Bioenergetics of a predatory beetle Nebria brevicollis (F) (Coleoptera, Carabidae)

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Bioenergetics of a predatory beetle
Nebria brevicollis (F)
(Coleoptera, Carabidae)

by

N. MANGA. M.Sc. (Dunelm)
Graduate Society

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

September, 1970.

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SUMMARY

1) Energy flux through a predatory beetle population was investigated. A population study of *Nebria brevicollis* (F.). (Coleoptera, Carabidae) was made on a old-field grassland. Population densities of $3.45/m^2$/larvae and $0.428/m^2$/adults were found.

2) The mean monthly soil/air interface temperatures were measured by means of the Pallmann/Berthet temperature integrator. Field temperatures were used to extrapolate metabolic data to the field situation.

3) The calorific values of *Nebria* increased with developmental stage. The pre-diapause female had the highest calorific value. The calorific values of *Nebria* material ranged between 4.5 - 6.1 K cal /g, which is in agreement with the range recorded for other Coleoptera.

4) Food preference experiments showed that *Nebria* preferred Collembola and dipterous larvae. Feeding periodicity was absent. The assimilation efficiency $(\frac{C - (F + U)}{C} \times \frac{100}{1})$ based on preferred foods was affected by temperature, size, and prey type. The percentage assimilation figure (50 - 90%) fell within the range shown by other terrestrial predators.

5) Adult consumption was estimated in both laboratory and field. Field consumption was estimated from field faecal production in

conjunction with gut clearance time and percentage assimilation. Feeding rates in the field were much lower than those recorded in the laboratory. The mean adult consumption in the field (2.41 mgs) during the pre-diapause period was only 66% of the value recorded in the laboratory.

6) Respiratory rates were affected by several factors. Metabolic acclimation to temperature was not shown. The Q_{10} values between 5° and 10°C was 3.37, and between 10° and 15°C it decreased to 2.90. The annual respiratory metabolism amounted to 414.70 cal $/m^2$.

7) The peak production occurred in January. The larvae contributed about 86% of the total population production (389.4 cal $/m^2/yr$). Exuvium production was only 2.16% of the total production. The production/respiration ratio $(^P/R)$ was 1 : 1.

8) The annual energy flux through the population was low (803.9 cal $/m^2/yr$). Ingestion peaks occurred when the adults were preparing for diapause, and during the reproductive period. The annual population consumption amounted to 1036.64 cal $/m^2$, of which 37% was channelled into production, 40% was lost as respiration, and 22.5% lost as faecal production. Population growth efficiencies were calculated as P/C = 37.6%, and P/A = 48.4%.

9) It was concluded that the contribution of *N. brevicollis* to the flux of energy through the studied ecosystem was relatively small.

CONTENTS

N.B. At no point in this thesis does the use of a capital letter in the word 'calories' imply Kilocalories.

Cals or cals = gram calories
Kcals or kcals = kilocalories

CHAPTER 1

Introduction

Lindemann (1942) proposed a trophic-dynamic model of an ecosystem, and since that time increasing attention has been paid to the measurement of energy flux, both through ecosystems and individual species populations. Energy flux (defined as the sum of production and respiration) is recognised as a reasonably reliable criterion for a functional comparison of different ecosystems, and as a means of evaluating the role of individual species in promoting energy flow within ecosystems.

Most of the available literature on energy flux studies concerns herbivores. Very little has been done on carnivores. The present investigation was made at the species population level, the species studied being the predatory carabid beetle *Nebria brevicollis* (F). It has a simple life history and is therefore ideal as the subject of an energy flux study. In terms of numbers it was the 'key' beetle in the study area. Carabid beetles are common in woodland litter and grassland. Most carabid species are carnivorous, therefore, a study on *Nebria brevicollis* would give some indication on the importance of Carabids in the ecosystem, particularly in terms of their contribution to total energy flux.

During the course of the study attempts were made to estimate independently all parameters of the energy flux equation $C = P + R + (F + U)$ for each of the life stages of N. brevicollis. The energy flux equation has been presented in a number of ways but the present formula $C = P + R + (F + U)$ follows Ricker (1968) where

C = energy of consumption
P = energy of production (growth + reproduction + exuvia)
F = energy of faeces
U = energy of urine

The sum of P + R is frequently termed assimilation and denoted by symbol A, hence

$$A = P + R$$

$$\text{or} \quad A = C - (F + U)$$

In many instances, particularly with invertebrates it is difficult in practice to separate egesta (F) and excretory products (U), consequently these are frequently measured together, hence (F + U). Theoretically U is a product of assimilation and should be included in A, i.e.

$$A = P + R + U$$

However, U is generally considered to be a small fraction of A and the error involved in including U with F is thought to be negligible.

In ecological evaluations of field situations it is clearly desirable to make as many measurements as is possible under field conditions. However, certain energetic parameters cannot at present be obtained with any accuracy in the field and must be measured under semi-natural and laboratory conditions. This is particularly true of soil dwelling organisms. The present study of N. brevicollis in all its life stages combined both laboratory and field estimates. Micro-climate (temperature), production (growth), and population density were determined in the field and percentage assimilation and respiration were measured in the laboratory. The respiratory data were used in conjunction with field temperature measurements to estimate annual respiratory metabolism in the field. Adult N. brevicollis consumption was obtained by combining faeces production in the field with laboratory determined percentage assimilation.

Each of the energetic parameters was determined independently and hence it was possible to check the different methods used in this study by combining various parameters, for example, P + R + F = C was used to check the accuracy of field and laboratory estimates of consumption.

The presentation of the information accords with the following pattern. Chapter 2 deals with the study area and its micro-climate (temperature). Information regarding the general biology of N. brevicollis is given in Chapter 3. Chapter 4 is devoted to bomb calorimetry. Individual energetic parameters of assimilation, consumption, production and respiration are discussed in Chapters 5 - 8. Data on population studies and energy flux through the population are presented in Chapter 9 and 10, respectively. Finally, Chapter 11 deals with the General Discussion.

CHAPTER 2

The Study Area and its Micro-climate

The present study was made in a section of the University of Durham Zoological Field Station (Grid ref. NZ 273404). It is situated some 2 km south of the University Science Laboratories at an altitude of 76.50 m. The whole area is quite small (1-2 hectares), slopes gently from east to west, and is primarily grassland overlying a light coloured sandy loam.

Prior to its acquisition by the University in 1962, the Field Station area was regularly grazed by cattle, but since 1965 only selective grazing has been allowed. From 1965 the management programme has been such that the whole area was divided into compartments by means of barbed wire fencing; certain of these compartments have been deliberately grazed, others have been free from grazing. The study area (see fig. 1) was located in an ungrazed compartment measuring 300 x 100 m.

Within the study area compartment the common grasses were *Agrostis stolonifera* (L), *Agrostis tenuis* (Sibth), and *Holcus lanatus* (L); other recorded, but less common, grasses were *Festuca rubra* (L), *Poa pratensis* (L), *Alopecurus pratensis* (L), *Dactylis glomerat~~e~~* (L) and *Arrhenatherum elatius* (L).

/a

Nebria brevicollis (F) was the dominant carabid beetle in the study area and it is studies of this species that are reported in the present work. Other carabids common on the area were *Feronia madida* (F), *Feronia melanaria* (Illig.), *Notiophilus biguttatus* (F), *Notiophilus quadripunctatus* (Dej.), *Loricera pilicornis* (F.) *Abax ater* (Vill.) and *Carabus violaceus* (L.).

To facilitate the study of *N. brevicollis* in the old-field grassland a study area of 75 x 75 m was delineated and marked into four grids.

On this area five temperature recording stations were sited at random. At each of the five temperature stations the soil/air interface temperatures were measured by means of a Pallmann/Berthet temperature integrator (Pallmann et al, 1940; Berthet, 1960).

The Pallmann/Berthet temperature integrator makes use of the temperature dependence, at a constant pH, of the inversion rate of a sucrose solution to monosaccharides

$$\text{Sucrose + water} \longrightarrow \text{fructose + glucose}$$

The amount of inversion as measured by a polarimeter over a known period of time permits calculation of the mean field temperature or, as it is sometimes termed, the ecological mean temperature.

In the present study the "rapid inversion" method was adopted, thereby allowing soil surface temperatures to be integrated over two week periods during the summer and four week periods during the winter. The initial procedure was to prepare two solutions as described by Berthet (1960):

(i) Buffer solution - 3.730 g KCl + 33.9 ml HCl .N made up to 500 ml with distilled water

(ii) Sucrose solution - 400 g sucrose dissolved in 260 ml distilled water + 10 ml formaldehyde (35%). The solution is filtered before storage.

The formaldehyde curbs the growth of micro-organisms and the two solutions, if kept separately in a refrigerator, can be safely used for periods of up to 3 months.

To prepare the integrators for field use on any one occasion, and obtain the required constants for purposes of calculating the mean field temperatures, the integrator fluids (which consisted of well mixed equal amounts of buffer and sucrose solutions) were used to fill nine screw topped bottles of 9 cm length and 25 ml capacity. One integrator was placed immediately in a deep freeze and one of each of another three were placed in constant temperatures of 5°, 10°, and 15°C. After an exactly known period of time the three integrators at temperatures above 0°C were placed in a deep freeze to prevent further inversion. Concurrently with the above procedure the remaining five identically prepared integrators were placed at the soil/air interfaces at the temperature stations.

These were carried to the field in a vacuum flask containing a freezing mixture of calcium chloride and ice, and were eventually transported back to the laboratory in a similar manner.

In the field, care was taken to place the integrators beneath grass cover so that they were sheltered from direct sunlight. After a two week period in the summer and a four week one in the winter the integrators were returned to the laboratory in order to determine their degree of rotation, and hence their inversion rate.

The mean field temperature (T) for each period of exposure was determined according to the equation

$$T = \frac{5854}{Kx - \log K'T}$$

where Kx is a constant and K T equals

$$\frac{1}{t} \log \frac{\alpha_0 - \beta_0}{\alpha - \beta_0}$$

K'T is the inversion constant at temperature T and the pH of the solution, t equals the time in days that the integrators were exposed to field temperatures, α_0 is the degree of rotation at t_0 , and β_0 is the degree of rotation at complete inversion, whereas α represents the degree of rotation at time t.

The value for kx given by Berthet (1960) was found unreliable in so far as it was not possible to replicate exactly the buffer pH used by Berthet. The integrators kept under constant temperature conditions in the laboratory were used to recalculate Kx according to the equation

$$Kx = \frac{5854}{T} + \left(\frac{1}{t} \log \frac{\alpha_0 - \beta_0}{\alpha - \beta_0}\right)$$

where T = temperature of constant temperature room

t = time in days that integrator was subjected to the constant temperature and

α_0, β_0, and α are the same as in the earlier equation.

Field temperatures were recorded from 14th October 1967 to 15th March 1969 and the data are given in Table 1 and Figure 2, for comparative purposes the air temperatures and rainfall recorded at the Durham University Observatory (91m above sea level and some 2 Km distance from the study area) are included.

The maximum mean soil surface temperature occurred in July/August 1968 - 17.60°C - and the mean minimum in February/March 1969 - 0.2°C. Although the mean maximum surface temperatures could on occasion be 3° - 4°C higher than the air mean maximum, the minimum mean temperatures were very similar - 0.1°C - different. The soil surface was cooler than the air from November 1967 to mid January 1968, and in January 1969 to March 1969. Generally the air temperatures followed the soil surface temperatures very closely during the winter and autumn months, diverging by about 1°C, except in February, 1968 and January 1969 when they diverge 2 - 3°C. From mid April 1968 to the beginning of September 1968 surface temperatures were much higher than the air temperatures, diverging about 2° - 4°C.

The monthly mean temperature of the air (6.97°C) was 2 - 3°C lower than the mean surface temperature (9.57°C). The annual range of temperatures were 17.27°C and 14.10°C for the soil surface and air respectively.

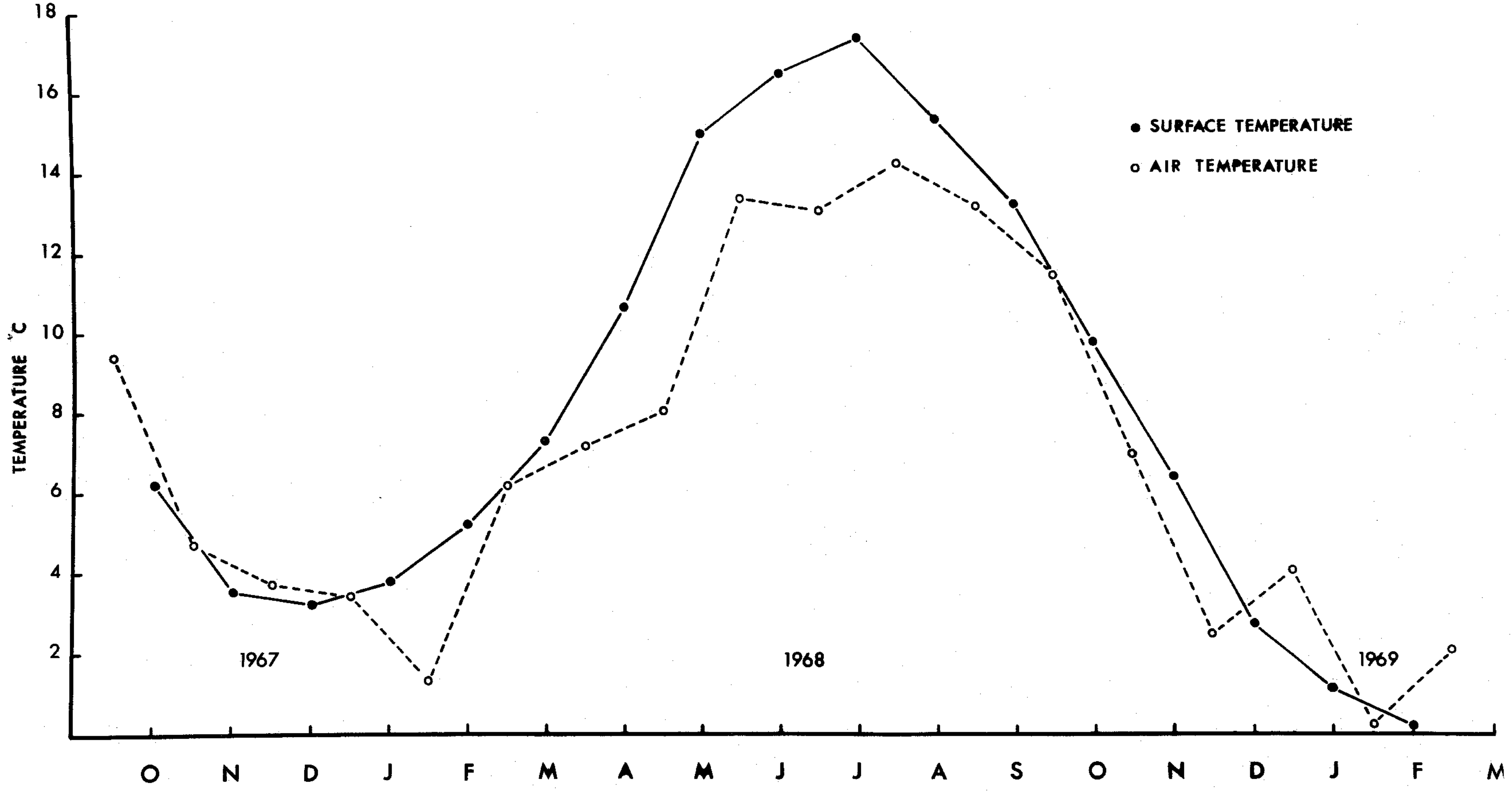
It is of interest to note that the mean field temperatures recorded never fell below 0°C, however, in view of the relatively lengthy winter integration periods (approx. 4 weeks) it should not be forgotten that temperatures probably fell below zero on a number of occasions during any one winter month. The effect of daily temperature changes on the *Nebria brevicollis* population remains unknown, but ecologically it is felt that use of mean temperatures (calculated by means of an integrator involving a biochemical reaction) for extrapolating laboratory obtained data to field conditions is at the present time a well tried and acceptable methodology (Qasrawi, 1966; and Bolton, 1969). Mean temperatures have been so used in the present work.

Mean soil surface temperature		Durham University Observatory records		
Period 1967- 69	Temperature in °C	Period 1967 - 69	Air temperature in °C	Rainfall in inches
(October November 1967 Mid-Month	6.21	October, 1967	9.4	3.42
(November December	3.52	November	4.7	3.20
(December January 1968	3.20	December	3.7	1.34
(January February	3.78	January 1968	3.4	0.99
(February March	5.23	February	1.3	2.13
(March April	7.32	March	6.2	1.18
(April May	10.69	April	7.2	1.87
(May June	15.02	May	8.1	1.94
(June July	16.56	June	13.4	1.99
(July August	17.45	July	13.1	4.03
(August September	15.38	August	14.3	1.66
(September October	13.42	September	13.2	4.47
(October November	9.81	October	11.5	2.55
(November December	6.43	November	7.0	2.57
(December January 1969	2.75	December	2.5	3.82
(January February	1.11	January 1969	4.1	3.38
(February March	0.33	February	0.2	3.48

Table 1 Mean monthly soil surface temperatures measured by the sucrose inversion method, and mean monthly air temperatures and rainfall at Durham University Observatory.

Fig. 1 Zoological Field Station in summer.

Fig. 2 Comparison of mean monthly air temperature and mean monthly soil surface temperature (1967-69).


18
16
14
12
10
8
6
4
2
TEMPERATURE °C
● SURFACE TEMPERATURE
○ AIR TEMPERATURE
1967
1968
1969
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M

CHAPTER 3

The General Biology of Nebria brevicollis (F).

(a) Introduction

Before detailed investigations are made of any animal species it is desirable to know as much as is possible of its general biology. The present chapter provides the background information about *N. brevicollis* that was deemed necessary before an ecological energetic study of it could be undertaken.

(b) Life History

Nebria brevicollis is commonly found in woodland litter (particularly beech and oak) and in grassland, especially areas grazed by cattle. The phenology of this species has been investigated in both Great Britain (Williams, 1959; Tipton, 1960; Greenslade, 1965; and Penney, 1965), and on the continent of Europe (Larson, 1939; and Van der Drift, 1951). This strictly nocturnal species is generally classified as an autumn breeder, its larvae being the overwintering stage.

In the present grassland study the life history pattern of *N. brevicollis* accorded with the earlier accounts and is shown diagrammatically in figure 3.

The adults emerge in Spring towards the end of May and are active for about five to six weeks before entering an obligatory diapause. During the active period the adults feed voraciously and build up large fat reserves for utilization during the period of diapause, which lasts anything from four to six weeks. The actual reason for the obligatory diapause is not clear and a number of theories have been advanced to explain this phenomenon. Gilbert (1958) suggested that diapause enabled the adult to develop its gonads, while Tipton (1960) suggested that it was to avoid the risk of dessication. Greenslade (1965) concluded from his study that the reason for diapause was to synchronise breeding activity. Penney (1966) who made the most detailed study of diapause in *N. brevicollis* suggested that its main function was to enable the adults to survive the period when food supplies (i.e. prey) occurred in their lowest densities.

Following diapause in the soil the adults re-emerge and feeding is resumed; during this period gonads develop rapidly and breeding occurs from mid-September to mid-November. By December very few adults survive although a few do over winter. However, as stated earlier the main overwintering stage is the larva. The larvae are active throughout the winter and early spring and pass through three larval stages (Williams, 1959) each of which can be readily identified according to its head-width (Williams,1959). From mid-April onwards pupation occurs and the next generation of adults appears at the end of May.

(c) Wet and dry weight relationship of N. brevicollis.

All weight measurements were first made in terms of wet weight. As energetic parameters are expressed in terms of dry weight and then calories, a conversion factor was necessary. Dry weights as Engelmann (1966) pointed out "........eliminates the possible variation in water content of the individual".

In the present study all weights were determined on

(a) Electromicrobalance - model E.M.B. - 1
(b) Mettler balance - Type H - 16

A few weight determinations were also made on the portable Cahn Electrobalance, M - 10. The wet weight measurements of adult N. brevicollis were made on the Mettler balance. The Electromicrobalance was used for all dry weight measurements.

(1) Larvae.

Before determining their wet weight the excess water on the body surface was removed with filter paper. A standard procedure was adopted for all weighings. Individuals after collecting from the field were kept unfed for 24 hours to allow gut clearance. Gut contents can alter weights and affect calorific values. After determining the wet weight they were placed in a vacuum oven at 60°C for 48 - 72 hours. The material was subsequently stored in a dessicator containing calcium chloride and self indicating silica gel, and left for at least 48 hours before weighing. Some material was left in the dessicator for several months before being weighed.

Figure 4 shows the wet/dry weight relationship of the larvae. Two regressions were calculated and the equations obtained were:-

Instar I $y = 2.63x + 1.33$ $r = +0.71$ y = wet weight
Instar II and III $y = 2.81x + 3.63$ $r = +0.98$ x = dry weight

(2) Adults

Samples of both sexes were taken during the pre-diapause, diapause, reproductive and post-reproductive periods. The weighing procedure as described in (1) was followed. The results are presented graphically in figure 5. The regression was calculated by the least square method and had a correlation co-efficient of $+0.92$. The equation obtained was:-

$$y = 1.84x + 14.66$$

y = wet weight
x = dry weight

(d) Food

In any ecological energetic study it is desirable that as many energy budget parameters as is possible are measured under field conditions; unfortunately this cannot always be achieved and one must resort to laboratory studies. Under such circumstances it is essential that the laboratory studies are made under conditions which are near natural. In the case of Nebria brevicollis it was not practicable to obtain sufficient data by direct observation of either adult or larval food and feeding, and laboratory studies were made.

With regard to adult food type Penney (1966) made detailed gut analyses and concluded that the diet was almost exclusively micro-arthropods. In her study area small Diptera formed 38% of the diet, Collembola 32% and Acari a further 32%; Collembola were considered the preferred food. In the present study area the densities of Collembola, Acari, Araneida, and larval Diptera, were adjudged high at all times but particularly during those periods when adults were actively feeding. It was thought that any or all of these four groups might be an important source of food for both larval and adult N. brevicollis, therefore food preference tests were made with Collembola, Acari, Araneida and Diptera larvae, from the study area.

A series of experiments was carried out in petri dishes, lined with moist filter paper, and kept at field temperatures. In all experiments, both with larval N. brevicollis and adults all prey items proffered were eaten. However, in more refined experiments (where equal numbers of prey items were presented to larvae and adult N. brevicollis) a distinct preference for Collembola was noted. Penney's (1966) conclusions regarding the food preference of Nebria are thus confirmed and extended to include larvae.

During these experiments it was observed that whereas the adult N. brevicollis consumed a collembolan or tipulid larvae completely, the carabid larvae eat only parts of Collembola and merely imbibed the body juices and soft parts of the tipulid larvae. Table 2 shows qualitatively the results of a further series of experiments designed to check the observations noted above.

	Adults	Larvae
Collembola	*	x
Blowfly larvae	*	x
Tipulid larvae	*	x
Earthworms	*	x
Enchytraeids	x	x
Spiders	x	x
Mites	x	-
Woodlice	x	x

Table 2

Food preference experiments

* = prey completely eaten

x = prey partly eaten

\- = prey rejected

It can be seen that whereas adult N. brevicollis normally consume the whole of their prey, this is not generally the case with the larvae.

From Penney's (1966) study and the results of the above experiments it was concluded that Collembola, and possibly dipterous larvae, were the most important food items in the Durham study area and these forms were used in all subsequent laboratory experiments on feeding.

(e) Feeding periodicity

When the probable field foods are known it is important to investigate whether the food intake is regular or periodic as this could affect, depending upon the period of observation, estimates of absolute consumption both in the laboratory and field. Nowak (1967), for example, showed that *Pterostichus nigrita* did not feed daily when supplied with excess food. On the other hand Penney (1965) found that adult *Nebria* guts contained food throughout active periods, whereas Ganagarajah (1966) intimated that adult *Nebria* fed little, during the breeding season. Clearly, in the case of *N. brevicollis* there is some doubt as to whether the adults feed regularly or not, and no information at all is available regarding the larvae. Consequently experiments were made to determine whether or not the larvae and adults of *N. brevicollis* showed a feeding periodicity. As before it was not possible to study this aspect under field conditions and the experiments were made in the laboratory.

The experiments were made in 7 cm diameter crystallizing dishes at 15°C and under conditions approximating natural photoperiod. The humidity of each dish was kept high by means of damp filter paper.

Both larval and adult Nebria were fed Tomocerus minor (Lubbock) and Isotoma viridis (Bourlet) which were obtained from laboratory cultures maintained at 15± 1°C. Prior to each experiment the experimental animals were kept without food for 36 hours.

In the experiments with larvae (3rd instar) a known weight of fresh but killed prey was supplied daily for a period of 8 days and the daily consumption was recorded. Figure 6 shows the results obtained and it is clear that consumption remained relatively stable from day to day and it can be concluded that N. brevicollis larvae do not show a feeding periodicity at least during periods in excess of 24 hours.

The adult experiments were somewhat more complex in that investigations were made with both pre-diapause and post-diapause (i.e. breeding) animals. In this case the daily ration of prey was not weighed and each individual Nebria was given 25 freshly killed Collembola per day. Every care was taken to ensure that the sizes of the offerred prey items were alike as was possible. Figures 7a and b respectively show the daily consumption of an adult pre-diapause male and female over a period of 15 days. After the first two days the daily food consumption of both males and females fluctuated about a mean level of approximately 20 Collembola per day; feeding certainly occurred every day and no evidence of a feeding periodicity was obtained. Similar tests with post-diapause males and females (Figures 8a and b) showed that daily feeding did occur but at a level approximately 50% of the pre-diapause condition.

These experiments confirm the tentative conclusions of Penney (1965) regarding a lack of periodicity in the feeding habits of *N. brevicollis* and indicate that Ganagarajah (1966) was justified in stating that adult *Nebria* consume relatively little during the breeding season. They also made easier the estimation of food consumption in later investigations (see Chapter 6).

Less extensive experiments made at 3°, 5° and 25°C showed (a) that larvae still feed at 3° ± 1°C, (b) adults stop feeding at 3° ± 1°C (c) adult feeding was depressed at 5 ± 1°C, and (d) at 25°C both larval and adults fed well providing the relative humidity was high. These reactions are well adapted to the phenology and micro-climatic conditions experienced by the different life stages at the soil surface (see Chapter 1 and 2).

Discussion

It is fairly clear that the larvae and adults of *N. brevicollis* can be considered general predators. Nevertheless it is probable that certain preferences are shown; the preferred food being Collembola and dipterous larvae. The fact that the larvae, unlike the adults rarely consume the whole of their prey and concentrate on softer body tissue suggests that the absolute mechanical strength of the larval mouthparts is not as great as that of the adult mouthparts. A similar phenomenon was observed by Phillipson (1960b) in his studies of the different life stages of the phalangiid predator *Mitopus morio* (F).

Unlike many invertebrate predators e.g. *Pterostichus nigrita* (Nowak in Andrzejewska et al, 1967); *Araneus quadratus* (Kajak, 1965); and *Melanotus rufipes* (Dutton, 1969), *Nebria brevicollis* does not show feeding periodicity in excess of 24 hours in any of its life stages. This could be related to the preferred prey of *N. brevicollis* i.e. Collembola and dipterous larvae one of which was potentially available at all times and seasons in the old-field grassland study area. Where feeding periodicities are known to occur the phenomenon is generally stated to be advantageous in that a single feed is such that it remains in the alimentary tract for a period of days and hence the maximum benefit, as demonstrated by high assimilation efficiencies, is obtained for the minimum of energy expenditure.

Although the present experiments were made in the laboratory it is of interest to note that there was not a significant difference in the daily consumption of male and female adults, even during the reproductive period. In contrast Mayashita (1968) working with *Lycosa - T - insignita* and Holling (1968) working with *Hierodula crassa* both noted a higher consumption by females just before, or during, the breeding period. No explanation can be offered for the present findings with regard to the reproductive activity of *N. brevicollis*.

Fig. 3 Life history pattern of *N. brevicollis*

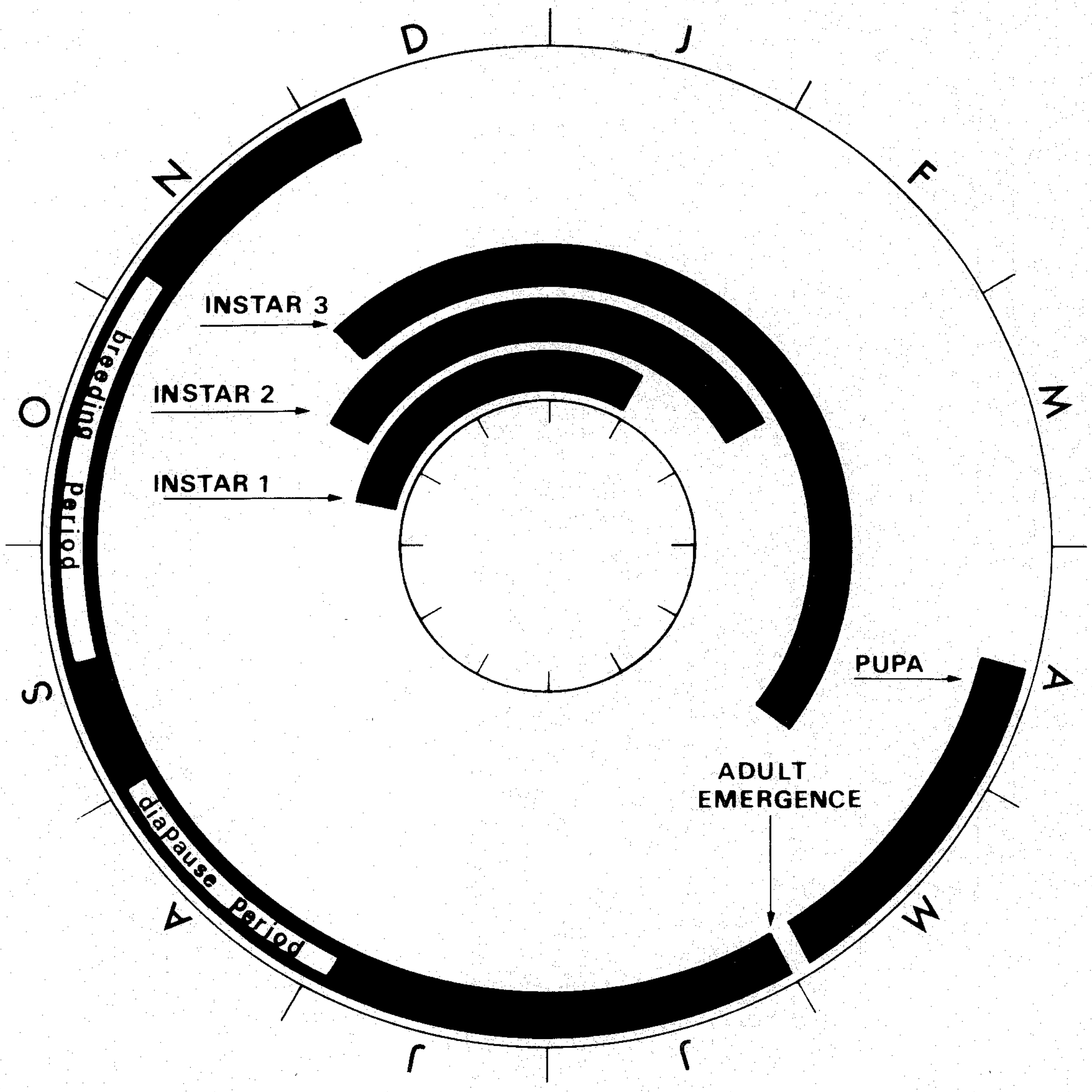
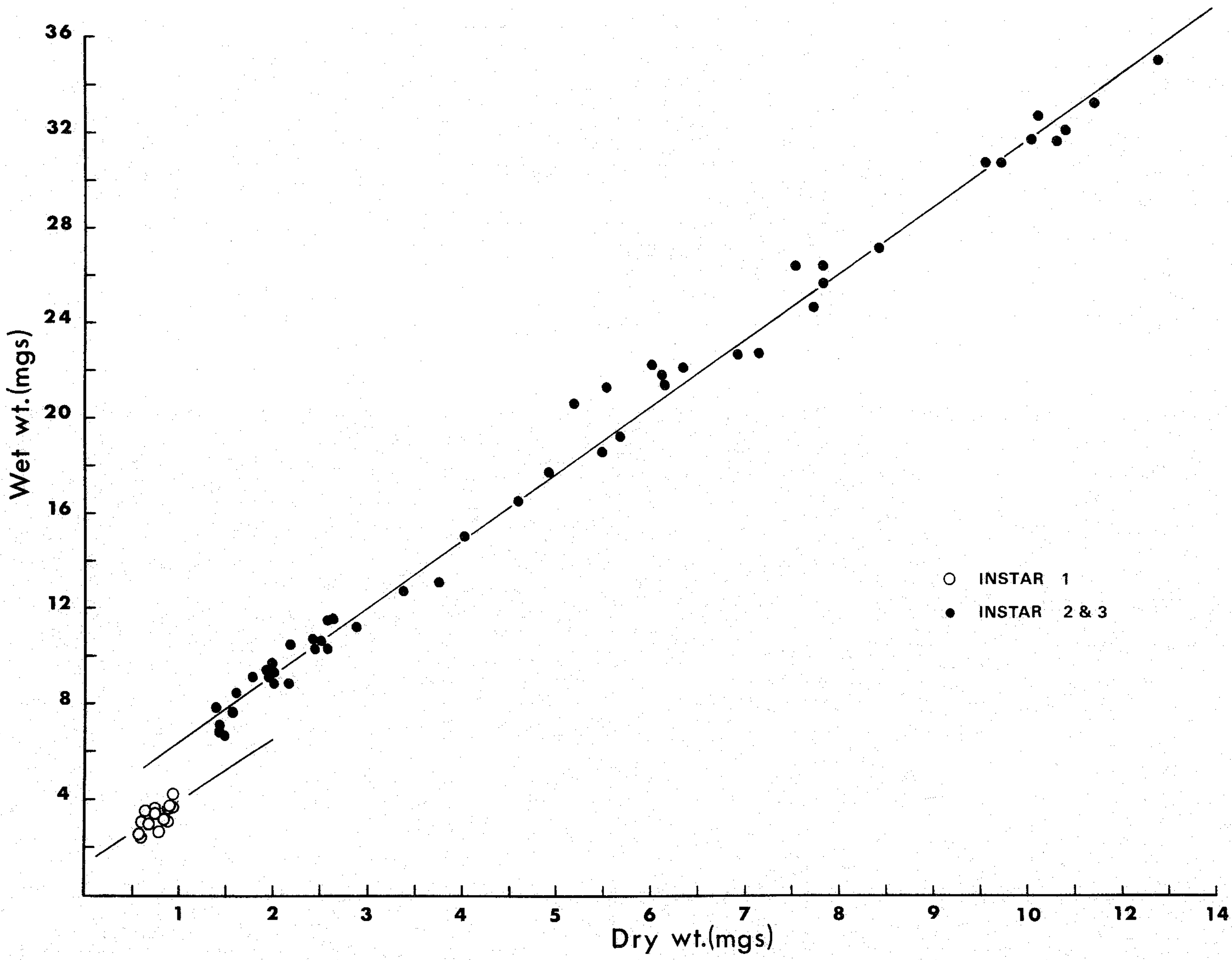

D
J
F
M
A
M
J
J
A
S
O
N
INSTAR 3
INSTAR 2
INSTAR 1
PUPA
ADULT EMERGENCE
breeding period
diapause period

Fig. 4. A wet and dry weight relationship of
N. brevicollis larvae



Wet wt.(mgs)
36
32
28
24
20
16
12
8
4
Dry wt.(mgs)
1
2
3
4
5
6
7
8
9
10
12
14
○ INSTAR 1
● INSTAR 2 & 3

Fig. 5 A wet and dry weight relationship of *N. brevicollis adults*

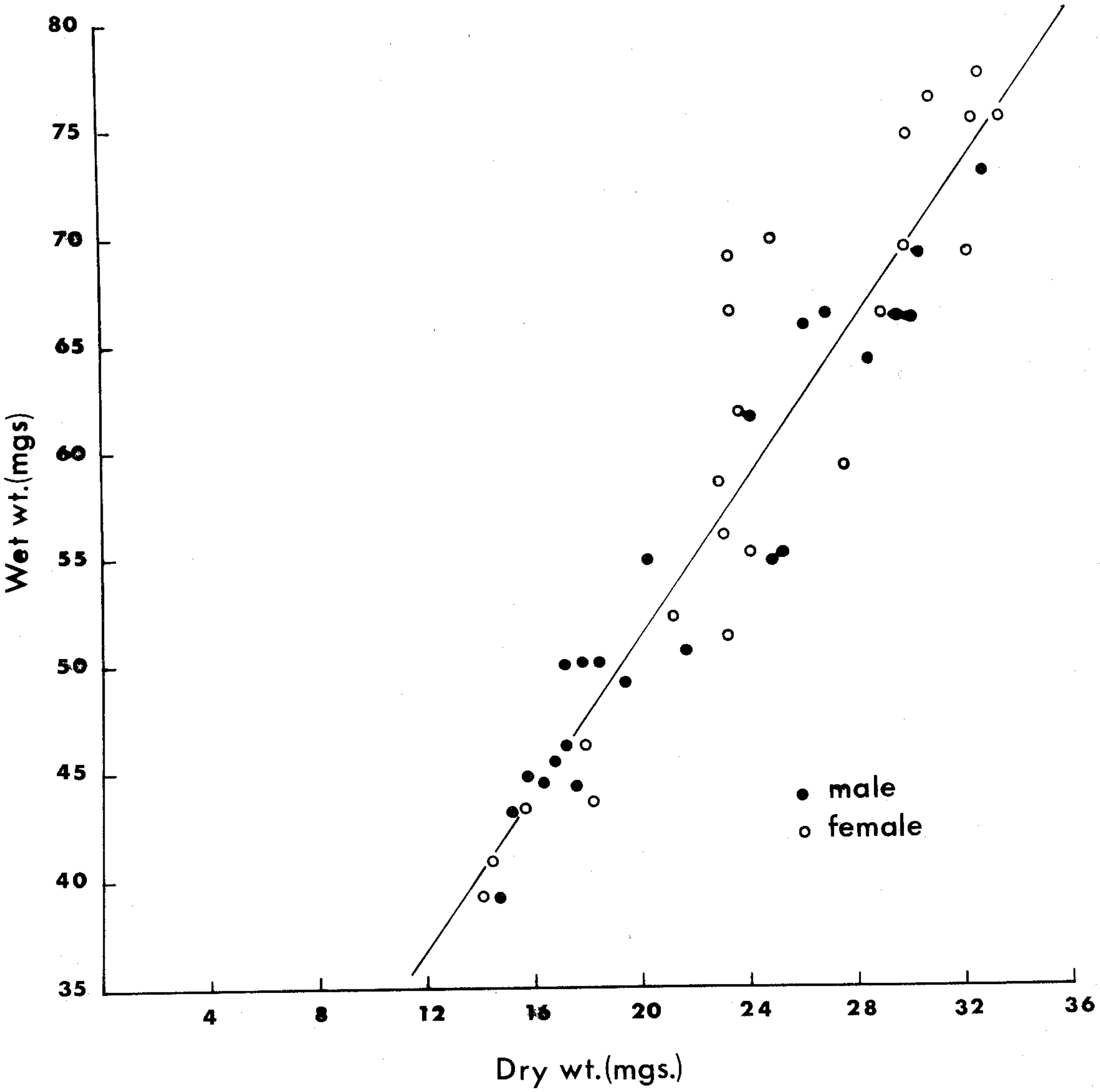

80
75
70
65
60
55
50
45
40
35
Wet wt.(mgs)
4
8
12
16
20
24
28
32
36
Dry wt.(mgs.)
● male
○ female

Fig. 6 The mean dry weight of prey (Collembola) eaten per larva (third instar larvae at 15°C) per day over a period of 8 days. Each point is the average value for 10 individuals.

