.69

Energy budget for Instar 2 larva

All values expressed as calories/individual of 0.29mgs/24hrs.

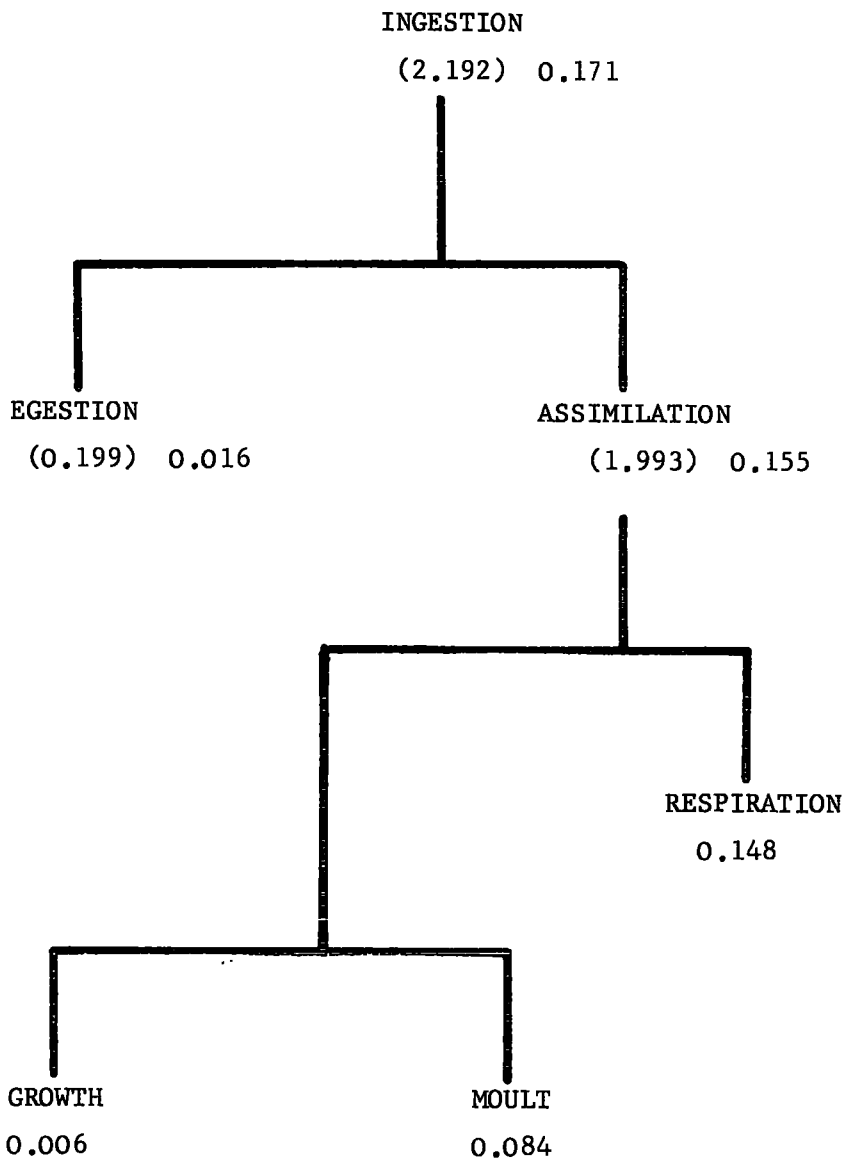


Fig.70

Energy budget for Instar 3 larva

All values expressed as calories/individual of 0.53mgs/24hrs.

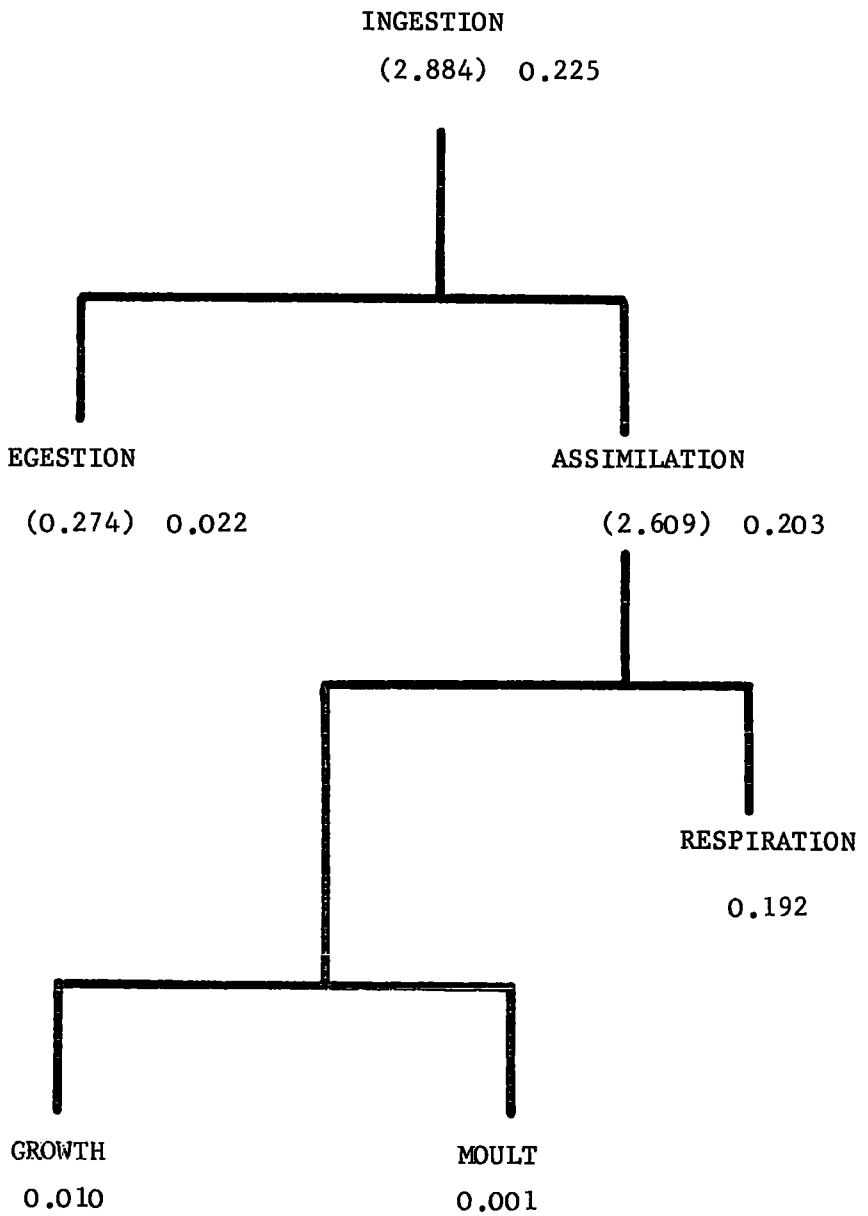


Fig.71

Energy budget for Instar 4 larva

All values expressed as calories/individual of 0.95mgs/24hrs.

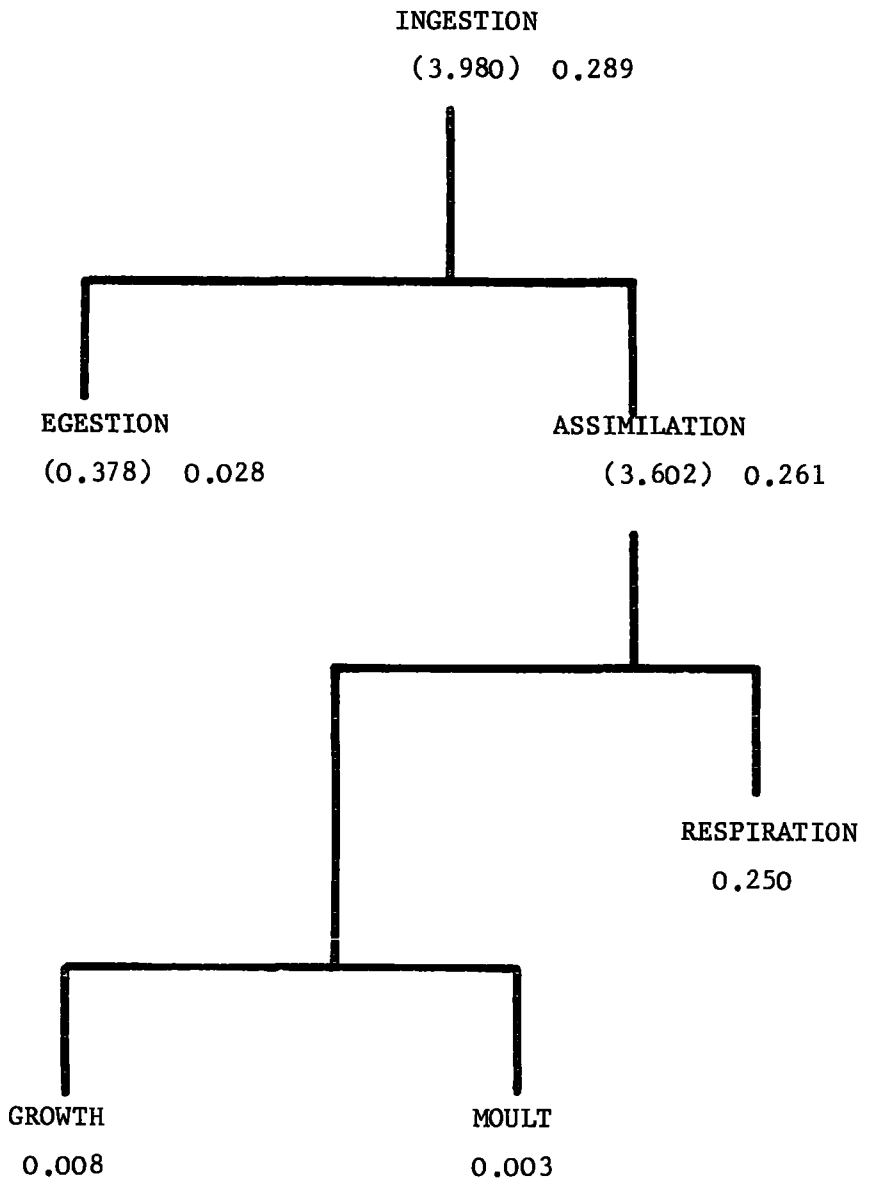


Fig.72

Energy budget for Instar 5 larva

All values expressed as calories/individual of 1.50mgs/24hrs.

