Energy dynamics of centipede populations (Lithobiomorpha – L. Crassipes and L. Forficatus) in woodland ecosystems

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ENERGY DYNAMICS OF CENTIPEDE POPULATIONS (LITHOBIOMORPHA - L. CRASSIPES AND L. FORFICATUS) IN WOODLAND ECOSYSTEMS

A thesis presented in the candidature for the degree of the Doctor of Philosophy

by

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Durham

December 1968

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Introduction

The functioning of organisms within ecosystems depends on the utilisation of energy, and the ultimate source of this energy is solar radiation. The absorption of solar energy by green plants and its subsequent use by living organisms is frequently expressed in terms of energy transfer through trophic levels, namely

solar radiation - producer - primary consumers - secondary consumers.

The transfer of this energy through each level (plant, herbivore and predator) relates to the classic concept of energy flow postulated by Lindeman (1942). The understanding of this type of energy transfer focuses its attention on ecology which, according to Odum (1962, 1968) is defined as the structure and function of the ecosystem. Structure embodies the composition of the biological community, the quantity and distribution of abiotic materials and the range or gradient of conditions of existence. While function incorporates the range of energy flow through ecosystems, the rate of material cycling and the regulation of the physical environment.

The pioneer work of Bornebusch (1930) at the species population level, although now known to be quantitatively inadequate, prepared the way for the development of ideas so succinctly expressed by Lindeman (1942). However, following the appearance of Lindeman's paper much work was directed towards the entire ecosystem (Odum 1957 and 1962 and Teal 1957), some towards food chains (Golley 1960), and

only recently have ecologists followed Bornebusch's lead by once more studying species populations. Three main approaches have been adopted in studying the energy flow through ecosystems: (1) The entire ecosystem (2) The simple food chain (3) The species population level.

In general, considerable progress has been made on the study of energy flow through primary producers and herbivores but investigations on predators are few. The present study was made in order to determine the energy flow through two populations of invertebrate predator, the centipedes Lithobius crassipes (L. Koch) and L. forficatus (L.).

In any detailed study of energy flow laboratory and field observations must be combined. Data on population density and size structure are essential as are data on microclimate, growth, respiration, assimilation and egg production. The populations chosen for study occurred in birch/alder woodland and on site measurements were made of (a) population density (b) microclimate, particularly temperature and (c) growth. The study area surrounding the sample area (Newbould 1967) was used for collecting centipedes for laboratory experiments. Macfadyen (1967) has stressed the need for care in linking field to laboratory data; particularly in connection with metabolic measurements and the effect of temperature. In this study all possible precautions were taken by measuring microhabitat temperature for later use in laboratory estimates of "field" metabolism.

It is well known that metabolic activity of different sized individuals varies and therefore to establish the role of each size class within a given population it is necessary to obtain some measure of population structure. In order to achieve this a study of the life history of the species under investigation is essential. Verhoeff (1925) showed the existence of ~~ten~~ twelve stadia for L. forficatus; and demonstrated that L. curtipes, a species similar to L. crassipes, had ~~eight~~ nine stadia. Recent work by Eason (1964) on the development of L. variegatus proposed a classification of stadia which was different from that used by Verhoeff. As Eason's system was preferred by the present author it was used in describing the development of L. crassipes, and to avoid confusion Verhoeff's descriptions of L. forficatus were grouped according to this scheme. L. crassipes was shown to possess ~~eight~~ nine stadia as was to be expected from its similarity to L. curtipes, and the presence of ~~ten~~ nine stadia in L. forficatus was ~~confirmed~~ suggested. In view of the large number of stadia in the development of each species and a relatively low population density it proved necessary, for the purpose of establishing the functional role of various size classes within each population, to group stadia into the three categories, thus dividing the population into juveniles (limb development), juniors (external genitalia and gonads) and adults.