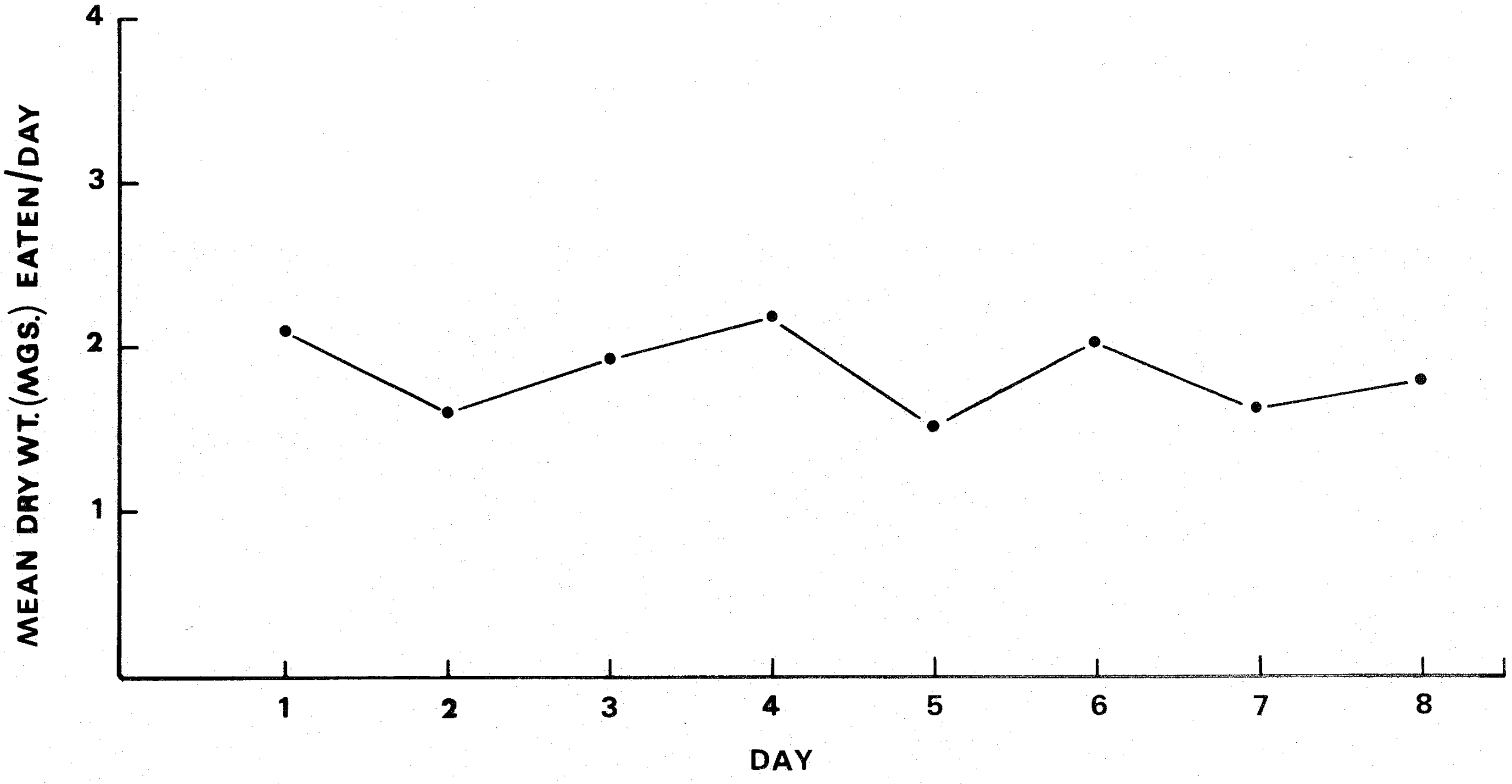
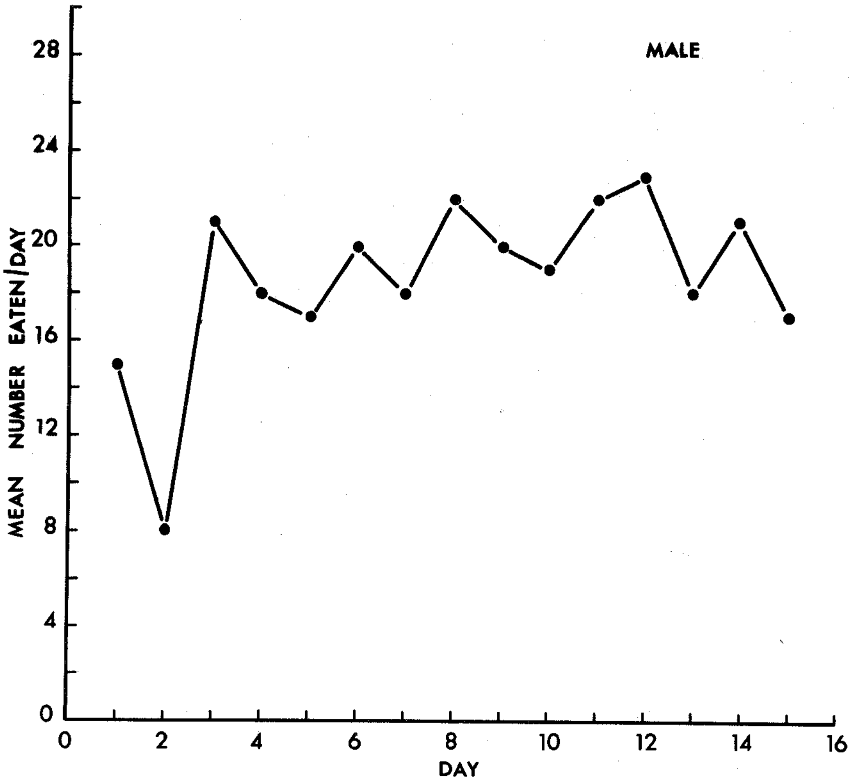

MEAN DRY WT.(MGS.) EATEN/DAY
4
3
2
1
1
2
3
4
5
6
7
8
DAY

Fig. 7a Daily consumption at 15°C (Collembola as prey) of a pre-diapause male over a period of 15 days. Each point is the average value for 5 individuals.

Fig. 7b Daily consumption at 15°C (Collembola as prey) of a pre-diapause female over a period of 15 days. Each point is the average value for 5 individuals.


MALE
MEAN NUMBER EATEN/DAY
0
4
8
12
16
20
24
28
0
2
4
6
8
10
12
14
16
DAY

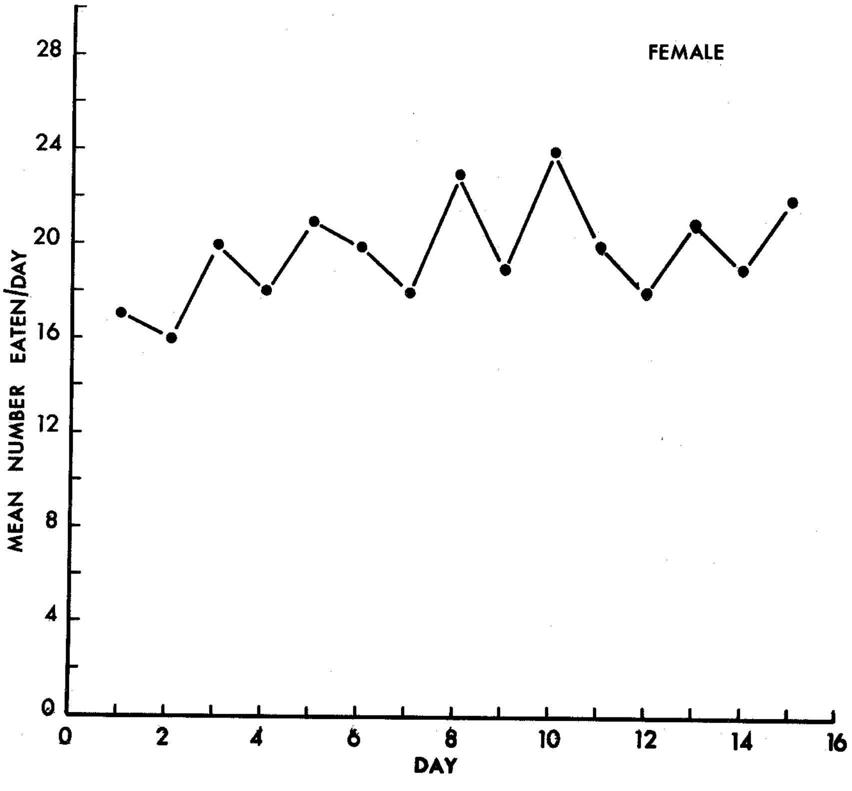
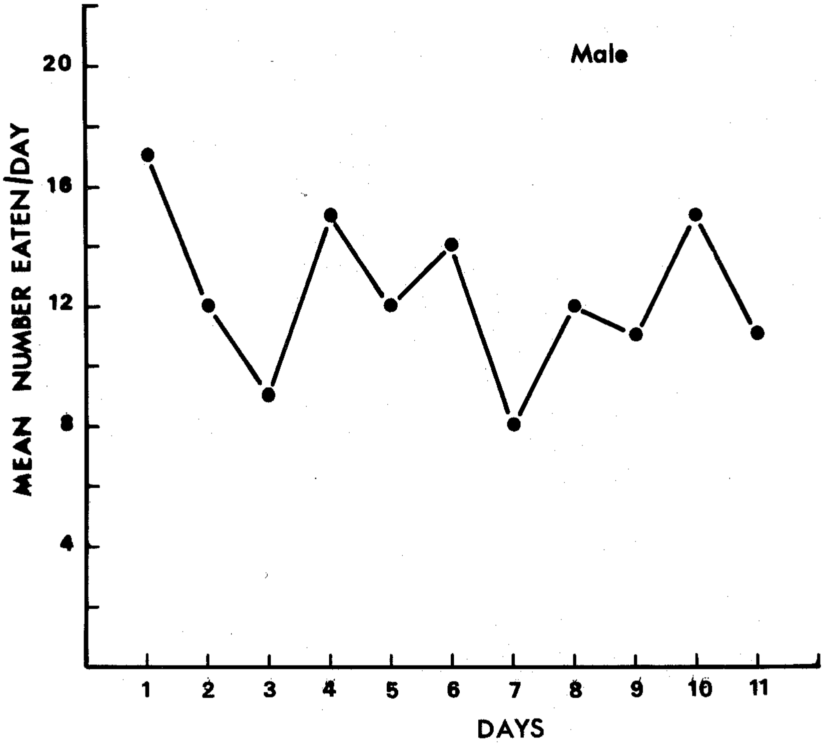
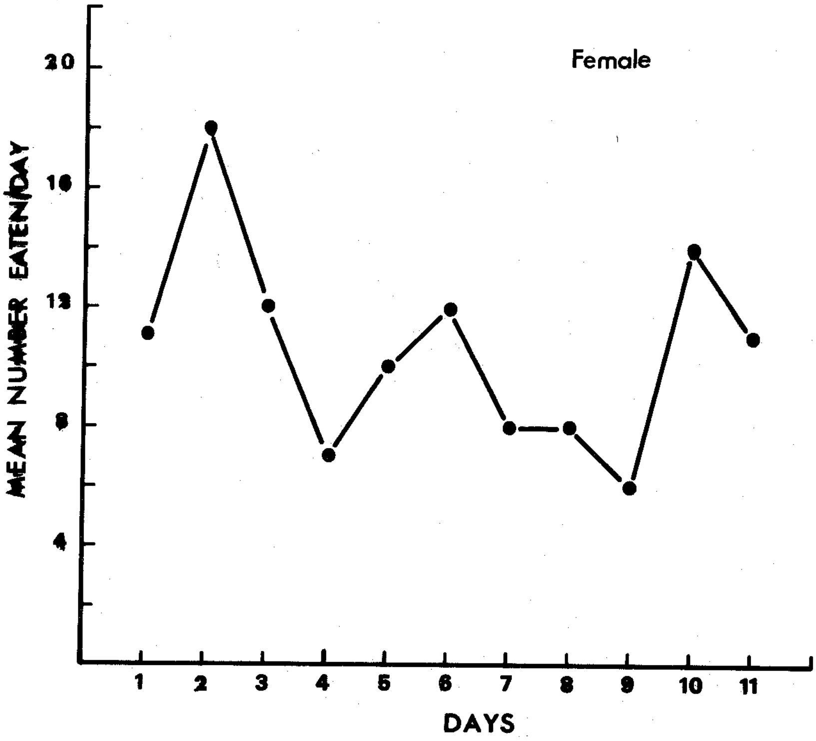

FEMALE
MEAN NUMBER EATEN/DAY
0
4
8
12
16
20
24
28
0
2
4
6
8
10
12
14
16
DAY

Fig. 8a Daily consumption of a post-diapause male at 15°C over a period of 11 days : Collembola as prey. Each point is the average value for 5 individuals.

Fig. 8b Daily consumption of a post-diapause female at 15°C over a period of 11 days : Collembola as prey. Each point is the average value for 5 individuals.


Male
MEAN NUMBER EATEN/DAY
20
16
12
8
4
1
2
3
4
5
6
7
8
9
10
11
DAYS


Female
MEAN NUMBER EATEN/DAY
20
16
12
8
4
1
2
3
4
5
6
7
8
9
10
11
DAYS

CHAPTER 4

Bomb Calorimetry

(a) Introduction

Ecological energetic studies require the conversion of all the measured parameters into comparable units of energy, the most widely used unit is the gramme-calorie. In the present study, the energy budget parameters C, P, and (F + U) were initially determined by gravimetric methods and hence the weights measured needed to be expressed in terms of energy content. For this purpose bomb calorimetry was preferred to the wet combustion method of Ivlev (1934).

(b) Methods

A micro-bomb calorimeter of the type described by Phillipson (1964) was used. The operational procedure was similar to that described by Phillipson (1964). The bomb was calibrated by burning benzoic acid pellets which were of known calorific value. The calibration figure was checked daily and was found to be constant throughout the experimental period. The ash free values were not calculated from the burnings as work carried out by Dutton (1969) on the same bomb showed that considerable variation in ash content estimates occurred when this procedure was adopted. The later reported energy content values are expressed therefore in kilo calories per gramme dry weight.

In all cases where energy content values were required the adults and larvae of the predator (N. brevicollis) and the prey species were allowed to evacuate their gut contents before killing and drying. All material to be combusted was first dried in a vacuum oven at 60°C. for 48 hours. The dried material was ground into powder using a mortar and pestle, and was then compressed into pellets and stored in a dessicator until required for analysis.

The size of the pellets varied from 8 - 22 mgs. Before each burning the sample pellet was weighed on an Electromicrobalance, model EMB-1.

Initially it was considered necessary to group male and female N. brevicollis faeces together, but this later proved unnecessary. Calorific determination of larval faeces (with Collembola as prey) was made with Instar III faeces only. Instar I and II produced such small quantities of faeces that collection for separate determination would have involved an excessive amount of work. Insufficient larval faeces (with Tipulid larvae as prey) were obtained for combustion.

Results

The mean value of twenty consecutive burnings of benzoic acid was:

$$0.5608\text{mV}/100 \text{ cal} \quad \text{SD}\pm 0.0071$$

This calibration factor was used for calculation of the calorific values of all material subsequently burned. The results expressed as k cal/g dry weight are shown in Table 3. Variations between burnings of a sample fell mostly within the 3-4% range. It is clear from Table 3 that:

1) The mean calorific value of each of the various life stages differ.

2) The females just prior to diapause had the highest calorific value - 6.1449 k cal/g-. Field faeces (September/October) had the lowest - 3.3082 k cal/g-. Generally the values for Nebria tissues fell within the 4.300 - 7.000 k cal/g range.

3) The mean value for females is higher than males in all four catagories determined.

4) In adults the calorific value was lowest at emergence, but increased and reached its maximum just prior to diapause, thereafter it decreased. No determinations were made in adults either in diapause or immediately after diapause.

5) The calorific value increased with larval development. Instar III had a higher value than the pupae, emerging adults, and male adults in all stages.

6) The laboratory faeces had a higher value than the field faeces. Calorific value of faeces was lower than that of the prey items.

7) The calorific value of exuvia decreased with increasing size of larvae, no doubt due to a higher percentage ash content.

The calorific value of larval faeces (Tipulid larvae as prey) was calculated by assuming that the percentage difference between adult and larval faeces with Collembola as prey would be the same with Tipulid larvae as prey.

Discussion

In *Nebria* the calorific value per gramme increased with developmental stage. Similar findings were made by Wiegert (1965) for *Philaenus spumarius*, Qasrawi (1966) for *Chorthippus parallelus*, Klekowski et al (1967) for *Tribolium castaneum*, Wignarajah (1969) for *Lithobius crassipes* and *Lithobius forficatus*, and Dutton (1969) for *Melanotus rufipes*. Qasrawi however found that the calorific value of instar III dropped below the value obtained for instar II. Other investigators have found no change or consistent change in calorific value with increase in size or instar number (e.g. Bolton, 1969; Lawton, 1969).

In *N. brevicollis* the highest calorific content was found for adults in a late pre-diapause stage. This high value is probably due to adults having built up large quantities of fat reserves for the diapause stage. The third instar of *Nebria* had a higher calorific value than the pupae and emerging adults probably also due to the higher fat content. A decrease in calorific value from pre-pupal stage to emerging adult was also found by Klekowski et al (1967) in *Tribolium* and Slobodkin (1965) in *Sarcophaga*. Slobodkin gave values for prepupae – 5.914 –, 11 day old pupae – 5.399 –. and newly emerged adult as – 5.079 – Kcal/ash free g.

The eggs did not have the highest calorific content of *Nebria* material. This corresponds with the result obtained by Dutton (1969).

However, some authors have shown that eggs have the richest energy content (Wiegert, 1965; Qaswari, 1966). Their values were also higher. The difference in the value is probably due to a lower fat content in the eggs of Nebria and Melanotus or higher ash content in the egg shell. It should be noted that while the latter took 2 - 4 weeks to hatch, Philaenus and Chorthippus took 6 - 7 months. This could probably explain ~~for~~ the difference in fat content in the eggs. The low calorific value of Tribolium castaneum eggs was explained by the very low calorific value of the egg shell. The calorific value increased by 20% without the eggshell (Klekowski en al, 1967).

The field faeces of Nebria had a lower calorific value than the laboratory faeces, probably because the mixed diet of the animal in the field had a lower mean calorific value than the laboratory food. Another probable reason is that material other than food material, which had a low calorific content, was taken in with the food. Watson (1965), Lawton (1969) also found laboratory faeces values higher than that of the field. The decrease in value of field faeces from June - July - September/October indicates a change in the quality of the diet in the field.

Material	Number of Samples	K cals./gm.	Standard Error (+) (-)
Larvae			
Instar I	6	5.2061	0.0396
Instar II	8	5.3644	0.0534
Instar III	6	5.8084	0.0383
Adults			
a) Male			
Emerging	1	4.9860	–
Pre-diapause	6	5.7356	0.0316
Reproductive	5	5.2147	0.0584
Post-reproductive	1	5.0556	–
b) Female			
Emerging	1	5.1105	–
Pre-diapause	6	6.1449	0.0236
Reproductive	8	5.4226	0.0283
Post-reproductive	2	5.2200	–
Eggs	5	5.6723	0.0406
Pupae	2	5.2873	–
Exuvia			
Instar I	1	4.9051	–
Instar II	1	4.7291	–
Instar III	2	4.4976	–
Prey Species			
Collombola	10	5.0387	0.0242
Tipulid larvae	9	5.3986	0.0466
Laboratory Faeces			
a) Adults			
Collembola	8	3.7599	0.0276
Tipulid larvae	2	4.0257	–
b) Larvae			
Collembola	2	3.9569	–
Tipulid larvae	–	–	–
Field Faeces			
Adults			
June	3	3.6051	0.0476
July	3	3.4666	0.0544
Sept./Oct.	3	3.3082	0.0380

Table 3   Calorific value determations

CHAPTER 5

Assimilation Efficiency

(a) Introduction

Knowing the probable food and feeding habits of *N. brevicollis* larvae and adults in nature it was possible to attempt reasonably realistic laboratory experiments to evaluate the assimilation efficiency of their life stages with a view to using the obtained figures to estimate absolute assimilation in the field and, in conjunction with estimates of faeces production, to calculate absolute consumption.

The difference between consumption and egestion is termed assimilation

$$C - (F + U) = A$$

Assimilation has been measured directly in the field by means of radionuclides (e.g. Hubbell, Sikora and Paris, 1965) but this has possible attendant dangers (Paris and Sikora, 1967). The evaluation of assimilation efficiency $\frac{C - (F + U)}{C} \times 100$ is generally done under laboratory conditions (e.g. Brocksen et al, 1968; Conover, 1966a and b; Davies 1964, Dutton 1969; Gerking, 1962; Nakamura, 1965; O'Neill, 1968; Qasrawi, 1965; Schindler, 1968; and White, 1968); and is most frequently calculated from dry weight determinations, or these values expressed in terms of energy content (e.g. Lawton, 1969; Paine, 1965; and Reichle, 1968).

However, some authors have used carbon content (e.g. Lasker, 1960 and 1966; and Sorokin and Panov, 1966), or nitrogen values (Corner, Cowey and Marshall, 1967). Gravimetric methods were used in the present study and results were obtained using both dry weight and energy content values.

A variety of factors can affect assimilation efficiency for example, food type, feeding rate, size, reproductive condition, and temperature. Some of these variables were investigated.

(b) General methodology

Experimental larvae and adults were acclimatized in the laboratory to the proposed experimental temperature for a period of not less than 24 hours. All experiments, excepting those designed to study the effect of temperature on assimilation efficiency, were made at 15± 1°C. The experimental chamber comprised a 7 cm. diameter crystallizing dish lined with aluminium foil; the foil being essential for the collection of faeces in that these were fluid or semifluid. Aluminium foil was considered the best means of ensuring that the total weight of faeces produced could be determined and had been employed in earlier studies by Wiegert (1964) and Dutton (1969). A high humidity inside the experimental chamber was maintained by means of a 'lid' of damp filter paper.

All animals were subjected to a period of 24 hours or more without food immediately before experimentation. The 'starvation' period varied with the type of experiment being made and details are given in the appropriate sections. Apart from the deliberate experimental variations of food type, temperature, etc. (see later) the experimental procedure for each experiment was as follows:

(1) Preweighed aluminium foil was placed in the experimental chamber.

(2) The experimental animal (*Nebria*) was placed in the chamber.

(3) The live weight of the prey was determined for later conversion to dry weight

(4) The prey item was immobilized by killing it in boiling water.

(5) The prey item was placed in the experimental chamber.

After a chosen interval of time, which varied with the type of experiment, the following measurements were made:

(6) The 'food remains' were removed from the chambers and their wet weight determined for later conversion to dry weight.

(7) The live weight of the experimental animal was obtained for later conversion to dry weight.

(8) The aluminium foil with the associated fluid faeces were placed in a vacuum oven at 60°C for 48 hours, and the dry weight of the faeces was subsequently determined by subtracting the dry weight of the foil from the dry weight of foil and faeces.

Before the obtained results could be substituted in the formula $\frac{C - (F + U)}{C} \times 100$ it was necessary to have a series of wet weight/dry weight regressions for the various items. These regressions were obtained from separate investigations, and the parameters of the above formula were calculated, using dry weights by means of the equations;

Consumption (C) = Food given - Food remains
Faeces (F + U) = Weight of foil and faeces - Weight of foil

(c) Effect of food type

The results given in Chapter III suggested that Collembola, and possibly dipterous larvae, were the main prey items of both larval and adult N. brevicollis. These two types of prey were therefore used in the experiments to determine assimilation efficiency. Two species of Collembola, Tomocerus minor (Lubbock) and Isotoma viridis (Bourlet) were grown in laboratory culture and used as food. One species of dipterous larvae (Ormosia bifurcata (Goetghebuer) was also employed. These larvae could be kept in the laboratory in damp soil and litter at 5 ± 1°C for periods of several months.

Figure 9 shows the wet weight/dry weight relationship of those sizes of Collembola used in the experiments and the appropriate least squares regression is expressed by the equation

$y = 4.309x - 0.3810$
y = wet weight
x = dry weight

Similarly figure 10 shows the wet weight/dry weight relationship of O. bifurcata larvae $<$ 4 mg live weight and $>$ 4 mg live weight.

The appropriate regressions are:

O. bifurcata < 4.0 mg

$$y = 5.5787x + 0.4756$$

y = wet weight

x = dry weight

O. bifurcata > 4.0 mg

$$y = 2.5719x + 1.6896$$

In experiments with *N. brevicollis* larvae, the larvae in addition to being acclimatized to the experimental temperature of 15 C were deprived of food 24 hours prior to the beginning of each experiment. Each experiment lasted a further 24 hours.

The results of these experiments are summarized in Table 4 and it can be seen that percentage assimilation, whether calculated from dry weight or energy content is significantly higher with soft bodied prey (*O. bifurcata*) than with relatively harder bodied prey (*Collembola*).

In the case of adult *N. brevicollis*, the experimental procedure in the food type experiments was the same as that described for larvae. The results are given in Table 5a and 5b, and it can be seen that during the pre-diapause period (June), there is no significant difference in the assimilation efficiency of males and females when fed the same type of prey item. However, as in the case of larvae, *O. bifurcata* was assimilated more efficiently than Collembola.

(d) Effect of feeding rate

The experimental procedure in larval feeding rate investigations was identical to that adopted for the 'prey type'

Instar Size	Prey type used	Number in Sample	Units	Mean percentage assimilation	Standard error
Instar II	Tipulid larvae	15	dry weight (mg)	86.11	0.6662
			calories	89.22	
Instar III	Tipulid larvae	25	dry weight (mg)	82.69	0.7708
			calories	86.76	
Instar III	Collembola	22	dry weight (mg)	65.38	1.00
			calories	72.81	

Table 4 Percentage assimilation in larvae at 15°C. Results expressed in terms of dry weight (mg) and calories.

Date of Experiment	Sex	Number in Sample	Units	Mean Percentage Assimilation	Standard error
June	Male	16	dry weight (mg)	57.59	0.84
			calories	68.35	
	Female	14	dry weight (mg)	58.91	1.17
			calories	69.34	

Table 5a Percentage assimilation in adults at 15°C with Collembola as prey. Results are expressed in terms of dry weight (mg) and calories

Date of Experiment	Sex	Number in Sample	Units	Mean Percentage Assimilation	Standard error
June	Male	13	dry weight (mg)	68.56	1.59
			calories	76.42	
	Female	12	dry weight (mg)	69.38	0.99
			calories	77.28	

Table 5b Percentage assimilation in adults with Tipulid larvae as prey. Results are expressed in terms of dry weight (mg) and calories.

experiments. However, in those experiments with adults when a low feeding rate was induced by keeping food in short supply a slightly different procedure was adopted. The experimental animals were kept at a low level of feeding for 2 - 3 days prior to the experiment; they were then starved for 36 hours. During the experiment they were fed at a low level for two days and a further period of 24 hours starvation was allowed to elapse before the experiment was terminated. Food consumption was determined for the initial two days of the experiment, whereas faeces production was measured over the full three days. All experiments were made at 15 ± 1°C.

Figures 11 and 12 show larval instar III percentage assimilation plotted against the dry weight of food consumed. The general levels of percentage assimilation for the two prey types used (O. bifurcata and Collembola) approximate those listed for the different prey types in Table 4. Moreover, it is clear that feeding rate had little influence on larval assimilation efficiency although in the case of tipulid prey there was a slightly positive relationship ($r = +0.2358$) and in the case of Collembola a slightly negative one ($r = -0.0809$).

Experiments on feeding rate in relation to assimilation efficiency were made with adults in both the pre-diapause and post-diapause phases. This was considered desirable in view of the findings on differential consumption reported earlier under "Feeding periodicity".

Figures 13a and 13b show the pre-diapause period results with Collembola and tipulid prey respectively. The general levels of percentage assimilation do not differ significantly from those reported under prey type and, as in the case of larvae, it would appear that feeding rate does not affect assimilation efficiency. The correlation coefficient for both Collembola (r = -0.3522) and tipulid larvae (r = -0.0269) indicate a slightly negative relationship.

Figures 14a and 14b show the post-diapause period results respectively for males and females with Collembola as the proffered prey item. In this instance males show an assimilation efficiency similar to that recorded for males in the pre-diapause period, but the mean percentage assimilation of females during October is approximately 10% lower than that recorded in June. Despite the different values of percentage assimilation shown by female adults in the two seasons it is once again evident that feeding rate does not affect percentage assimilation values. The correlation (r) for males is - 0.0032 and for females - 0.0119.

A further experiment was made with adult Nebria with Collembola as prey in October. The results are shown in figure 15 and accord closely with those obtained in pre-diapause and post-diapause experiments.

It must be concluded for both larval and adult N. brevicollis that feeding rate does not affect assimilation efficiency.

Date of Experiment	Sex	Number in Sample	Units	Mean Percentage Assimilation	Standard Error
September	Male	12	dry weight (mg)	55.08	1.25
			calories	66.48	
	Female	15	dry weight (mg)	43.51	1.34
			calories	57.84	
October	Male	15	dry weight (mg)	55.13	1.08
			calories	66.52	
	Female	10	dry weight (mg)	52.05	1.28
			calories	64.22	

Table 6 Percentage assimilation in adults (post-diapause stage) at 15°C with Collembola as prey. Results expressed in terms of dry weight (mg) and calories.

(c) Effect of size

With Instar I larvae it was possible to calculate the dry weight of food consumed in the laboratory experiments at $15^{\circ} \pm 1^{\circ}C$ but the quantity of faeces produced was so small that accurate weighing proved impracticable. In the case of instar II and III and adults estimates of mean percentage assimilation could be readily determined from the figures given in table 4. and 5.

Figure 16 shows these mean percentage assimilation figures plotted against life stage. Clearly, the assimilation efficiency of approximately 89% shown for Instar I was obtained by extrapolation and too much confidence should not be placed on this estimate. It is evident however that size does influence assimilation efficiency, the efficiency of the larval stages ($> 80\%$) being higher than that shown by adults ($< 70\%$).

(f) Reproductive condition

Table 5a summarizes the pre-diapause assimilation efficiency of adult N. brevicollis when fed Collembola and Table 6 shows the results obtained from similar experiments made during mid-September (early post-diapause period) and late October (late post-diapause period). It should be noted that the females used during September were later shown to have mature and developing eggs in their ovaries, whereas the October females were in a post peak reproductive period.

Date of Experiment	Temperature	Number in Sample	Units	Mean Percentage Assimilation	Standard Error
June	15	25	dry weight (mg)	68.95	0.94
			calories	76.83	
	20	10	dry weight (mg)	61.52	1.74
			calories	71.53	
	25	10	dry weight (mg)	52.47	1.33
			calories	64.79	

Table 7 The effect of temperature on percentage assimilation in adults with Tipulid larvae as prey.

Comparison of male dry weight percentage assimilation of Collembola in the three periods, June (57.59%) September (55.08%) and October (55.13%) indicates a slight decline in efficiency but none of these values were significantly different. A similar comparison of female dry weight percentage assimilation, June (58.91%), September (43.51%), and October (52.58%) suggests that the September figure, which is significantly lower than the June and October values, is probably related to the active reproductive state. An alternate explanation might be in experimental error during the September series of experiments in that these females produced a yellow secretion (quite distinct from faeces) which could not be excluded from the estimates of faeces production and hence the value (F + U) would be high and result is an under estimate of true percentage assimilation.

Effect of temperature

Experiments were made to determine the percentage assimilation of tipulid larvae (O. bifurcata) by pre-diapause adult N. brevicollis at different temperatures. In these experiments the procedure described for 'prey type' was followed except for the different acclimatization and experimental temperatures. The experimental temperatures were 15°, 20° and 25°. The results are shown in Table 7 and it is clear that assimilation efficiency declines with increasing temperature.

Discussion

The fact that percentage assimilation in N. brevicollis does vary with prey type, size, possibly reproductive condition, and temperature, is of the utmost importance in the extrapolation of laboratory data to field conditions. Under present circumstances it is not practicable to know the relative proportions of prey type taken in nature by the different life stages of N. brevicollis and it is only possible in the extrapolation of laboratory data to use a mean assimilation efficiency, based on known preferred foods, for each life stage. Size and reproductive condition can clearly be allowed for, providing the size class composition of the natural population is known. The microclimate data reported in Chapter 2 could be used in conjunction with known assimilation efficiencies at particular temperatures, but in this case it should be noted that the experimental temperatures of 20° and 25°C were higher than the integrated mean value recorded in the field. Unfortunately the experiments which were made at 5°C proved unsuccessful and the influence of temperature lower than 15°C on assimilation efficiency in N. brevicollis requires further study.

The mean percentage assimilation in instar I (77.65) and instar II (75.27) with Collembola prey was estimated by assuming that the percentage difference between assimilation efficiencies with Collembola and Tipulid larvae was the same as in instar III.

The percentage assimilation figure (50 - 90%) recorded for N. brevicollis are, as might be expected, higher than those found for herbivorous beetles e.g. Tenebrio molitor; 46.3% (Evans and

Goodliffe, 1939), and *Chrysochus auratus*, 48% (William and Reichle, 1968). They do however fall within the range shown by other terrestrial predators (47 - 95%) e.g. *Mitopus morio*, 47 - 75% according to life stage (Phillipson 1960a and b), *Oryzomys palustris*, 88 - 95% (Sharpe, 1967) and *Melanotus rufipes*, 86.6% (Dutton, 1969). The wide range of assimilation efficiencies shown by invertebrate predators is frequently related to food type and predator life stage. Generally speaking the softer the body tissues ingested the higher the assimilation effiency; *N. brevicollis* accords with this situation in that with a soft bodied prey, *O. bifurcata* percentage assimilation was significantly higher (larvae 84.4%, adults 68.9%) than with Collembola (larvae 65.4%, and adults 58.0%).

Fig. 9 Wet weight/dry weight relationship of Collembola used in the assimilation and consumption experiments with _N. brevicollis_.

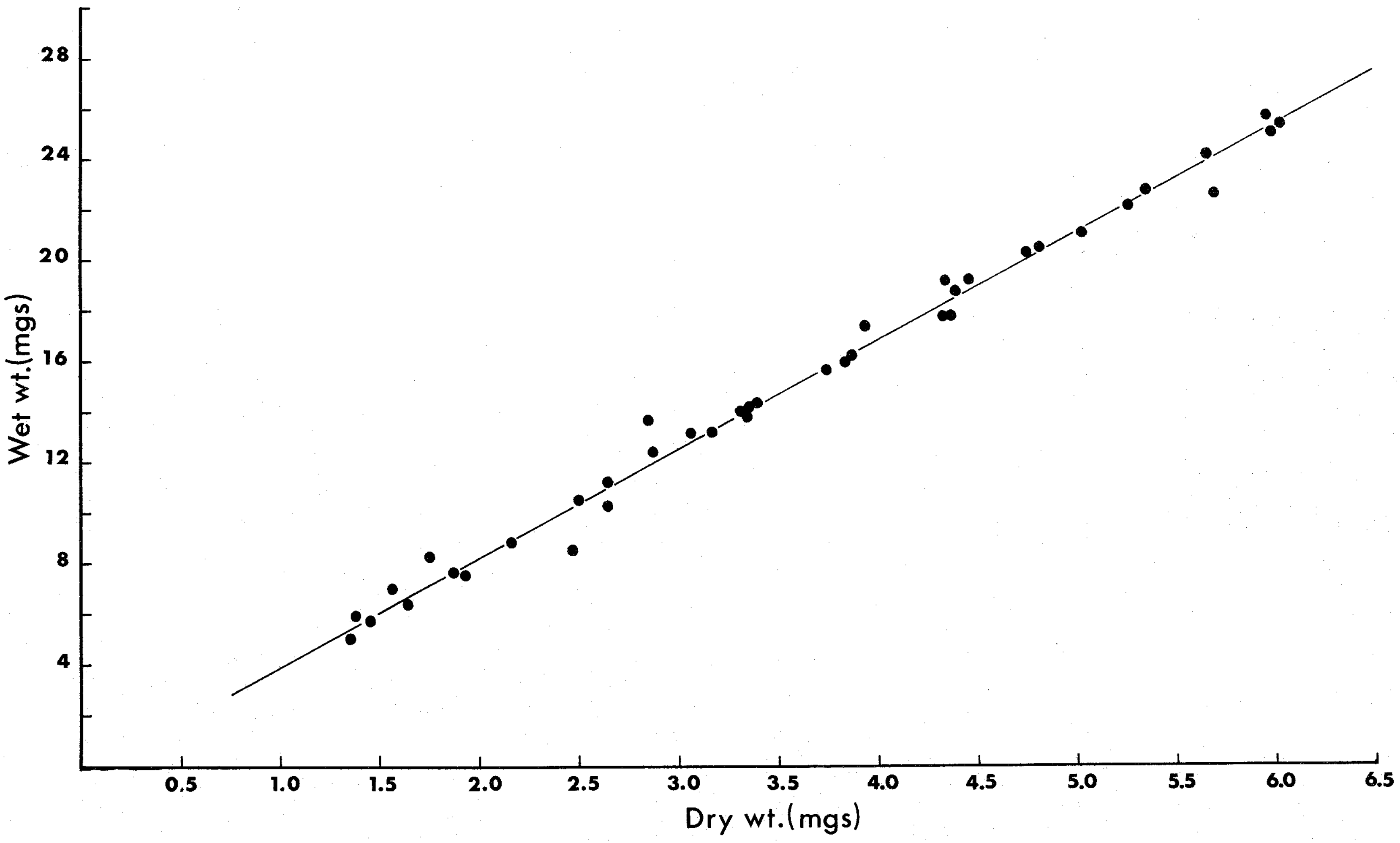

28
24
20
16
12
8
4
Wet wt.(mgs)
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
4.5
5.0
5.5
6.0
6.5
Dry wt.(mgs)

Fig. 10 Wet weight/dry weight relationship of Tipulid larvae (<u>O. bifurcata</u>) used in the assimilation experiments with <u>N. brevicollis</u>.

○ < 4mgs ● > 4mgs

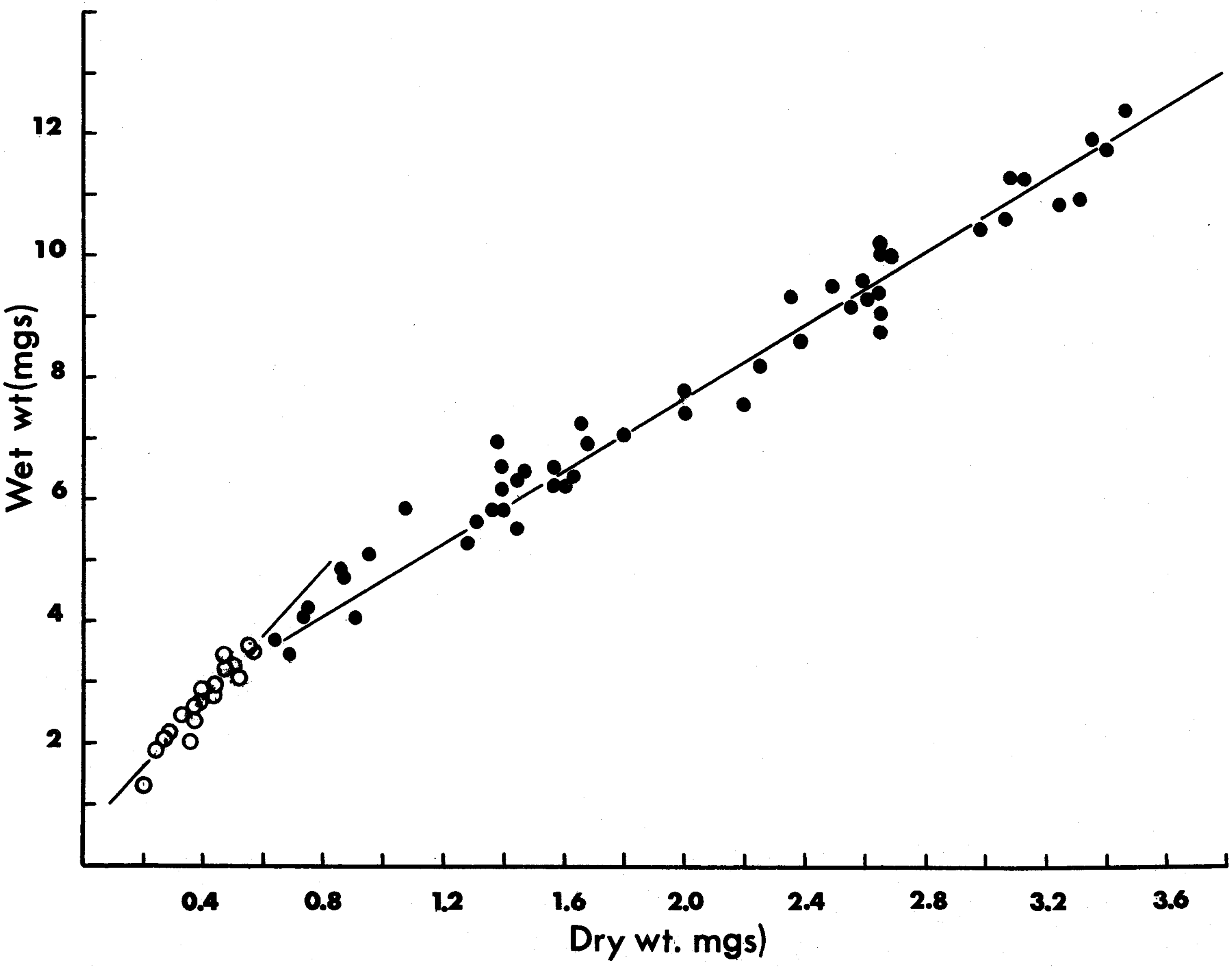
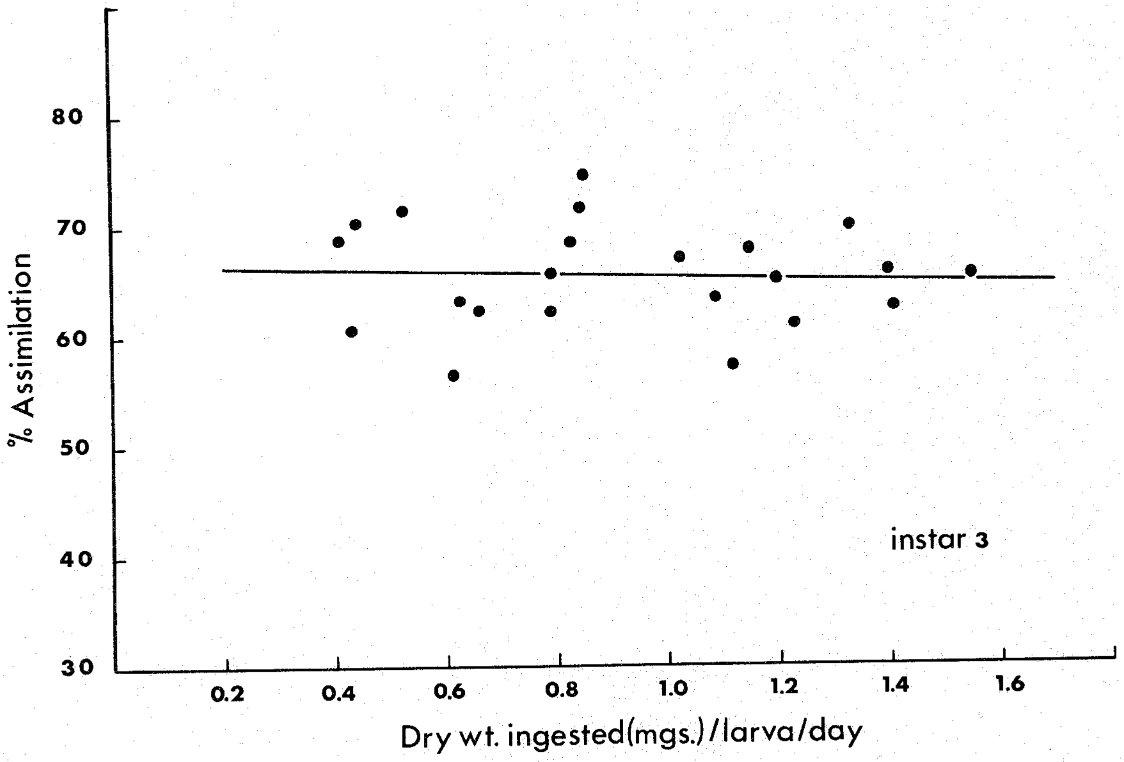

Wet wt(mgs)
12
10
8
6
4
2
0.4
0.8
1.2
1.6
2.0
2.4
2.8
3.2
3.6
Dry wt. mgs)

Fig. 11 Relationship between feeding rate and assimilation efficiency in third instar larvae with Collembola as prey.