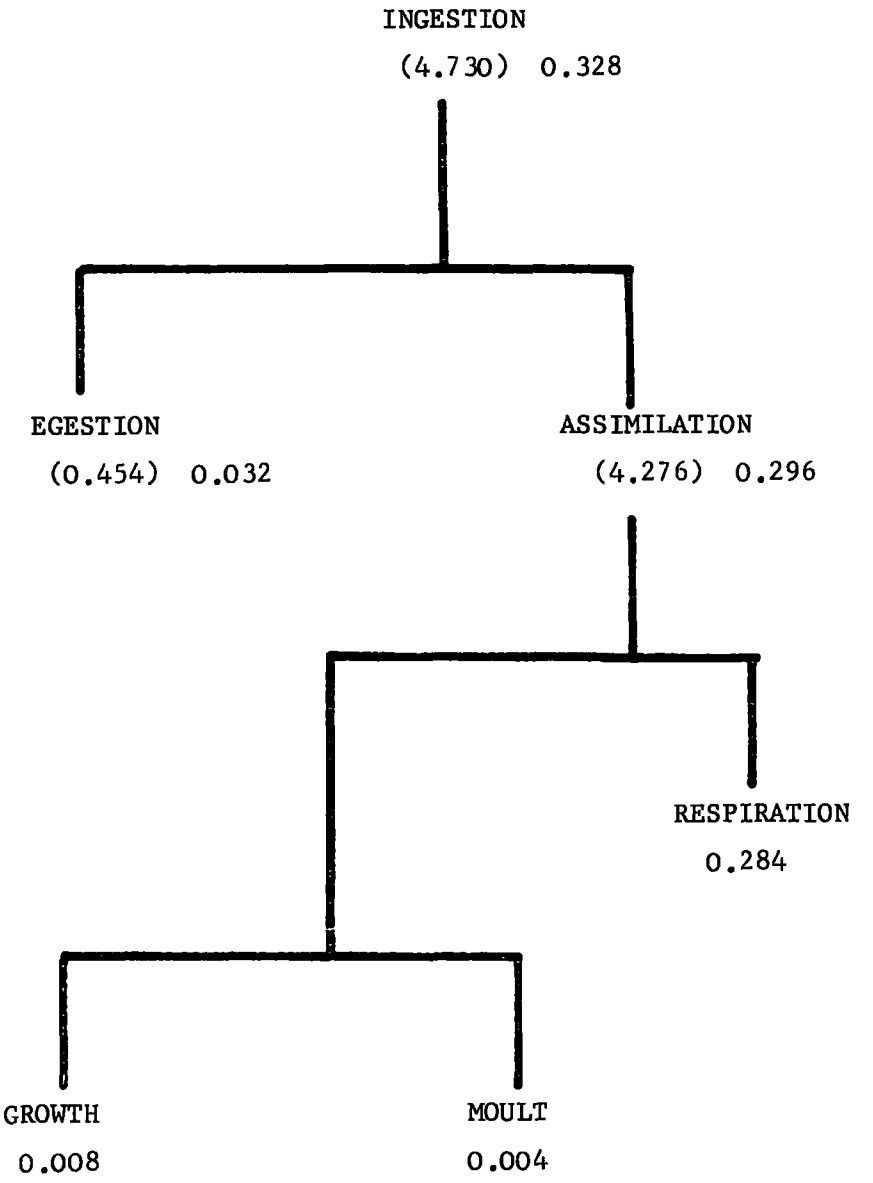


Fig.73.

Energy budget for Instar 6 larva

All values expressed as calories/individual of 2.10mgs/24hrs.

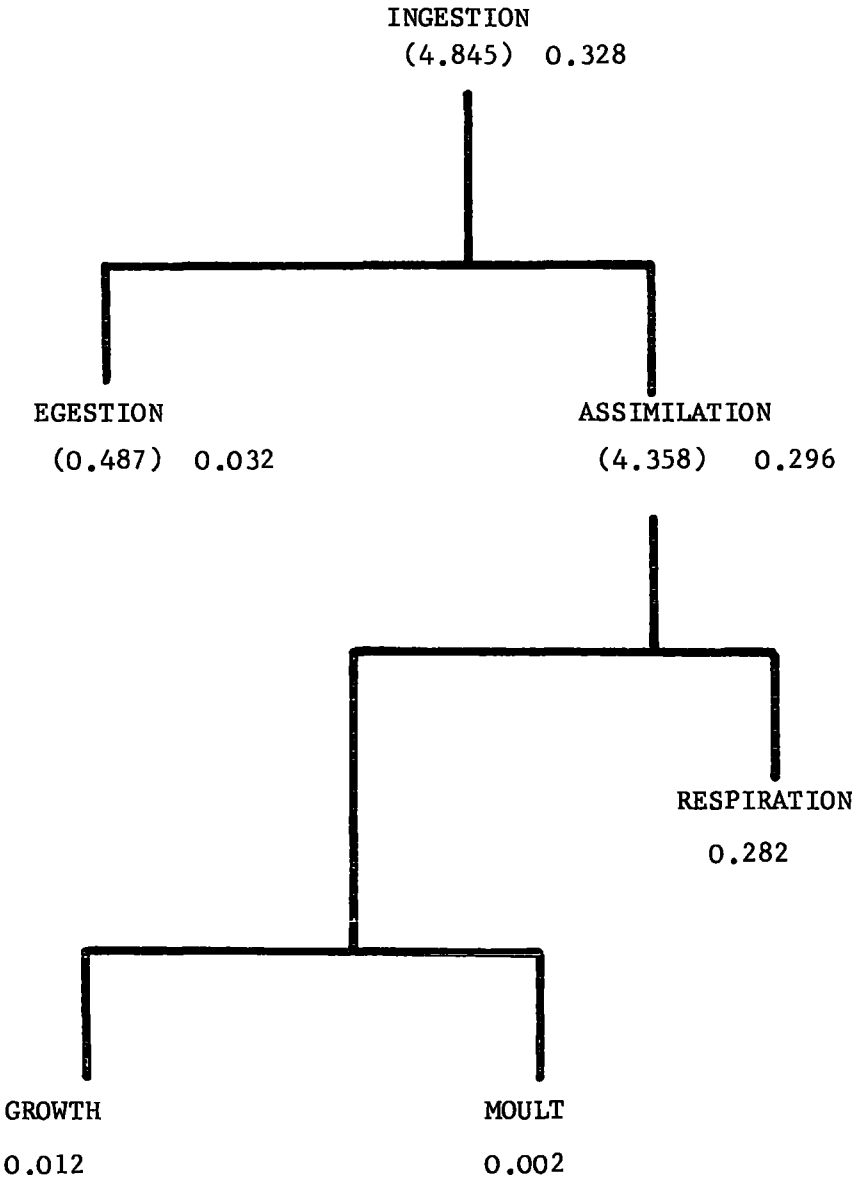


Fig.74.

Energy budget for Instar 7 larva

All values expressed as calories/individual of 3.10mgs/24 hours.

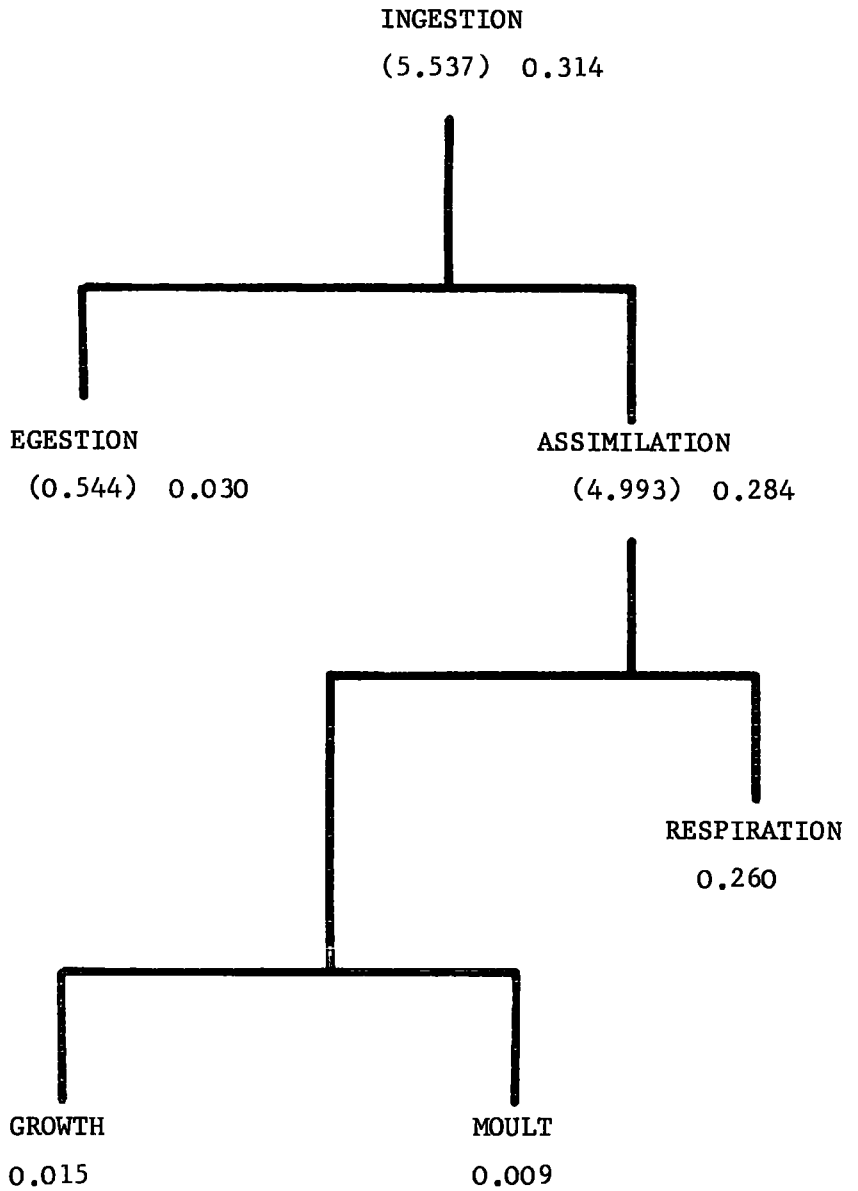


Fig.75.