The data for the population density for each species of centipedes were obtained from stratified random samples of logs and

cylindrical soil cores. The extraction of lithobiids was based on the methods described by Macfadyen (1955) and Murphy (1956 and 1962). The centipedes were collected from monthly extractions identified to stadia, and weighed. The validity of the population curve was checked using the data from ova production. A percentage standard error less than 25% was observed for L. crassipes while a range of 25 to about 40% in standard error was recorded for L. forficatus. A percentage error of less than 30% can be considered sufficiently accurate for population studies (Southwood 1966). The higher percentage standard error for L. forficatus was unavoidable. Both species were shown to be randomly distributed over the sample area.

The population biomass of each species was calculated from wet weight/dry weight regressions and expressed in calories per m^2, in terms of the three stated size categories. The calorific value of lithobiid material was determined seasonally using the Phillipson bomb calorimeter (Phillipson 1964). Phillipson (1962, 1963) stressed the need for continuous respirometry in determining the metabolic activity of the various life stages within a single species. In the present study oxygen consumption was determined for all stadia using the Phillipson respirometer at 15°C, 10°C and 5°C. The lithobiids were acclimatised at the temperatures mentioned. Metabolic activity was found to vary with temperature. A regression analysis of the rate of respiration with temperature was used to compute field respiratory data for lithobiids. The oxycalorific

value (Carpenter 1939) used in the calculations was a mean for the combustion of glycogen (5.06 Kcal/1), animal fat (4.72 Kcal/1) and protein (4.60 Kcal/1).

Respiratory activity normally utilises a large percentage of assimilated food (Macfadyen 1963). The balance of energy of assimilation is channelled into production which is ultimately utilised by the next trophic level. Various workers have defined production in several ways (Wiegert 1964, Odum and Smalley 1959, Davis 1963, Engelmann 1966, Macfadyen 1963 and 1967). In the present study production is defined as growth or rate of increase of biomass with time. The increase in biomass with time for L. crassipes and L. forficatus was determined by taking monthly mean weights of individuals kept in field enclosures; and by collation with field population data an estimate of production was obtained. Over the calculated life span of five years for L. crassipes and about six years for L. forficatus the net production efficiency of both species populations was calculated and shown to approximate 6%.

The energy assimilated by each species population was determined using the energy flow equation of Slobodkin (1962) when production

I	=	Y	+	R
Energy of assimilation in cals.		Energy of production in cals.		Energy of respiration in cals.

and respiration were known. Thus the energy budgets of the two species were computed.

CHAPTER I

FIG. 1. WYNYARD ESTATE WITH SAMPLE AREA (S).

KEY TO FIG. 1.

1. CLOSE WOOD
2. NEWTON HANZARD PLANTATION
3. MIDDLE SWAINSTON PLANTATION
4. TILERY WOOD
5. BRIERLY WOOD
6. THORPE MOOR LARCHES
7. BLACK SQUARES
8. BRIERLY WOOD
9. WELFIELD PLANTATION
10. NEWTON HANZARD
11. WYNYARD PARK