Fig. 12 Relationship between feeding rate and assimilation efficiency in third instar larvae with Tipulid larvae as prey.


80
70
60
50
40
30
% Assimilation
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
Dry wt. ingested(mgs.)/larva/day
instar 3

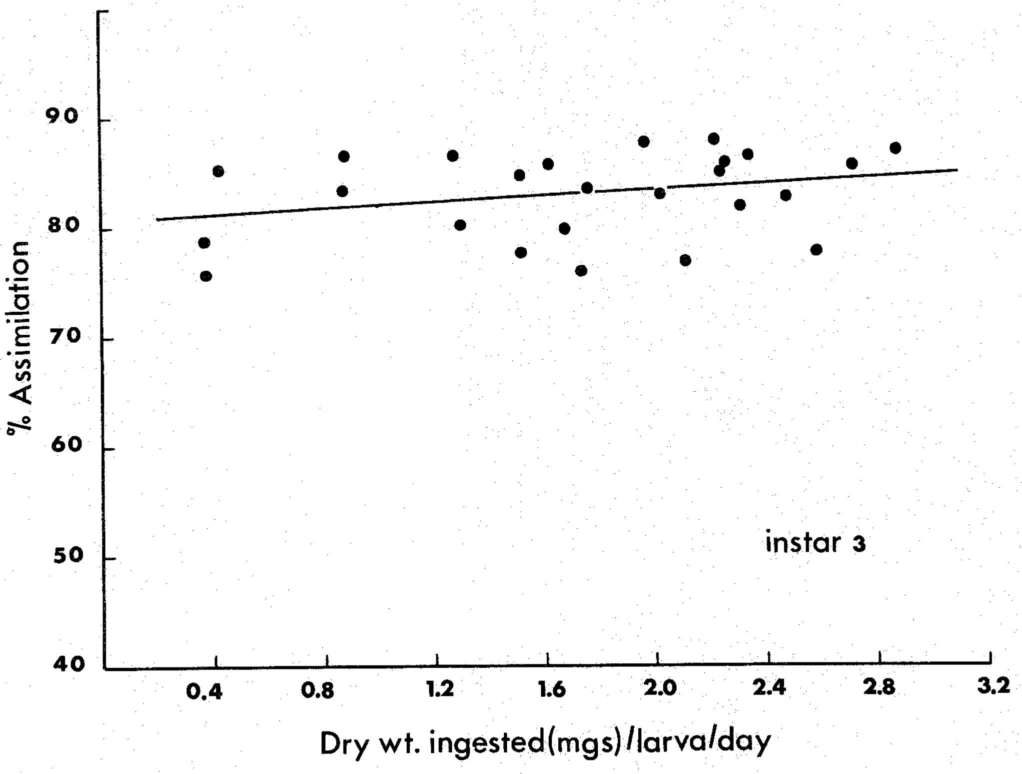
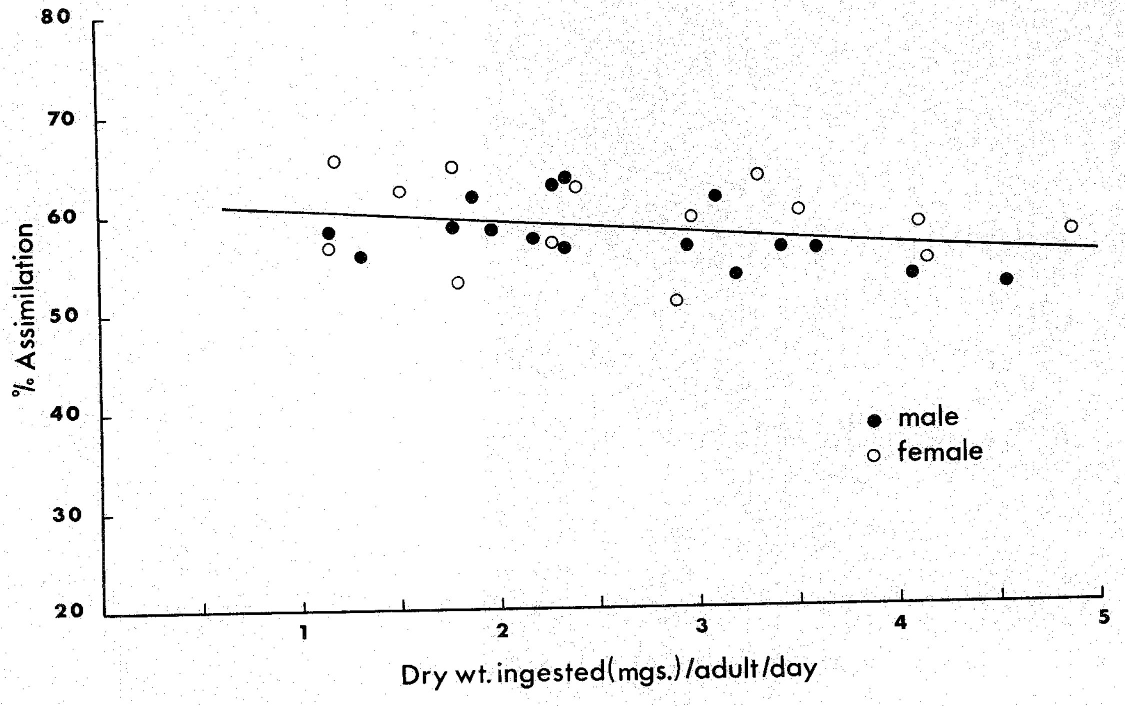

90
80
70
60
50
40
% Assimilation
0.4
0.8
1.2
1.6
2.0
2.4
2.8
3.2
Dry wt. ingested(mgs)/larva/day
instar 3

Fig. 13a Relationship between feeding rate and percentage assimilation in pre-diapause adults with Collembola as prey.

Fig. 13b Relationship between feeding rate and percentage assimilation in pre-diapause adults with Tipulid larvae as prey.


80
70
60
50
40
30
20
% Assimilation
1
2
3
4
5
Dry wt. ingested (mgs.) / adult / day
● male
○ female

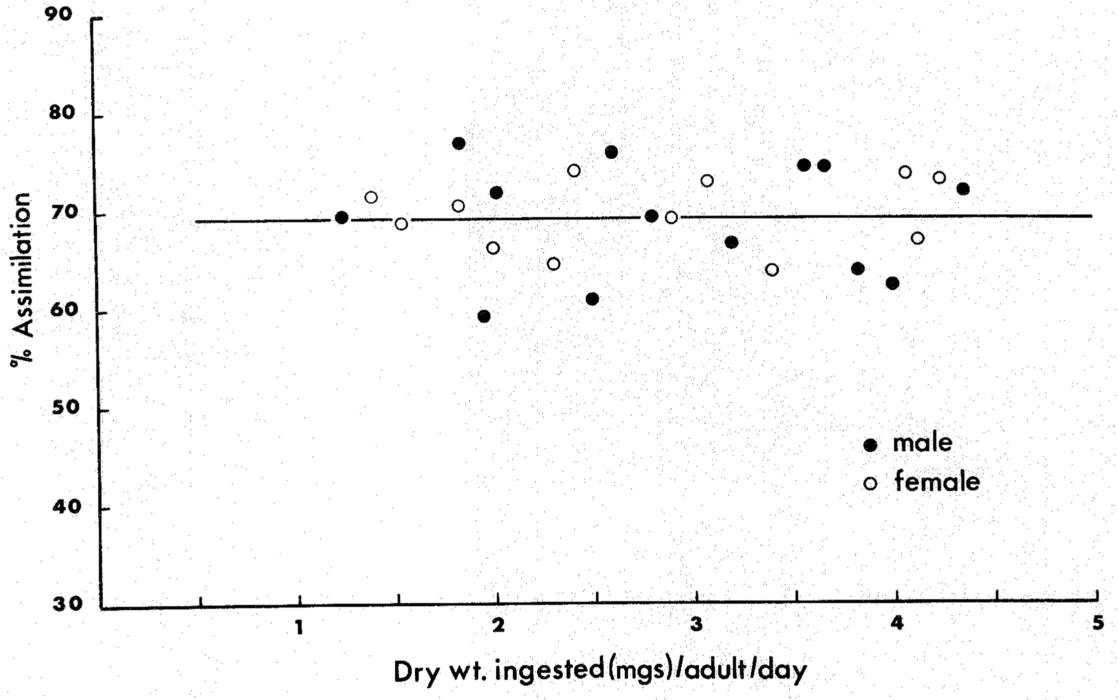
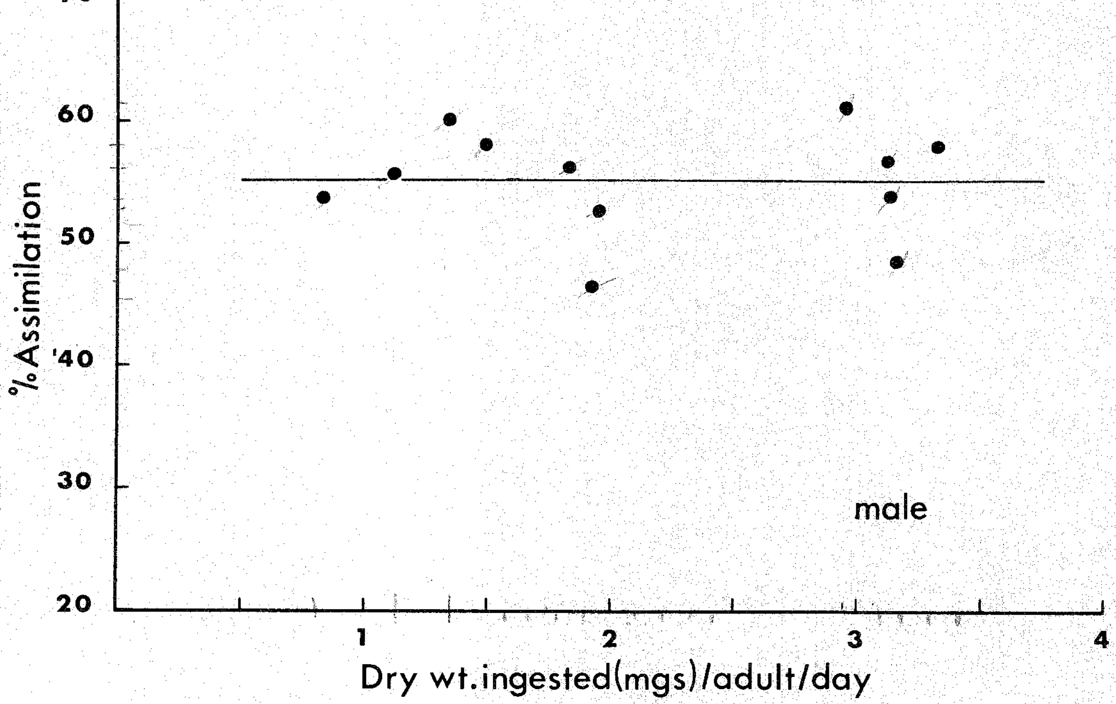

90
80
70
60
50
40
30
% Assimilation
1
2
3
4
5
Dry wt. ingested (mgs) / adult / day
● male
○ female

Fig. 14a Relationship between feeding rate and assimilation efficiency in post-diapause males (September) with Collembola as prey.

Fig. 14b Relationship between feeding rate and assimilation efficiency in post-diapause females (September) with Collembola as prey.


70
60
50
40
30
20
% Assimilation
male
1
2
3
4
Dry wt. ingested(mgs)/adult/day

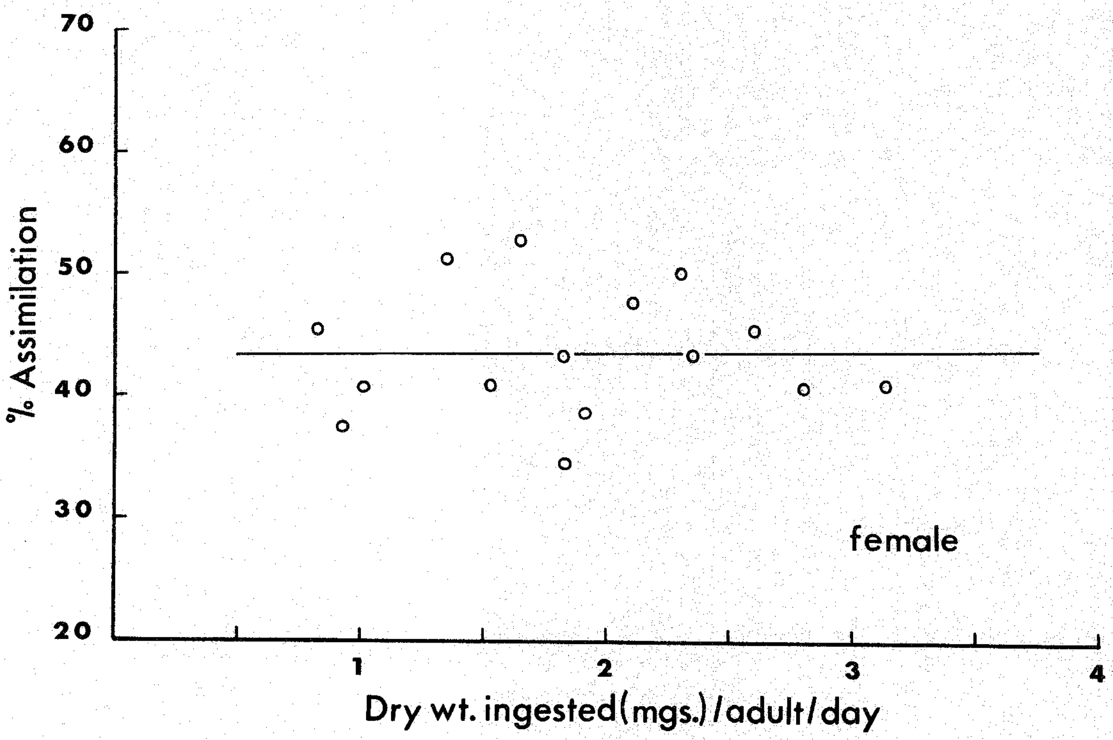

70
60
50
40
30
20
% Assimilation
female
1
2
3
4
Dry wt. ingested(mgs.)/adult/day

Fig. 15 Relationship between feeding rate and percentage assimilation in post-diapause adults (October) with Collembola as prey.

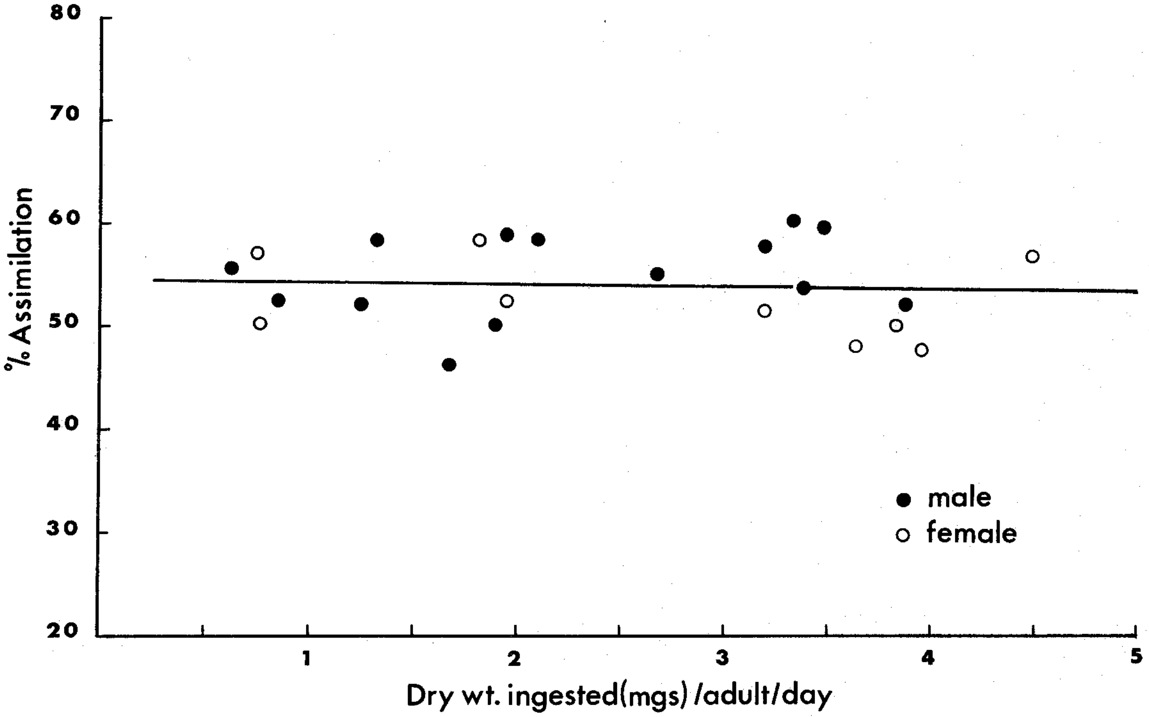
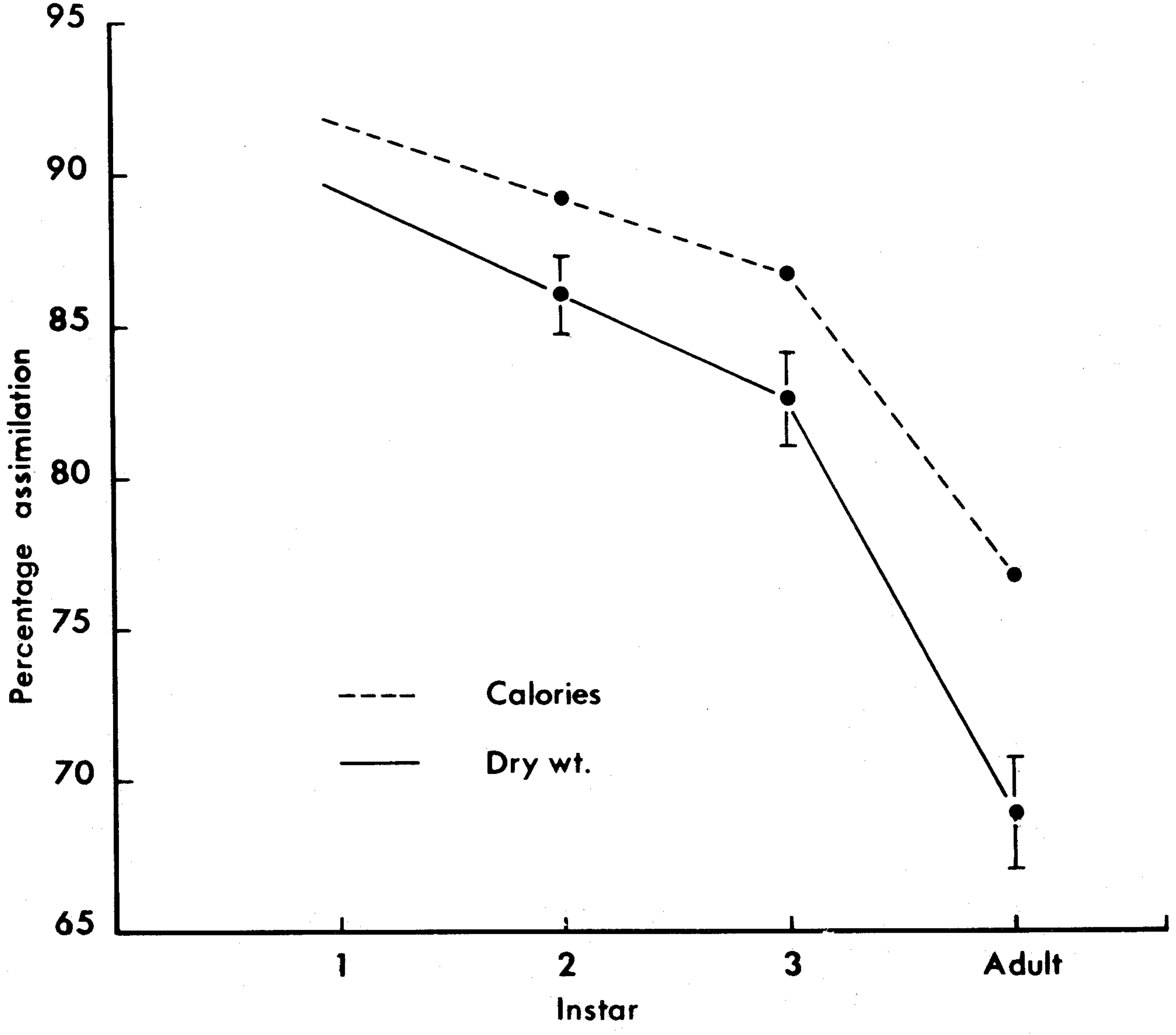

80
70
60
50
40
30
20
% Assimilation
1
2
3
4
5
Dry wt. ingested(mgs) /adult/day
● male
○ female

Fig. 16 Relationship between size and assimilation efficiency in N. brevicollis, calculated in terms of dry weight and calories : vertical lines are ± 2 standard errors. Regression drawn by eye. Tipulid larvae as prey at 15°C.


95
90
85
80
75
70
65
Percentage assimilation
Calories
Dry wt.
1
2
3
Adult
Instar

CHAPTER 6

Consumption

(a) Introduction

Consumption (C) is the major input energy pathway of any animal population and as indicated in Chapter 1

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

$$\text{or} \quad C = A + (F + U)$$

Attempts to estimate consumption have been made in the laboratory with later extrapolation to field conditions (e.g. Gerking, 1962; Nakamura, 1965; O'Neill, 1968; Pond, 1961; and Smith, 1959). In other cases field consumption has been measured directly (Paine, 1965; Kajak, 1967; and Petal, 1967). When, as is most usual, ingestion cannot be measured directly in the field, use is made of gut volume and gut clearance time or faeces production per unit time.

In the present study of N. brevicollis consumption was estimated in both the laboratory and the field.

(b) Laboratory Studies

Laboratory experiments were made with third instar larvae and adults of N. brevicollis. In all cases the experimental animals were deprived of food for 24 hours before the 1 week long experiment was conducted at either 5° or 15°C.

Collembola were offered daily as prey items and daily consumption was recorded gravimetrically according to the equation

Consumption = Weight of food proffered - Weight of food remains

The results obtained with third instar larvae are shown in Table 8 and Figure 6 and 17a. It is of interest to note that at any one temperature the daily consumption did not fluctuate markedly, however the mean daily consumption at 15°C was almost twice that recorded at 5°C.

Table 9 and Figure 17 show the results of laboratory consumption experiments with adult *N. brevicollis*. No significant difference was found in the daily consumption by the two sexes at 15°C and the consumption was reasonably stable throughout the experimental period. Unfortunately the experiments made with adults at 5°C were, for some inexplicable reason, unsatisfactory however it would seem reasonable to assume that a Q_{10} relationship of approximately 2.0 holds for adults as well as larvae.

As Phillipson (1967) has indicated with *Oniscus asellus*. L. laboratory determined consumption can give estimates of consumption much higher than those actually attained under field conditions and so the extrapolation of laboratory data to field consumption must be carried out with caution.

An alternative and preferable laboratory approach is the determination of gut clearance times with known foods at known

Mean Weight of larvae	Temperature	Number in sample	Units	Mean amount eaten per day	1 Standard error
22.50	5°	15	dry weight (mg)	0.88	.081
			calories	4.41	.40
23.26	15°	10	dry weight (mg)	1.87	.076
			calories	9.35	.44

Table 8 Mean daily consumption (dry weight and calories) of instar III : estimated in the laboratory with Collembola as prey.

Sex	Mean weight of adult	Number in Sample	Units	Mean amount eaten per day	1 Standard error
Male	56.66	10	dry weight (mg)	3.50	0.09
			calories	17.64	0.50
Female	64.11	10	dry weight (mg)	3.77	0.10
			calories	18.97	0.51

Table 9 Mean daily consumption (dry weight and calories) of adults : estimated in the laboratory at 15°C with Collembola as prey.

temperatures and to use this figure to determine consumption in the field indirectly.

It was known that with larval and adult N. brevicollis the feeding history of the experimental animal could influence gut clearance time (for example a 3 to 5 day period of starvation lengthened the time period that food remained in the gut). However, the following experiments were made.

Third instar larvae were acclimatized in the absence of food for 24 to 36 hours at the experimental temperature (5°, 10°, 15°, or 20°C). The larvae were offered Collembola as food for one hour, after which the remaining food was removed from the feeding chamber. The time interval between the end of feeding period and the appearance of the last faecal 'pellet' was termed 'gut clearance time'.

Figure 18 shows gut clearance time in hours plotted against larval weight in experiments made at 15°C. The mean gut clearance time did not alter with weight and was 14.8 hours within a range of 11 to 20 hours. Figure 19 shows the effect of temperature on larval gut clearance time. As was to be expected, temperature did influence gut turnover, the time of turnover being reduced by approximately one third for every 10°C increase.

Experiments with adults were made at 15° ± 1°C after a period of acclimation and starvation. Each individual was fed freshly killed Collembola, and after 30 minutes all uneaten food was removed;

following this blowfly larvae which led to the production of yellow coloured faeces was proffered. Collembola and blowfly larvae were fed alternatively and the yellow faeces were used according to the marker technique of Phillipson (1960); it was thus possible to determine adult gut clearance time with Collembola as the primary food source. The obtained results are shown in Figure 20 where it can be seen that the mean gut clearance time was 28 ± 4.3 hours within the range of 22-38 hours.

(c) Field Studies

Gut clearance time and percentage assimilation (See Chapter 5) can be used in conjunction with measurements of faeces production in the field to estimate absolute field consumption. A series of investigations were made therefore to determine egestion (F + U) under field conditions.

Adult N. brevicollis are known to be mainly nocturnal in their feeding activities and so an attempt was made to observe adults during a period which began after the animals were considered to have fed in the field. Accordingly dry pitfall traps were set at approximately 0300 hours and were emptied at dawn. Individual adults were placed in small dishes lined with pre-weighed aluminium foil and left under field conditions for such periods that permitted complete gut evacuation.

The weight of the resulting faeces was determined by subtract-

Month	Sex	Mean weight of animal (mg)	Faecal production (mg)	
June	Male	54.56	0.981	Not significant
	Female	66.39	1.078	
September	Male	46.35	0.839	
	Female	70.77	1.123	Significant

Table 10 Comparison between mean faecal production (under natural conditions) of Male and Female *N. brevicollis.*

ing the vacuum dry weight of aluminium foil from the vacuum dry weight of foil and faeces. Investigations of this type were made in the pre-diapause (June-July) and post-diapause (September) periods.

Table 10 and figures 21a and b show the results obtained. During the pre-diapause period the males and females showed no significant difference in faecal production, but in the post-diapause period there was a significant difference. It could be concluded that females in the field consume a greater quantity of food per day but this is not necessarily so as the assimilation efficiency experiments (Chapter 5) showed that the egg carrying females assimilate at a lower rate than the males. If this is correct then the difference in faecal production is due to the lower assimilation rate rather than a greater amount of food eaten per day by the females.

Some of the captured adults produced no faeces and stomach analysis showed food to be absent. There are a few possible reasons that could account for this:

(a) Feeding stops a few days before going into diapause
(b) Females stop feeding just before and when ovipositing eggs
(c) Starvation
(d) Senescence with attendant inability to feed

Most adults in the field were feeding well below the feeding rate obtained in the laboratory. The laboratory value can be considered as the maximum rate. The mean field feeding rate of both sexes during the pre-diapause period (males 2.31 mg, females 2.52 mg) was only 66% of the maximum rate. This value decreases during the reproductive stage, when the male rates fell to 52% of the maximum rate. This decrease is probably due to reproductive activities and senescence rather than decrease in the availability of food. Penney (1960) showed that the number of micro-arthropods available to the adults during the pre-diapause and reproductive periods did not vary greatly.

(d) Estimated field consumption

Knowing percentage assimilation for a given food at known temperatures, gut turnover time at known temperatures and field faeces production it is possible to estimate absolute consumption and assimilation in the field.

It was assumed that the gut clearance time found in the laboratory would be applicable to animals in the field. As the gut clearance time of the adult was more than 24 hours, the amount of food ingested per day would actually be less than the amount suggested by the quantity of food material in the gut at the time of capture by the turnover factor of 0.8347 $(\frac{24.00}{28.75})$. Therefore the dry weight of food in the gut before assimilation (calculated from field faeces and percentage assimilation data) multiplied by 0.8347 gives the quantity of food ingested per day by the adults in the field.

The same data were recalculated in terms of calories using

Month	Sex	Mean weight of animal (mg)	Units	Ingestion	Assimilation
June/ July	Male	54.56	dry weight (mg)	2.3098	1.3290
			calories	11.6383	8.1708
	Female	66.39	dry weight (mg)	2.5217	1.4433
			calories	12.7060	8.8930
September	Male	46.35	dry weight (mg)	1.8188	0.9795
			calories	9.1643	6.3881
	Female	70.77	dry weight (mg)	2.4236	1.3004
			calories	12.2117	8.4963

Table 11 Estimated field ingestion and assimilation of adult *N. brevicollis*.

the calorific values of field faeces and Collembola. The estimated calorific value of field faeces was 3.5358 and 3.3082 in June/July and September/October respectively. These values are only slightly lower than the calorific values obtained for laboratory faeces (Collembola 3.7599, Tipulid larvae 4.0257). Table 11 summarizes the estimates obtained.

(d) Discussion

The measurement of Consumption (C) directly in the field is a difficult task especially when dealing with an invertebrate predator. In the laboratory it is difficult to reproduce the complex pattern which exists in the field. The laboratory results which reflect maximum feeding rate provide little information of the feeding rates in the field. In the present study, the results show that N. brevicollis in the field was feeding well below the feeding rate in the laboratory.

There are many variables that can affect the passage of food through the gut. Darnell and Meierotto (1962) discuss some variables known to affect fish. In the present investigation because of limited time only two variables were considered (temperature and starvation). Both consumption and gut clearance time were affected by temperature. Between 5° and 15°C gut clearance time of the larvae decreased by 31% while food intake decreased by 53% between 15° and 5°C. In the millipede Narceus americanus, food consumption first increased with rising temperature between 10 - 25°C and then fell between 25 - 35°C. (O'Neill, 1968).

Several workers, for example, Smalley (1960), Wiegert (1965), Mann (1965) estimated field consumption by combining the relevant components of the energetics equation

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

If consumption is estimated independently as in this study, the above method can serve as a check.

Fig. 17a The mean dry weight of prey eaten per larva (third instar at 5°C) per day over a period of 10 days. Each point is the average value for 15 individuals.

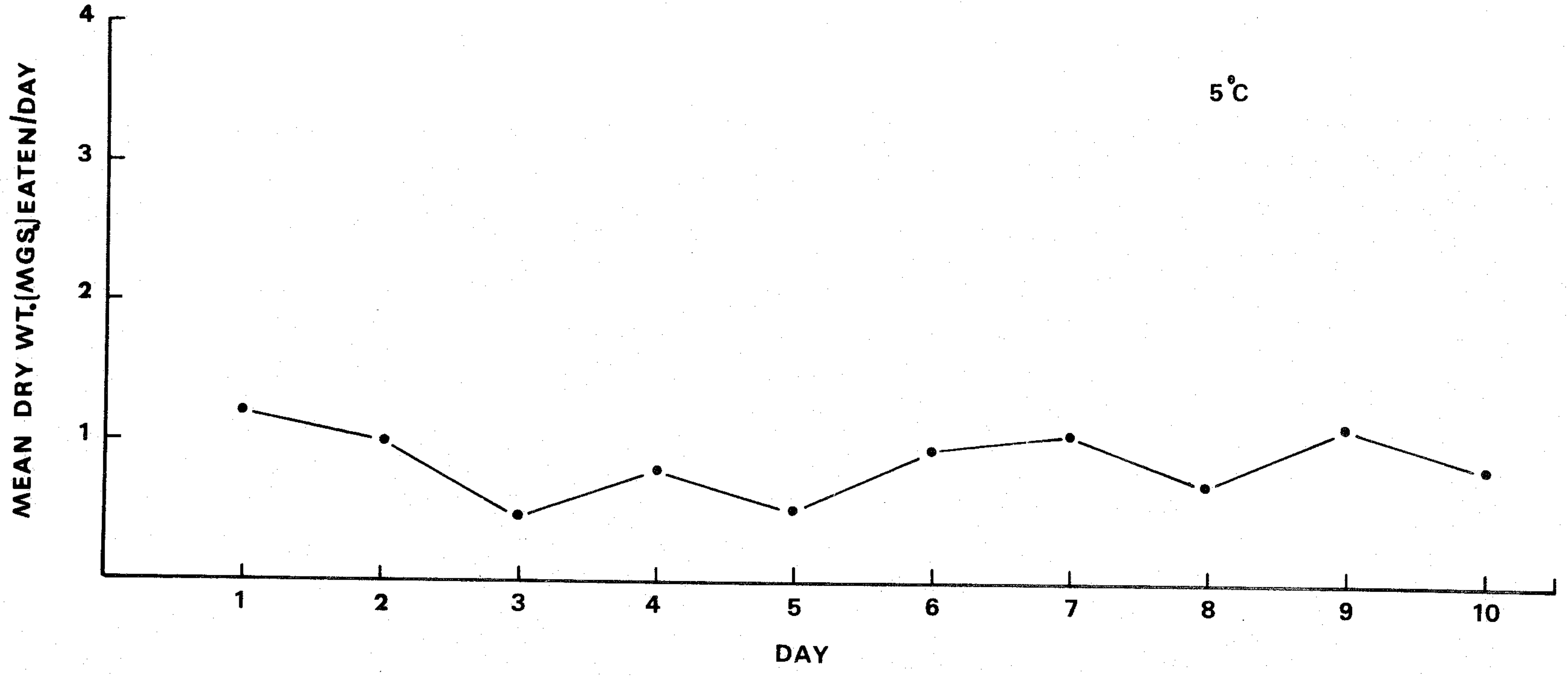

5°C
MEAN DRY WT.(MGS.)EATEN/DAY
4
3
2
1
1
2
3
4
5
6
7
8
9
10
DAY

Fig. 17b The mean dry weight of prey eaten per adult (pre-diapause stage at 15°C)per day over a period of 7 days. Each point is the average value for 10 individuals.

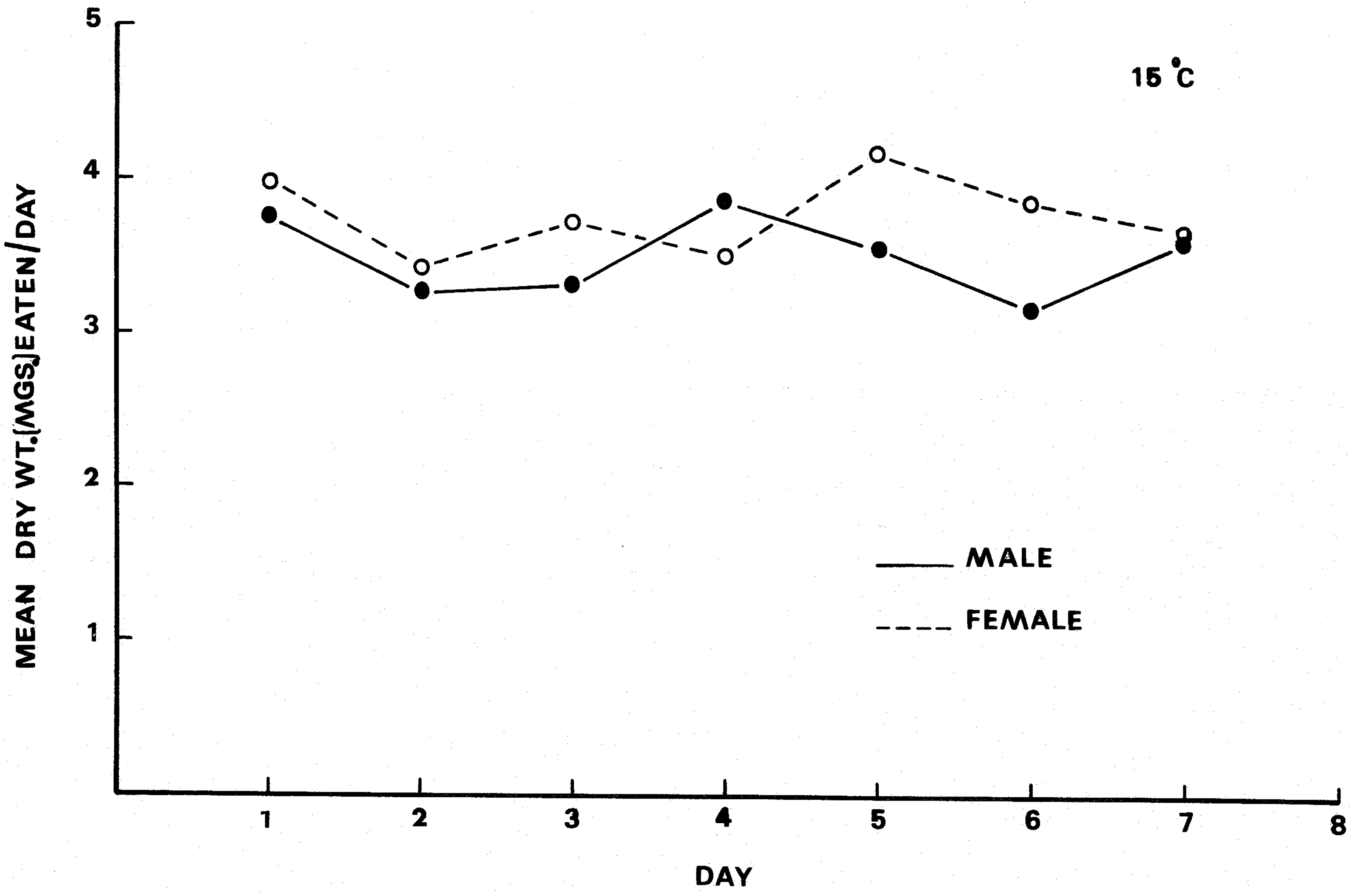

15 °C
MEAN DRY WT.(MGS.)EATEN/DAY
5
4
3
2
1
DAY
1
2
3
4
5
6
7
8
MALE
FEMALE

Fig. 18 Larval gut clearance time experiment with Collembola as prey at 15°C.