Energy budget for Instar 8 larva

All values expressed as calories/individual of 4.90mgs/24 hours.

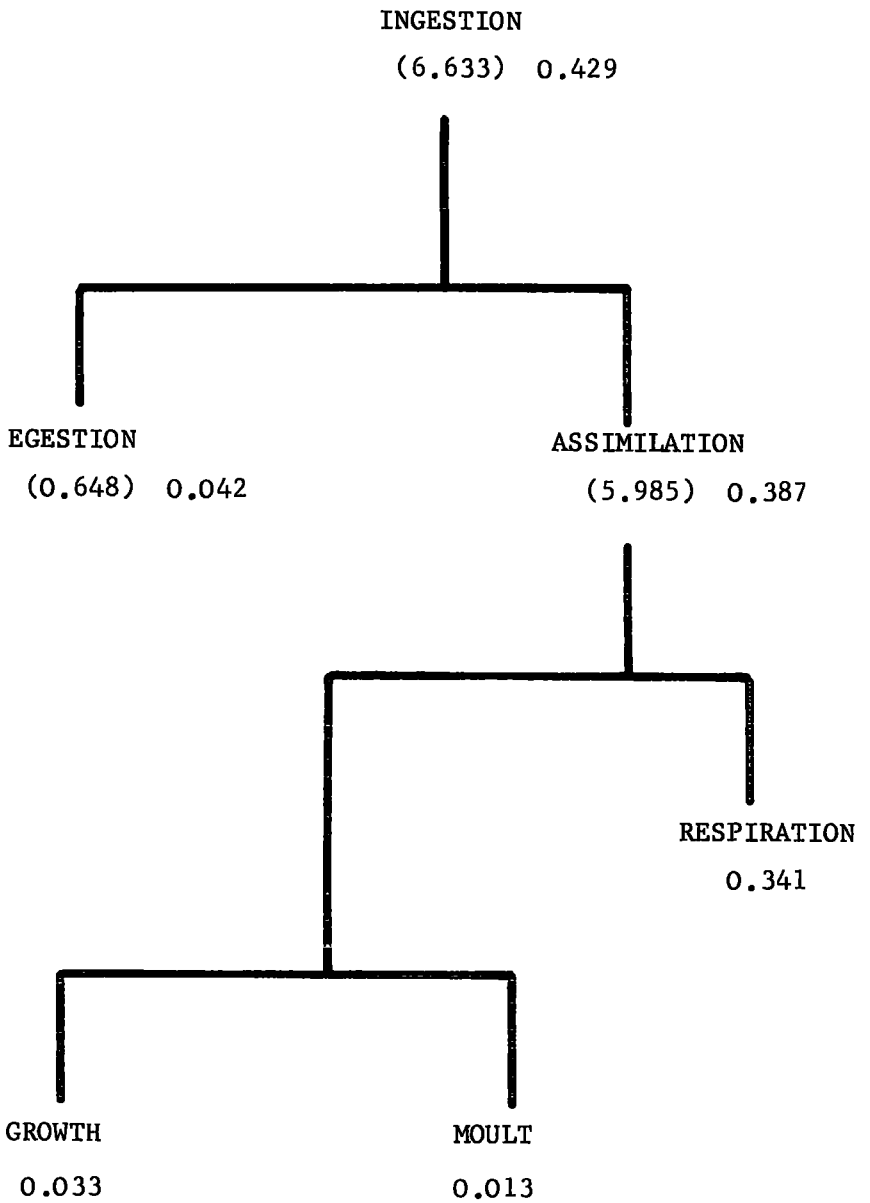


Fig.76.

Energy budget for Instar 9 larva

All values expressed as calories/individual of 7.10mgs/24 hours.

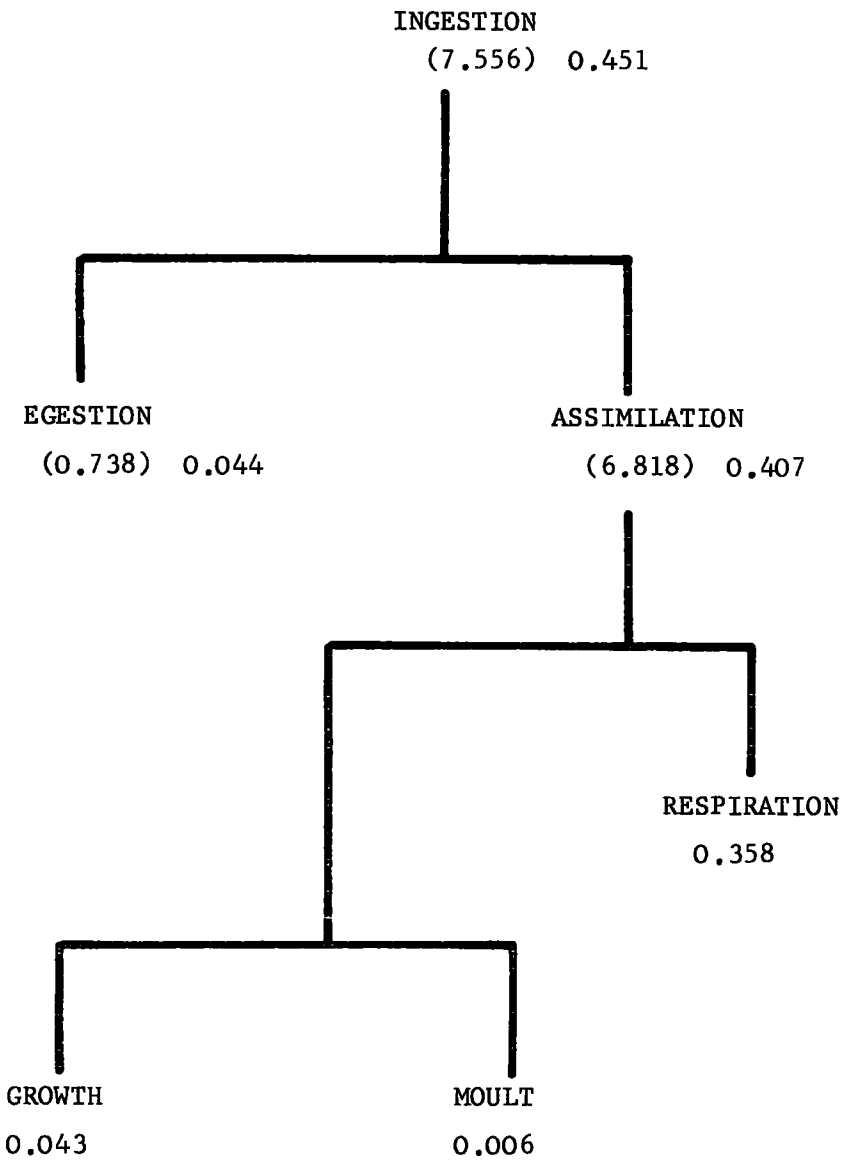


Fig.77.

Energy budget for Instar 10 larva

All values expressed as calories/individual of 14.00mgs/24 hours.