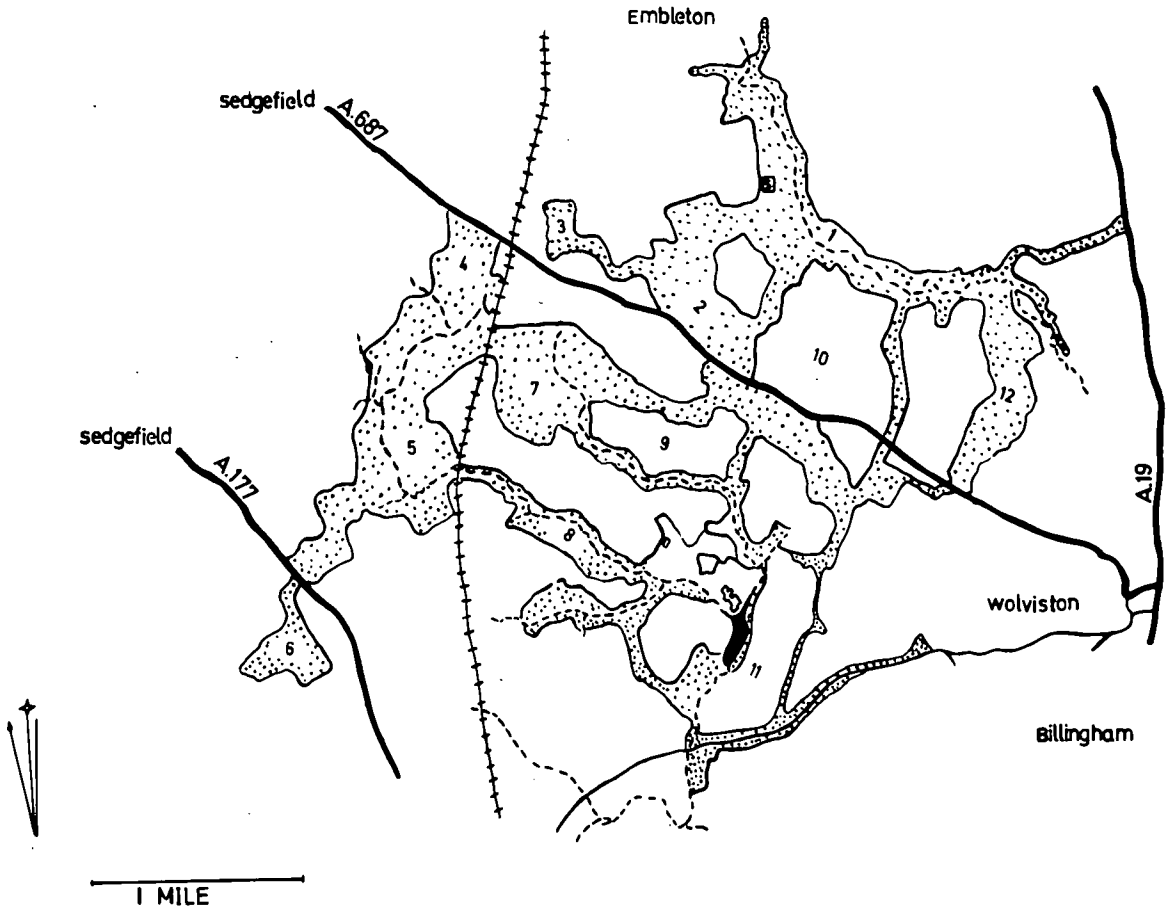


FIG. 1 WYNYARD ESTATE WITH SAMPLE AREA(s)

The Study Area

(a) Location

Wynyard Estate lies about 15 miles south-east of the University of Durham between Sedgefield and Wolviston (Fig.1). It was on this estate, arranged by the kind permission of the Forestry Commission, that the study was made. The study area (25,000 m^2) which bordered the Newton Hanzard Plantation (Grid Reference NZ. 424287) was a mixed birch/alder woodland growing on boulder clay and the sample area (Newbould 1967) was a large grid of a total area of 2,400 m^2. No large stones or rocks were found in the sample area but fallen logs of varying diameter were common. Plant litter varied in thickness with season. The soil was acidic (pH 2.0-4.5), and total annual rainfall for the estate falls within the range of 71.1 to 78.7 cm (meteorological stations of Durham and Hartlepool - monthly weather reports). However the land is low lying and the water table was usually never more than 20 cm below the surface.

(b) Vegetation

Figures 2 and 3 show general views of the sample area and the nature of the dense undergrowth during the summer is clear. According to the classification of Elton and Miller (1954) the vegetation of the sample area was stratified. The high canopy was dominated by birch (*Betula* sp.) and alder (*Alnus* sp.), oak

FIG. 2. VEGETATION IN SUMMER SHOWING DENSE UNDERGROWTH.

FIG. 3. VEGETATION IN WINTER WITH SPARSE UNDERGROWTH.


A4

(Quercus sp.), hawthorn (Crataegus monogyna Jacq.) and sycamore (Acer pseudoplatanus L.) also occurred but were sparsely distributed.