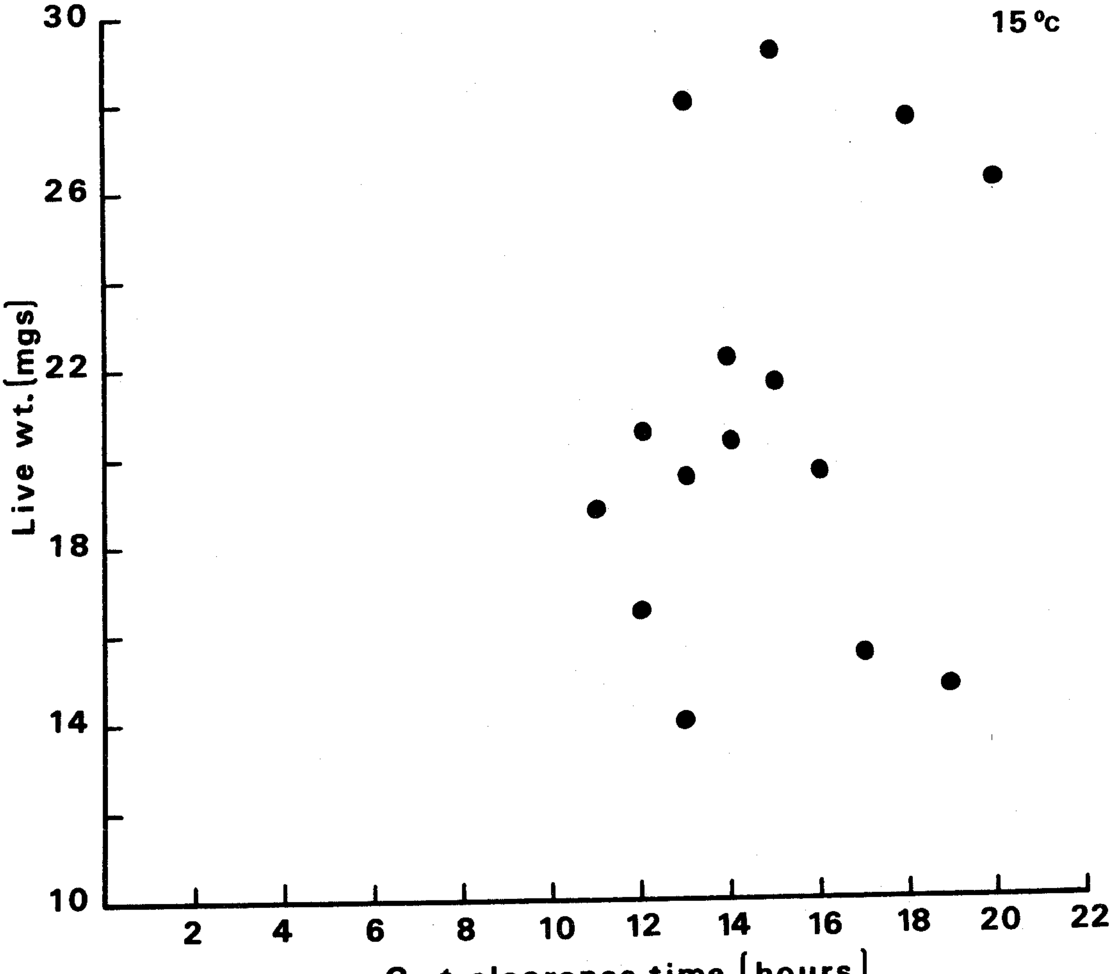

15 °c
Live wt. (mgs)
30
26
22
18
14
10
2
4
6
8
10
12
14
16
18
20
22
Gut clearance time (hours)

Fig. 19 The effect of temperature on larval gut clearance time with Collembola as prey : vertical lines are ± 2 standard errors. Regression drawn by eye.

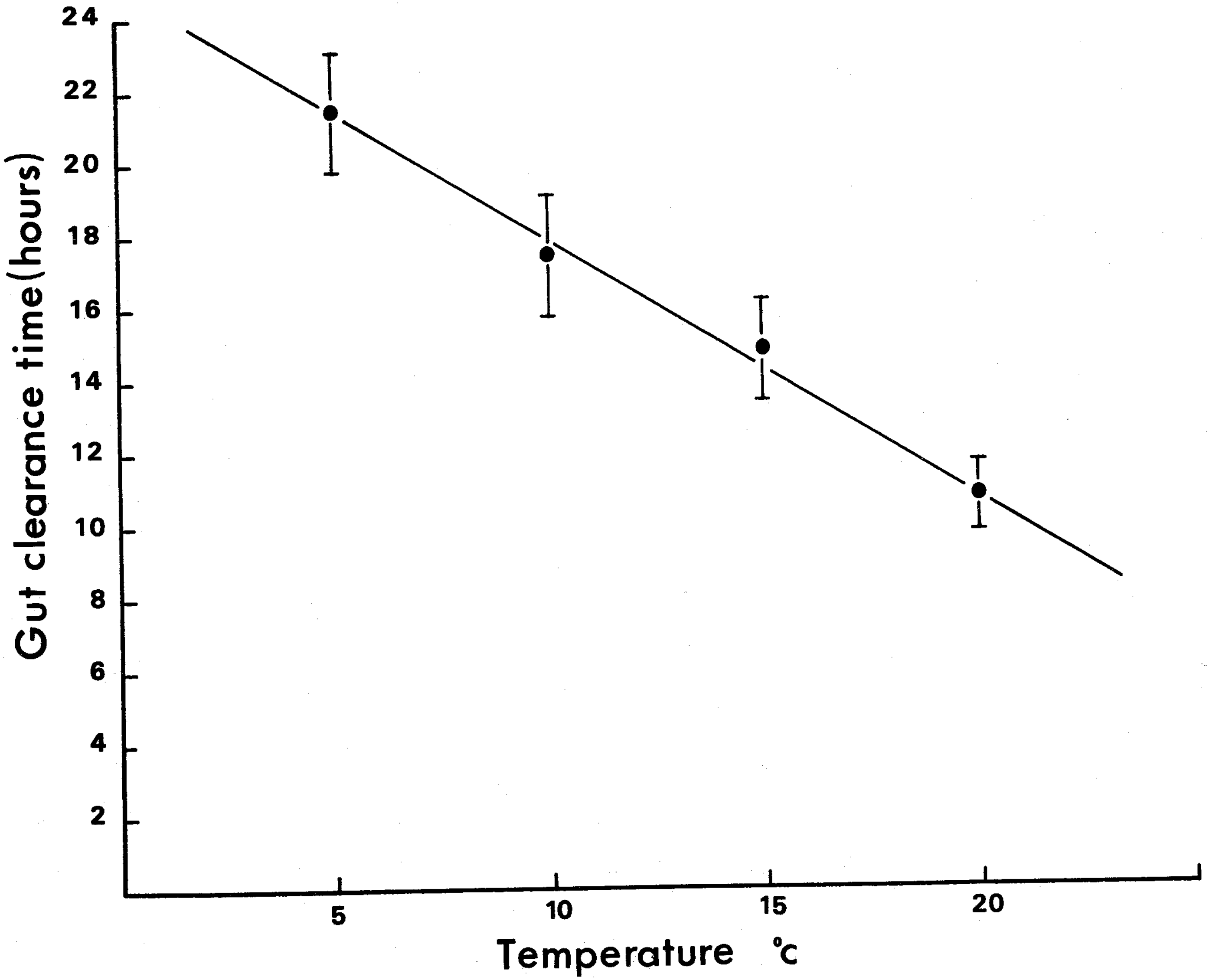

Gut clearance time (hours)
24
22
20
18
16
14
12
10
8
6
4
2
5
10
15
20
Temperature °c

Fig. 20 Adult gut clearance time experiment with Collembola as prey at 15°C.

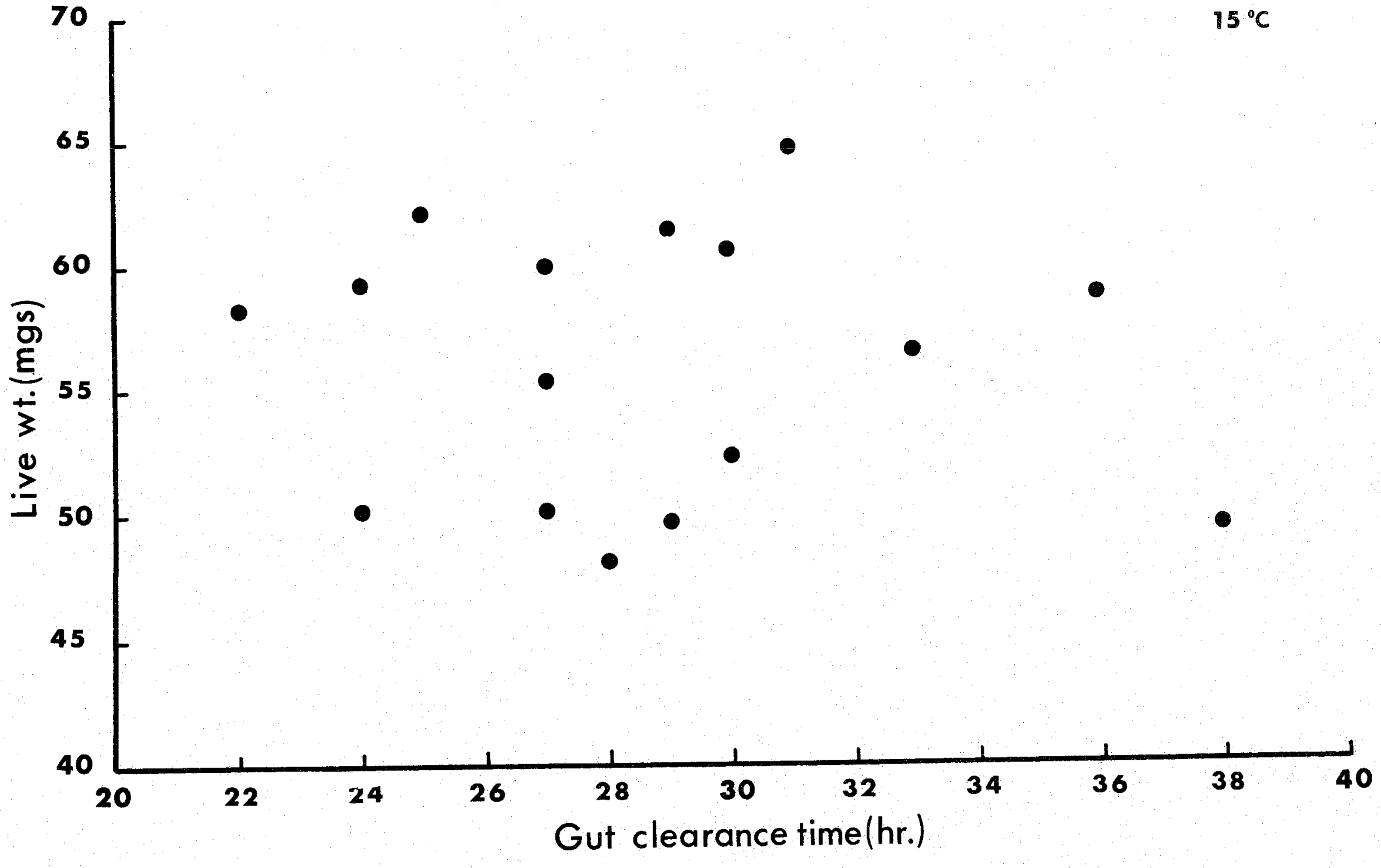
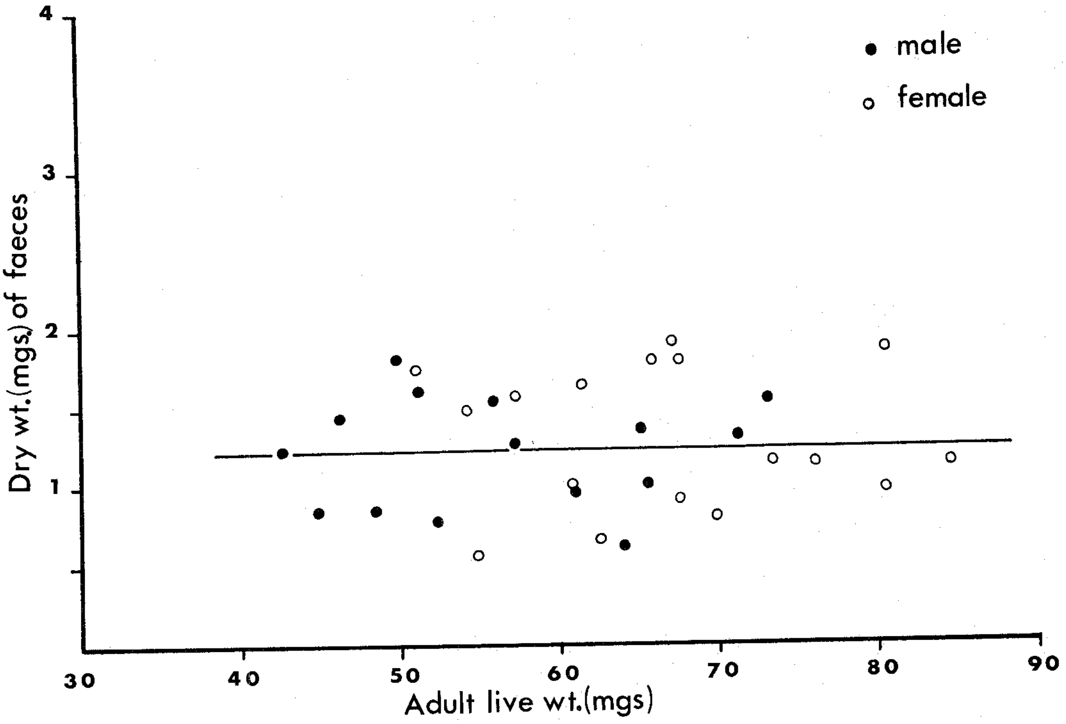
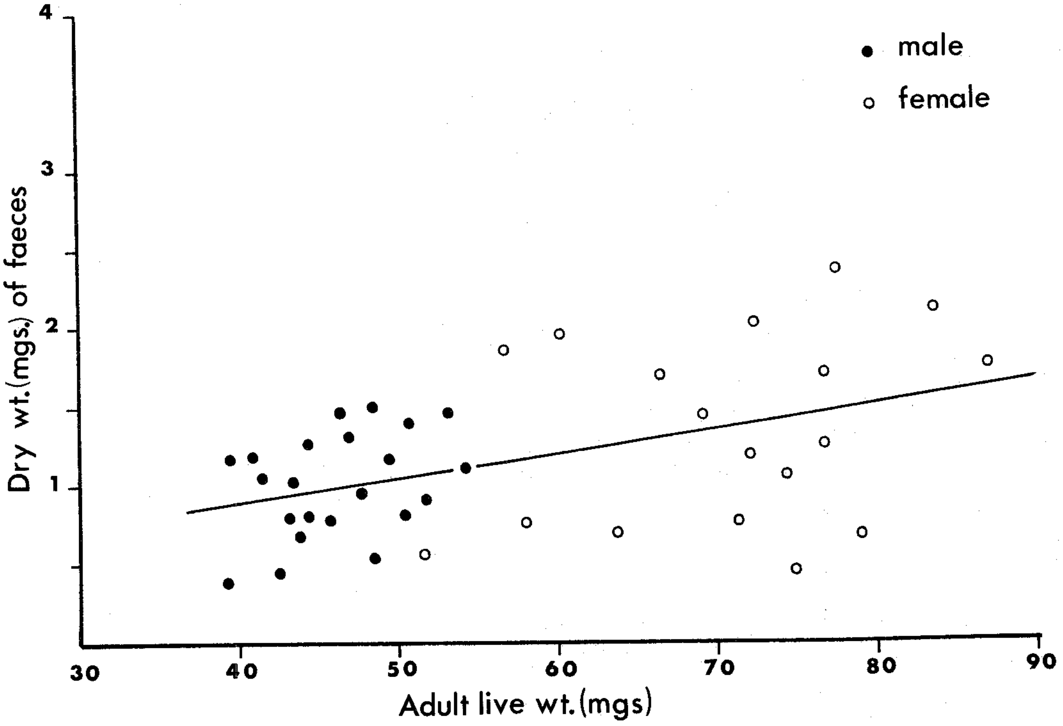

15 °C
Live wt.(mgs)
70
65
60
55
50
45
40
20
22
24
26
28
30
32
34
36
38
40
Gut clearance time(hr.)

Fig. 21a Faeces production of pre-diapause adults under natural conditions.

Fig. 21b Faeces production of post-diapause adults under natural conditions.


● male
○ female
Dry wt.(mgs.) of faeces
4
3
2
1
30
40
50
60
70
80
90
Adult live wt.(mgs)


● male
○ female
Dry wt.(mgs.) of faeces
4
3
2
1
30
40
50
60
70
80
90
Adult live wt.(mgs)

CHAPTER 7

Production

(a) Introduction

The term production has been used variously in the literature, Odum and Smalley (1959) and Smalley (1960) equated it with growth (the increase in population biomass per unit time), whereas Wiegert (1964) defined production as growth or increase in biomass plus moulted exoskeletal material. In later works Wiegert (1965) excluded exuviae and Saito (1965) included egg production along with growth.

In the present attempt to quantify the parameters of the energy budget equation $C = P + R + F + U$, production (P) include (a) growth of individuals per unit time (P g), (b) larval exuviae (E_V), and (C) egg production (Pr) hence:

$$P = Pg + Pr + Ev$$

(b) Growth (Pg)

Measurement of the larval growth under field conditions proved impractical because of the prolonged oviposition period, and further the population data (See Chapter 9) was not good enough for the calculation of Pg. Experiments were made therefore in semi-natural conditions. The synchronised adult emergence allowed this parameter (adult Pg) to be measured under field conditions. Adult growth rate measurements were also made in semi-natural conditions.

Initially twenty larvae were collected soon after hatching and four placed in each of 5 growth chambers. Each growth chamber consisted of a 5 cm diameter crystallizing dish, partly filled with soil. To simulate natural conditions a few stones and litter were added. To avoid injury to the newly hatched forms the experimental animals were not themselves weighed, instead separate weighings were made of newly hatched, non experimental individuals. The mean weight was found to be 1.30 mg and this was taken as the initial weight of the experimental larvae.

Following preparation the growth chambers were placed in the field, a regular supply of food in the form of Collembola was provided. Larvae were then weighed every ten days.

A duplicate set of experiments was also prepared and run in the laboratory at 15 ± 1°C.

In the case of adults thirty newly emerged individuals were collected in the first week of June and one male and one female were placed in each of 15 prepared growth chambers, prepared as for larvae. The growth chambers were placed in the field, food was supplied regularly and weighings were made every 10 days. It was known that adult body growth ceases after the onset of diapause and so experiments were stopped at this time.

The mark and recapture samples used in obtaining the adult population estimates were also used to provide field growth data. Twenty individuals were taken from each sample (10 of each sex) and weighed.

The wet weight measurements were converted to dry weights by using the regressions in Chapter 3, and to calories from the information in Chapter 4.

Table 12 - 13 and figures 22 - 24 show the obtained results. In the case of the larvae under semi-natural conditions (Table 12 and fig. 22) it can be seen that growth was fairly steady up to the prepupal stage. The first moult occurred after about 17 days (range 15 - 19 days), the second moult between 40 - 55 days. The experiment was terminated once the larvae reached the prepupal stage. Feeding stops during this period and the animal loses weight.

As was to be expected, in the laboratory experiment with larvae (Figure 23), growth was much faster than in the field, indeed the temperature dependence of growth rate is well documented (e.g. Rasmussen, 1967 demonstrated this for Hylotrupes bajulus). It should be noted however, that despite the different development times the final recorded weights of Instar III in the two types of experiment was not significantly

Mean dry weight	In calories	Growth increment in dry weight (mg)	In calories	Growth per day in dry weight (mg)	In calories
0.0700	.3644				
0.8364	4.3543	0.7664	3.9899	0.0766	0.3989
1.1118	5.9641	0.2754	1.6098	0.0275	0.1609
1.8356	9.8468	0.7238	3.8827	0.0724	0.3882
2.9206	15.6672	1.0850	5.8204	0.1085	0.5820
3.9766	23.0976	1.0560	7.4304	0.1056	0.7430
5.8578	34.0244	1.8812	10.9268	0.1881	1.0926
6.8220	39.6249	0.9642	5.6005	0.0964	0.5600
7.7768	45.1707	0.9548	5.5458	0.0954	0.5545
8.4380	49.0112	0.6612	3.8405	0.0661	0.3840
8.3847	48.7016				

Table 12 Growth data of larvae under semi-natural conditions.

Mean dry weight	In calories	Growth increment dry weight (mg)	In calories	Growth per day dry weight (mg)	In calories
16.09	98.871				
24.86	152.76	8.77	53.89	0.88	5.38
30.53	187.60	5.67	34.84	0.56	3.48
33.47	219.18	5.14	31.58	0.51	3.15
35.47	217.46				

Table 13a Female growth data under semi-natural conditions.

Mean dry weight	In calories	Growth increment dry weight (mg)	In calories	Growth per day dry weight (mg)	In calories
13.97	80.12				
19.66	112.76	5.69	32.64	0.57	3.26
24.48	140.41	4.82	27.65	0.48	2.76
29.32	168.17	4.84	27.76	0.48	2.78
29.67	170.18	0.35	2.00	0.04	0.20

Table 13b Male growth data under semi-natural conditions.

different.

Table 13 a b and figure 24 show that adult growth was fairly steady up to diapause stage. The field growth rate was faster (fig. 24). The female growth was faster and weighed approximately 9 - 11 mgs heavier than the male on reaching diapause. Feeding ceases during the diapause period and the animal loses weight.

The loss of weight or decreased growth at moulting could be due to several factors.

a) The larvae stops feeding some 24 hours before moulting.

b) Loss of water during the moulting period.

c) Feeding activity is delayed up to 24 hours after moulting whilst the mandibles become sclerotized.

For the population growth calculation it was necessary to know the growth rate of each instar and adult per day. This was estimated from the growth data in figures 22 and 24 by use of the regression analysis. The equations obtained were as follows:

Instar I $y = 0.0276x + 0.56$ $r = +0.65$

Instar II $y = 0.0884x - 0.10$ $r = +0.84$

Instar III (until prepupae) $y = 0.1264x - 2.11$ $r = +0.79$

Male

June $y = 0.4239x + 15.63$ $r = +0.86$

July $y = 0.0006x + 28.17$ $r = +0.002$

Female

June $y = 0.5549x + 17.18$ $r = +0.89$

July $y = 0.0113x + 32.88$ $r = +0.04$

where $y = ax + b$

y = dry weight (mgs.)

x = days since hatching (instar I) or last moult.

thus a = mg. growth per day.

Therefore for each instar/adults growth rate (mgs./day) is

Instar I = 0.0276

Instar II = 0.0884

Instar III = 0.1264

Males

June = 0.423

July = 0.001

Females

June = 0.5549

July = 0.0113

c) *Reproduction* (Pr)

Two methods were used to estimate the reproductive potential of *Nebria*.

1) Females were collected from the field after mid-September and dissected to estimate the number of eggs present in the body. Only females weighing 80 mg wet weight were dissected. This was to avoid dissecting females that had already laid a batch of eggs. Ten specimens were dissected and only mature and well developed eggs were counted. The mean number of eggs per female was 27.3 ± 3.79. It can be assumed that some eggs were still to develop or a few eggs had already been laid. The maximum number of eggs in a female was 34.

2) In the second method, females were kept in glass dishes lined with filter paper. An inverted tube filled with water was placed in the centre of the dish to keep the filter paper moist. The glass dishes were covered and placed in the field. They were fed (collembola) alternate days. Eggs were laid in holes chewed into the filter paper. The total number of eggs laid by the five females was 167, a mean of 33.4 per female. The females were dissected after 40 days and were found spent. Penney (1965) estimated that egg production took an average of 27 days. The percentage of eggs that hatched was high.

It was noted that the eggs laid on the surface of the filter paper failed to develop and were probably infertile. The total number of eggs 167 minus the number of infertile eggs 14 divided by 5 gave a mean of 30.6 eggs per female. This figure was taken as an estimate of the reproductive potential of

Number of Eggs	Dry weight (mgs) of eggs	Mean weight of 1 egg
5	1.35	.2700
10	2.63	.2630
8	2.25	.2812
10	2.55	.2550
10	2.25	.2250
8	1.85	.2312
5	1.24	.2480
3	0.85	.2833
4	0.95	.2375
4	0.97	.2425
3	0.76	.2533
8	1.75	.2187
5	1.10	.2200
5	1.22	.2440
8	2.00	.2500
	mean	.2481

Mean dry weight of 1 egg = 0.2481 mg.

Table 14 Wet/dry weight relationship of *N. brevicollis* eggs.

Instar No.	Dry Weight (mgs) of larvae	Dry Weight (mgs) of moult	In terms of calories
I	0.939	0.0722	0.3541
II	2.623	0.1889	0.8933
III	8.139	0.5159	2.2303

Table 15 Exuvium data of *Nebria brevicollis*

N. brevicollis. The figure agrees with the estimate obtained by Penney (1965) of 31 eggs per female.

A wet and dry weight relationship of eggs gave the mean dry weight of one egg as 0.2481 mgs. (See table 14). The total calories of eggs produced per female is 43.10.

d) Exuviae (E_V)

N. brevicollis undergoes four moults;-

Instar I II III pupa

It was found that the pupal exuvium was very small, and its contribution to total production was assumed negligible. Only the larval exuviae were therefore considered in the present study.

Larval exuviae are rarely found in the field and in order to obtain sufficient data it was necessary to rear larvae under laboratory conditions. Occasionally larvae moulted during feeding and respiration experiments, and the resulting exuviae were incorporated in the final results.

Each exuvium was dried in a vacuum oven at 60°C before it was weighed, and eventually the mean weight of each stadial exuvium was calculated.

Table 15 and figure 25 show the obtained results. The weight of the exuviae increased from 0.072 mg (No.1 instar) to 0.5159 mg (third instar). The rate of increase in weight of the exuviae was not constant but was similar to the rate of increase of body weight. The exuviae of Instar I, II and III represented about 7.69, 7.20, 6.33% of the larval dry body weight respectively. The total calories lost in moulting during development was approximately 3.42 calories. The total production of a single individual was approximately 251.62 calories (Pg (205.10) + Pr (43.10) + Ew (3.42), therefore exuvium production amounted to 1.4% of the total production.

(c) Discussion

The method of measuring production of known individuals per unit time was used by several workers (Watson, 1965; Rasmussen, 1967; Teal, 1965 etc.). In spite of the simple life history, growth of the larval *Nebria* could not be measured in the field because of the long oviposition period. Elliott (1967) working with some *Plecoptera* and *Ephemeroptera* was faced with a similar problem but overcame it by looking at the changes in modes rather than means, which revealed periods of slow and rapid growth. Growth rate calculated from mean weights can lead to a reduced estimate of population growth rate, and for bioenergetic purposes this method is unsatisfactory.

Another problem in the present investigation was the failure to sample all three instars equally. Instar I was not well represented in the samples taken from the field. An error like this no doubt will also affect the population production curve.

The energy lost through moulting is small in terms of total energy budget; a conclusion which accords with the findings of a number of investigators who found that the energy loss due to moulting was small. (Teal, 1957; Wiegert, 1964; Whittaker, 1965; Rasmussen, 1967; Dutton, 1969; Lawton, 1969).

Fig. 22 Growth data of larvae under semi-natural conditions. Vertical lines are ± 2 standard errors : curve drawn by eye.

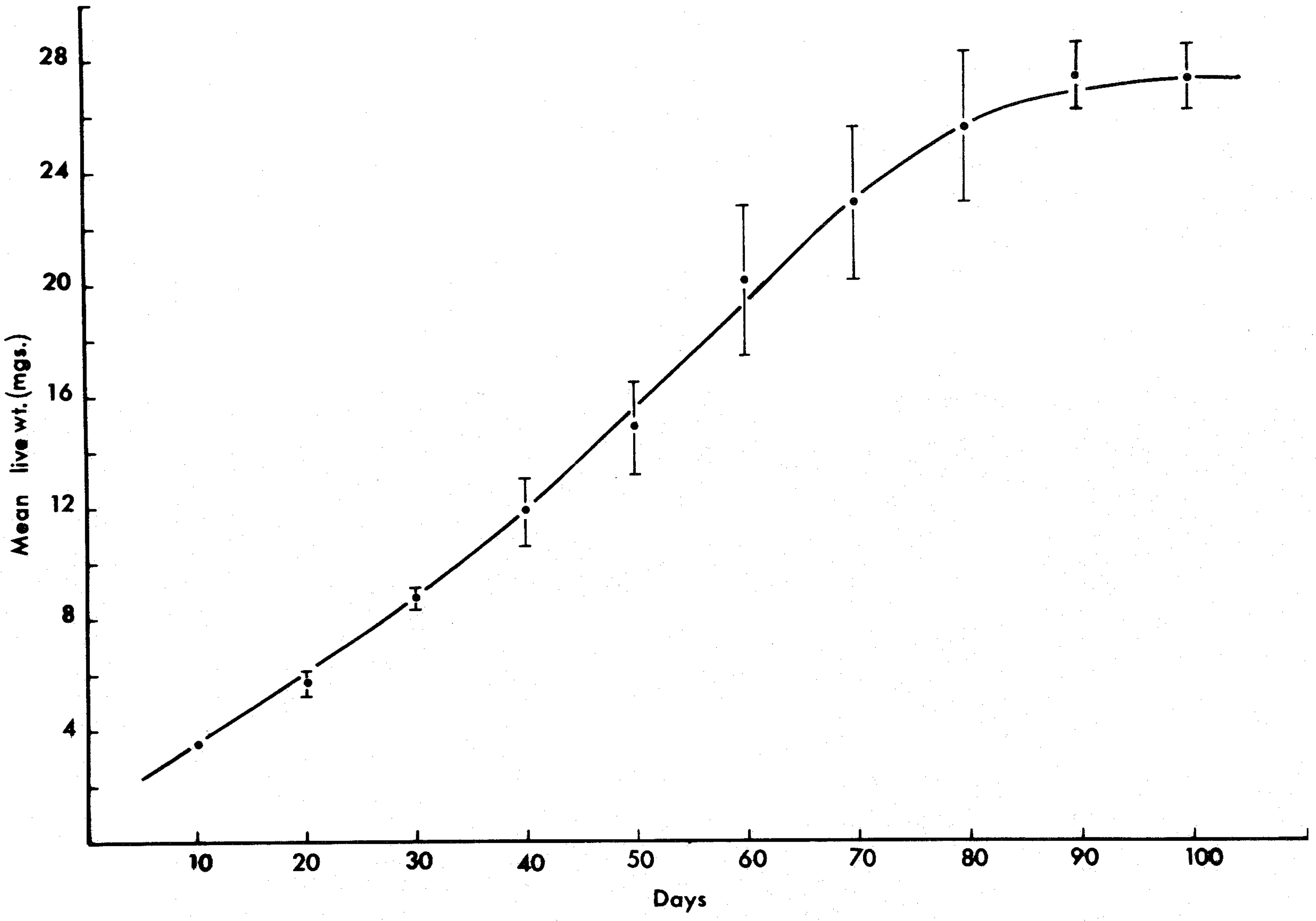

Mean live wt. (mgs.)
28
24
20
16
12
8
4
10
20
30
40
50
60
70
80
90
100
Days

Fig. 23 Growth data of larvae at constant temperature ($15 \pm 1^{\circ}C$). Vertical lines are ± 2 standard errors : curve drawn by eye.

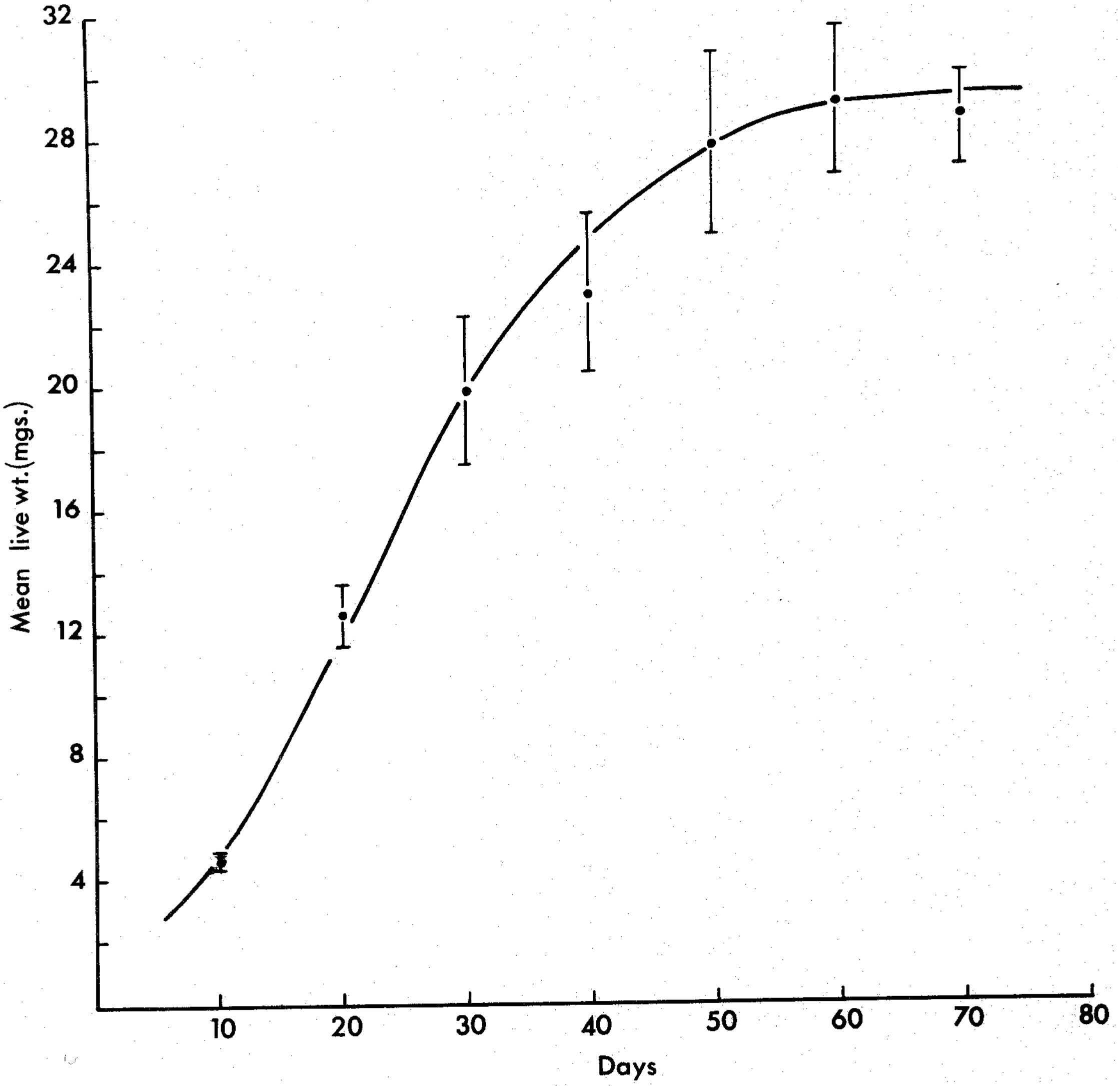

32
28
24
20
16
12
8
4
Mean live wt. (mgs.)
10
20
30
40
50
60
70
80
Days

Fig. 24 Adult field growth data : vertical lines are ± 2 standard errors.

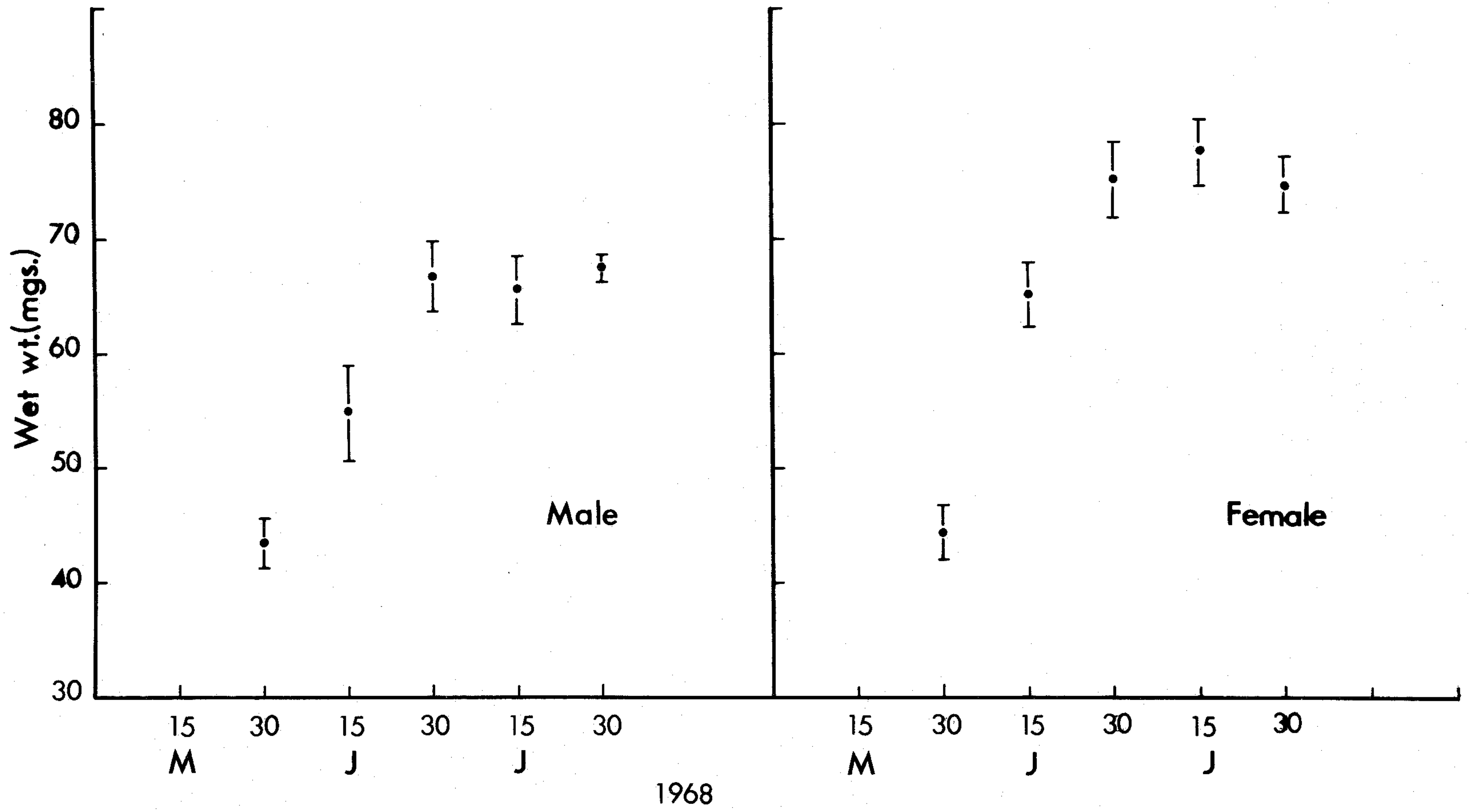
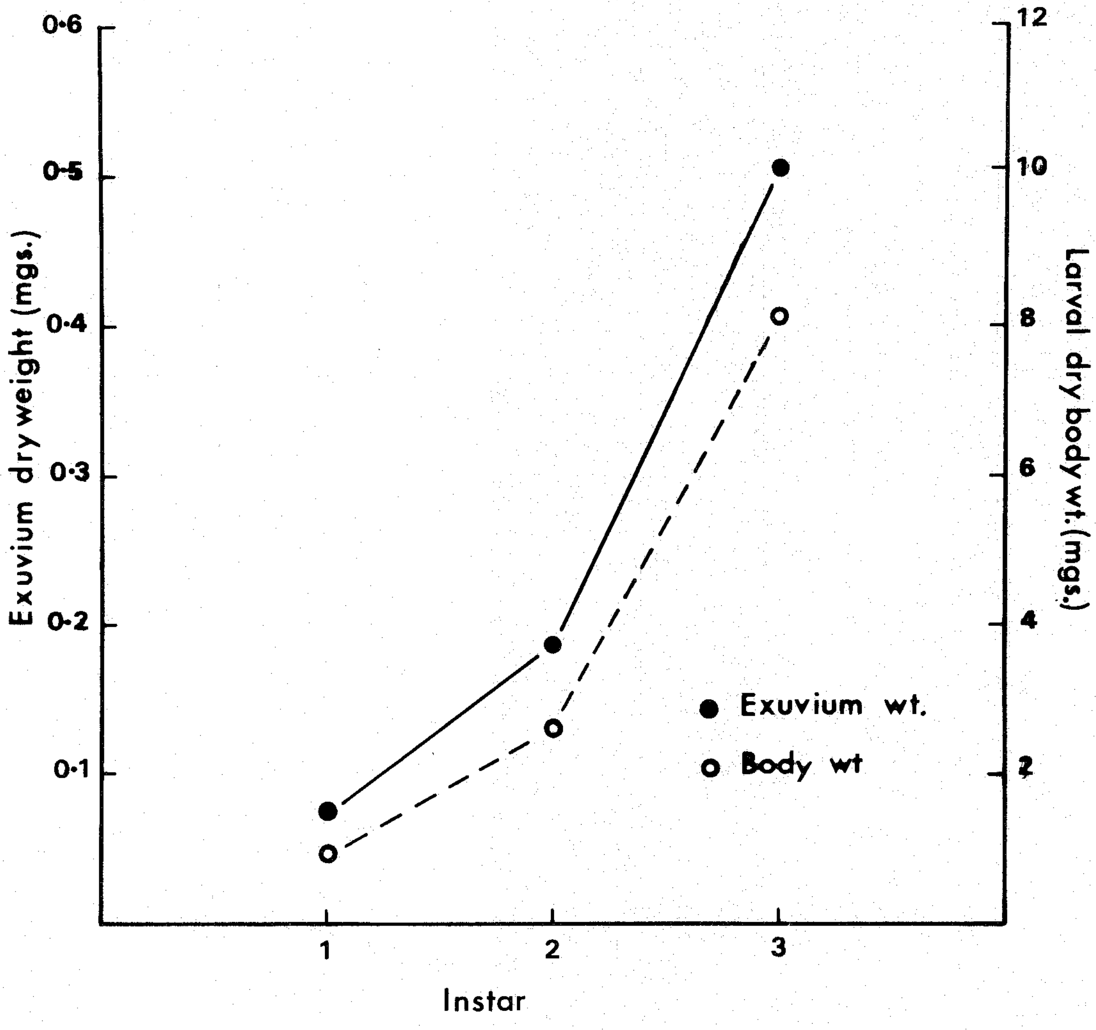

Wet wt.(mgs.)
80
70
60
50
40
30
Male
Female
15
30
15
30
15
30
M
J
J
1968

Fig. 25. Larval body weight and exuvium weight with regards to instar number of *N. brevicollis*.