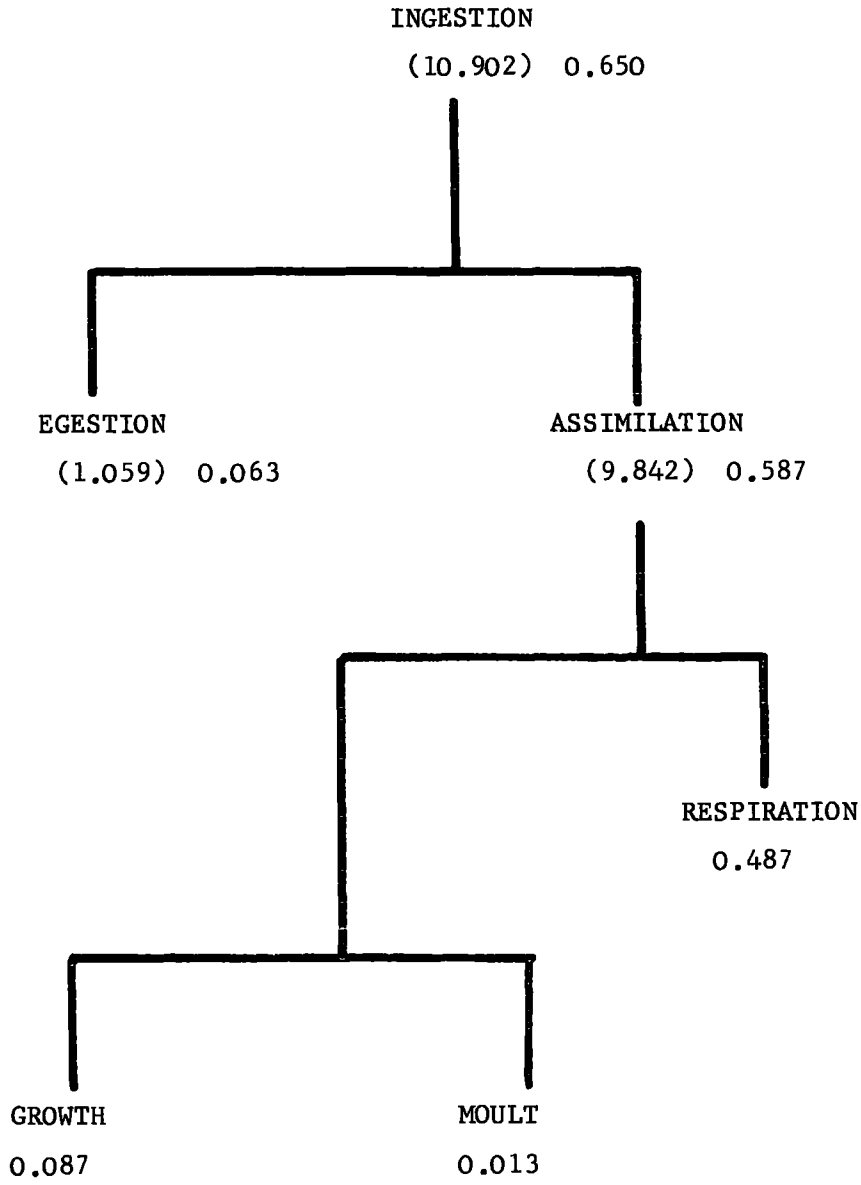


Fig.78.

Energy budget for an Instar 11 larva

All values expressed as calories/individual of 20.50mgs/24 hours.

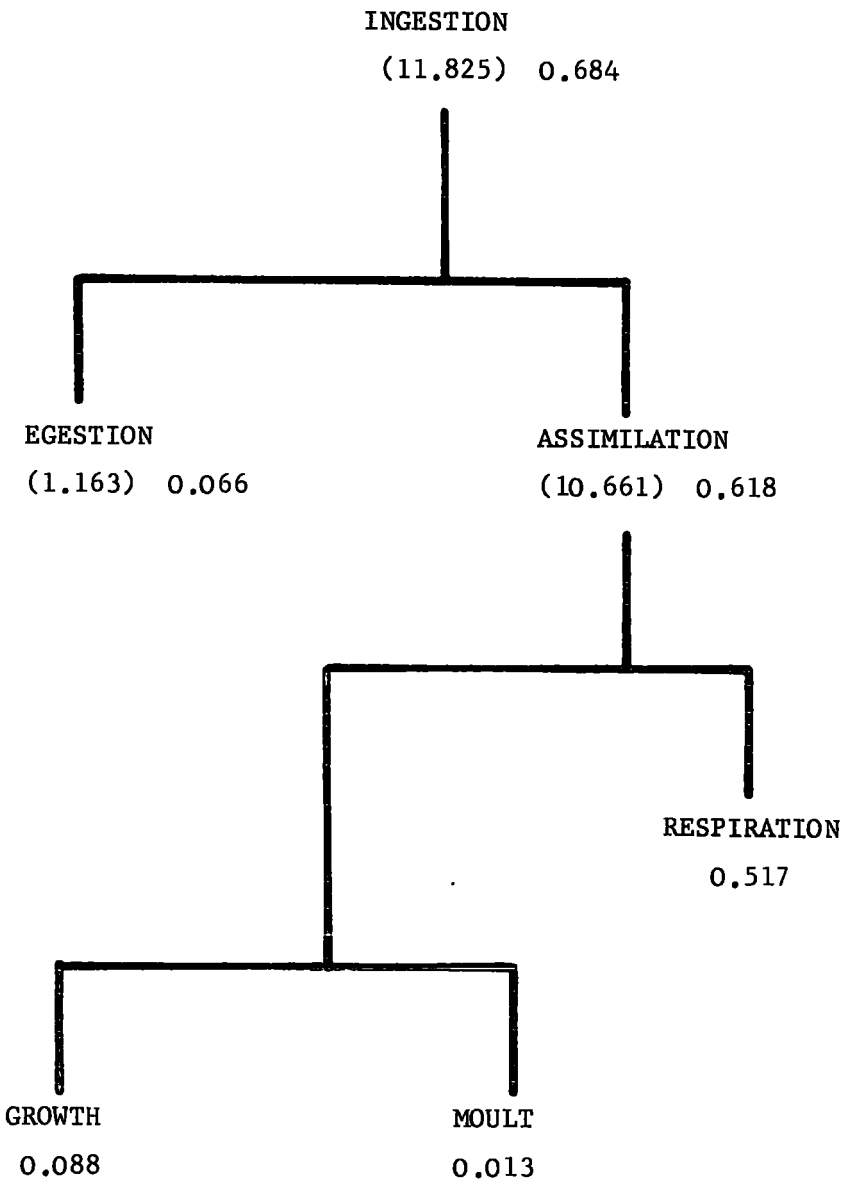


Fig.79.

Energy budget for an Instar 12 larva

All values expressed in calories/individual of 34.50mgs/24 hours.

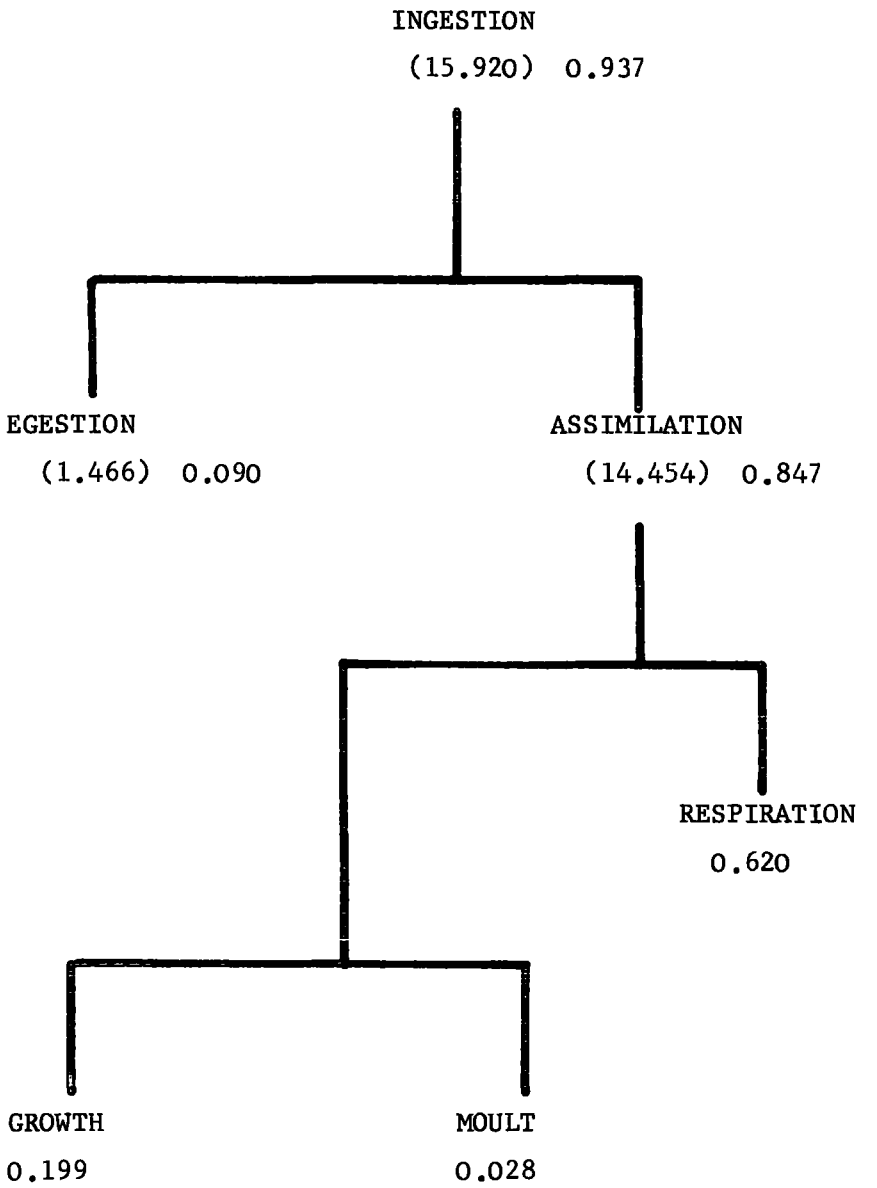


Fig.80.

Energy budget for Instar 13 larva

All values expressed as calories/individual of 59.20mgs/24 hours.