0·6
0·5
0·4
0·3
0·2
0·1
Exuvium dryweight (mgs.)
12
10
8
6
4
2
Larval dry body wt. (mgs.)
1
2
3
Instar
● Exuvium wt.
○ Body wt

CHAPTER 8

Respiration

(a) Introduction

The measurement of respiratory heat loss in bioenergetic studies is of prime importance as it is one of the major pathways of energy flow.

Respiration studies on all life stages of beetles have been made amongst others by Gromadzka (1968) in *Leptinotarsa decemlineata*, (Dutton (1969) in *Melanotus rufipes*, Klekowski et al (1967) in *Tribolium castaneum*, and Tipton (1960) measured the respiration of *Nebria brevicollis* adults prior to diapause. In all cases except Dutton (1969) respiration was measured over a short period. It has been shown by several investigators (e.g. Macfadyen, 1963; Phillipson and Watson 1965; Webb, 1968) that respiration varies with weight, sex, age, season and physiological condition. Phillipson (1963 and 1967) therefore stressed the importance of measuring respiration continuously over 24 hours on all life stages throughout the year. This procedure was adopted in the present study, except where the inter-relationships of temperature and respiratory rate were being investigated.

(b) Methods

Oxygen consumption measurements were made throughout the year using the continuously recording respirometer of the type described by Phillipson (1962). The majority of measurements were made at 15 ± 1°C and the light regime was regulated by an automatic time-switch thus allowing the experiment to run close to the natural photoperiod. In the examination of temperature effects on oxygen consumption, the Warburg respirometer technique described by Umbreit et al (1947), was used.

The experimental animals were collected in grazed fields around Durham City one day prior to the experiments. They were fed and kept overnight at the experimental temperature. Oxygen consumption measurements were made on different life stages of N. brevicollis, and approximately 700 animals were used in the experiments. With instar I and early instar II it was not possible to make measurements on single individuals as the apparatus was not sensitive enough to record the oxygen consumption of animals of 3 - 7 mg wet weight. Determination of O_2 consumption by such small individuals were made on groups of 3 to 4 larvae. In these cases cannabalism was avoided by placing each larvae in a small glass tube containing damp filter paper. In addition both ends of the glass tube were covered with perforated parafilm paper. The animals were not fed during the experiment.

Each experiment ran for 48 hours. The first 10 hours of readings of each experiment was ignored as this was considered the time required by the animal to settle down in the respirometer. The live weight, instar number, sex, of each experiment was recorded, and subsequently its respiration rate per 24 hours calculated.

c) Results

All results are expressed as $O_2 mm^3/mg/hr$

1) Larvae

Figures 26 - 29 show the oxygen consumption per unit wt/unit time of the individual larvae plotted against live weight for each of the months they were present in the field. The graphs show an L shaped curve similar to those obtained by O'Connor (1963, 1964), Nielsen (1961), Phillipson (1963), Phillipson and Watson (1965). An inflexion occurs at about 5 mg live weight. Over 10 mg the respiratory rate per unit weight was more or less constant.

These data are summarized in Table 16 and figure 30 where the mean monthly rate of each instar is shown. The respiratory rate of instar I remained more or less constant, and seasonal effects on the respiration of Instar II and III were not very marked either.

The mean respiratory rate of the larvae at 15°C in each month is shown in table 17 and figure 30. Despite the constant

Month	Instar I	Instar II	Instar III	Male	Female
October	.9786	.8570			
November	.9550	.8257	.5281		
December	.8604	.6217	.4414		
January	.9017	.5152	.4108		
February	.9060	.5817	.4835		
March		.5008	.4490		
April		.7184	.3772		
May			.4119		
June				.3842	.3733
July				.2176	.2239
August					
September				.7080	.5771
October				.4776	.4215
November				.4511	.3587

Table 16 Mean monthly respiration data (1967-68) for larvae and adults of *N. brevicollis*. All values expressed as $O_2mm^3/mg/hr$.

Month	Mean respiratory rate ($O_2 mm^3/mg/hr$)
October	0.9178
November	0.7696
December	0.6411
January	0.6092
February	0.6570
March	0.4749
April	0.5478
May	0.4119

Table 17 Mean monthly respiration data of *N. brevicollis* larvae

experimental conditions, seasonal effects are quite clear, the oxygen consumption rate being highest in Autumn (October-November) - 0.8437 $O_2mm^3/mg/hr$, and lowest in spring (March - May)- 0.4782 $O_2mm^3/mg/hr$.

There is an exponential decrease in the weight specific respiration rate with increasing weight. The highest respiratory rate occurs in Instar I, the rate decreased from 0.9202 to 0.4431 $O_2mm^3/mg/hr$ in the third instars. No periodicity in respiration was observed during the 24 hour period. Moulting often occurred in the respiratory chamber, but it did not affect the result significantly.

2) Pupae and adults

Figures 31 - 34 show the individual oxygen consumption per unit weight/per hour at 15°C.

The mean respiratory rate of the pupal stage (see fig. 31) is low (0.2121 $O_2mm^3/mg/hr$.). The mean rate of the pupae corresponds with the prepupal larvae (approx. 0.2500 $O_2mm^3/mg/hr$) and diapause adults (0.2207 $O_2mm^3/mg/hr$). Pupal respiration was highest a few days before the adult emerged, probably due to the reorganisation of organs.

The variability of the adult respiratory rate can be correlated with season and physiological condition. Table 17 and figure 35 show the mean oxygen consumption per month. There is a significant difference between the monthly means.

In June/early July the increased oxygen consumption is presumably associated with the active feeding of the adult. Feeding ceases after ± 4 weeks. The adult becomes inactive (locomotor and feeding activity stops) and goes into diapause for about 4-6 weeks. This is reflected in the low respiratory rate in August (see figure 31). The peak of respiratory activity occurred in September; this coincides with the peak of the reproductive period. In September the males showed a significantly higher respiratory rate than the females. The males had a higher respiratory rate than the females at any comparable stage except diapause.

The respiratory rate of the males and females in a breeding condition was about 45% and 35% respectively higher than that of non-breeding adults (pre-diapause). The mean oxygen consumption rate decreased in October and November. The high respiratory rate shown by some individuals in October is probably due to their reproductive condition, but this would not be so for those males who had a high respiratory rate in November. This high rate can be correlated with senescence as most of the November individuals are in a post-breeding condition.

No periodicity in respiration was detected in the 24 hour experiment, although in the field the adult activity is nocturnal.

The mean oxygen consumption of the males was 0.4476 mm^3/mg/hr compared with 0.3909 mm^3/mg/hr for the females. The amount of oxygen consumed by individual males was 22.34 mm^3/hr against 26.96 mm^3/hr by the females.

d) Temperature effects

1) Larvae

The Warburg apparatus was used to determine oxygen consumption of each life stage at different temperatures. For each instar one group of animals was used in all three temperature measurements. Oxygen consumption was plotted as $O_2 mm^3$/mg/hr against temperature. The results are presented in table 18a and figure 36. Regression lines were fitted by the method of least squares. The equations obtained were as follows:

Instar I $y = 0.0874x - 0.2173$
Instar II $y = 0.0575x - 0.1142$
Instar III $y = 0.0409x - 0.0705$

y = respiration rate
x = temperature

In conformity with the often observed phenomenon, all larval stages showed an increased oxygen consumption with rise in temperature.

The data plotted on a semi-logarithmic grid (see figure 37) show the almost parallel nature of the curves, which means that the influence of temperature on the respiratory rate is similar irrespective of the size.

Developmental stage	10°C	15°C	20°C
Instar I	.6462 ± .0630	1.1050 ± .1046	1.5250 ± .1302
Instar II	.4688 ± .0510	.7328 ± .0838	1.0469 ± .1180
Instar III	.3477 ± .0342	.5284 ± .0520	.7685 ± .0688

Table 18a Respiration data of *N. brevicollis* larvae in relation to temperature. All values expressed as $O_2 mm^3/mg/hr$

Developmental stage	5°C	10°C	15°C	20°C
Prediapause	.1867 ± .0304	.3037 ± .0568	.4311 ± .0474	.5927 ± .0778
Diapause	.0911 ± .0308	.1449 ± .0148	.2086 ± .0396	.2652 ± .0234
Reproductive				
Male	.2306 ± .0548	.5081 ± .0758	.8156 ± .0447	
Female	.2348 ± .0274	.3966 ± .0356	.5915 ± .0564	

Table 18b Respiration data of *N. brevicollis* adults in relation to temperature. All values expressed as $O_2 mm^3/mg/hr$.

There is a decrease in Q_{10} with rising temperature, the lines in figure 37 becoming less steep. The Q_{10} calculated were as follows:-

between 5 - 10°C = 3.19
and between 10 - 15°C = 2.83

<u>Adults</u>

The oxygen consumption of adult individuals in a pre-diapause, diapause, and reproductive stage was determined at temperatures of 5, 10, 15, and 20°C. The results of these experiments are given in Table 18b and figures 38a, b and 39a, b which also show ± 2 standard errors.

As no difference was found in the oxygen consumption between the sexes when in a non-reproductive condition, the results were combined. Similar results were obtained with the continuously recording apparatus. Separate regressions were calculated and the equations obtained were as follows:-

Pre-diapause $y = 0.0269x + 0.0422$
Diapause $y = 0.0118x + 0.0289$ y = respiration rate
Reproductive Male $y = 0.0586x - 0.0671$ x = temperature
Reproductive Female $y = 0.0359x + 0.0493$

The oxygen consumption of the adults increased significantly with rise in temperature. The influence of temperature on the rate of respiration of diapause animals was similar to that of active animals, although the temperature influence was slightly greater on animals in a reproductive condition. The Q_{10} values were as follows:-

between 5 and 10 = 3.55
10 and 15 = 2.97

The Q_{10} values of *N. brevicollis* fall within the range of values found for most anthropods.

e) Oxygen consumption and body weight

The Warburg respiratory data for both larvae and adults at 15°C were also drawn on a double logarithmic plot. The relationship between oxygen consumption (O_2mm^3/ind/hr) and body weight was non-linear. In figure 40 the points which deviate from linearity are those obtained from adults in a reproductive condition. Diapause respiratory data was not included. The relationship is however, linear between the three larval stages.

In the present study the respiratory quotient (RQ) was not measured. To convert the respiratory data to calories a conversion factor (oxy caloric co-efficient) of 4.825 cal/ml/O_2 was used. This assumes a RQ of 0.82 (Brody 1945). This value (4.825 cal/ml/O_2) has been used by other workers when RQ was not determined (e.g. Healey, 1967; Menhinick, 1967). For an accurate value of the co-efficient it is necessary to know the RQ which varies with growth depending on the relative amounts of fat, protein and carbohydrates being metabolised.

f) Acclimatization

It is well known that animals respond within certain limits to variations in the environment by modifying their metabolic rates. Such responses are referred to as acclimation or acclimatization. Experiments were carried out to see if *N. brevicollis* possessed such responses.

Twenty third instar larvae were brought into the laboratory. Ten were kept at 5 ± 1°C and ten at 15 ± 1°C. During this period of acclimation, both groups of larvae were fed daily. After 1 week the respiratory rate of both groups were determined at 15°C, using the Warburg apparatus. Two larvae were placed in each flask. Table 19 shows the results of this experiment.

There was no significant difference in the respiratory rate of the two groups. From this result it was concluded that acclimatization does not occur in *N. brevicollis*. For this reason it was necessary to adjust the laboratory respiratory data when extrapolating to the field using the relevant data.

g) Respiration corrected to field temperatures

For the purpose of calculating the overall energy budget

GROUP A

Acclimatised at 5°C

	O_2 mm^3/mg/hr	Wt. of larvae (mg)
1	.6198	24.20
2	.5497	28.05
3	.5533	27.00
4	.6568	21.10
5	.6134	24.50
Mean	.5986	24.97

GROUP B

Acclimatised at 15°C

	O_2 mm^3/mg/hr	Wt. of larvae (mg)
1	.6313	26.00
2	.6072	23.35
3	.5672	23.87
4	.4486	28.22
5	.5839	25.25
Mean	.5676	25.34

Table 19 Acclimatization data. See text for details.

Month	Instar I	Instar II	Instar III	Male	Female
October	10.5168	7.6128			
November	5.0616	4.0200	3.1176		
December	1.9152	1.9512	1.6440		
January	2.1264	2.0880	1.7424		
February	4.2240	3.4680	2.7240		
March		5.9520	4.5000		
April			7.1424		
May			10.8720		
June				11.2128	11.2128
July				11.9232	11.9232
August				5.3376	5.3376
September				18.4992	13.5024

Table 20 Mean monthly field respiration of *N. brevicollis*. All values expressed as O_2mm^3/mg/day.

of N. brevicollis, the laboratory respiratory data were adjusted to field rates, by using the data in Chapter I on field temperatures and from the above regression equations (See figures 36, 38 & 39). Table 20 and figure 41 and 42 show the results.

The field respiratory rates of the larvae follow the pattern of the field temperature curve (see fig. 41). This was expected as the larvae was temperature dependent. Seasonal effects are quite evident, high respiratory rates occurring in Autumn (October - November) - 0.2527-, and Spring (March - May) - 0.3178-, and low rates in Winter (December-February) - 0.1013-, O_2mm^3/mg/hr.

However, the field respiratory rates of the adults do not follow the field temperature curve closely. The two peaks (temperature and respiratory rate) do not coincide (see Figure 42). This is caused by the physiological condition of the adult. The adult respiration is influenced not only by temperature but also by physiological factors such as diapause, reproduction, senescence etc.

The field temperature peak is reached in July/August. This period coincides with the diapause stage of the adult, hence the low field respiration. The peak field respiration occurs in September when reproductive activity in the field is at its peak. The rate decreases thereafter.

h) Discussion

The use of the Warburg respirometer served as a check on the electrolytic respirometer. A comparison of results obtained from the two respirometers (see table 21) show that the Warburg data is higher in all stages except diapause. There are several reasons for this higher rate.

1) The animals were allowed a shorter period of time (15 - 20 minutes) compared with the electrolytic respirometer, to settle down before oxygen consumption measurements were made.

2) When measuring the larval respiration several animals had to be placed in one flask and this no doubt caused a certain amount of activity.

3) Fewer animals were used in the Warburg determinations.

In spite of the higher rate the trend is very similar to the electrolytic respirometer results. At 5°C respiration measurements (Warburg apparatus) on Instar I and II were abandoned because too many animals were required per flask (10 ml flask) before any oxygen consumption was recorded. Too many animals per flask increased activity and also resulted in cannabalism.

The respiratory rate of N. brevicollis was affected by several factors - a) weight b) age c) temperature d) reproductive condition e) diapause f) senescence. The variability

Developmental stage	Warburg data $O_2mm^3/mg/hr$	Electrolytic data $O_2mm^3/mg/hr$
Larvae		
Instar I	1.1050	.9202
Instar II	.7328	.6180
Instar III	.5280	.4431
Adult		
Prediapause	.4311	.3789
Diapause	.2086	.2207
Reproductive	.8156	.7080
	.5915	.5771

Table 21 Comparison of the Electrolytic and Warburg respirometer data.

of oxygen consumption with size, physiological condition and season have been shown by Phillipson (1962 and 1963), Phillipson and Watson (1965) Wiegert (1964) etc.

Acclimatization was absent or possibly very rapid but it did not affect the respiration rates. It was, therefore, possible to correct laboratory measurements of metabolism to field temperatures. Compared to other poikilotherms "insects are considered to be relatively poor in their ability to compensate for differences in temperature" (Bursell 1964).

The Q_{10} values of N. brevicollis fall within the range of values obtained for most arthropods.

Fig. 26a Larval respiratory rate per unit weight plotted against live weight (Oct. 1967).

Fig. 26b Larval respiratory rate per unit weight plotted against live weight. (Nov. 1967).

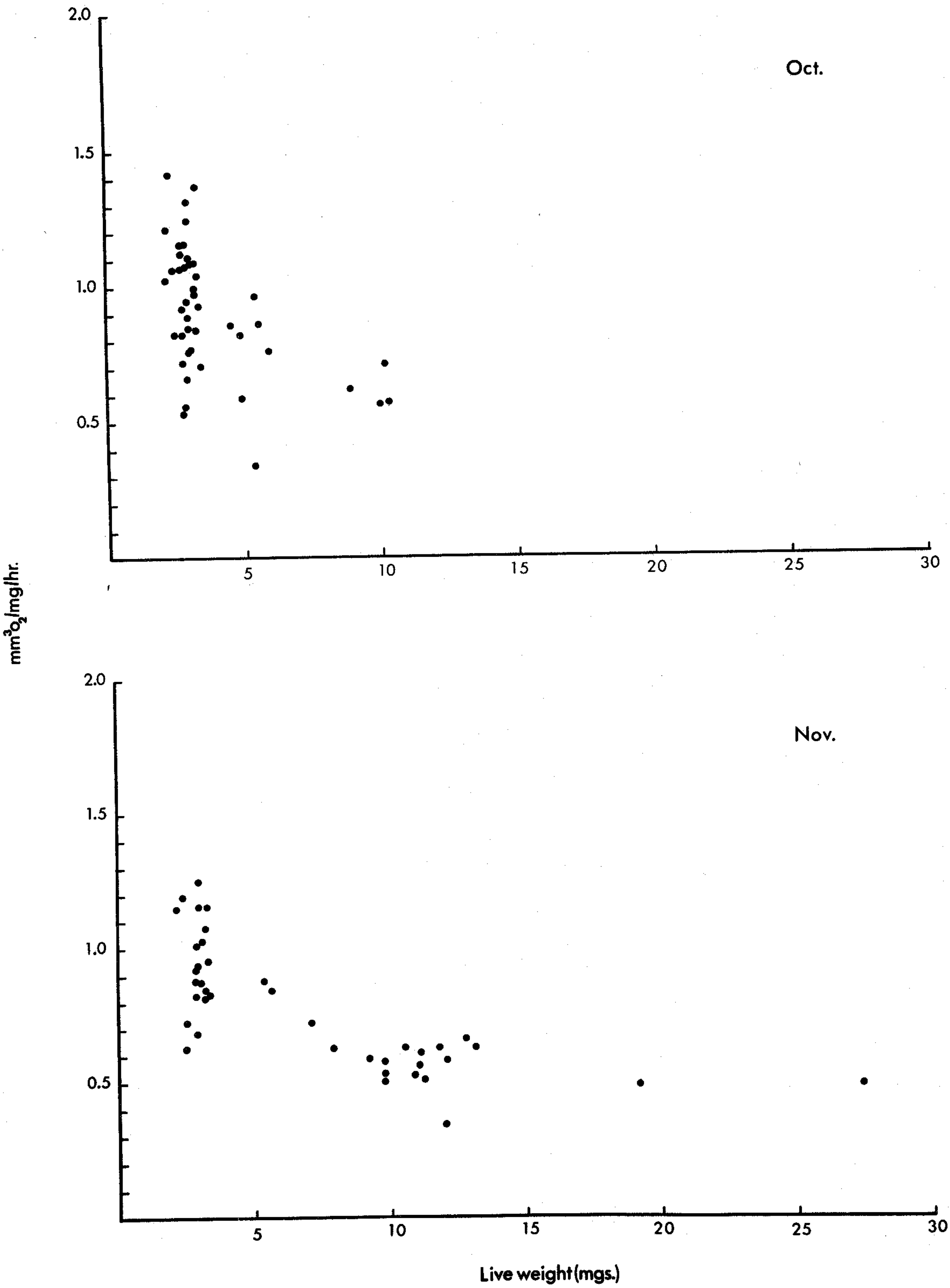
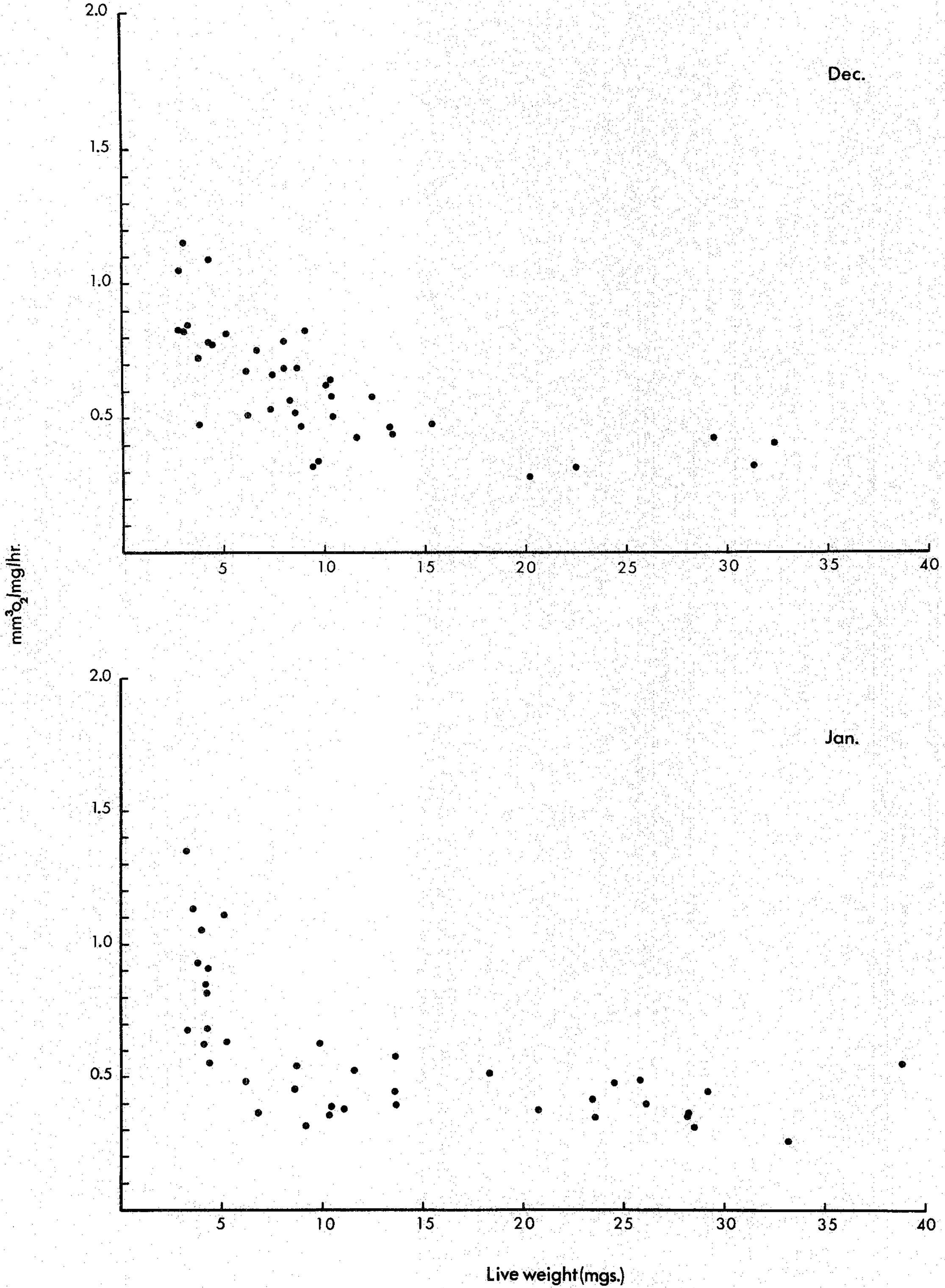

2.0
1.5
1.0
0.5
Oct.
5
10
15
20
25
30
mm^{3}O$_2$/mg/hr.
2.0
1.5
1.0
0.5
Nov.
5
10
15
20
25
30
Live weight (mgs.)

Fig. 27a Larval respiratory rate per unit weight plotted against live weight (Dec. 1967)

Fig. 27b Larval respiratory rate per unit weight plotted against live weight (Jan. 1968)



Dec.
Jan.
2.0
1.5
1.0
0.5
5
10
15
20
25
30
35
40
mm³O₂/mg/hr.
Live weight (mgs.)

Fig. 28a Larval respiratory rate per unit weight plotted against live weight (Feb. 1968)

Fig. 28b Larval respiratory rate per unit weight plotted against live weight. (Mar. 1968)

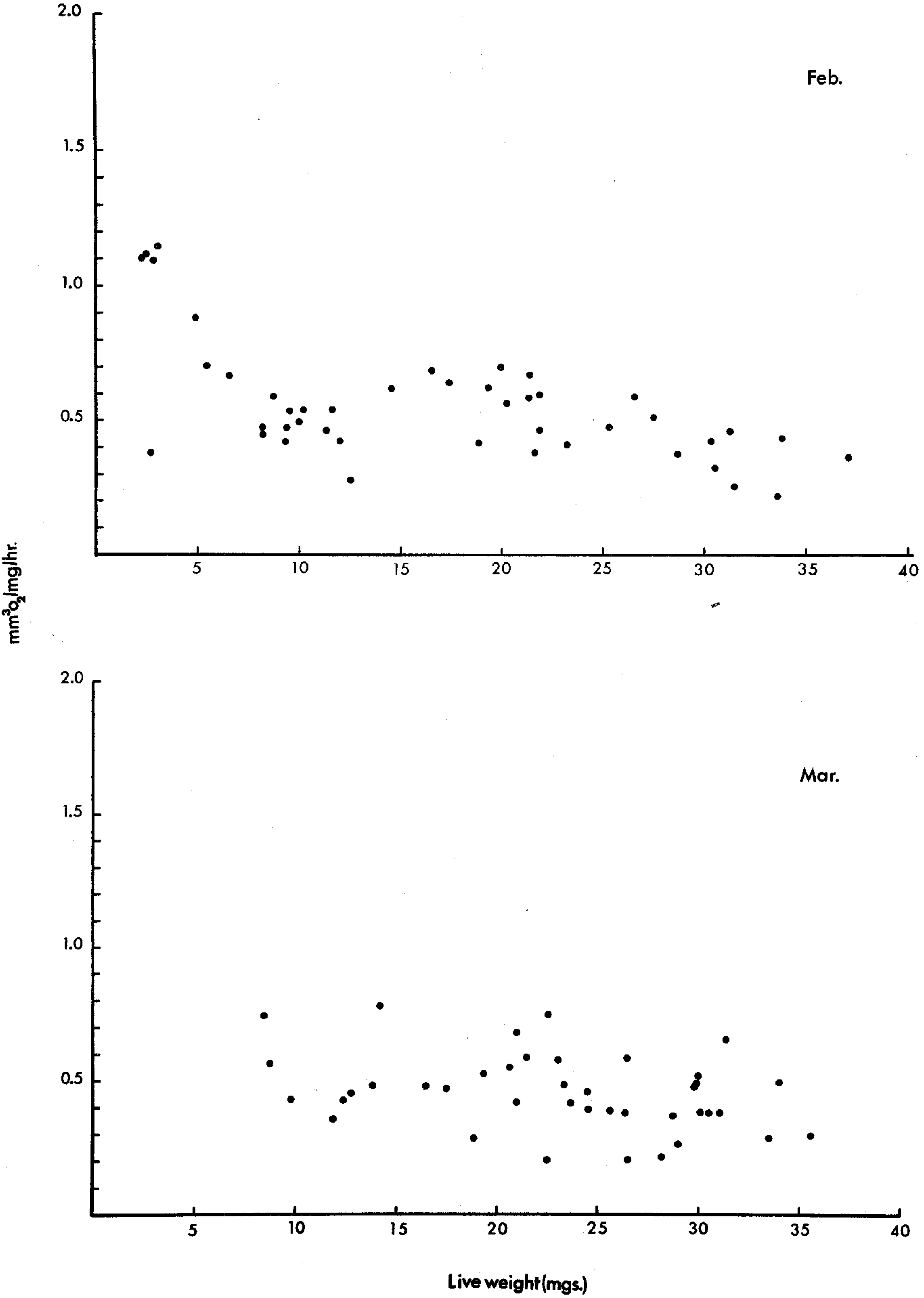

2.0
1.5
1.0
0.5
Feb.
5
10
15
20
25
30
35
40
mm^{3}o$_2$/mg/hr.
2.0
1.5
1.0
0.5
Mar.
5
10
15
20
25
30
35
40
Live weight (mgs.)

Fig. 29a Larval respiratory rate per unit weight plotted against live weight (April 1968)

Fig. 29b Larval respiratory rate per unit weight plotted against live weight (May 1968)

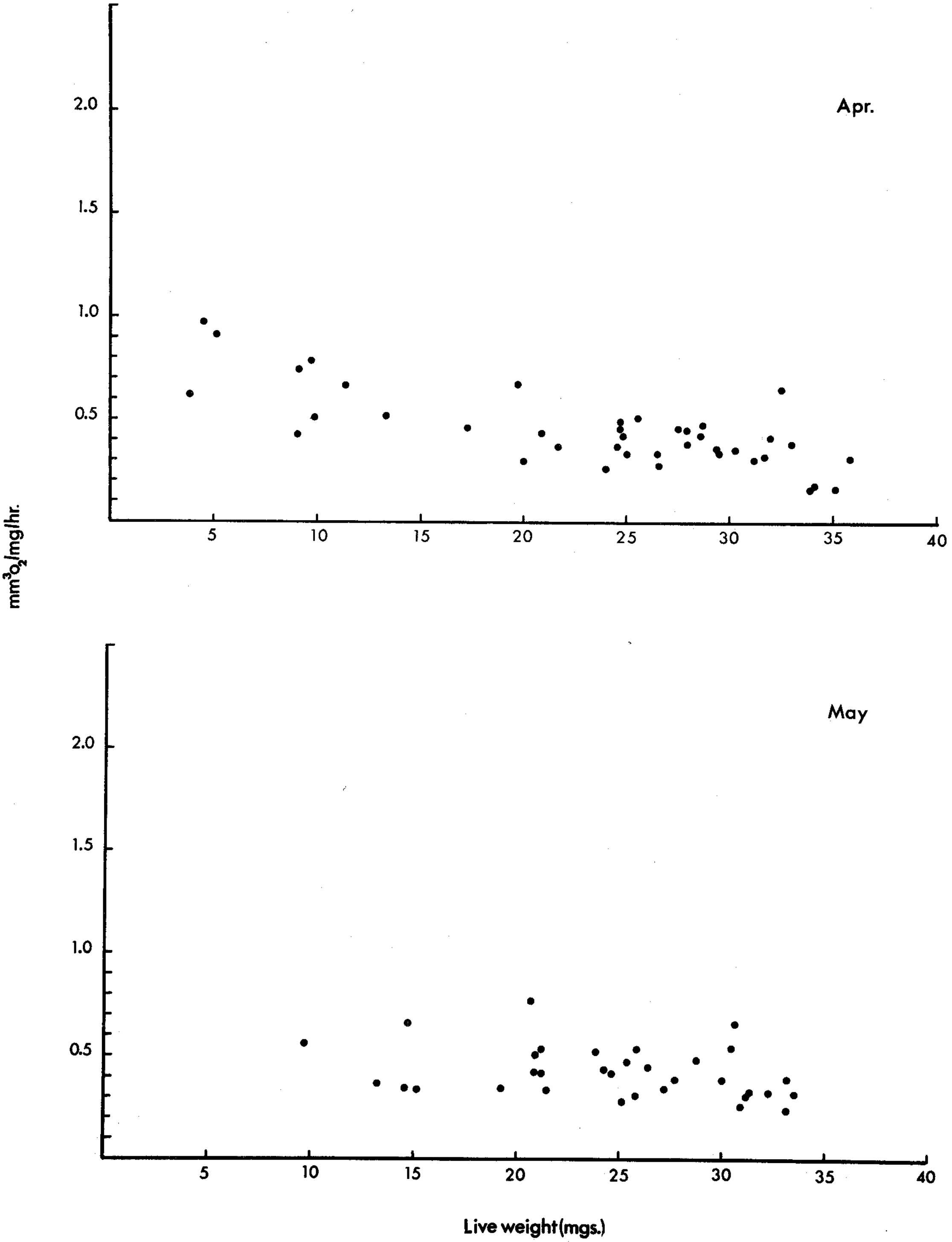

Apr.
May
2.0
1.5
1.0
0.5
mm^{3}O$_2$/mg/hr.
5
10
15
20
25
30
35
40
Live weight (mgs.)

Fig. 30 Mean monthly respiration data ($15^{\circ}C$) of *N. brevicollis* larvae.

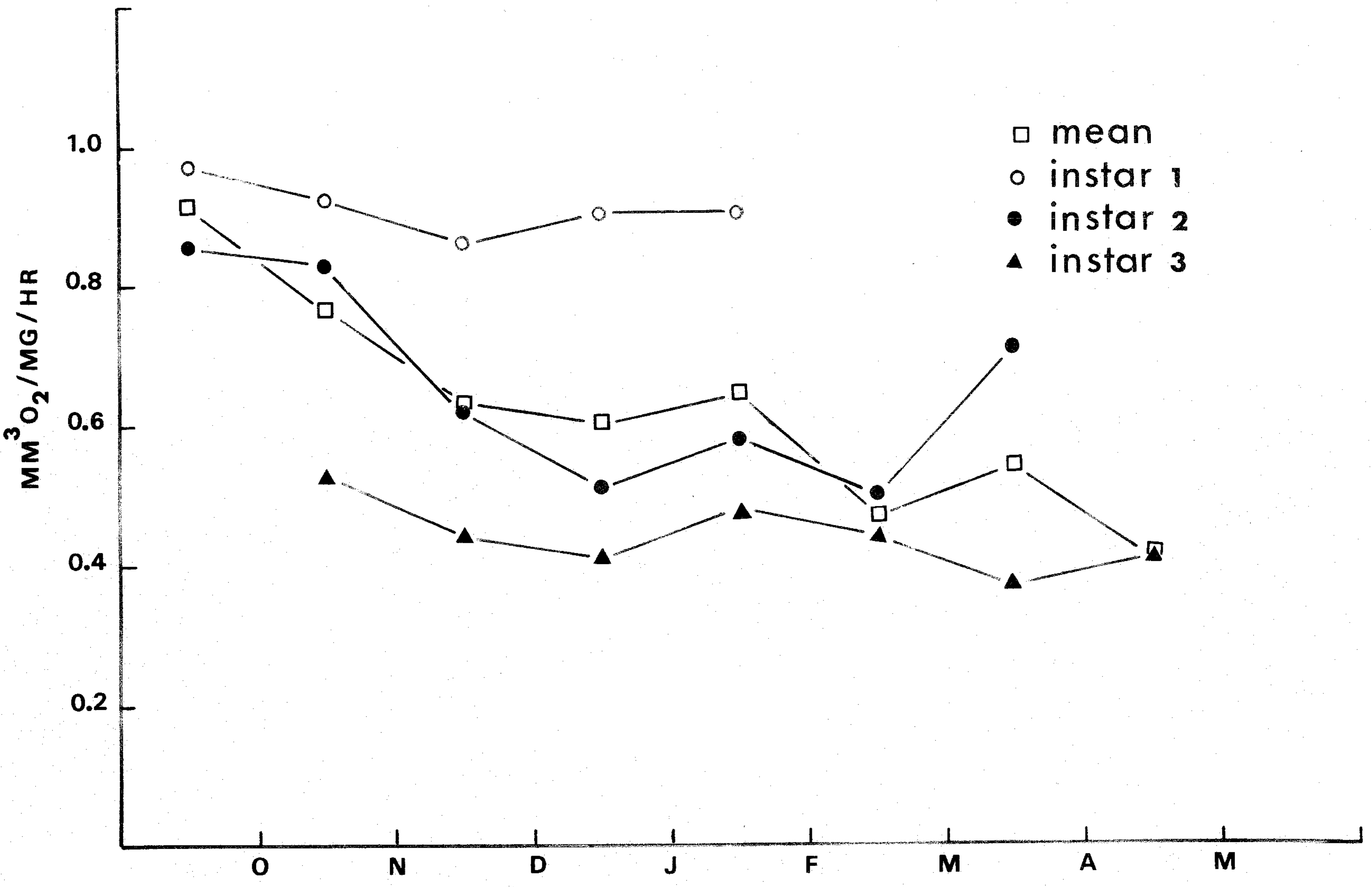

□ mean
○ instar 1
● instar 2
▲ instar 3
$MM^3O_2/MG/HR$
1.0
0.8
0.6
0.4
0.2
O
N
D
J
F
M
A
M

Fig. 31 Pupal respiratory rate per unit weight plotted against live weight (May 1968)

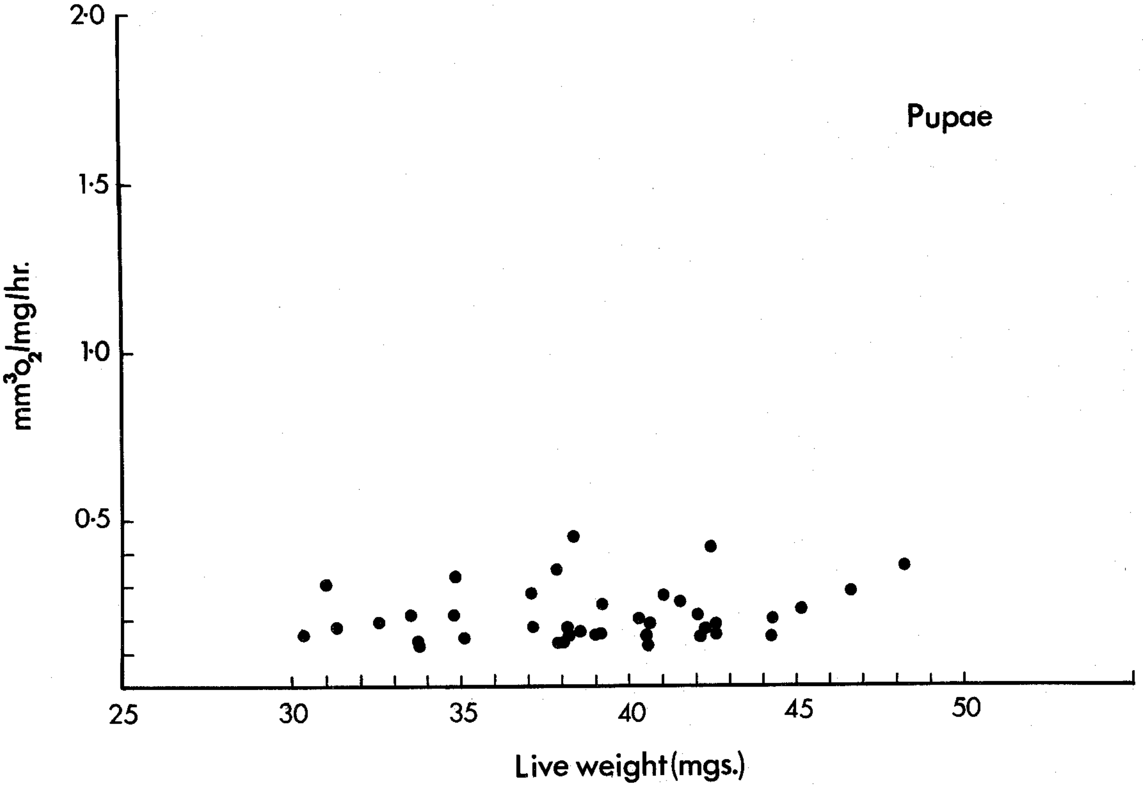

Pupae
2·0
1·5
1·0
0·5
$mm^3O_2/mg/hr.$
25
30
35
40
45
50
Live weight (mgs.)

Fig. 32a Adult respiratory rate per unit weight plotted against live weight (June/July 1968)

● Male ○ Female

Fig. 32b Adult respiratory rate per unit weight plotted against live weight (Aug. 1968)

● Male ○ Female

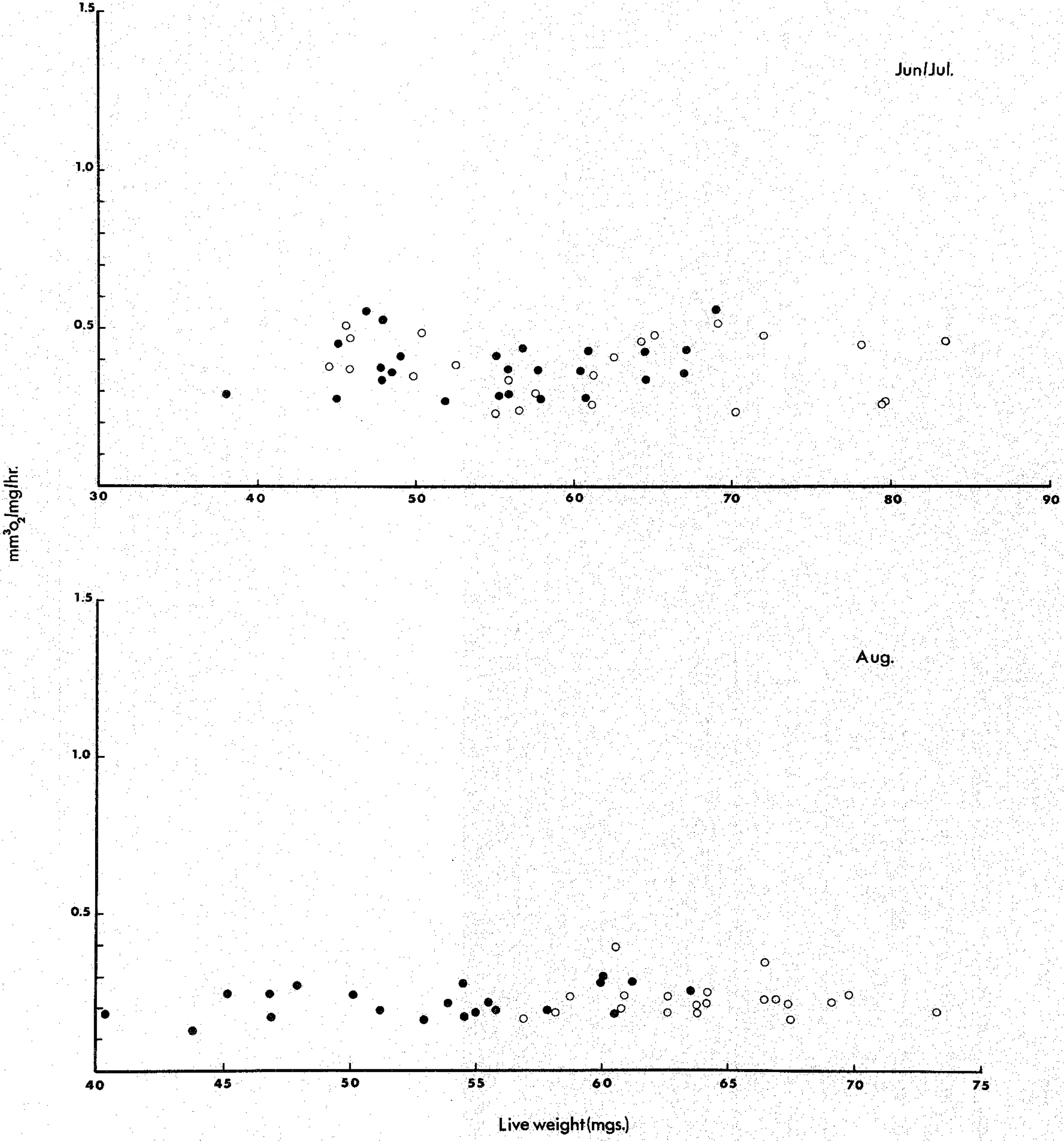

Jun/Jul.
1.5
1.0
0.5
30
40
50
60
70
80
90
mm^{3}O$_2$/mg/hr.
Aug.
1.5
1.0
0.5
40
45
50
55
60
65
70
75
Live weight (mgs.)

Fig. 33a Adult respiratory rate per unit weight plotted against live weight (Sept. 1968)

● Male ○ Female

Fig. 33b Adult respiratory rate per unit weight plotted against live weight (Oct. 1968)

● Male ○ Female

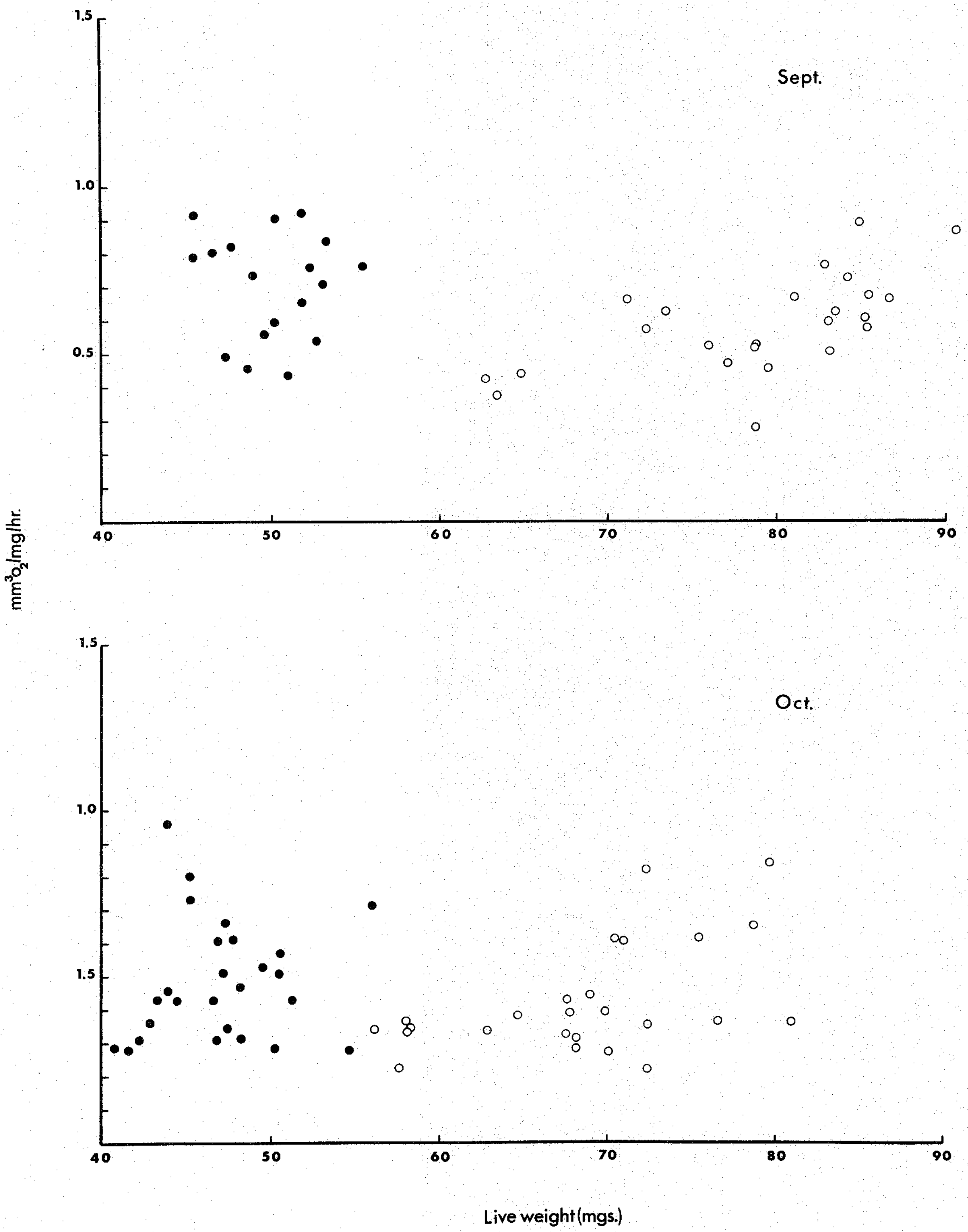

1.5
1.0
0.5
Sept.
40
50
60
70
80
90
mm3o2/mg/hr.
1.5
1.0
1.5
Oct.
40
50
60
70
80
90
Live weight (mgs.)

Fig. 34 Adult respiratory rate per unit weight plotted against live weight (Nov. 1968)

● Male ○ Female

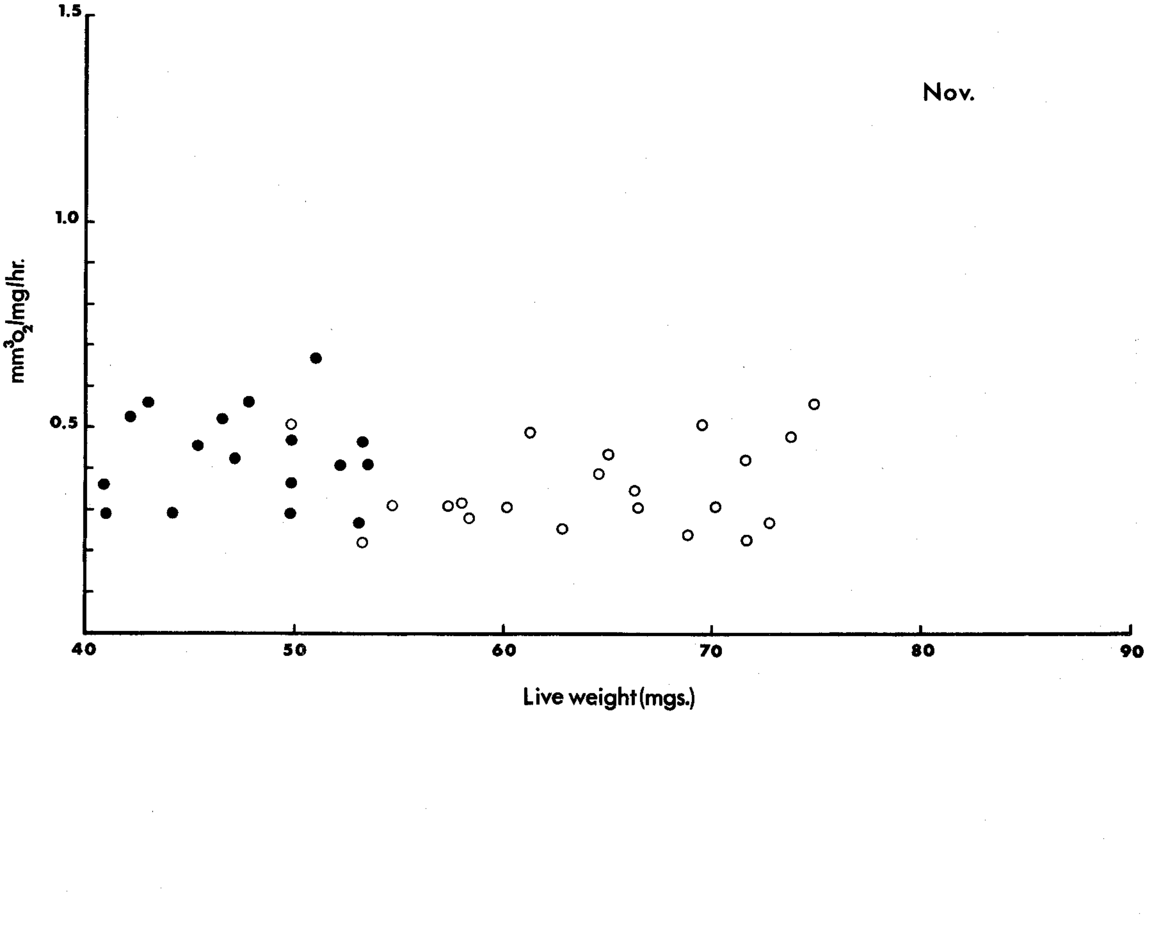
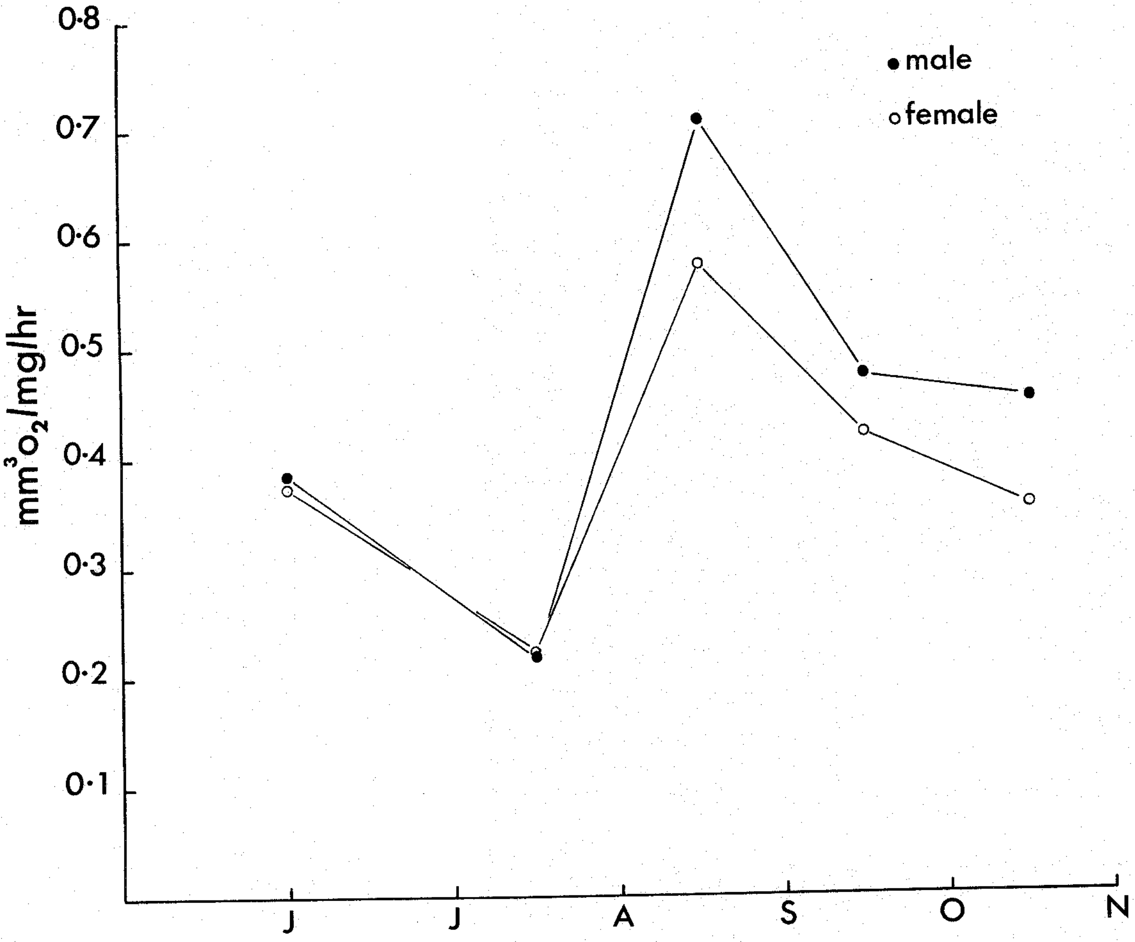

1.5
1.0
0.5
mm³o₂/mg/hr.
Nov.
40
50
60
70
80
90
Live weight (mgs.)

Fig. 35 Mean monthly respiration data($15^{\circ}C$) of adult *N.brevicollis.* (June – November 1968)



0·8
0·7
0·6
0·5
0·4
0·3
0·2
0·1
mm³O₂/mg/hr
● male
○ female
J
J
A
S
O
N

Fig. 36 Respiration rate in relation to size and temperature : vertical lines are ± 2 standard errors.

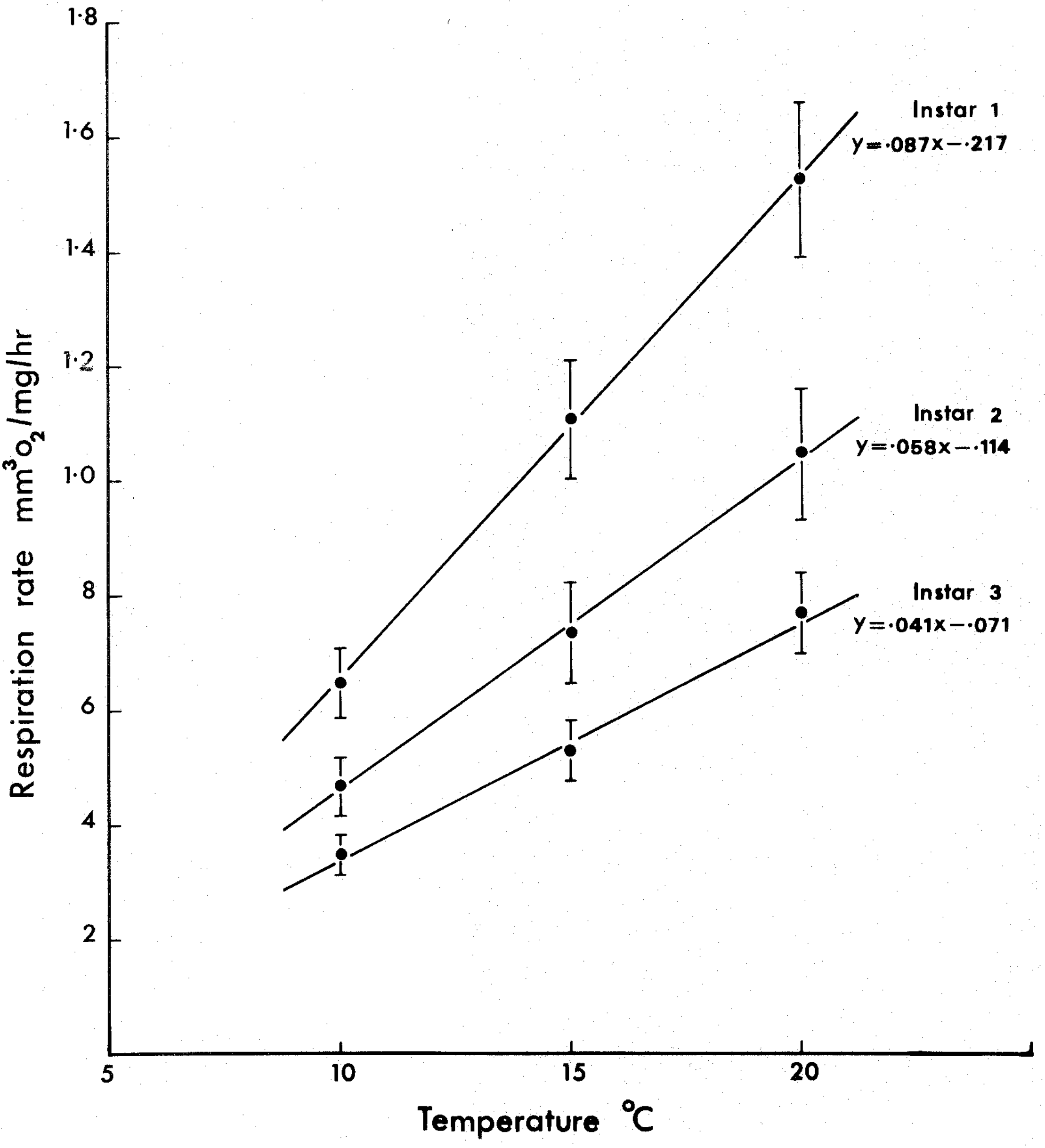

Respiration rate mm^{3}o$_2$/mg/hr
1·8
1·6
1·4
1·2
1·0
8
6
4
2
5
10
15
20
Temperature °C
Instar 1
y=·087x−·217
Instar 2
y=·058x−·114
Instar 3
y=·041x−·071

Fig. 37 Oxygen consumption in relation to size and temperature on a semi-logarithmic plot : curves drawn by eye.

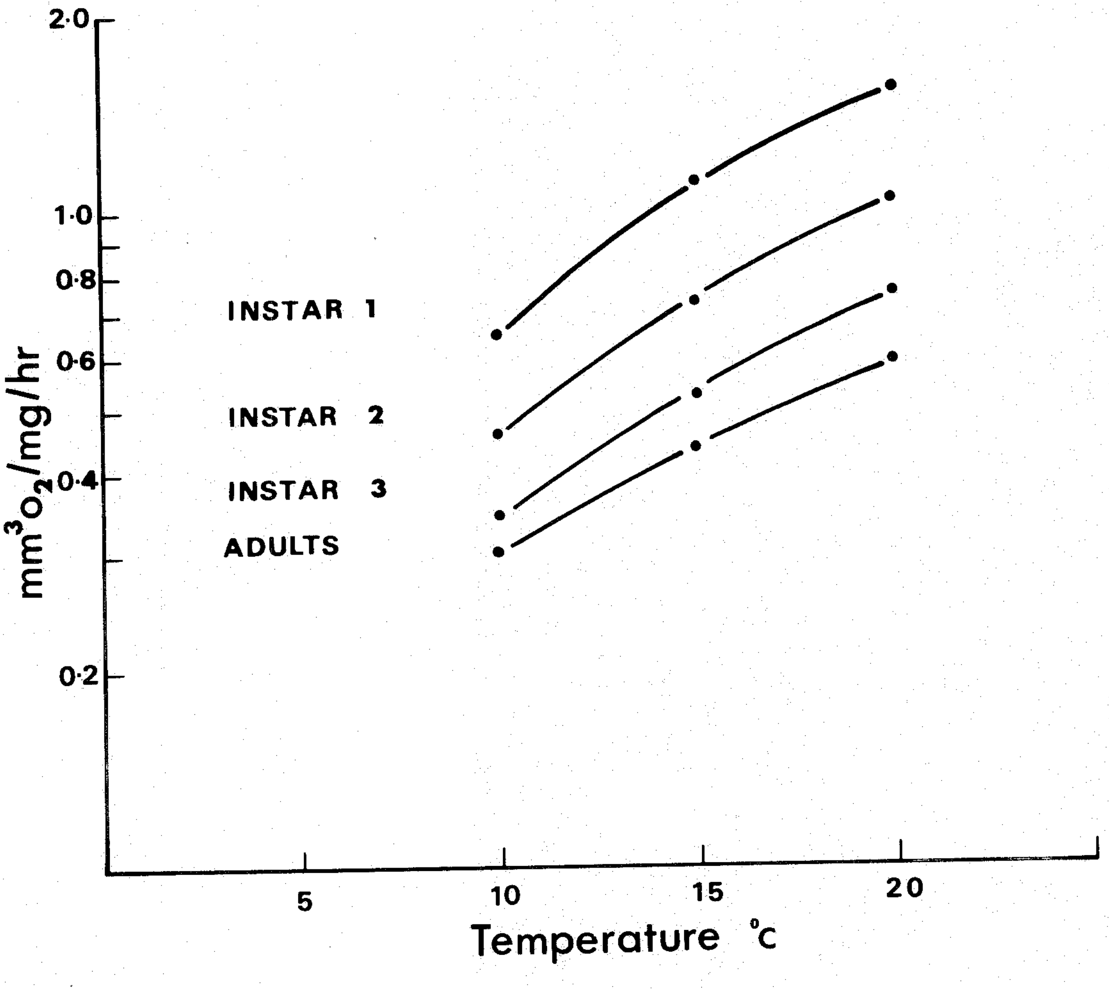
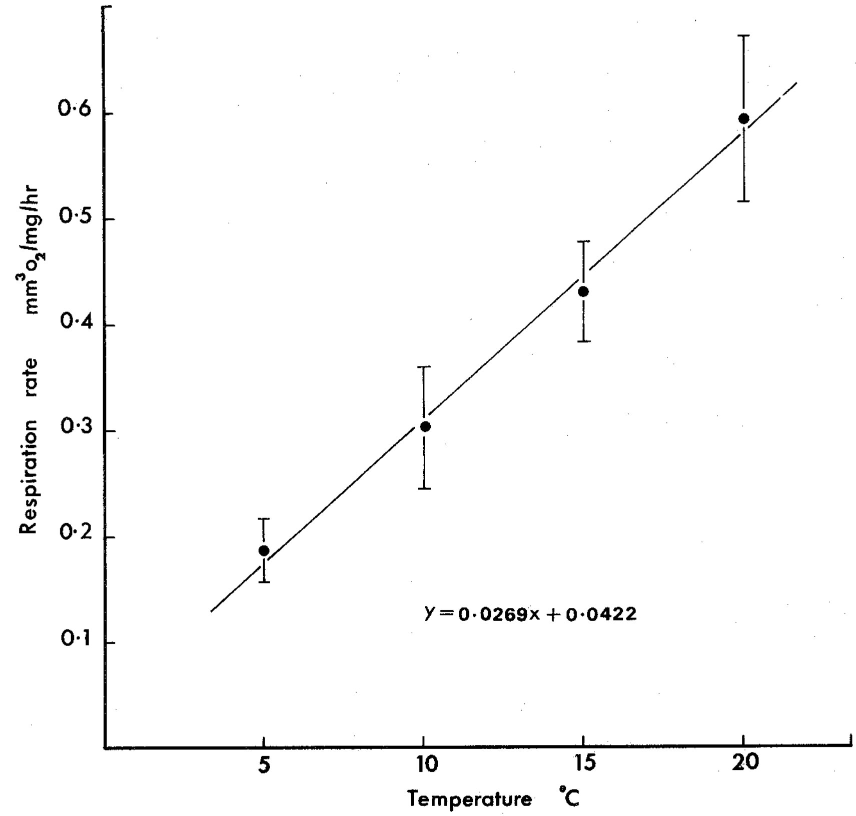
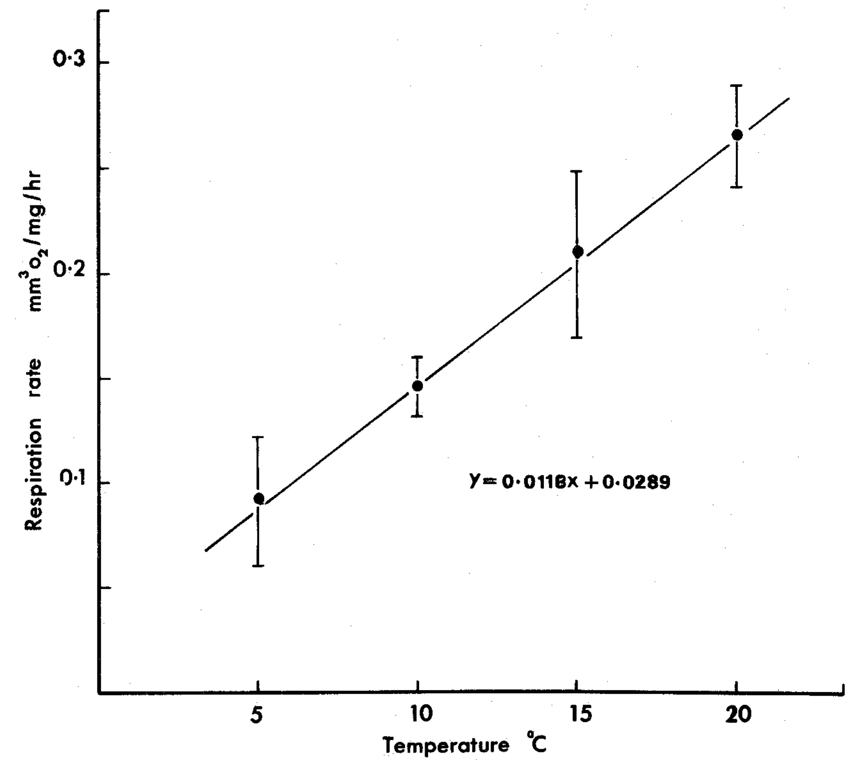

2·0
1·0
0·8
0·6
0·4
0·2
$mm^3 O_2/mg/hr$
INSTAR 1
INSTAR 2
INSTAR 3
ADULTS
5
10
15
20
Temperature °c

Fig. 38a Respiration rate of pre-diapause adults in relation to temperature : vertical lines are ± 2 standard errors.

Fig. 38b Respiration of diapause adults in relation to temperature : vertical lines are ± 2 standard errors.



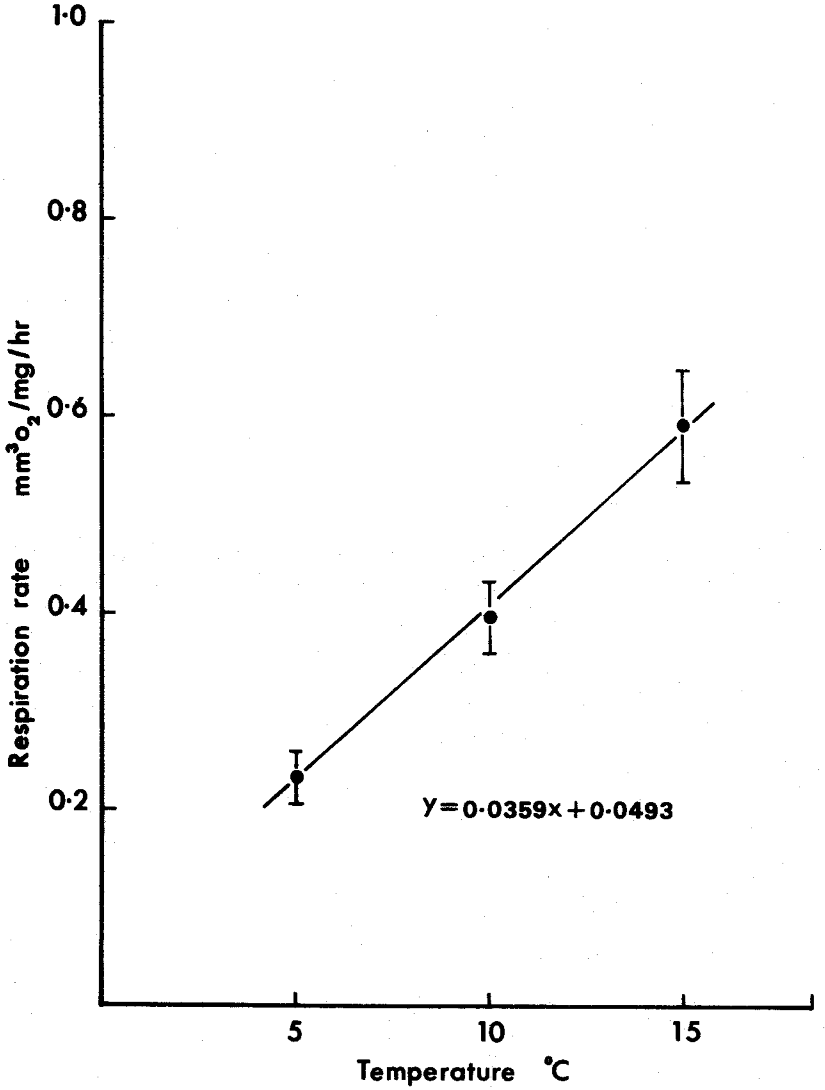
Respiration rate mm^3 O$_2$/mg/hr
0·6
0·5
0·4
0·3
0·2
0·1
$y = 0.0269x + 0.0422$
5
10
15
20
Temperature °C



Respiration rate mm^3 O$_2$/mg/hr
0·3
0·2
0·1
$y = 0.0118x + 0.0289$
5
10
15
20
Temperature °C

Fig. 39a Respiration rate of reproductive males in relation to temperature : vertical lines are ± 2 standard errors.

Fig. 39b Respiration rate of reproductive females in relation to temperature : vertical lines are ± 2 standard errors.


1·0
0·8
0·6
0·4
0·2
Respiration rate mm^{3}o$_2$/mg/hr
$y = 0{\cdot}0359x + 0{\cdot}0493$
5
10
15
Temperature °C

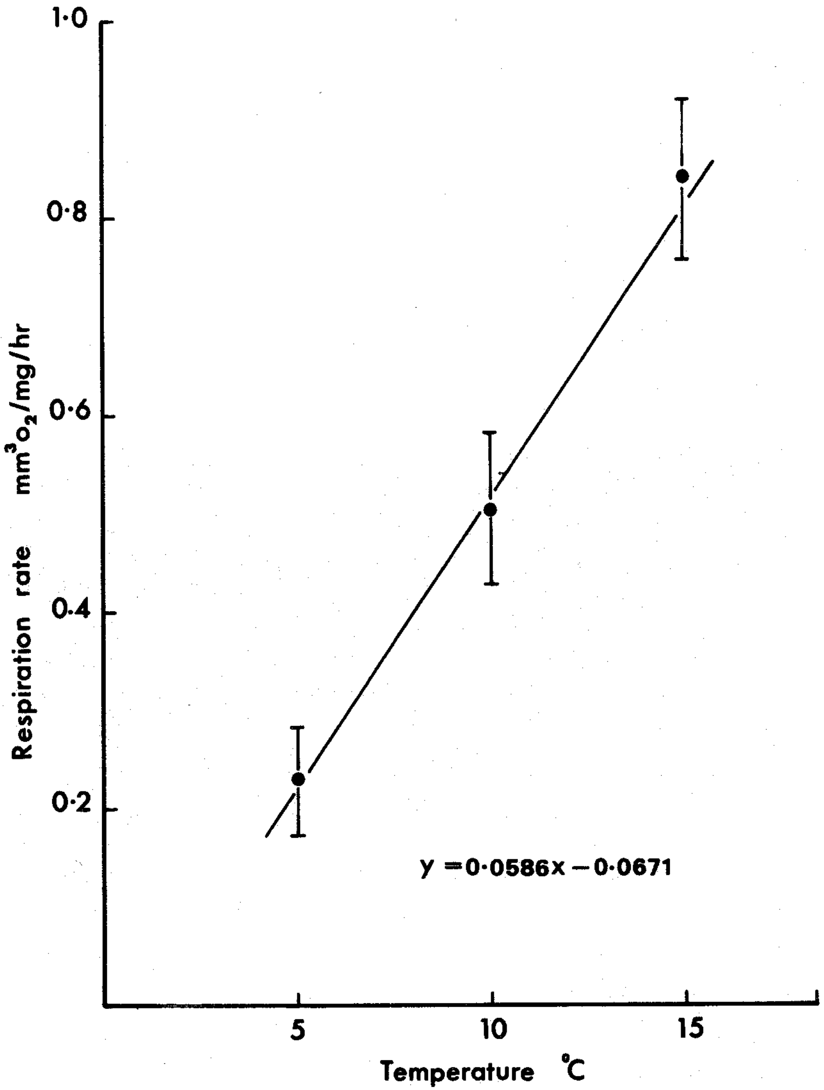
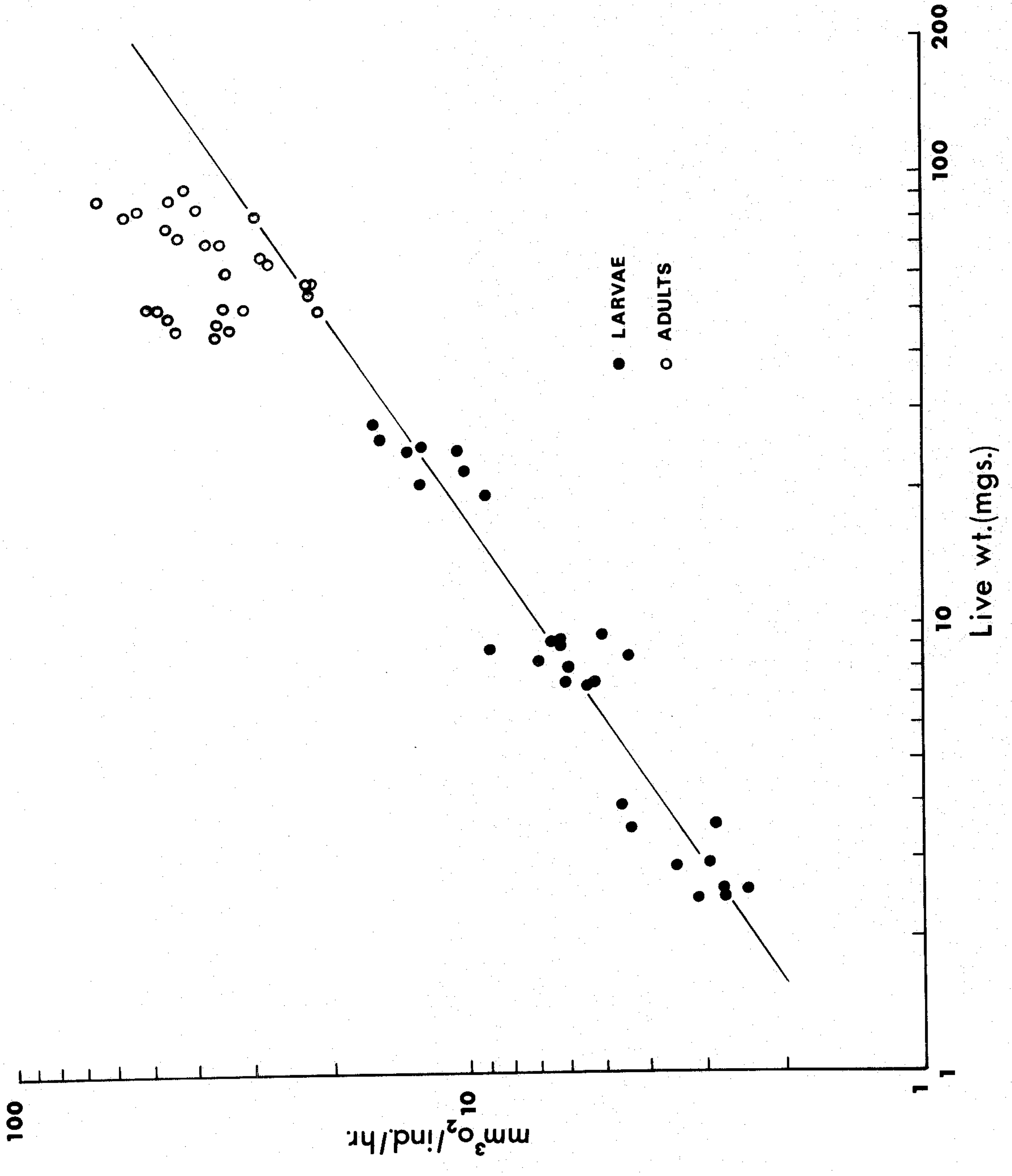

1·0
0·8
0·6
0·4
0·2
Respiration rate mm^{3}o$_2$/mg/hr
$y = 0{\cdot}0586x - 0{\cdot}0671$
5
10
15
Temperature °C

Fig. 40 Oxygen consumption ($mm^3 O_2$/ind./hr) against body weight drawn on a double logarithmic scale.



100
10
1
mm³O₂/ind./hr.
1
10
100
200
Live wt.(mgs.)
● LARVAE
○ ADULTS

Fig. 41 Mean monthly field respiration of <u>N. brevicollis</u> larvae : mean monthly field temperatures are also shown.