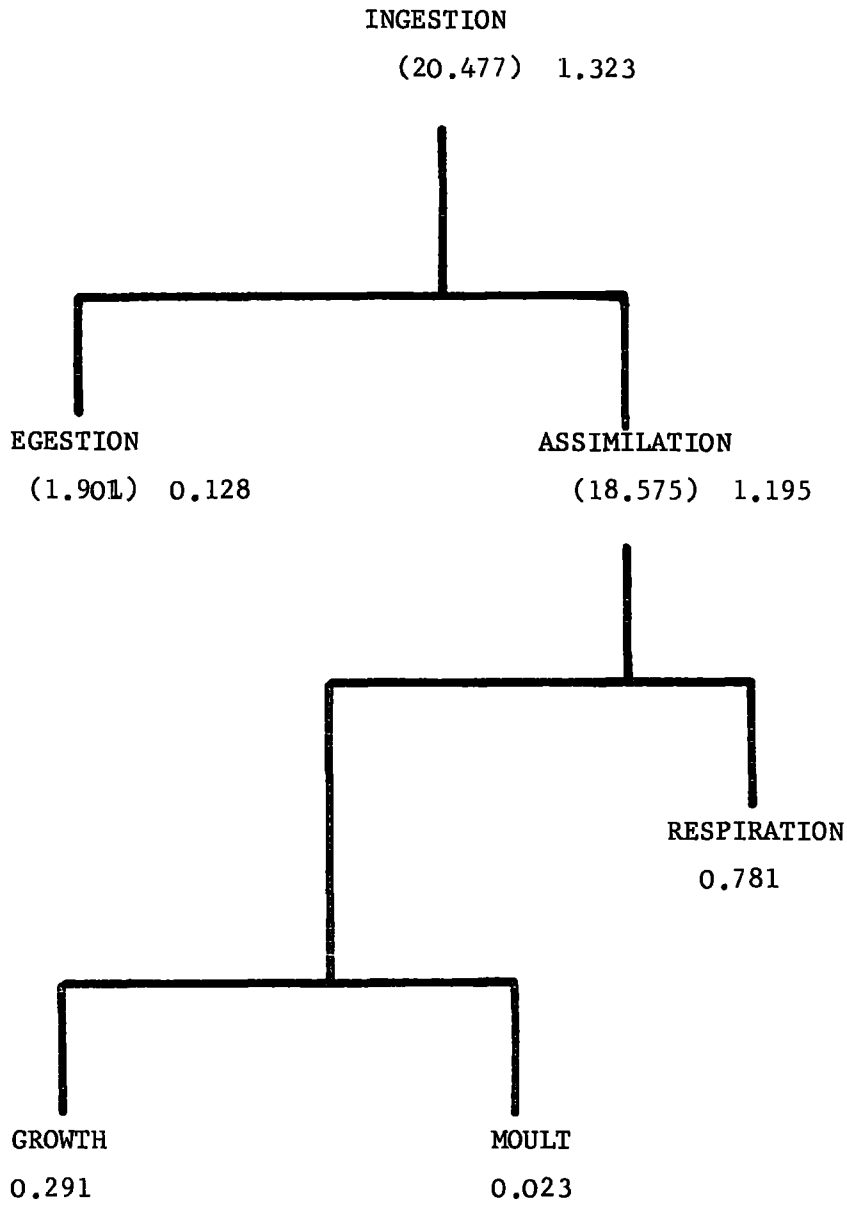


Fig.81.

Energy budget for an Instar 14 larva

All values expressed as calories/individual of 88.50mgs/24 hours.

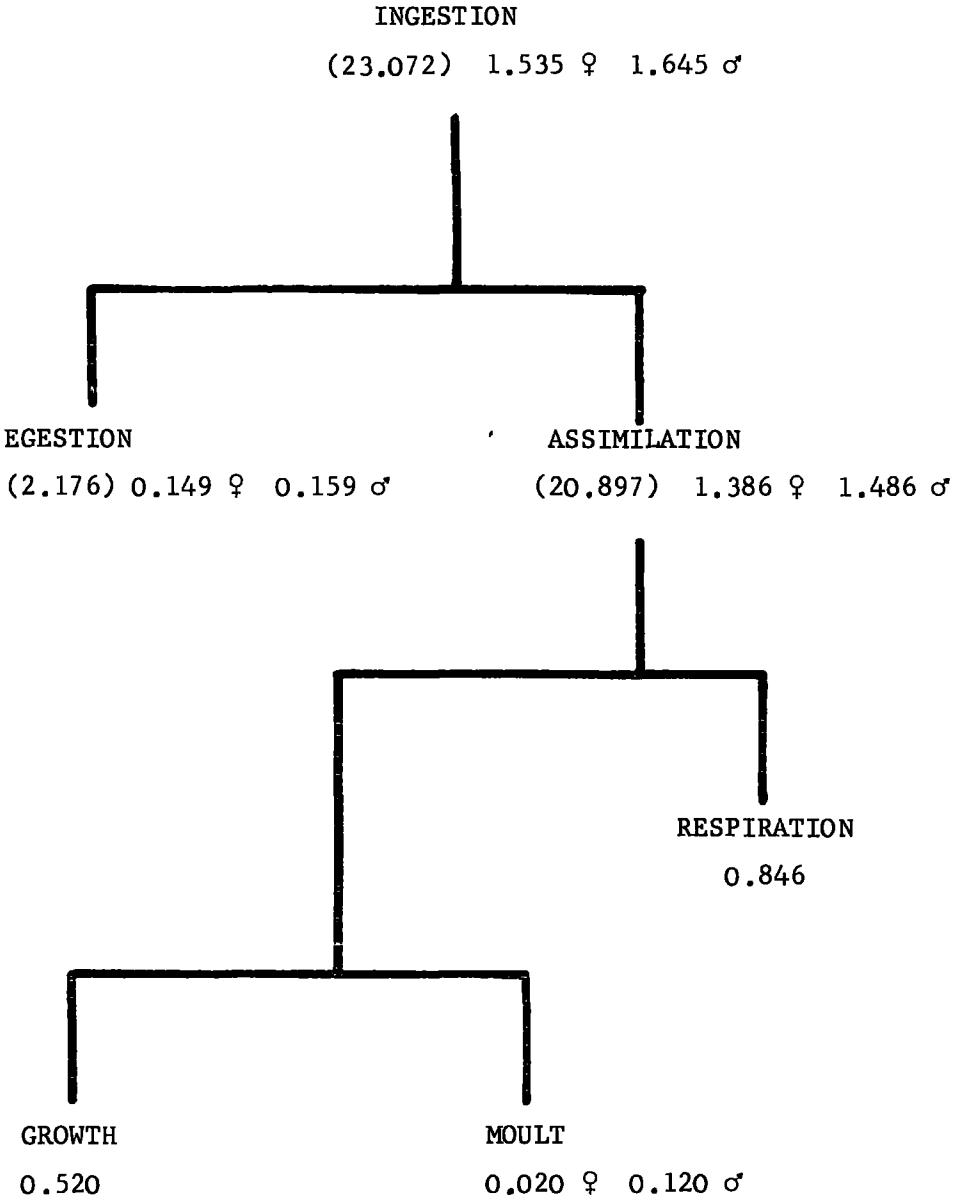
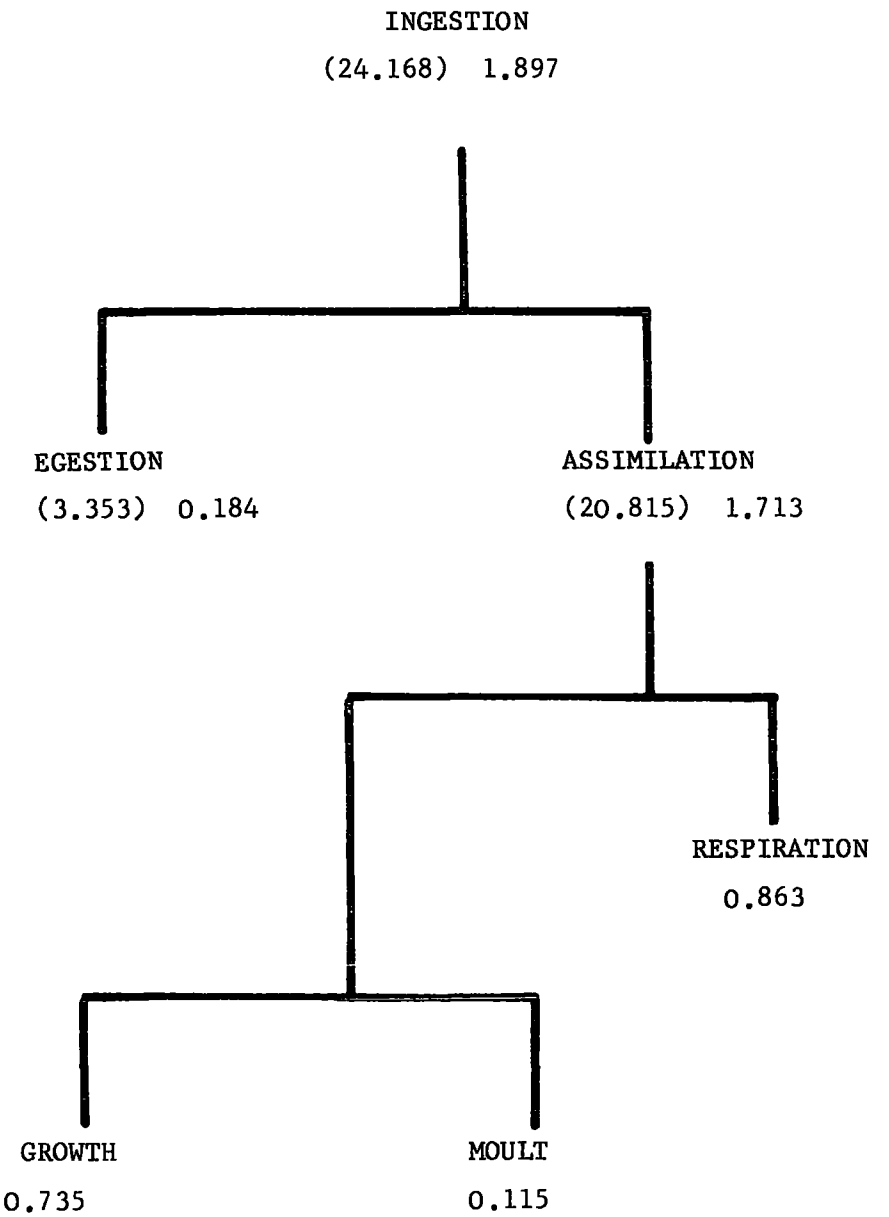


Fig.82.

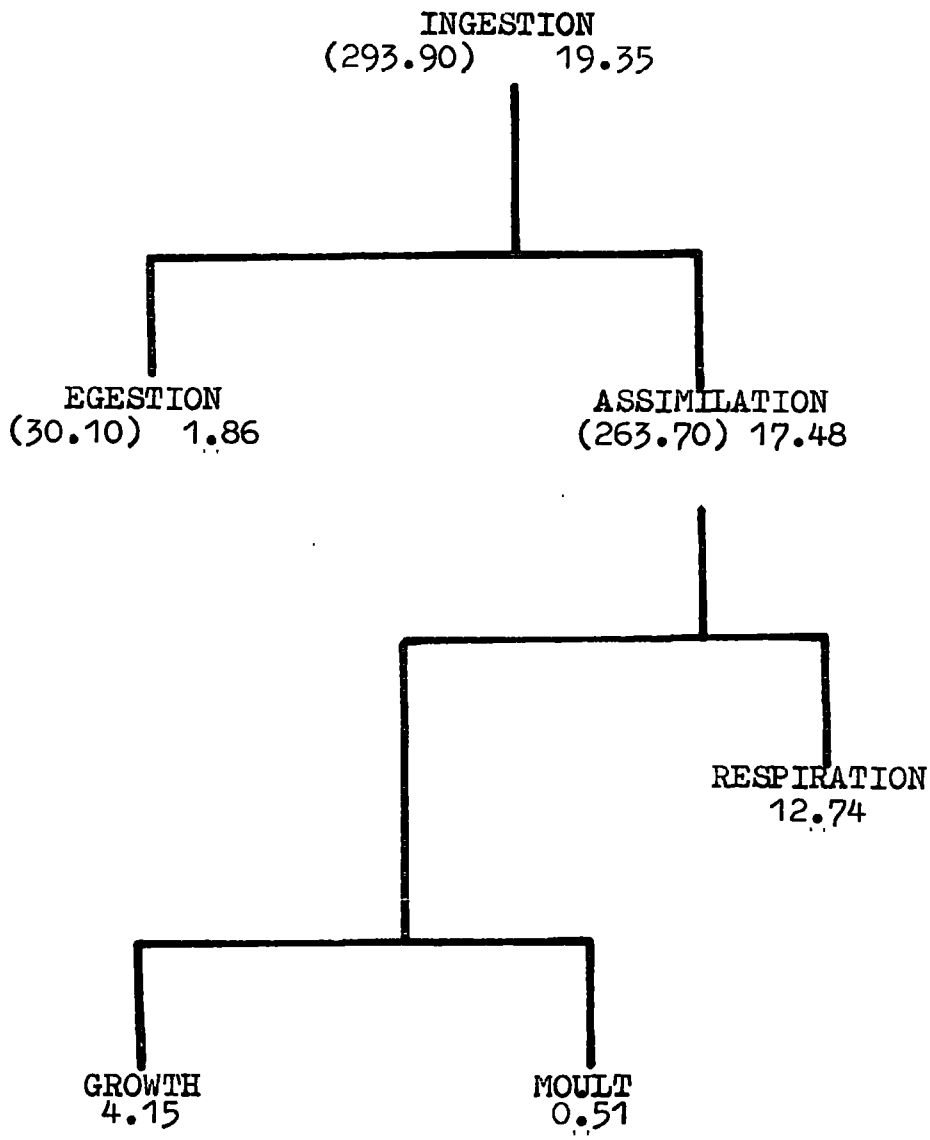
Energy budget of an Instar 15 larva

All values expressed as calories/individual of 119.80mgs/24 hours.



Mean energy budget of larval M.rufipes applied to biomass data. Fig.83.

Mean biomass = 1.966 gms./100L. timber/yr. (Chap.6.)
Mean weight M.rufipes =23.81mgs. Mean ingest.=0.642cals/day.
Mean assim.=0.580cals/day. Mean egest.=0.062cals/day.
Mean resp.=0.423cals/day. Mean moult =0.017cals/day.
Mean growth =0.138cals/day.
∴ Energy turnover K.cals/100L.timber/year =



Discussion

The assimilation percentage of 90.3%, on a calorific basis for M.rufipes is one of the highest yet recorded for a carnivorous invertebrate. However, it is comparable to the data of Lawton (pers.comm.1968) who obtained a range of 87 - 95% assimilation, in calories, by Pyrrhosoma nymphula (Sulz), a damsel fly. A probable explanation of the twelve to fourteen-fold difference, found between the laboratory experimental feeding rates and those found by summation, can be put forward. Evans and Gough (1942) and Zacharuk (1965) have all stated that wireworms are sporadic feeders and during the moult and pre-moult periods are known to fast for up to ten weeks, even in the presence of food. Clearly this could account for up to 20% of the discrepancy.

In the laboratory feeding experiments data was collected only from the 28.9% of animals which fed, those not feeding being ignored. However, if all the laboratory experiments are taken into account, it is possible to reduce the discrepancy by approximately 70%. As an example, it is possible to use the data in Fig.83 for assimilation. In this figure the experimental value was 263.70 Kcals/yr as opposed to the calculated value of 17.48 Kcals/yr. Thus a reduction of the difference by 70% would mean that the experimental value would become 79.1 Kcals/yr as opposed to 263.70 Kcals/yr, which reduces the discrepancy to only 4 times the amount obtained by summation (17.48 Kcals). The calculation of the feeding rates also assumed that daily feeding

occurred in M.rufipes, however all the available evidence indicates that a single meal will last the animal much longer than 24 hours. The histological data presented in Chapter 1 revealed the presence of large fat bodies, which are probable metabolic stores, thus energy could be stored for use at a later time. It appears to be characteristic of many carnivores that they eat as much food as they can, when it is available; obviously the values obtained in the laboratory feeding experiments represent maximum feeding values. It is probable that M.rufipes will take in such quantities of food, when it is available in the field, but will not feed daily. It is not clear whether M.rufipes feeds during the winter months or not. Certainly larvae could not be induced to feed in the laboratory below 7.5°C. The temperature data (Chapter 1) shows that the field temperature commonly falls below 7.5°C during the winter. The calculation of animal feeding rates from laboratory data assumes that feeding occurs throughout the year.

Thus it is possible to trace a number of variables, which would account for the high feeding rates obtained in this study. Clearly further work is necessary to isolate these errors. At this time the most meaningful estimate is probably that calculated by summation although the laboratory rates should be noted for comparison even though they are very high.

SECTION IV.

Discussion

M.rufipes was shown to have 14 or 15 instars, depending on the sex of the animal, and that a considerable time was necessary, 7 - 8 years, to complete these stages. Basden (1950) stated that an animal with a complex life history can be studied, if a number of larvae from each growth stage are observed and that data can be amassed to give a complete picture of the life history. This approach has been adopted and extended in the present study, to encompass bioenergetic measurements at each growth stage. Data concerning the general biology and ecology of M.rufipes are also presented, as little previous data was available and to provide a background for the study.

Of special note was the use of polymodal analysis methods (Harding 1949) to determine the numbers of instars present during the life-cycle of M.rufipes. This method proved most valuable and would clearly be of use in the solution of similar problems in other species. Dyar (1890) demonstrated that the head capsules of certain insects grow in a regular geometrical fashion, accordingly, if the logarithm of head width is plotted against instar number, a straight line is obtained. Such a plot was carried out for M.rufipes (Fig.27), which agrees with Dyar's principle, in that the growth of the head capsule was linear. A graph of this type is also of use

as a check, to see if all instars are accounted for, in a range of measurements. Such a procedure formed the basis of the pilot study (Chapter 2), which gave the approximate instar groupings.

Przibram (Wigglesworth 1965) states that the weight of an insect doubles at each instar and that the linear dimensions are increased by 1.26 or $^{3}/_{2}$. Using data obtained during the present study, the increase in linear dimensions of M.rufipes was found to be 1.18 ± 0.08 at each moult, not 1.26 as predicted by Przibran (Table VII). From this it was possible to calculate the theoretical weight increase at each instar:-

$$\frac{1.18}{1.26} \times 2$$

$$= 1.88$$

Data presented in Chapter 10 showed that the measured weight increase at each instar for M.rufipes was 1.57 times. Both values of Przibram's rule are therefore over-estimates for M.rufipes.

Data concerning the moulting activity of M.rufipes indicated that the moulting pattern changes with age. Fernando (1963) believes that optimum size may be the factor controlling moulting. Thus any animal has to reach an optimum size before it can moult to the next instar; it is probable that the optimum size is reflected by Przibram's factor of 1.18 obtained in this study. Clearly the length of time taken to fulfil this increment

will depend on such factors as food availability, quantity and quality, and other environmental factors such as temperature. The variability of these factors will lead in extreme cases to variability in moulting, overlapping of instars, and an increase in the length of the life cycle. In the present study certain individuals moulted without any increase in their linear dimensions or weight (Chapter 10). Usually these animals ceased to feed and died. This is the first report of the phenomenon in M.rufipes, but it has been found in other wireworm species by Hyslop (1917), Strickland (1939), Thomas (1940), Evans and Gough (1942), Begg (1956), Zacharuk (1962), and Fernando (1963). It may be a characteristic phenomenon of wireworms. Begg (1956) believes it is the result of adverse conditions. Possibly the optimum size of that particular instar is not reached, but hormonal influences cause the animal to moult before it is ready.

The programme of population sampling was carried out to provide biomass data for application to the bioenergetics data. As reported, the programme was modified to include random samples and "whole log" samples. In the latter programme it was only possible to remove one "whole log" a month to avoid habitat destruction and depletion of M.rufipes resources. The total volume of timber removed in any "whole log" by sample was at least equivalent, and often exceeded, the total volume of 18 random samples removed from Wynyard.