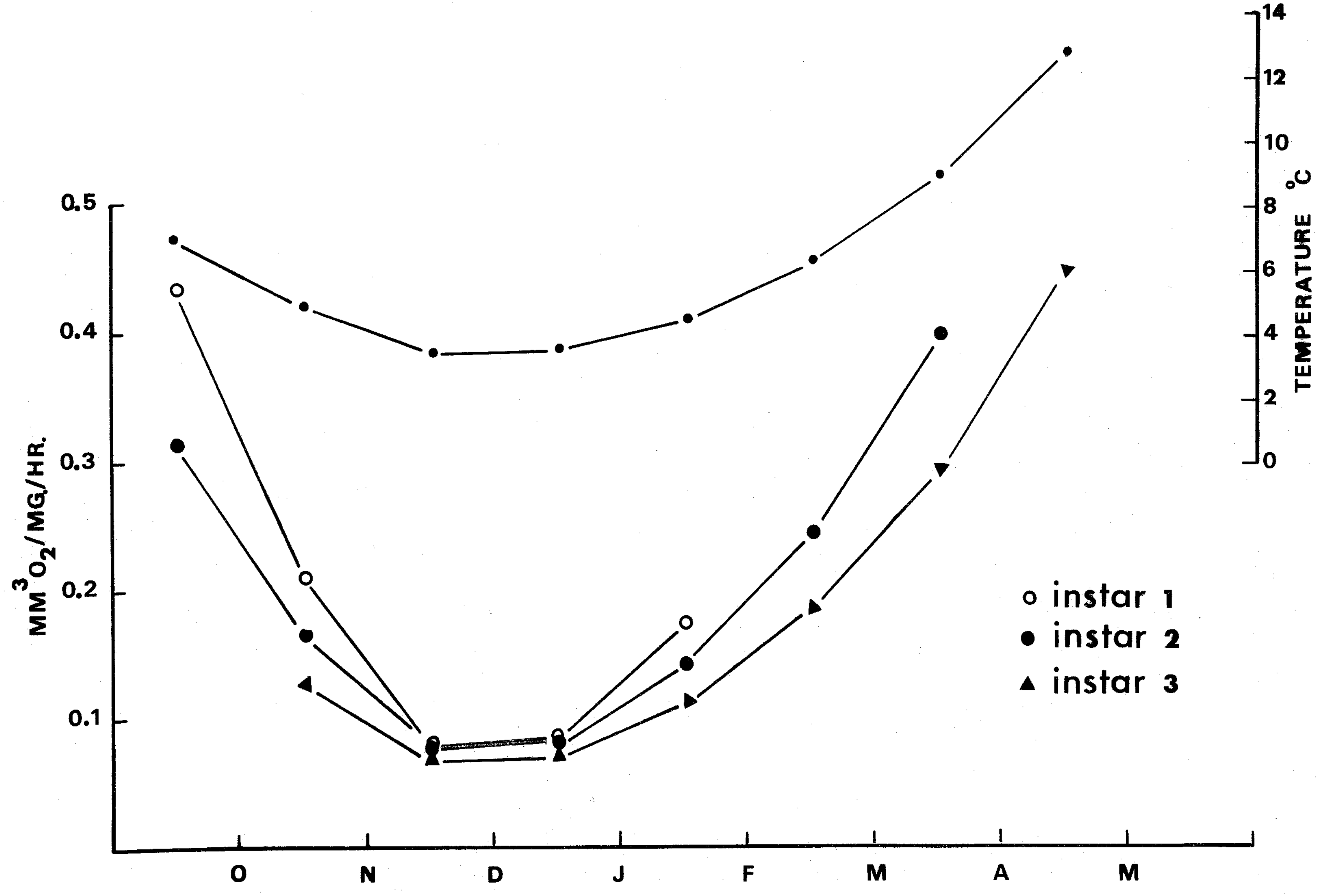
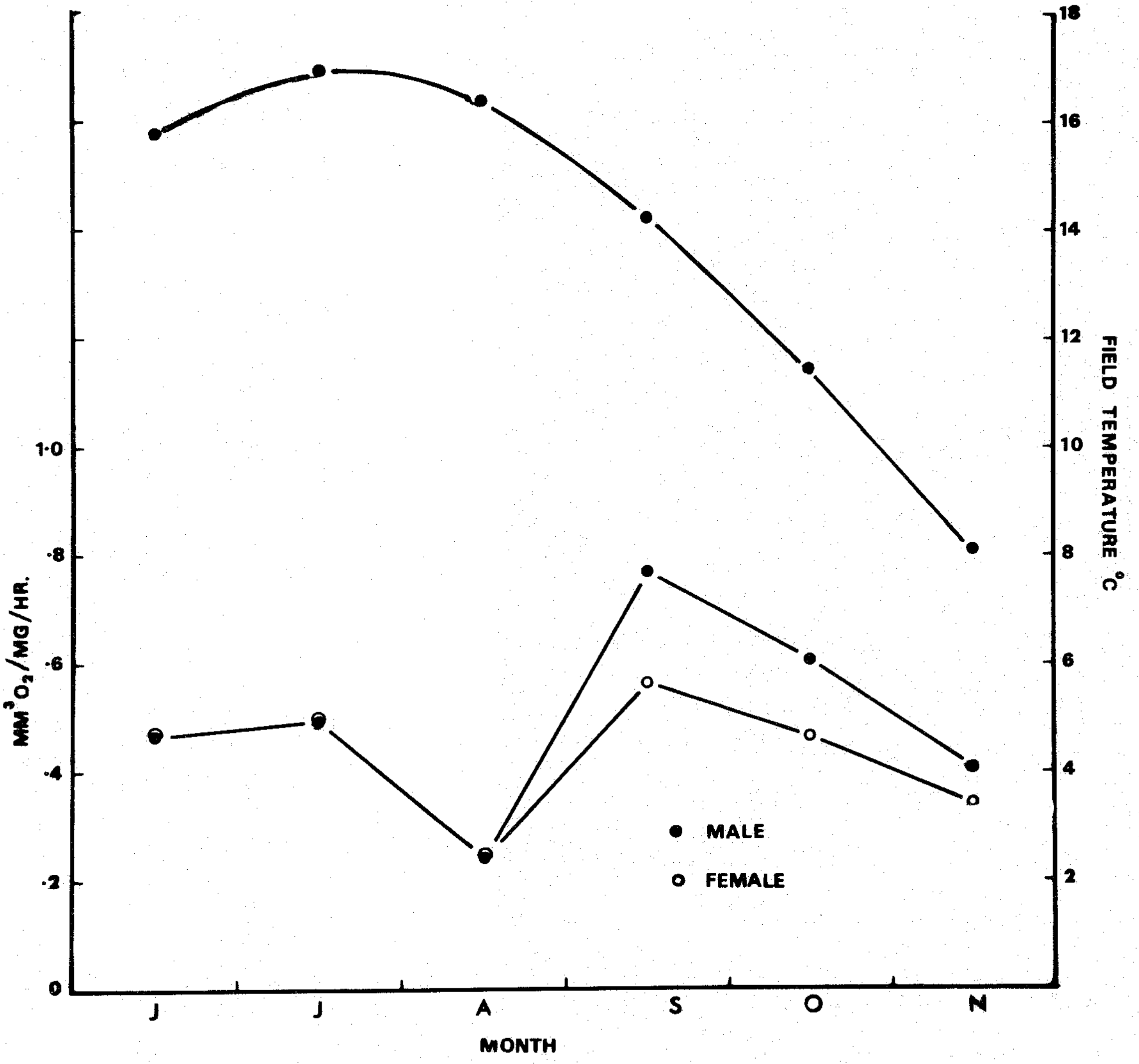

0.5
0.4
0.3
0.2
0.1
MM^{3}O$_2$/MG/HR.
O
N
D
J
F
M
A
M
14
12
10
8
6
4
2
0
TEMPERATURE °C
○ instar 1
● instar 2
▲ instar 3

Fig. 42 Mean monthly field respiration of adult *N. brevicollis* : mean monthly field temperatures are also shown.


MM^{3}O$_2$/MG/HR.
1·0
·8
·6
·4
·2
0
FIELD TEMPERATURE °C
18
16
14
12
10
8
6
4
2
J
J
A
S
O
N
MONTH
● MALE
○ FEMALE

CHAPTER 9

Population studies

(a) Introduction

As the object of the present study was to evaluate energy flow through a population of N. brevicollis, it was necessary to obtain estimates of population density so that they could be used in conjunction with the metabolic data.

(b) Methods

Preliminary investigations showed that mark, release, and recapture methods were unsuitable for the study of the larval population. It was necessary, therefore, to employ different methods in the estimation of the population density of different life stages. These were :

(1) Soil extraction - to obtain estimates of larval population density.

(2) Mark, release and recapture - to obtain estimates of adult population density.

The larval population of the study area was sampled at monthly intervals. The samples were taken from three square each with an area of 400 m^2. Each square was equally subdivided, and a stratified random method of sampling was employed (Macfadyen, 1962). Fifteen samples each 625 cm^2 (10 cm in depth) were taken on each sampling occasion. Each sample was placed in an enamel tray and brought back to the laboratory for extraction. The extraction was carried out in a Tullgren funnel apparatus under a steadily increasing heat regime. The bottom of the collecting dish was lined with filter paper which was kept moist throughout the extraction by an inverted glass tube of water. The extraction was checked regularly and the larvae removed and weighed. Instar number was also noted. The extraction was terminated after 10 days.

To estimate the density of the adult population on the study area 50 pitfall traps were laid, five rows of ten traps each 25 cm apart, covering an area of 625m. Each trap consisted of a glass jar (5.5 cm in diameter at the mouth) sunk into the ground until the rim was flush with the ground surface. The traps were left dry, unbaited, and cleaned after each sampling occasion.

Marking was carried out in the laboratory using a branding technique where a battery operated gas lighter was used. The filament of the lighter was exposed by removing the metal cap and then uncoiled and carefully bent into a V shape.

The adult N. brevicollis were very active, and marking was found difficult without the animal being immobilized. Before each marking operation the beetle was anaesthetized with CO_2 gas produced from 'dry ice'. The mark was then carefully applied on the thoracic shield or elytra. Only a touch of the filament on the body was required to produce a small mark. When the marking was successful the beetle recovered within a few minutes, but if the hot filament pierced the elytra or thoracic shield, the animal recovered but died within a short time. The behaviour of the beetle in the laboratory appeared not to be affected by CO_2 gas but for the purpose of ensuring that the beetles were healthy they were kept in the laboratory for 2 days before being released.

The beetles were fed and released during the day from a central point on the grid. All traps were closed during this period. Time was allowed for the released adults to mix with the rest of the population before the next sample was taken. The mark and recapture data were analysed according to Jolly's (1965) stochastic method. In this method there is no restriction in the length of time between successive samples, nor need the time between samples be equal.

Each beetle released has to be marked so that it may be individually recognised or as in Parr (1965) a system of recording multiple recaptures may be employed. Each sample taken is assumed to be random, and that the marked animals after release become mixed with the rest of the field population so that they have the same probability as the others of being recaptured in the next sample.

In order to estimate the population parameter N_i, ϕ_i and B_i, the information required is contained in a series of estimates, $\hat{\alpha}_i$ and m_i

$\hat{\alpha}_i$ = the proportion of marked animals in the population at the time i, thus

$$\hat{\alpha}_i = \frac{m_i}{n_i} \qquad (1)$$

when m_i = Number of marked animals in the population at time i

n_i = Number captured in the i th sample

M_i = Total of marked animals in the population at time i

thus

$$\hat{M}_i = \frac{s_i \quad Z_i}{R_i} + m_i \qquad (2)$$

where s_i = Number released from the i th sample after marking

Z_i = Number marked before time i which are not caught in the i th sample but are caught subsequently.

R_i = Number of the s_i animals released from the i th sample that are caught subsequently.

$\hat{N}_i$ = the estimate of the population on day i .

The total population each day is estimated as

$$\hat{N}_i = \frac{M_i}{\alpha_i} \qquad (3)$$

$\hat{\phi}_i$ = The probability that an animal alive at the moment of release of the i th sample will survive till the time of capture of the $i + 1$ th sample; thus

$$\hat{\phi}_i = \frac{\hat{M}_{i+1}}{\hat{M}_i - m_i + s_i} \qquad (4)$$

This rate can be converted to loss rate (the effect of death and emigration) by

$$\hat{y}_i = 1 - \hat{\phi}_i$$

$\hat{B}_i$ = The number of new animals joining the population in the interval between the i th and $i + 1$th samples and alive at a time $i + 1$ thus;

$$\hat{B}_i = \hat{N}_{i+1} - \hat{\phi}_i(\hat{N}_i - n_i + s_i) \qquad (5)$$

The approximate standard errors were calculated by

$$V(\hat{N}_i/N_i) = \sqrt{N_i \; (N_i - n_i \; (\frac{M_i - m_i + s_i}{M_i}(\frac{1}{R_i} - \frac{1}{S_i}) + \frac{1 - \alpha_i}{m_i})} \qquad (6)$$

The recapture data is tabulated according to Jolly (1965) in tables 22 - 25 for each sex.

The various estimates of the population parameters are derived by substituting the relevant values obtained from tables 22-25 in equations 1 -6.

(c) Results

(1) Larvae

Table 26 shows the monthly population estimates in terms of number per m^2. The results are also presented graphically in fig. 43. Standard errors were very low and therefore are not shown.

The population density per m^2 was low but the pattern of the larval population was as expected. The highest density occurred in October - 6.39 larvae per m^2-. The higher density values obtained in October and November are due to the large number of eggs hatching after the peak breeding period. Most of the eggs were laid in September and early October and the hatching period in the field at this time of the year is between 3 - 4 weeks. The density per m^2 gradually decreased until it reached zero at the end of May. By May most larvae had reached the pupal stage.

(2) Adults

Estimates of the various population parameters are shown in Tables 27 - 29. Table 27 and figure 44 give the population density per m^2.

The adult density was lower as one would expect than that of larvae. The highest density for both sexes occurred in June. The numbers gradually decreased in July as they went into diapause. No beetles were trapped on August 15th. They started to reappear at the end of August and another peak was reached in September. The density again decreased in October. No estimates were obtained for October 30th because of the failure to recapture any marked individuals.

The high standard errors are due mainly to the low number of marked beetles recaptured. Death rates were unreliable using this method and calculations were abandoned.

Discussion

Because of moulting the mark and recapture method could not be used to study the larval population. Marking the adults with cellulose paint was found unsatisfactory for long term mark and recapture analysis. The marks came off after a short period, especially when the animal burrowed into the soil. Similar observations were made by Springett (1967) and Davies (per comm.).

The branding technique was successfully used to mark the N. brevicollis adults. As great care had to be taken not to damage the beetle with the hot filament, the marking operation was slow. Schotz-Christensen (1965) used a much more sophisticated branding device to mark carabid beetles. The behaviour of the beetles was not affected by the CO_2 gas. After recovering the beetle appeared normal both in activity and feeding.

The adult population pattern was similar to that observed by other investigators (Greenslade, 1964; Tipton, 1960.) The highest density occurred in June - 0.6374 beetles per m^2. This value is lower than that recorded by Penney (1966) in Woodland - 0.945 (1962) - , 0.827 (1963) - beetles per m^2. Adult population estimates showed high standard errors. Parr (1967) and Springett (1967) who also used Jolly's method obtained similar results on days when recaptures of marked individuals were low.

Negative death rates were expected from this method because of the behaviour of the adult. The negative death rate is caused by the marked individuals going into diapause and then reappearing later. Death rates would also be inaccurate because of the low number of marked animals recaptured.

n_i	s_i	May	June		July		Aug.		Sept.		Oct.		Nov.
11	11	30											
38	38	2	15										
36	36	2	4	30									
20	18	0	1	3	15								
7	6	0	0	0	2	30							
0	0	0	0	0	0	0	15						
8	8	0	0	1	0	0	0	30					
34	34	0	2	0	1	0	0	2	15				
35	35	0	0	0	0	1	0	0	3	30			
14	13	0	0	0	0	0	0	1	0	2	15		
8	8	0	0	0	0	0	0	0	0	2	0	30	
4	4	0	0	0	0	0	0	0	0	0	2	0	15
	Ri =	4	7	4	3	1	0	3	3	4	2	0	

Table 22 Capture and recapture data of males tabulated according to Jolly's method (1965).

	May	June		July		Aug.		Sept.		Oct.		
	30											
	(2)	15										
	2	(6)	30									
	0	1	(4)	15								
	0	0	0	(2)	30							
	0	0	0	0	(0)	15						
	0	0	1	1	1	(1)	30					
	0	2	2	3	3	3	(5)	15				
	0	0	0	0	1	1	1	(4)	30			
	0	0	0	0	0	0	1	1	(3)	15		
	0	0	0	0	0	0	0	0	2	(2)	30	
	0	0	0	0	0	0	0	0	0	2	0	15
Z_{i+1} =	2	3	3	4	5	4	2	1	2	2	0	

Table 23 Data from table 22 re-arranged according to Jolly (1965).

n_i	s_i	May	June		July		Aug.		Sept.		Oct.		Nov.
12	12	30											
33	33	3	15										
34	34	1	4	30									
26	26	0	2	3	15								
6	6	0	0	0	2	30							
0	0	0	0	0	0	0	15						
14	14	1	0	0	0	1	0	30					
30	28	0	0	1	2	0	0	1	15				
24	24	0	0	0	0	0	0	1	2	30			
12	12	0	0	0	0	0	0	0	1	2	15		
8	8	0	0	0	0	0	0	1	0	1	1	30	
3	3	0	0	0	0	0	0	0	0	0	1	0	15
Ri =		5	6	4	4	1	0	3	3	3	2	0	

<u>Table 24</u> Capture and recapture data of females tabulated according to Jolly's method (1965).

	May	June		July		Aug.		Sept.		Oct.		Nov.
	30											
	(3)	15										
	1	(5)	30									
	0	2	(5)	15								
	0	0	0	(2)	30							
	0	0	0	0	(0)	15						
	1	1	1	1	2	(2)	30					
	0	0	1	3	3	3	(4)	15				
	0	0	0	0	0	0	1	(3)	30			
	0	0	0	0	0	0	0	1	(3)	15		
	0	0	0	0	0	0	1	1	2	(3)	30	
	0	0	0	0	0	0	0	0	0	1	0	15
Z_{i+1} =	2	3	2	4	5	3	2	2	2	1	0	0

Table 25 Data from table 24 re-arranged according to Jolly (1965).

Month	Instar I	Instar II	Instar III	Male	Female
September	3.20				
October	4.26	2.13			
November	3.20	1.06	1.06		
December		2.13	2.13		
January		1.06	2.13		
February		1.06	1.06		
March			1.06		
April			2.13		
May					
June 15				.3910	.2464
June 30				.3169	.3319
July 15				.1760 (.3095)*	.1497 (.3190)*
July 30				.1456 (.3050)*	.1258 (.3065)*
Aug. 15				(.3045)*	(.2940)*
Aug. 30				.1493 (.3015)*	.1793 (.2825)*
Sept.15				.3011	.2721
Sept.30				.1786	.2432

* Population estimates extrapolated from graph (see figure 44) and used in energy budget calculations.

Table 26 Population estimates/per m^2 of N. brevicollis (1967-68).

Date	$\hat{\alpha}_i$	$\hat{M}_i$	$\hat{N}_i$	$\hat{\phi}_i$	$\hat{B}_i$	$\sqrt{V(Ni/Ni)}$
May 30						
June 15	.0526	12.86	244.4	.6753	33.02	214.99
June 30	.1666	33.00	198.1	.3492	40.84	134.45
July 15	.2000	22.00	110.0	.7222	13.01	80.49
July 30	.2857	26.00	91.0	-	-	102.17
August 15	-	-	-	-	-	-
August 30	.1250	11.66	93.33	1.4823	50.07	98.09
September 15	.1470	27.66	188.20	.2250	69.29	151.71
September 30	.1142	12.75	111.64	.3657	33.86	91.63
October 15	.2142	16.00	74.69	-	-	65.60
October 30						
November 15						

Table 27 Male population parameters obtained using Jolly's method (1965)

Date	$\hat{\alpha}_i$	$\hat{M}_i$	$\hat{N}_i$	$\hat{\phi}_i$	$\hat{B}_i$	$\sqrt{V(Ni/Ni)}$
May 30						
June 15	.0909	14.00	154.02	.6931	100.73	116.75
June 30	.1470	30.50	207.48	.3025	30.83	147.08
July 15	.1923	18.00	93.60	.6666	15.60	62.63
July 30	.3333	26.00	78.00	-	-	85.27
August 15	-	-	-	-	-	-
August 30	.1428	16.00	112.04	.8092	79.37	98.70
September 15	.1333	22.66	170.04	.4072	82.76	169.84
September 30	.1250	19.00	152.00	.3750	3.00	132.73
October 15	.2500	15.00	60.00	-	-	49.75
October 30						
November 15						

Table 28 Female population parameters obtained using Jolly's method (1965).

Date	Male	Female	Total number per m^2
May 30th 1968	–	–	–
June 15th	244.4 ± 214.9	154.02 ± 116.75	.6374
June 30th	198.1 ± 134.5	207.48 ± 147.08	.6488
July 15th	111.0 ± 80.49	93.60 ± 62.63	.3257
July 30th	91.0 ± 102.17	78.00 ± 85.27	.2704
August 15th	–	–	–
August 30th	93.33 ± 98.09	112.04 ± 98.70	.3286
September 15th	188.2 ± 151.71	170.04 ± 169.84	.5732
September 30th	111.64 ± 91.63	152.00 ± 132.73	.4218
October 15th	74.69 ± 65.60	60.0 ± 49.75	.2155
October 30th	–	–	–

<u>Table 29</u> Population estimates of adult <u>N. brevicollis</u> (June - October 1968).

Fig. 43 Population estimates (per /m^2) of

N. brevicollis larvae.

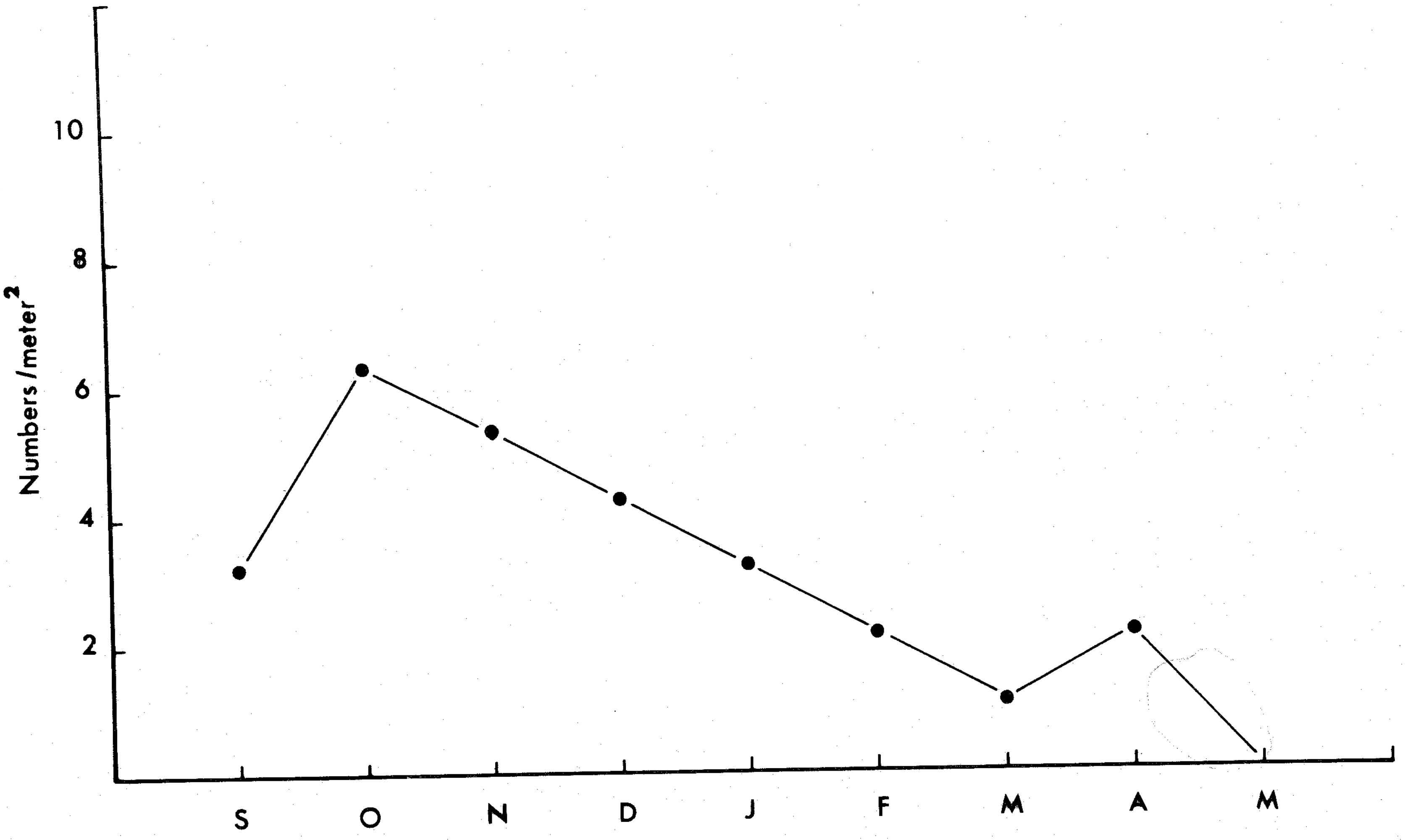
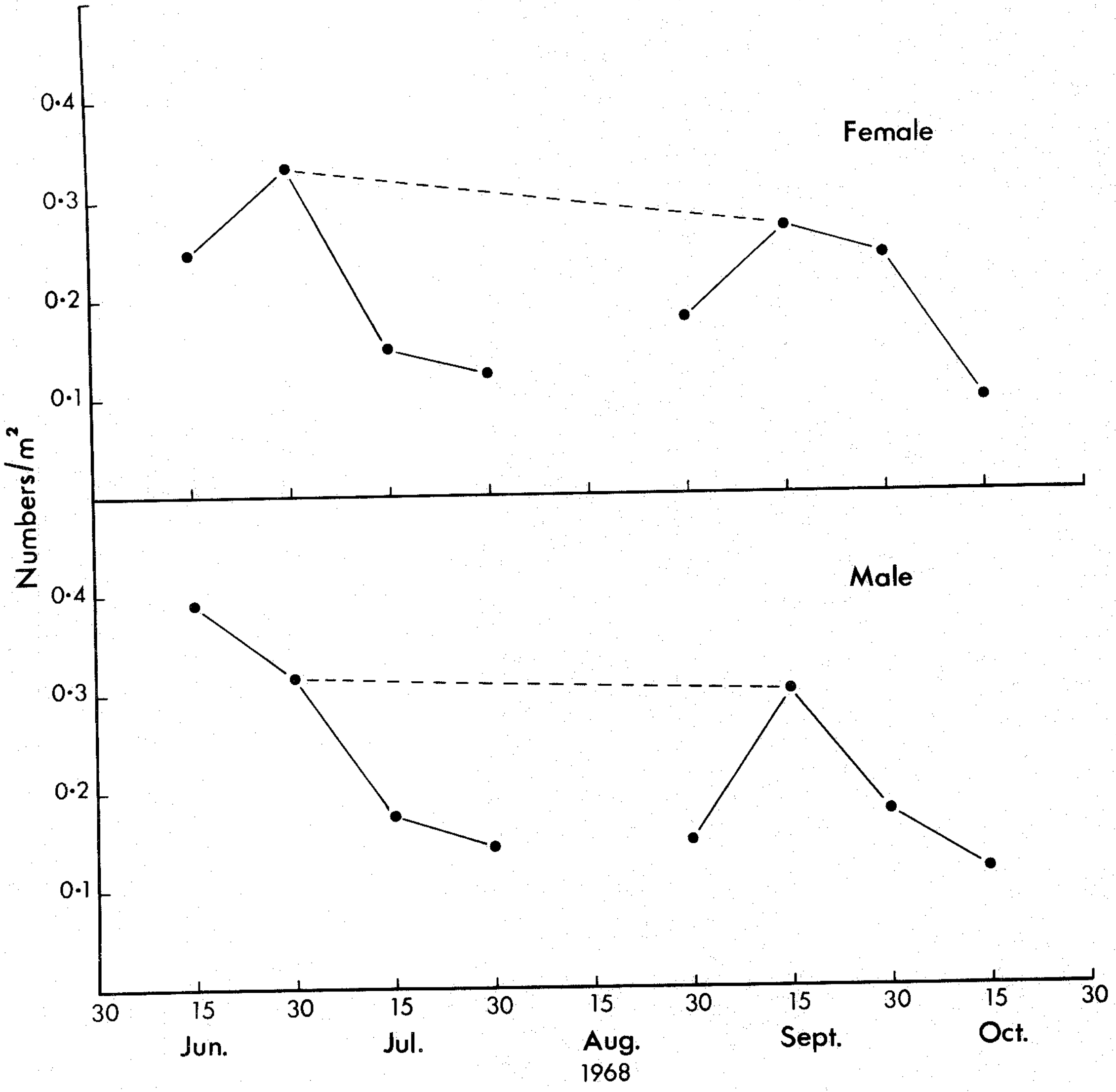

Numbers /meter^2
10
8
6
4
2
S
O
N
D
J
F
M
A
M

Fig. 44 Population estimates (per/m^2) of *N.brevicollis* adults. Dotted line show probable trend of population density during the diapause period.


Female
Male
Numbers/m²
0·4
0·3
0·2
0·1
0·4
0·3
0·2
0·1
30
15
30
15
30
15
30
15
30
15
30
Jun.
Jul.
Aug.
Sept.
Oct.
1968

CHAPTER 10

Energy flux through the Population

An energy budget according to the formula $C = P + R + (F + U)$ was calculated separately for each larval instar and adults. These budgets were subsequently summed to obtain the total energy budget of the N. brevicollis population. The energy flux parameters are expressed in cals/m^2/month and the mean monthly biomass or standing crop in calories/m^2.

The calculation of the energy budget for each life stage was as follows:-

1) The mean number of each instar and adults per m^2 each month was calculated from :

$$N = \frac{n_1 + n_2}{2}$$

N = Monthly mean number per m^2

n_1 = Number per m^2 at end of month 1.

n_2 = Number per m^2 at end of month 2.

The numbers of each instar/adults at the end of each month were obtained from chapter 9, table 26.

2) The mean monthly biomass per m^2 in terms of dry weight for each life stage was calculated from ;

$$\frac{n_1 \text{ x dry weight of each life stage at the end of month 1} + n_2 \text{ x dry weight of each life stage at the end of month 2}}{2}$$

where n_1 and n_2 are the same as in (1)

Dry weights converted to calories gave the monthly mean biomass in calories. The caloric data for each instar and adults were taken from chapter 4, table 3. The results in terms of dry weight and calories are presented in table 30 and 31 respectively.

3) Production (P)

The growth rate per day (mgs dry weight) of each instar and adults (taken from chapter 7) when applied to the population data (i.e. growth rate x the mean number of each instar and adults per m^2) gave production in mgs/m^2/day. The results were converted to mgs/m^2/month. Using the calorific data of each instar/adults (Chapter 4), production was expressed in calories/m^2/month. The results are shown in tables 32 and 33.

4) Respiration (R)

The field respiratory rates expressed as $mm^3 O_2$/mg/day (chapter 8, table 20) were converted to $mm^3 O_2$/ind/month. Respiration per m^2 each month by each life stage was obtained by multiplying the calories respired per individual per month by the monthly mean number /m^2. To convert the data to calories, a conversion factor (oxy caloric co-efficient) of 4.825 cals/ml/O_2 was used. The results are presented in table 34 as cals resp/m^2/

month.

5) The total calories assimilated by each life stage per m^2 per month was obtained by summation R + P = A (3 and 4 above).

6) Knowing the mean percentage assimilation for each instar and adults (chapter 5), it was possible to calculate the total calories consumed, and the caloric equivalent of faeces produced per m^2 per month by each life stage.

7) It was also possible to compare the adult consumption estimates as calculated in 6, with two independent estimates of consumption.

a) The calories eaten per day in the laboratory was converted to calories eaten per month x the number of males/females per m^2.

The caloric equivalent of food eaten/day is given in chapter 6, table 9.

b) Similarly calories eaten per day estimated from field faeces and percentage assimilation was converted to calories eaten/month x the number of males/females per m^2.

The calories consumed/day was taken from chapter 6, table 11.

8) Exuvium production (E_v)

The number of larvae moulting per m^2 was calculated from the population data. For example;

	Instar I	Instar II	Instar III
September	3.20		
	$\xrightarrow{a}$		
October	4.26	2.13	
		$\xrightarrow{c}$	
November	3.20	1.06	1.06
	$\xrightarrow{b}$		
December		2.13	

a = 2.13 moulted from Instar I - Instar II

b = 1.07 moulted from Instar I - Instar II

c = 1.06 moulted from Instar II - Instar III

This method gives the minimum estimate ofexuvium production. The number of animals moulting per m^2 x the calories per exuvium gave the calories lost in exuvium production per m^2. The results are presented in table 35.

The dry weight of each instar exuvia is shown in chapter 7, table 15. The calorific values of the exuvia was taken from chapter 4, table 3.

9) Egg production (P_r)

The total female emergence from diapause x the caloric equivalent of eggs produced by one female gave calories of egg production per m^2. The calories of eggs produced per female is given in chapter 7.

The total female emergence from diapause was taken from chapter 9, table 26.

N.B. Cals or cals = gram calories
Kcals or kcals = kilocalories

b) Results

The energy flux data for each instar and adults are given in tables 36 - 40. The energy flux of the total population is shown in table 41. All data are expressed in g.cals/m^2/month.

The population consumption estimates based on laboratory consumption experiments were 1.8 - 2.5 times greater than the figures obtained through summation (see tables 39 and 40). The high estimates may be explained by the fact that animals in the laboratory were feeding in optimum conditions, a condition probably not realised in the field, and therefore the high values can be regarded as an overestimate. The population consumption estimates, based on field faeces and percentage assimilation, represent animals feeding at different rates and are probably more reliable. The figures recorded from this method agrees more closely to the values obtained by summation.

The peak population energy flux occurred in June, and did not correspond with peak numbers, biomass, or peak field temperature. Energy flux, as might be expected, reached a low level during the diapause period. The larval energy flux followed the larval biomass fluctuations closely, and the two peaks coincided (see figs. 45 and 46). Adult energy flux was more influenced by field temperature although the two peaks did not correspond. (see fig. 46).

Figure 46 shows that peak larval consumption took place in December and January, and the peak adult consumption in June and September. The maximum population biomass coincided with the peak field temperature. The June biomass figure is underestimated because of the failure to obtain a population estimate on May 30th. The maximum population production occurred in January (see table 33), the larvae contributed about - 86% - of the total population production. The production - respiration ratio ($^P/_R$) was high 93.8%.

The total calories lost due to exuviae production was 7.9768 cals/m^2, which was only 2.16% of the total population growth. Exuviae and egg production amounted to 19.6956 cals/m^2, hence population production due to growth was 369.51 cals/m^2/yr. The total population consumed 1036.64 cals/m^2/yr, of which 37.5% was utilized for production, 40% was lost as respiration, and 22.5% as faeces production. The contribution of Instar I to total energy flux was small (see table 42). The major contribution was made by instar III.

Population growth efficiencies were calculated as :

a) Gross growth efficiency $^{P}/C$ = 37.6%

b) Net growth efficiency $P/_{A}$ = 48.4%

Growth efficiencies calculated separately for larvae and adults are shown in table 43.

Figure 48 shows a double logarithmic relationship between annual population production and annual population respiration in k.cals/m^2. The regression line was drawn according to the equation given by McNeill and Lawton (1970), for comparatively short-lived poikilotherms (aquatic and terrestrial forms).

$$\text{Log } R = 1.1740 \text{ Log } P + 0.1352$$

The data obtained for N. brevicollis ($R = \bar{1}.5901$ $P = \bar{1}.6177$) fitted very closely to this line.

Month	Instar I	Instar II	Instar III	Male	Female	Total
October	2.4714					2.4714
November	2.5280	2.6026				5.1306
December	1.1088	2.3146	10.6559			14.0793
January		2.6613	12.8853			15.5466
February		2.1386	10.4106			12.5492
March		1.1626	8.9973			10.1599
April			12.8479			12.8479
May			8.1493			8.1493
June				6.5388	6.1109	12.6479
July				8.6936	10.6718	19.3654
August				7.7030	9.0942	16.7972
September				5.7180	8.8756	14.5936
						144.3401

Table 30 Monthly biomass data of *N. brevicollis*.
All values in mgs. dry weight/m^2

Month	Instar I	Instar II	Instar III	Male	Female	Total
October	12.8665					12.8665
November	13.1609	13.9613				27.1222
December	5.7725	12.4164	61.8939			80.0828
January		14.2762	74.8429			89.1191
February		11.4725	60.4691			71.9416
March		6.2369	52.2598			58.4967
April			74.6259			74.6259
May			47.3343			47.3343
June			-	37.5043	37.5512	75.0555
July			-	49.8634	65.5777	115.4411
August			-	44.1815	55.8830	100.0645
September			-	30.6828	52.6228	83.3056
						835.4558

Table 31 Monthly biomass data of *N. brevicollis*.
All values given in cals./m^2.

Month	Instar I	Instar II	Instar III	Male	Female	Total
October	3.1913					3.1913
November	3.0844	4.2166				7.3010
December	1.7967	4.3572	6.2302			12.3841
January		4.3572	8.3461			12.7033
February		2.7174	5.8283			8.5457
March		1.4524	4.1535			5.6059
April			6.0292			6.0292
May			4.1535			4.1535
June				3.3090	3.3255	6.6345
July				0.0172	0.0600	0.0772
August				-	-	-
September					2.0657*	2.0657
						68.6914

* Egg production

Table 32 Monthly production of *N. brevicollis*.
Values in mgs dry weight/m^2.

Month	Instar I	Instar II	Instar III	Male	Female	Total
October	16.6142					16.6142
November	16.0576	22.6195				38.6771
December	9.6187	23.3737	36.1874			69.1798
January		23.3737	48.4774			71.8511
February		14.5772	33.8530			48.4302
March		7.7912	24.1251			31.9162
April			35.0200			35.0200
May			24.1251			24.1251
June				20.0287	21.2367	41.2654
July				0.0172	0.3870	0.4042
August				-	-	-
September					*11.7188	11.7188
						389.2024

* Egg production

Table 33 Monthly production of N. brevicollis.
Values in cals./m^2.

Month	Instar I	Instar II	Instar III	Male	Female	Total
October	18.0606					18.0606
November	8.1210	7.6224				15.7434
December	1.8476	3.8192	9.3775			15.0443
January		3.9579	13.3176			17.2746
February		4.2340	14.5406			18.7746
March		3.8840	17.1213			21.0053
April			39.4470			39.4470
May			41.3664			41.3664
June				26.8740	24.2775	51.1515
July				32.1660	39.9840	72.1500
August				12.5505	14.8740	27.4245
September				35.9025	41.3592	77.2620
						414.7042

Table 34 Monthly respiratory data of *N. brevicollis*.
All values expressed as cals. resp./m^2.

Month	Instar I	Instar II	Instar III	Total
September	-	-	-	-
October	.7539	-	-	0.7539
November	-	.9467	-	0.9467
December	.3786	.9557	-	1.3343
January	-	-	-	-
February	-	-	-	-
March	-	-	-	-
April	-	-	-	-
May	-	-	4.9419	4.9419
				7.9768

Table 35 Exuvium production of *N. brevicollis* values in cals/m^2.

Month	Number/m^2	Cals growth/ m^2/month	Cals resp/m^2 /month	Assimilation	Egestion	Consumption
				All as cals/m^2/month		
October	3.73	16.6142	18.0606	34.6748	6.2974	40.9722
November	3.73	16.0576	8.1210	24.1786	4.3911	28.5697
December	2.10	9.6187	1.8476	11.4663	2.0824	13.5487
		42.2905	28.0292	70.3197	12.7709	83.0906

Table 36 Energy flux through the instar I population.

Month	Number/m^2	Cals growth/ m^2/month	Cals resp/m^2 /month	Assimilation	Egestion	Consumption
				all as cals/m^2/month		
November	1.59	22.6195	7.6224	30.2419	6.5263	36.7682
December	1.59	23.3737	3.8192	27.1927	5.8683	33.0612
January	1.59	23.3737	3.9570	27.3307	5.8981	33.2288
February	1.06	14.5772	4.2340	18.8112	4.0595	22.8707
March	0.53	7.7912	3.8840	11.6752	2.5195	14.1947
		91.7353	23.5166	115.2519	24.8717	140.1236

Table 37 Energy flux through the instar II population.

Month	Number/m^2	Cals Growth/ m^2/month	Cals resp/m^2 /month	Assimilation	Egestion	Consumption
				All as cals/m^2/month		
December	1.59	36.1874	9.3775	45.5649	11.5482	57.1131
January	2.13	48.4774	13.3176	61.7950	15.6617	77.4569
February	1.59	33.8530	14.5406	48.3936	12.2652	60.6588
March	1.06	24.1251	17.1213	41.2462	10.4537	51.7001
April	1.59	35.0200	39.4470	74.4670	18.8734	93.3404
May	1.06	24.1251	41.3664	65.4915	16.5986	82.0901
		201.7880	135.1704	336.9584	85.4008	422.3592

Table 38 Energy flux through the instar III population.

Month	Cals growth/ m^2/month	Cals resp/m^2 /month	Assimilation	Egestion	Consumption
			All as cals/m^2/month		
June	20.0287	26.8740	46.9027	18.2852	65.1879
July	0.0172	32.1660	32.1832	12.5467	44.7299
August	-	12.5505	12.5505*	4.8928*	17.4433*
September	-	35.9025	35.9025	13.9967	49.8992
	20.0459	107.4930	127.5389	49.7214	177.2603

<u>Independent consumption estimates</u> (Cals/m^2/month)

(a) From laboratory consumption experiments

June = 145.3712
July = 107.7451

(b) From field faeces and % assimilation

June = 95.9112
July = 71.0867
September = 63.9209

* = put into the August calculation for convenience

Table 39 Energy flux through the male population.