Standard food preference studies aided by flame photometry investigations indicated clearly that M.rufipes has a distinct preference for animal foods. The use of flame photometry was very successful and could be used to solve similar problems in other feeding studies. King (1959) tried to change the ionic ratios of Na : K by feeding the normally carnivorous Limonius agonus Say on potato but was not successful. Therefore flame photometry should be a reliable indicator of the true diet of M.rufipes and other insects.

Wireworms are normally thought of as being rampant herbivores, howeverKring (1922) reported that Melanotus spp. were carnivorous, feeding on any wood-boring larvae. Subklew (1934) noted that a large number of elaterids were carnivorous, especially those inhabiting rotting timber. A number of authors believe that a protein meal is necessary for proper growth in wireworms. Dobrovsky (1954) found C.vagus (Cand) was unable to grow until a protein meal was taken, even if it was cannibalistic. Kring (1959) reported that L.agonus Say would not moult or survive without a protein meal. Zacharuk (1963) made a similar observation on D.linearis L. Cannibalism is found in many wireworm species, but according to Fernando (1963), not in M.rufipes; however in the present study cannibalism was noted in this species, at least in the laboratory. This may be a phenomenon of overcrowding as suggested by Horst (1922) or a need for a protein meal.

During the present feeding studies unforeseen difficulties were found such as lack of data for early instars. This was remedied as far as possible by extrapolation from late instar feeding data. Of particular note was the high assimilation percentage of 86.5% by weight or 90.3% by calories. This is comparable to the data of Phillipson (1960a : b) and Lawton (pers. comm. 1968). This figure is higher than data for assimilation in terrestrial herbivores, which range from 12% - 45%. However, high assimilation percentages have been found in some herbivorous planktonic animals by Lasher (1960), Marshall and Orr (1963) and Conover (1964 : 1965a : b), who found assimilation percentages ranging from 50% - 80%. Even fewer records have been made of assimilation in carnivores, apart from those quoted above. Mainly data has been collected on carnivorous vertebrates. Ivlev (1939), Gerking (1955), Davies (1960 : 1964 : 1965) and Mann (1965) found values of 80% - 97.3% for various fish. It appears that many carnivores, particularly those feeding on soft or'fluid' food, have a high assimilation rate. Plant material tends to contain more unusable material which lowers the assimilation rate in herbivores. It is thought, in the present study, that M.rufipes is an "efficient" feeder as the evidence indicates that pre-digestion occurs, therefore fluid food is ingested, which will contain little waste material, leading to the high assimilation percentage found.

Respiratory measurements were made to estimate the annual respiratory loss. Macfadyen (1960), Phillipson (1961) and Phillipson and Watson (1965) advocate the measurement of respiratory rates on a 24 hour basis as many animals exhibit diurnal rhythms. M.rufipes was also treated in this way but showed no diurnal changes. Diurnal rhythms will be characteristic of animals subjected to a day and night regime, but not M.rufipes which inhabits a burrow where darkness is continuous. Phillipson (1967a) has also stressed the need to carry out respiratory measurements throughout the year. This was done in the present study, the results showed that marked seasonal differences were apparent, reinforcing the viewpoint that respirometry on a seasonal basis ensures reliable data.

Phillipson (1963) described four methods of computing respiratory data. In the present study, three of these are considered; the fourth method based on gonad condition is not applicable. Method 1, oxygen consumption/unit weight/unit time plotted against weight, and Method 2, the oxygen consumption/unit weight on a monthly basis, are already discussed. Method 3, the oxygen consumption/individual/unit time against weight, plotted logarithmically, was also calculated. Instead of the expected straight line relationship, a curve was found. This was substantiated by Warburg check data. Bertalanffy (1957) gave examples of data treated in this way for Tenebrio sp., but larvae below 20mgs were not considered. It is these animals which show

the greatest change. As Phillipson (1963) pointed out, data treated in this manner assumes a linear relationship, which may not exist. Clearly, in M.rufipes, consideration of data in this way could have led to an under-estimate of early instar respiration.

It is clear from the micro- climate data (Chapter 1) that respirometry carried out at 15°C may not reflect the field condition. In order to make this data comparable to the field situation, a compensation factor was calculated and applied, using the known field temperatures. The respiratory rate was seen to be dependent on temperature (Fig.52) and acclimatization did not appear to affect the respiratory rate. This phenomenon may be due to the stable temperature conditions found inside the larval galleries in logs (Macfadyen 1957).

Both Evans and Gough (1942) and Zacharuk (1963) have reported on the fasting periods of various wireworm species, leading to a sporadic feeding pattern. It was also noted by Evans and Gough (1942) that animals even gained weight during these fasts. This, they explained, was caused by absorption of water through the cuticle and that shortly after moulting the water was replaced by an equivalent amount of tissue, as soon as feeding recommenced. This would explain why wireworms and in particular M.rufipes can undergo notable weight changes, as shown in the laboratory growth data (Chapter 10).

Bertalanffy (1957), in his theories concerning metabolism and growth, stated that in insects catabolism and anabolism increase at the same rate, therefore growth rates do not decrease with time, but in fact increase. According to Bertalanffy growth in insects is not limited, at least not in the larval stages, but is exponential, no steady state being attained. Growth is brought to an abrupt halt by metamorphosis, during which there may even be a decrease in weight as large amounts of tissue are broken down to form the imago. This pattern is evident in the growth curve presented for M.rufipes (Fig.65), from which it was possible to calculate the growth rates per instar.

Once all the bioenergetic parameters were calculated and converted to calories, it was possible to construct energy budgets for all the life stages of M.rufipes. The mean calorific data was applied to the mean biomass data (Fig.83). According to this, the energy stored by M.rufipes as growth per year, (excluding moulted exoskeleton), was 3.64 Kcals/100L of timber, the energy ingested being 19.35 Kcals/100L/year. Respiratory loss accounted for 12.74 Kcals/100L/year or approximately 60% of the energy ingested.

In the present study M.rufipes had a secondary production/respiration ratio of 28.6%. Wiegert (1965) found this ratio to vary between 53% - 63% in grasshoppers, which is in agreement with Smalley (1960) who obtained a value of 58% for marsh grasshoppers.

In a previous study Wiegert (1964) obtained the very high value of 71% for meadow spittlebugs. Engelmann (1961) obtained a value of 22% for oribatid mites and explained that a long generation time will lower the value. The figure of 28.6% for M.rufipes is low, but M.rufipes has one of the longest generation times ever investigated from a bioenergetic viewpoint. Even lower values have been recorded by Golley (1961) and Odum, Connell and Davenport (1962), for rodents, but as these are homiotherms they are not strictly comparable as their metabolism is much higher. However, Golley and Gentry (1964) found values of 1% for the southern harvester ant, this low value probably being correlated with the extreme activity exhibited by the group.

Clearly, according to the bioenergetic equations, the rates of ingestion, assimilation and faeces production do not equate with the remaining parameters of respiration and growth. The reasons for this were discussed in Chapter 12. This emphasizes the fact that laboratory feeding data for bioenergetic studies must be considered with care, at least for carnivores of this type. It is probably more difficult to design feeding experiments for carnivores than herbivores, especially to be able to simulate near-natural conditions and make accurate measurements of the parameters. Too little is known of carnivores and feeding. Holling (1961 : 1965 : 1966) has illustrated the complexity of the feeding responses of carnivores and has divided them into four main exponents :-

1) the time the predator and prey are exposed

2) the searching rate

3) the handling time

4) hunger

Nos. 1 - 3 are self-explanatory, indicating the time taken up with these activities. Especially important to M.rufipes is the searching rate. The number of contacts made with any prey animal must be fairly low as the timber is ramified by many interlacing passageways. Component 4, hunger, is of special note as it is affected by the rate of assimilation and the food capacity of the gut. Holling (1961 : 1965 : 1966) showed that the more hungry an animal, the more it eats when food is available. Prey density is also shown by Holling to affect the feeding rate. According to Holling (1966), these factors alone can account for a difference in feeding rates of up to 10 times. Clearly these introduce great variables in any feeding experiments on a carnivorous animal. Watson (1966) and Phillipson (1967a) emphasize that laboratory feeding rates do not necessarily reflect field conditions. Richman (1959) and Slobodkin (1960) have both shown that laboratory feeding rates tend to reflect maximum feeding rates, not usually characteristic of field conditions. Thus the high feeding rates of ingestion, assimilation and egestion, obtained in the present study, are maximum feeding rates but are affected by many variables.

Kuenzler (1961), Wiegert (1964) and Saito (1965) calculated the feeding rates of ingestion, assimilation and egestion from the remaining bioenergetic parameters of respiration and growth. This approach was adopted in the present study, so that comparisons between data calculated in such a way, and data calculated by laboratory experiment, could be compared. It is thought by the author that the rates derived from the other bioenergetic parameters are more meaningful, reflecting the true status quo, as they are comparable in magnitude with data obtained by other authors. Clearly the feasibility of laboratory feeding studies, on carnivores of this type, in the laboratory, must be questioned. It appears that rates derived from respiration and growth data are better estimates of field rates with terrestrial carnivores. With these animals it is well nigh impossible to simulate natural or near natural conditions and measure the parameters accurately.

The question arises as to how and when bioenergetic measurements should be measured. A review of methods used to measure bioenergetic parameters has been published by Golley (1968). At present two approaches are available :- 1) All bioenergetic data can be measured in the laboratory at a constant temperature. It may be possible to convert such data to field rates by use of a temperature compensation factor or Q_{10}, providing field temperatures are known. The main objection to this approach is the falsely high values, reflecting

maximum rates, which may be obtained. For certain animals this can be overcome by carrying out experiments under near natural conditions. The use of radio-isotopes to determine metabolic rates may prove of value in such experiments under near natural conditions.