Month	Cals growth/ m^2/month	Cals resp/m^2 /month	Assimilation	Egestion	Consumption
			All as cals/m^2/month		
June	21.2367	24.2775	45.5142	17.7438	63.2580
July	0.3872	39.9840	40.3712	15.7388	56.1100
August	-	14.8740	14.8740*	5.7986*	20.6726*
September	11.7188•	41.3595	53.0783	20.6927	73.7710
	33.3427	120.4950	153.8377	59.9739	213.8116

<u>Independent consumption estimates</u> (Cals/m^2/month)

(a) From laboratory consumption experiments

June = 117.2915
July = 107.5599

(b) From field faeces and % assimilation

June = 78.5611
July = 72.0430
September = 88.5104

* = put into August calculation for convenience
• = egg production

<u>Table 40</u> Energy flux through the female population.

Month	Production	Respiration	Assimilation	Faeces production	Consumption
October	16.6142	18.0606	34.6748	6.2974	40.9722
November	38.6771	15.7434	54.4205	10.9174	65.3379
December	69.1798	15.0443	84.2241	19.4989	103.7230
January	71.8511	17.2746	89.1257	21.5598	110.6855
February	48.4302	18.7746	67.2048	16.3247	83.5295
March	31.9163	21.0053	52.9216	12.9732	65.8948
April	35.0200	39.4470	74.4670	18.8734	93.3404
May	24.1251	41.3664	65.4915	16.5986	82.0901
June	41.2654	51.1515	92.4169	36.0290	128.4459
July	0.4044	72.1500	72.5544	28.2855	100.8399
August	-	27.4254	27.4245*	10.6915*	38.1160*
September	11.7188	77.2620	88.9808	34.6894	123.6702
	389.2024	414.7042	803.9066	232.7388	1036.6454

* put into August calculation for convenience.

Table 41 Energy flux through the total population of N.brevicollis
All values in gram cals/m^2/month

	All as k cals/m				
	Production	Respiration	Assimilation	Faecal production	Consumption
Instar I	0.0423	0.0280	0.0703	0.0128	0.0831
Instar II	0.0917	0.0235	0.1153	0.0249	0.1401
Instar III	0.2018	0.1352	0.3369	0.0854	0.4224
Male	0.0200	0.1075	0.1275	0.0497	0.1773
Female	0.0334	0.1205	0.1538	0.0599	0.2138
Total	0.3892	0.4147	0.8038	0.2328	1.0367

Table 42 Energy budget of *N. brevicollis*

	P/C	P/A
Instar I	50.9%	60.1%
Instar II	65.4%	79.5%
Instar III	47.7%	59.9%
Male	11.3%	15.7%
Female	15.62%	21.7%

Table 43 Growth efficiencies of each life stage, calculated from the energy flux parameters (see table 42).

Fig. 45 Monthly biomass data (cal /m^2) of

N. brevicollis

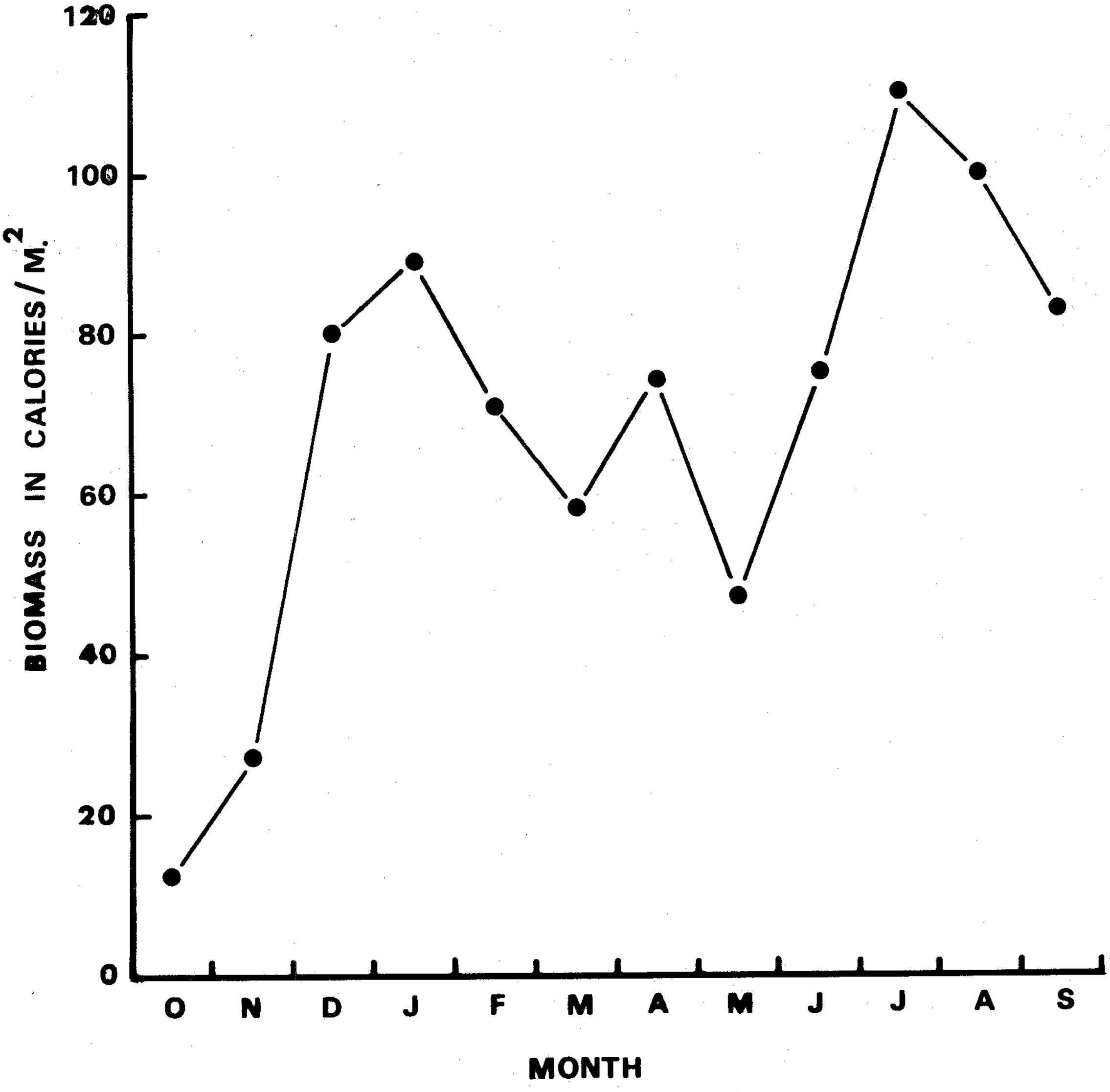
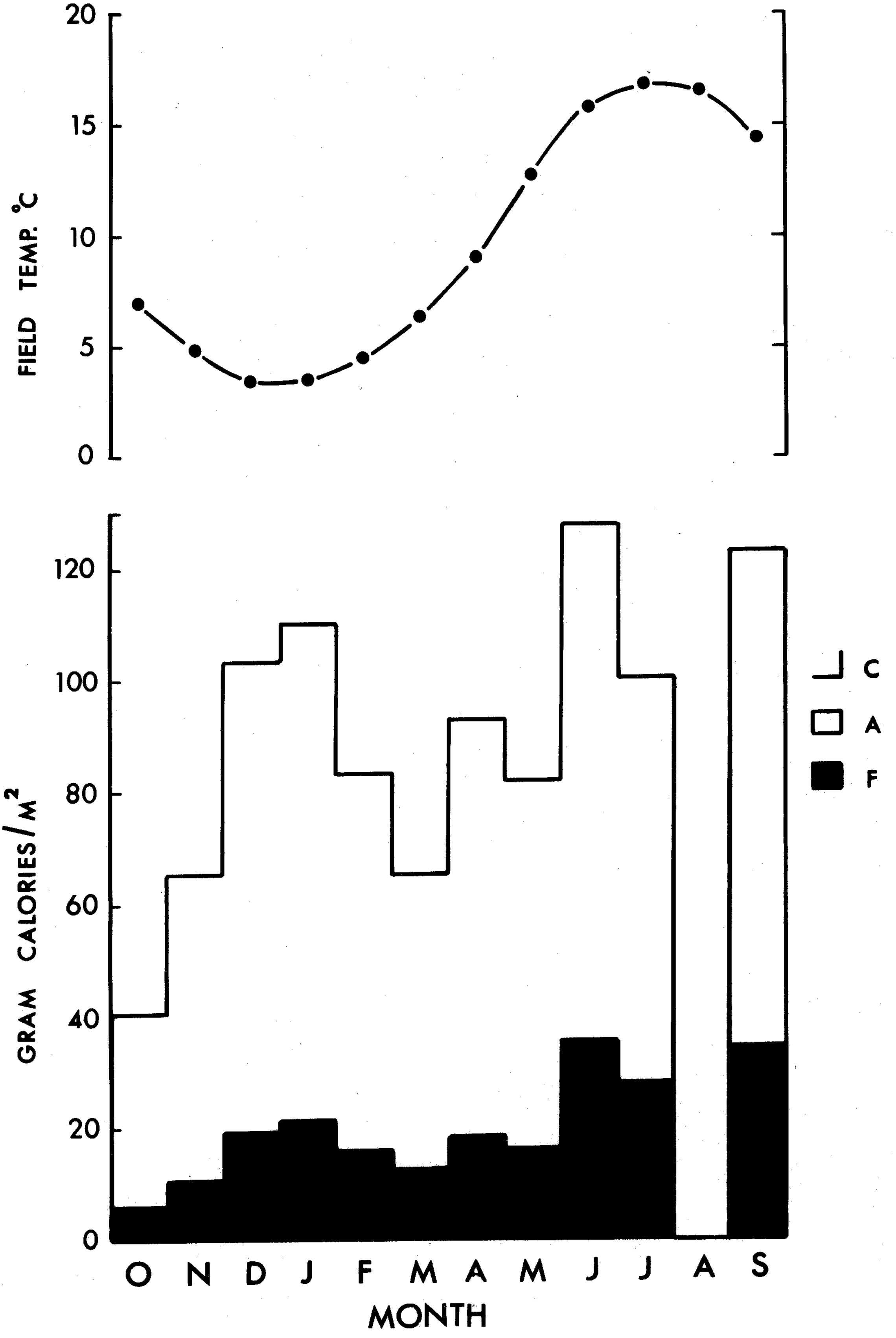
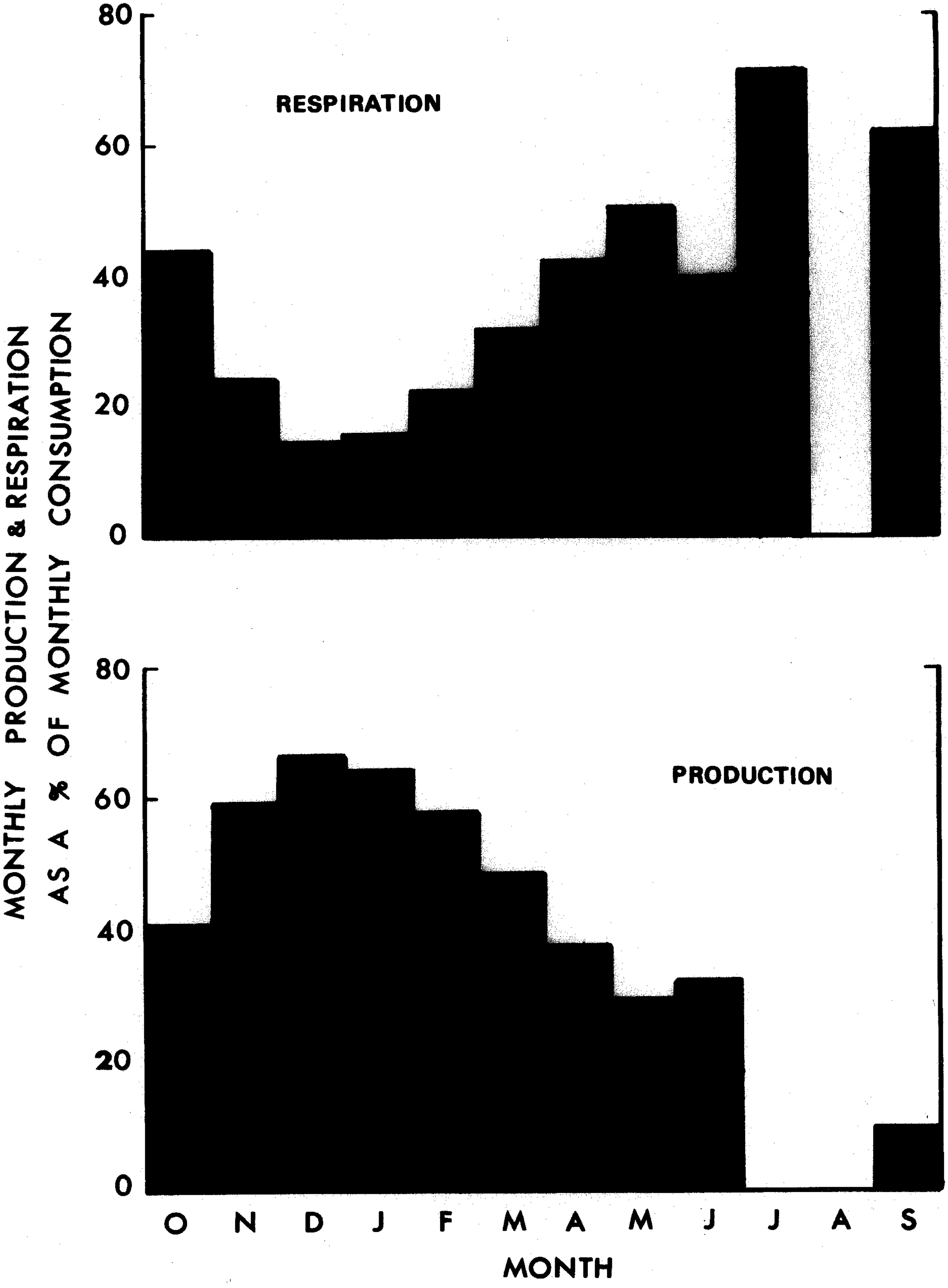

120
100
80
60
40
20
0
BIOMASS IN CALORIES/M.^{2}
O
N
D
J
F
M
A
M
J
J
A
S
MONTH

Fig. 46 Changes in monthly consumption, assimilation and faecal production : mean monthly field temperatures are also shown. C = consumption, A = assimilation, F = faecal production.



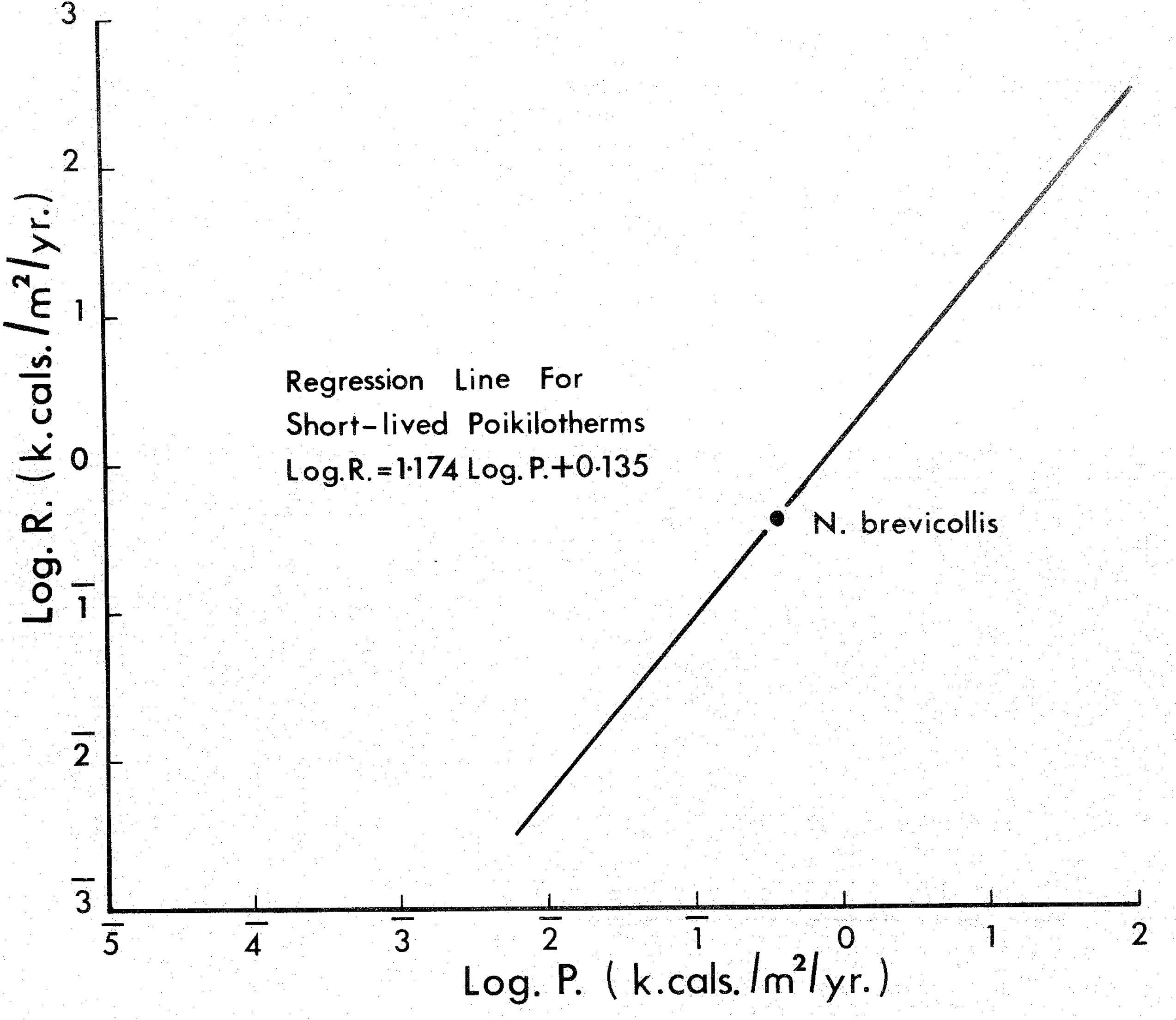
FIELD TEMP. °C
20
15
10
5
0
GRAM CALORIES/M^2
120
100
80
60
40
20
0
C
A
F
O
N
D
J
F
M
A
M
J
J
A
S
MONTH

Fig. 47 Monthly production and respiration as a % of monthly consumption.



RESPIRATION
PRODUCTION
MONTHLY PRODUCTION & RESPIRATION AS A % OF MONTHLY CONSUMPTION
0
20
40
60
80
O
N
D
J
F
M
A
M
J
J
A
S
MONTH

Fig. 48 Logarithmic relationship between annual population production and annual population respiration (K cal /m^2). Regression line drawn according to equation given by McNeill and Lawton (1970), for short lived poikilotherms.


Regression Line For
Short-lived Poikilotherms
Log.R.=1·174 Log.P.+0·135
N. brevicollis
Log. R. (k.cals./m²/yr.)
3
2
1
0
$\bar{1}$
$\bar{2}$
$\bar{3}$
$\bar{5}$
$\bar{4}$
$\bar{3}$
$\bar{2}$
$\bar{1}$
0
1
2
Log. P. (k.cals./m²/yr.)

CHAPTER 11

General Discussion

(1) Field Temperature

It was necessary to obtain field temperature data so that the laboratory measurements could be extrapolated to field conditions. The mean monthly soil/air interface temperatures of the study area were measured by means of the Pallmann/Berthet temperature integrator. These were compared with the monthly air temperatures recorded at the Durham University Observatory. Generally the air temperatures followed the soil surface temperatures closely during the winter. In summer soil surface temperatures were higher, diverging by 2.4°C. This is probably caused by the thicker grass cover in the summer acting as a blanket thus preventing rapid thermal changes and thereby reducing daily fluctuations in temperature.

Mean monthly temperatures have been used in energy flux studies by several investigators (Bolton, 1969; Saito, 1965 and 1967; Qasrawi, 1966; O'Neill, 1968).

(2) Bomb Calorimetry

Published data on calorific determinations of Coleoptera are limited. Kendeigh (in Cummins 1967) estimated a value of 5.926 kcal/g for *Megilla maculata* (Coccinellidae). No mention is made of stage or condition of the animal. Slobodkin (1961) recorded a figure of 6.314 kcal/g for Tenebrio molitor larvae about to pupate. Klekowski et al (1967) and Dutton (1969) give values for Tribolium castaneum (range 5-6.7 kcals/g) and Melanotus rufipes (range 4.3 - 6.5 kcal/g) respectively, through its developmental stages.

The calorific values of N. brevicollis material ranged between 4.5 - 6.1 kcal/g which is in agreement with the values indicated above. The literature indicates that values for animal tissues ranged between 4.0 - 7.0 kcal/g(Golley, 1961; Slobodkin and Richman, 1961; Cummins, 1967).

In Nebria, the calorific value per gramme increased with developmental stage, which accords with the data recorded by Wiegert (1965), Klekowski et al (1967), and Dutton (1969). The pre-diapause stage adult and instar III had the highest calorific value, probably due to the higher fat content. Slobodkin (1961) pointed out that animals about to pupate or diapause generally have high calorific values. This was evident in N. brevicollis.

(3) Feeding and Assimilation efficiency

Before attempting to determine the assimilation efficiency of each life stage, it was important to determine the probable food and feeding habits of N. brevicollis. Food preference experiments revealed that larvae and adults showed preference for Collembola and dipterous larvae. Nebria did not show feeding periodicity in excess of 24 hours, the exact opposite to the situation noted by Kajak (1965), Nowak (1967) and Dutton (1969). This lack of periodicity in feeding could be related to the preferred prey of *Nebria* being potentially available at all times.

The assimilation efficiency of *N. brevicollis* was not affected by feeding rate. This phenomenon also occurs in many aquatic forms, for example, *Calanus finmarchicus* (Marshall and Orr, 1955), *Lepomis macrochirus* (Gerking, 1955), *Salmo clarkii* (Brocksen et al, 1968).

The assimilation efficiency of some terrestrial invertebrates decreases with increasing feeding rate, e.g. *Armadillidium vulgare* (Hubbel et al, 1965); *Oniscus ascellus* (Hartenstein, 1964). A similar response to increased feeding rate has been reported for aquatic invertebrates (Richman, 1958; Schindler, 1968). Decreasing assimilation can be explained by the faster rate at which food passes through the gut. Prosser and Brown (1962) and Hartenstein (1964) showed that the level of feeding can affect the rate at which food passes through the gut. Large amounts of food passes through the gut more rapidly resulting in poor digestion, hence a lower percentage assimilation. At lower feeding levels, food passes through slowly, and allows the animal to assimilate more efficiently.

Davies (1964) working with *Carassius auratus,* found percentage assimilation increasing with increased feeding rate, and suggested that the decreased assimilation at low feeding levels, was due to the small quantities of food having a "sub-optimum stimulatory effect" on the gut, resulting in poor digestion.

The assimilation efficiency of *Nebria* was significantly affected by different prey items. This was also observed by Marshall and Orr (1955), Conover (1965b), Schindler (1968). In *Nebria* assimilation efficiency was higher with a soft bodied prey. With soft bodied prey the nature of food entering the gut is mainly in a fluid form which is easily digestible, thus giving a high assimilation efficiency. Carnivores feeding on soft bodied prey have shown a high assimilation efficiency value, for example, *Lepomis macrochirus* - 94.4% - (Gerking, 1955), *Carassius auratus* - 93.3% - (Davies, 1964), *Oryzomys palustris* - 88% - (Sharpe, 1967), *Melanotus rufipes* - 86.5% - (Dutton, 1968).

While the feeding rates of Nebria increased with rising temperature, the assimilation efficiency decreased. This type of response to temperature has been shown by White (1968) in *Tracheoniscus rathkei*, O'Neill (1968) in *Narceus americanus*. However, feeding rates in the millipede (*N. americanus*) decreased after 25°C. The decreasing assimilation efficiency can be attributed to the faster passage of food through the gut. White (1968) found the calorific value of faeces increase with rise in temperature, which indicates, that not only food was passing more rapidly through the gut, but digestive efficiency was also decreasing. In *Daphnia magna*, assimilation efficiency increased with rise in temperature, although feeding rates were unaffected.

N. brevicollis females were found to assimilate less efficiently when carrying a large number of eggs. This occurred despite the increase in respiratory rate during this period. Several workers have found that increase in assimilation efficiency coincided with an increase in respiratory rate. (Phillipson, 1962; Watson, 1965). The lower assimilation efficiency of Nebria females carrying eggs can be related to the active reproductive state or due to experimental error (discussed in chapter 5). Schindler (1968) showed that percentage assimilation was significantly higher in Daphnia magna carrying large broods although respiratory rates did not increase.

Size was another factor which influenced the assimilation efficiency of N. brevicollis. A similar phenomenon occurred in Daphnia magna (Schindler, 1968), Mitopus morio (Phillipson, 1962), Chorthippus parallelus, (Qasrawi, 1966), Porcellio scaber (Watson, 1965). Phillipson (1962) pointed out, that in Mitopus morio, the earlier instar could not tear up the hard parts of the prey, and only ingested the soft parts which were easily digestible. Wiegert (1964) reported that assimilation efficiency in P. spumarius increased as animal size increased, whilst in A. brama larvae assimilation efficiency was unaffected by size (Sorokin and Panov, 1966).

The assimilation efficiency figures (50 - 90%) recorded for N. brevicollis are higher than the value suggested by Engelmann

(1966) for poikilotherms. The literature indicates that the digestive efficiency of most invertebrate carnivores are high. It appears that Engelmann (1966), based his assumption on terrestrial invertebrate herbivores, which generally speaking have a low assimilation efficiency value ranging from 6 - 50%. This low efficiency can be attributed to two factors.

a) Their diet which contains some relatively indigestible cellulose.

b) The fact that in nature they are not necessarily limited by food results in consumption of large quantities which leads to a low assimilation value.

Wiegert (1964) obtained a high assimilation value for adult Philaneus, but it should be noted that Philaneus is a fluid feeder and probably ingests less unusable material. High assimilation percentages have been found in some aquatic invertebrate herbivores, e.g. Oxytrema silicula - 59.6% - (Brocksen et al, 1968), Calanus hyperboreus - 70% - (Conover, 1966). Vertebrate herbivores too, have very high efficiencies (Golley, 1959 and 1960; Conell, 1959; West, 1968).

In nature predators commonly utilize several prey species, however, in bioenergetic studies it is difficult for one worker to estimate percentage assimilation on several prey species, because of the magnitude of such an undertaking. Most investigators have used a soft bodied prey to estimate percentage assimilation of carnivores.

High values were obtained (80 - 95%). It would be desirable to get values on two distinctly different prey types as in the present investigation. It is also necessary to consider other variables such as temperature, feeding rate, animal size and reproductive condition.

(3) Consumption

In the field N. brevicollis was feeding well below the feeding rate in the laboratory. The laboratory results on consumption which are maximum feeding rates provide very little information on the feeding rates in the field.

In the field feeding rates of predators are affected by prey density. As prey density increases the number of prey attacked or eaten also increases, called functional response by Holling (1963, 1966, 1967). The functional response to prey density arises from the action of five basic and five subsidiary variables (see Holling 1967). Most of these variables are absent in laboratory experiments. The complex pattern (between predator and prey) which exists in the field is impossible to reproduce in the laboratory. It is probably more difficult to design feeding experiments for terrestrial predators like Nebria than it is for herbivores and aquatic predators. With herbivores, laboratory data can be extrapolated to the field, as most herbivores in the field are not usually limited by food. If laboratory studies are carried out to obtain some indication of consumption in the field, then they should duplicate natural conditions as closely as possible with regards to food, temperature and light.

Radio-isotopes have been used by some investigators to estimate field consumption of herbivores (Crossley, 1963, 1966 & Reichle, 1967). The field estimates obtained by Crossley using radio-active techniques agreed closely with the laboratory results (weighing technique). Radio-active techniques could be used to study feeding rates of predators directly in the field, but for such purpose, a suitable experimental animal is necessary.

Several workers used gut contents to estimate field consumption (Golley 1960, Lawton 1969, Paine 1965, Phillipson 1960). In the present study the method employed was similar to the one used by Phillipson (1960)and Lawton (1969). Paine (1965) did not incorporate the laboratory assimilation data in his calculation of field ingestion. Field feeding rates were measured directly from stomach contents and gut clearance time. Hard parts of the prey that could not be digested were recovered from the faeces, identified, measured, and then correlated with the size of the prey. With the calorific information of each prey type he was able to estimate the calories of each prey type consumed. This method is only feasible when all prey consumed leave some recognisable remains which can be correlated with their size.

Some sources of error which may arise when using gut contents and gut clearance time to estimate field consumption are discussed by Darnell and Meierotto, 1962; Gerking, 1962.

In the field *Nebria* was only nocturnally active and feeding coincided with this period. In the laboratory *Nebria* would accept food in daylight and showed no periodicity in defaecation. Periodicity in feeding can complicate the study of field feeding rates by the gut contents and gut clearance time method. Lawton (1969) pointed out, that this method gives the most reliable estimates when there is no periodicity in feeding, when gut clearance times are relatively long, and when several prey types are attacked.

5) Growth and Moulting

In the present investigation, because of low population numbers, it was necessary to conduct separate growth experiments to obtain an accurate estimation of the growth rate of *N. brevicollis*. Mary workers have used field data to study the growth rate. (Teal, 1957; Smalley, 1960; Wiegert, 1964 and 1965; Mann, 1965; Saito, 1965 and 1967). Their data was based on accurate and reliable sampling methods. Wiegert (1964) calculated growth of *P. spumarius* nymphs from the increase in the mean weight of nymphs between successive samples, i.e. $\left(\frac{\Delta W}{\Delta T}\right)$ where ΔW = weight increase, ΔT = time. Saito (1967) calculated growth rate in *L. japonicam* (life span of 2 years) by measuring the increase in mean weights for each year class between consecutive samples.

In the present study, errors may have been introduced into the calculation of production, because the growth curve used (see chapter 7) was derived from semi-natural conditions, that is, whilst temperature was as in the field, feeding was artificial.

The total calories lost in moulting through development was small (3.4 cals.), and amounted to 1.4% of the total production per individual. This is in agreement with most investigators. In Philaneus the exuviae was - 3.5% - of the total production due to growth (Wiegert, 1964). In Neophilaenus lineatus, it was higher - 9.0% - (Whittaker, 1967), and in Anatopynia it represented only 3% of the total ingestion (Teal, 1957). In other Coeloptera, for example, Hylotrupes bajalus exuviae was found to represent less than 1% of the larval weight (Rasmussen, 1967), and in Melanotus rufipes 4.9% of the body dry weight (Dutton, 1969).

However, in Euphausia pacifica, the amount of calories lost in moulting is large (Lasker, 1966). The dry weight of each moult is approximately 10% of the body dry weight, and since moulting occurs about every five days, the exuviae accounted for 20 - 25% of the production due to growth. In some animals the energy loss due to exuviae production was considered zero because,

a) The animals eat their moult after casting it. (Saito, 1965; Watson, 1965; Wignarajah, 1969).

b) The moults contain a high percentage of mineral, thus having no significant caloric value (Watson, 1965).

6) Respiration

The annual respiratory metabolism was estimated at 15°C, but this hardly reflects the field situation where temperature varies considerably. With N. brevicollis showing no acclimatization, it was possible to extrapolate to the field situation using the field temperature data and the regressions obtained from the respiratory measurements made at different temperatures. A similar approach was employed by Smalley (1960), Wiegert (1964, 1965) and Saito (1965). Various other methods have been used to correct laboratory measurements of respiration to field temperatures. Bornebusch (1930) and Nielsen (1961) used Krogh's curve, while Berthet (1964) and Healey (1965) employed a Q_{10} relationship.

The respiratory measurements at different temperatures were made on animals, that had been kept at the temperature at which the measurements were made, for 24 - 48 hours prior to the experiment. Several investigators, for example, Wiegert (1964), Healey (1965), Berthet (1963), Dutton (1969), made measurements of a single individual at different temperatures, allowing only 30 - 90 minutes for the animal to "acclimatize" at the new temperature. Although this method reduces individual variation, the sudden change in temperature can effect the respiratory rate. For example, in some crustacea a rapid change in temperature initially caused an overshoot in oxygen consumption, followed by a period of minor oscillations, before a steady level characteristic of the new temperature was reached (Grainger, 1956). Berthet

(1964) found that a sudden 10° rise in temperature resulted in the respiratory rate of mites increasing by about five times.

In ecological work it is desirable to measure oxygen consumption on normal animals approaching conditions as far as possible to those in the field. If the experimental animals in the field always contain food in their guts then it is justified to use fed animals in the respirometer. It is difficult to duplicate the exact field situation. However, the important thing in metabolic studies is to standardize the material used. In the present study, all the animals were fed the night prior to the experiment. Nielsen (1961) used enchytraeids with empty gut contents. Phillipson (1962 and 1963) used phalangiids immediately after collecting in the field. Mann (1965) fed fish before placing them in the respirometer. Feeding animals just prior to the experiment could have an effect on the metabolic rate. Warren and Davis (1967) found that the metabolic rate in fish increases following food consumption, and this increase was attributed to the specific dynamic action of the food. In this situation a short duration experiment would show a high respiratory rate.

The effect of starvation on the respiratory rate of *Nebria* was not investigated, but several workers found a decrease in oxygen consumption due to starvation (Healey, 1966; Mann, 1965). The respiratory rate of *N. brevicollis* was affected by several factors (weight, temperature, reproductive condition, diapause, senescence), a result which accords with the findings of several investigators (Phillipson, 1962 and 1963; Watson, 1965; Wiegert, 1965; Webb, 1969). For accurate and reliable estimates on the respiratory metabolism of a population, it is necessary to study respiration continuously over 24 hours, and on all life stages throughout the year (Phillipson, 1967).

The metabolic rate of *Nebria* was temperature dependent. Contrary to this often observed phenomenon, Newell and Northcroft (1967) found that the basic metabolic rate of certain marine invertebrates (*A. equina*, *N. bombergi*, *L. littorea*, and *C. edula*) was independent of temperature over much of the normal environmental temperature range (7 - 22.5°C). This was probably due to rapid acclimatization (see Bullock 1955).

N. brevicollis males had a higher respiratory rate than the females at any comparable stage except diapause. This is not atypical of insects. Siew (1968) made similar observations on the beetle (*Galeruca tanacetti* (chrysomelidae), and Phillipson (1962 and 1963) on the phanlagiids *Mitopus morio* and *Oligolopus tridens*. During the reproductive period the male rates were 18.48% higher than the females. The much lower respiratory rate of the females, can be explained by the fact that the eggs, although contributing to the total body weight, do not have a high respiration rate thereby lowering the oxygen consumption per unit weight. (Edwards, 1956; Phillipson, 1962).

The response of the different life stages to temperature change was more or less similar. This is comparable to the results found by Edwards (1946) in the click beetle Melanotus communis, and Job (1955) in the fish Salvelinus fontinalis. However, in some species the effect on different life stages vary. Wiegert (1964), for instance, noted that the respiratory rate of the adult Philaneus was more affected by temperature rise than the nymphs. In the sunfish the metabolic rate of larger individuals showed more response to temperature change than the smaller individuals (O'Hara (1968).

The Warburg respiratory data were also plotted on a double logarithmic scale. This method was used by several workers in estimating respiratory metabolism. (Engelmann, 1961; Job, 1955; Ito , 1964; Saito, 1965; Smalley, 1960). The above mentioned authors obtained a linear relationship between oxygen consumption and body weight. With N. brevicollis a non-linear relationship was revealed. Klekowski et al, (1967) obtained a similar result in the beetle Tribolium castaneum. This is not atypical of insects as shown by the work of Phillipson (1963) and Wiegert (1965).

In figure 40 the points which depart from linearity are those obtained from the reproductive animals. This also occurred in L. rotundum. However, in Philaenus spumarius, the same explanation did not apply. The cause is explained by the increase in the amount of chitin on the bodies of older nymphs and adults, which increases the body weight but contributes metabolically very little (Wiegert 1964).

To assume that a linear relationship exists between the log. of the respiration rate and log. of body weight could lead to errors when estimating the shares contributed by different stages. In the case of N. brevicollis the reproductive stage individuals would be underestimated.

7) Comparison of Energy flux

The total energy flux of the studied population of N. brevicollis was low (.803 K cal/m^2/yr) when compared with the aquatic Coleopteran Rhanatus (Tilley, 1968), which had an annual energy flux of 11.0 Kcal/m^2. The work of Wignarajah (1969) on centipedes is the only comparable study of a terrestrial invertebrate carnivore. The total energy flux (defined as R + R) of the two species L. crassipes (1.3 Kcal/m^2/yr) and L. forficatus (2.1 Kcal/m^2/yr) was slightly higher than the figure found for N. brevicollis.

The major contribution to the total lithobiid energy flux came from respiratory metabolism, 3 - 5 times greater than the value found for Nebria. Although the Lithobiids had a higher mean standing crop (.856 Kcal/m^2/yr), the total production of the two species (.158 kcal/m^2/yr) was lower than Nebria (.389 Kcal/m^2/yr).

The total energy flux values of the Lithobiids and Nebria are low when compared with other terrestrial invertebrates, for example, *P. badius* - 31.0 Kcal/m^2/yr (Golley, 1960), *P. spumarius* - 38.9 - Kcal/m^2/yr - (Wiegert, 1964), *L japonicam* - 19.5 - Kcal/m^2/yr. - (Saito, 1965), *J. laminata armigera* - 57.8 - Kcal/m^2/yr. - (Saito, 1967). Both *Nebria* and the Lithobiids being predators had a very low population density per m^2 compared with the above mentioned herbivores (*except P. badius*), and therefore a low energy flux per m^2/yr. was expected. In the case of *P. badius*, the high energy flux was due to the high respiratory metabolism.

The influence of changes in population numbers, biomass and field temperature on population energy flux was examined. In *N. brevicollis*, larval energy flux followed the biomass fluctuations closely, and the two peaks coincided. Adult energy flux was found to be more influenced by field temperature and physiological condition. In *L. crassipes* and *L. forficatus* changes in population numbers and biomass coincided with changes in energy flux. This was due mainly to the stable age composition of the lithobiid population throughout the year (Wignarajah, 1969).

In *Euphausia pacifica*, size structure of the population was found to have more influence on the annual energy flux than temperature (Small, 1967), and in *Pyrrhosoma nymphula*, the population energy flux was influenced by field temperature although the two peaks did not correspond (Lawton, 1969). In the grasshopper *O.fidicinium*, peak energy flux did not correspond with maximum numbers or biomass, but occurred when the population was composed of a medium number of medium sized nymphs (Odum and Smalley, 1959).

The peak energy intake in *N. brevicollis* took place in June when the adults emerged and were rapidly preparing for diapause. Generally speaking there is close correlation between energy dynamics and life cycle events. This is comparable to the situation found in *N. americanus*. Peaks of energy occurred during the breeding season and in preparation for hibernation. Energy flux reached a low level during the moulting period. (O'Neill, 1968).

The gross population growth efficiency ($^P/C$) of *Nebria* was higher than the value found in *P. spumarius* - 17.8% - (Wiegert, 1964), *J. laminata* - 9.5% - (Saito, 1965), *A rosea* - 0.14% - (Bolton, 1969). These low figures are probably due to a lower assimilation efficiency. *A.rosea*, for example had an assimilation efficiency of less than 1%. The net growth efficiency ($^P/A$) value accords with those obtained for short-lived poikilotherms. (Smalley, 1960; Wiegert, 1964; Healey, 1966; Qasrawi, 1966; McNeill, 1969).

Although the $^P/R$ ratio of *Nebria* was high (94%), it was lower than the figures recorded in other comparatively short-lived poikilotherms, for example, *Leptoterna dolobrata* - 103.2% -

(McNeill, 1969), *Chorthippus parallelus* – 124% – (Qasrawi, 1966). These values are greatly in excess of those found by Wiegert (1965) in Orthoptera – 53.55% –, Smalley (1960) in *O.fidicinium* – 58% –. Short-lived poikilotherms with a high $^P/R$ ratio tend to have a very low annual production, and probably for this reason have to maximize production efficiencies (McNeill and Lawton, 1970). Most long-lived poikilotherms have low $^P/R$ and $^P/A$ values due mainly to their high annual respiratory costs. (Bolton, 1969; Mann, 1965; Wignarajah, 1969).

The logarithmic relationship of annual population respiration and annual population production was examined, and the data from *N. brevicollis* fitted very closely to the comparatively short-lived poikilotherm regression line, thus showing agreement with data obtained by other workers on short-lived poikilotherms.

As carabid beetles are preyed upon by small mammals such as field mice, voles, shrews, moles etc. (Ashby, pers.comm.), it is likely that *N. brevicollis* will form a prey source to these mammals. Their contribution to energy flux in the ecosystem appears to be as food for higher trophic levels. Since the biomass present at any one time small, and energy flux through the population low, their contribution to the flux of energy through the studied ecosystem was relatively small.

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