2) The alternative is to make determinations under field conditions, as few as possible. It may now be more feasible to adopt this approach more often, by the use of radio-isotopes. But to do this successfully, a very amenable experimental animal has to be found, and it is well known that these are rare.

At the present time the laboratory approach seems to offer the best solution to the problem. Such data can be applied to field measurements of population numbers and temperature.

In the present study a partial attempt was made to do this and respiratory data was calculated in the laboratory and compensated to the known field temperatures. As time was the limiting factor, the approach was not extended to the other bioenergetic parameters, but some indication of the magnitude of compensation may be gained from this data.

It is hoped that the present study makes some contribution to further the knowledge of energy flow in a carnivorous invertebrate. Further comparisons may be made when data is available for other carnivorous invertebrates.

SECTION VIII

Summary

1) An outline of the present study was presented, together with reviews of bioenergetic principles and previous bioenergetic studies.

2) Little previous data was available concerning the general biology and ecology of M.rufipes. In order to provide background data for this study, the morphology and anatomy of the larvae was studied and described, together with information on the ecology of this animal.

3) The adult morphology and anatomy were described with special reference to egg production and the reproductive apparatus. The mean value of egg production was 260.4 eggs/female. The mean weight of a single egg was 0.0624 mgs.

4) Information was presented on decay of timber and its effect on the distribution of M.rufipes. Details of the habitat microclimate were also given.

5) Analyses of the head width frequency distribution, in relation to the instar number, revealed that M.rufipes has 14 instars in males and 15 instars in female animals. Data were presented giving the mean head width per instar, and its range.

6) The head width data was discussed with special reference to Dyar's Law.

7) Data concerning the moulting frequency of M.rufipes revealed that two moulting peaks were found during the year, in spring and autumn. In addition, a summer moult was found in the early instars. Therefore the moulting pattern of 3 - 2 - 1 was seen to change with age.

8) The length of the life cycle was found to be 7 years in males and 8 years in females, females undergoing an extra moult, probably due to the larger size of their reproductive apparatus.

9) The major study areas of Wynyard Wood, Great High Wood and Park End Wood were described.

10) In order to gain population estimates, random samples were made to ascertain distribution, and 'whole log' samples taken to determine numbers of M.rufipes. Details were presented concerning the annual change in biomass.

11) In order to determine the energy flow through a population of M.rufipes, it was necessary to solve the bioenergetic equations :-

$$C = A + F \qquad \ldots\ldots\ldots 1$$

$$A = R + Pg + Pr + U \qquad \ldots\ldots\ldots 2$$

C = energy consumed

A = energy assimilated

F = energy egested

R = energy respired

Pg = energy of bodygrowth

Pr = energy of reproduction

U = energy of excretion

12) Feeding rates were determined in order to fulfil the first equation.

13) Simple food preference trials indicate that M.rufipes has a definite carnivorous preference.

14) By using the technique of flame photometry to determine the ratios of Na : K it was possible to make further dietary investigations. It was concluded that this method has a great potential in discovering the feeding regimes of insects.

15) The mode of feeding was described. It was noted that the products of ingestion and faeces production were fluid.

16) Feeding experiments were designed in which the rates of ingestion, assimilation and faeces production could be determined. The rates for the early instars were extrapolated from data collected on the later instars.

17) A very high assimilation percentage of 86.3% by weight was found.

18) The measured values of ingestion, assimilation and faeces production appeared to be high. This was probably due to the sporadic nature of feeding as well as the assumption that the animal feeds daily.

19) No evidence could be found that the adults feed. No feeding was observed in the laboratory.

20) The annual respiratory loss of the larvae and adults was determined using a continuously recording respirometer over a 24 hour period. No respiratory diurnal rhythm was detected.

21) On plotting the oxygen consumption per unit weight for each month the expected L-shaped curve was found.

22) The effect of temperature on larval respiratory rates was determined and a compensation factor calculated. The annual respiratory metabolism was corrected by the known field temperature, using this data.

23) The annual respiratory metabolism was calculated for both larvae and adults. The former showed a low winter-spring rate and a high summer-autumn rate. The latter showed varying rates which were correlated with the developmental stages.

24) Data was presented on the daily respiratory loss of each instar both per unit weight and per individual. A straight line relationship was found between the respiratory rate and instar, when plotted on a single log plot.

25) Investigations were made into the effect of size on respiration. A curved relationship, rather than the expected straight line relationship, was found. This was corroberated by short-term Warburg experiments. It was thought this may be due to a greater efficiency of growth, in the early instars, for only a little extra respiratory loss.

26) Additional respiratory data was given. It was shown that the release of CO_2 by M.rufipes is in short bursts, rather than being continuous.

27) It was shown that feeding and starvation had little or no effect, on the respiratory rate of M.rufipes.

28) Investigations suggested that acclimatization is not shown, in M.rufipes, as respiratory compensation.

29) In order to make all data comparable, a series of weight determinations was made. These were presented as wet weight - head width data, wet weight - instar data, and wet weight - dry weight data for whole animals. Exuvium weight data was also presented.

30) Growth rate studies were set up in the laboratory but were not successful. The growth rates for energetic purposes were calculated from laboratory and field data. A growth curve for M.rufipes was presented. Daily growth rates were calculated from this data.

31) The calorific values of whole animals, larvae and adults, as well as exuvia, food, faeces and eggs were determined using a Phillipson micro-bomb calorimeter.

32) The calorific equivalents for all parameters of the energetic equations were presented. From these data individual energy budgets were constructed for each instar.

33) The percentage assimilation, on a calorific basis, was 90.3% and was comparable to 87% - 95% obtained by Lawton (pers.comm. 1968) for P.nymphula.

34) The mean energy budget as applied to the mean biomass data was presented as a 'best estimate'. Mean ingestion was found to be 19.35 Kcals/100L/yr., assimilation 17.48 Kcals/100L/yr., egestion 1.86 Kcals/100L/yr, respiration 12.74 Kcals/100L/yr,

and growth 4.15^{5} Kcals/yr. All values from summation of respiration and growth.

35) On a calorific basis the rates of ingestion, assimilation and egestion were found to be twelve to fourteen times greater than the remaining parameters. This was thought to be due to the sporadic nature of feeding and the incorrect assumption that M.rufipes fed daily.

36) Respiration was shown to account for 60% of the energy ingested, or 74% of the energy assimilated.

37) A value of 28.6% was found for the ratio of secondary production/respiration.

38) It was noted that M.rufipes was an interesting animal bio-energetically as it is a carnivore and in addition has a complex life-history.

39) The feasibility of laboratory and field studies for bio-energetic studies was discussed.

40) It was finally concluded that laboratory studies in conjunction with field data are, at present, the best approach to bioenergetic studies.

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Appendix 1.

Wynyard site - plant species 1965-68. (after M.K.Hughes).

Trees

Betula spp - hybrid variety.
Alnus glutinosa (L) Gaeitn.

Ferns

Dryopteris felix-mas (L). Polystichum setiferium (Forsk)
Pteridium aquilinum (L) Kuhn.

Forbs and shrubs

Mercurialis perrenis L.	Ajuga reptans L.
Viola riviniana Rchb.	Circaea lutetiana L.
Potentilla sterilis(L) Gorche.	Potentilla reptans L.
Geum urbanum L.	Rubus fructicasus agg.
Chamaenerion angusti-folium(L) Scop.	Cirsium sp.
Rosa canina L.	

Grasses

Deschampsia caespitosa(L) Beauv.	Arrhenatherium elatius(L).J&C Presl.
Holcus mollis L.	Holcus lanatus L.
Agrostis tenuis Sibth.	Poa trivialis L.

Tree species in field layer

Crataegus monogyna Jacq.	Acer pseudoplatanus L.
Quercus spp.	Sambucus nigra L.

Mosses and leafy liverworts

Mnium hornum Hedw.	Polytrichum formosium Hedw.
Eurhynchium striatum (Hedw) Schp.	Eurhynchasum praelongum (Hedw) Hobk.
Dicronum scoparium (Hedw)	Hypnum cupressiforme Hedw.
Dicronella heteronalla (Hedw) Schp.	Thuidium tamariscinum (Hedw) Bad
Pellia sp.	Fissidens sp.
Lophocollen heterophylla (Schras) Dorn.	

Appendix 2.

Summary of species found during log extraction

OLIGOCHAETA

Denorobaena rubida tenuis (Eisen)
Various Enchytraeid worms

ARACHNIDA

Nemastoma lugubre (Mull)
Various unidentified spiders and speudoscorpions
Various Acarina in large numbers

ISOPODA

Oniscus asellus L.
Trichoniscus pusillus provisonus (Raeovitza)

DIPLOPODA

Cylindroiulus punctatus (Leach)
Julus sp.
Polydasmus sp.

CHOLOPODA

Lithobius crossipes L.
L.forticatus (L)
Brachygeophilus truncorum (Bergso on Meinert)

COLLEMBOLA

Isotoma sp.
Various other spp.

DIPLURA

Campoden sp.

COLEOPTERA

Melanotus rufipes Hbst.
Dolopius marginatus L.
Linonius minutus L.
Denticollis linearis L.

COLEOPTERA (Contd.)

Athous haemorrhoidalis (F)
Various Staphylinidae spp.
inc. Tachyponus sp.
Boetrychroae sp.

DIPTERA

Tipulidae spp.
Cecidomyidae spp.
Ceratopogonidae spp.
Chironenidae sp.

Xylophogidae sp.
Rhagionidae spp.
Asilidae sp.
Empidae sp.
Lonchopteridae sp.
Symphidae sp.
Farnica caralicularis L.
Various Muscid spp.

GASTROPODA

Agrion subfuscus (Drap.)