The low canopy was represented by a few individuals of briar (Rosa canina L.). Plants of the field layer were numerous and were dominated by ferns, herbs and grasses. Prominent were the co-associated pteridophytes Pteridium aquilinum L. and Dryopteris filix-mas L. Kuhn. A species of Polystichum was also quite common. Species of perennial herbs were dog's mercury (Mercurialis perennis L.), the violet (Viola riviniana Rchb.), the common enchanter's nightshade (Circaea lutetiana L.), the barren strawberry (Potentilla sterilis L. Garcke), and the wood avens (Geum urbanum L.). Often within the field layer was the blackberry (Rubus fruticosus Agg.) and the rose bay willow herb (Chamaenerion angustifolium L. Scop.). The grasses included the tufted hair grass (Deschampsia caespitosa L. Beau.), the creeping soft grass (Holcus mollis L.), Yorkshire fog (Holcus lanatus L.), the common bent grass (Agrostis tenuis Sibth.) and the meadow grass (Poa trivialis L.).

The vegetation of the ground zone was mainly mosses and leafy liverworts which occurred in patches in various sections of the sample area. The species of mosses include Mnium hornum Hedw., Hypnum cupressiforme Hedw., Dicranella heteromalla Hedw. and Thuidium tamariscinum Hedw. The common liverworts were Pellia sp., Fissidens sp., and Lophocollea heterophylla Schrad. Dum. Lying in the ground zone were logs, the surface litter and

organic debris (for details see Hughes 1968).

(i) Species studied

Those aspects of plant cover of great importance to the present study were the fallen logs, the litter layer and the A-horizon of the soil. It was in these microhabitats that the most common lithobiids (L. crassipes and L. forficatus) in the sample area were found. The only other lithobiid recorded was L. calcratus but occurred very rarely. Chilopods such as geophilomorphs were extremely common in the sample area occurring under bark in decayed timber, in the leaf litter and in the soil. The lithobiomorpha under investigation were found living under bark, in decayed logs, in the litter and the top surface of the soil. The only centipedes living in the soil were the [redacted] geophilids, [redacted] which are morphologically adapted to burrow. Lithobiids appear to be numerous in the litter and logs during the summer, but in the winter are less obvious and migrate into the crevices in decaying logs and litter, and the humus layer of the soil.

(ii) Microclimate

Before the relevant measurements of metabolic parameters essential to population energy flow studies could be made it was necessary to consider the microclimate normally experienced by L. forficatus and L. crassipes. Previous workers, Auerbach (1951) and Roberts (1957) showed that centipedes were very sensitive to

temperature, rainfall and humidity. Microclimate measurements were considered necessary to explain population fluctuations as well as being essential for the calculation of field respiratory rates from laboratory oxygen consumption data. Figures for rainfall were obtained from meteorological records at West Hartlepool (approximately four miles from the site). It was not possible to obtain mean monthly humidity measurements due to the lack of suitable apparatus. Temperature measurements of the microhabitat were determined monthly using the technique adopted by Berthet (1960).

(a) Berthet's Technique

Berthet (1960) described an improved technique for the measurement of mean field temperatures based on the rate of inversion of saccharose

$$\text{sucrose} + H_2O \longrightarrow \text{fructose} + \text{glucose}$$

The rate of inversion was at constant pH and the measurement of the angle of ~~inversion~~ rotation of the solution of saccharose determined by the use of a polarimeter. The constant of inversion K'T was calculated by applying formula I.

$$K'T = \frac{1}{t} \log \frac{Ao - Bo}{A - Bo} \qquad \text{I}$$

where t = time of exposure to temperature in days.

Ao = rotatory power of the solution at time = 0.

Bo = rotatory power of the solution at complete inversion.

A = rotatory power of the solution at time t.

The temperature was calculated using the second formula.

$$\log K'T = B + m\theta \quad \text{——————————} \quad II$$

where B and m are constants and θ is the temperature in degrees centigrade.

(b) Procedure

The solution to be exposed to the temperature of the microhabitat consisted of a buffer solution and a sucrose solution mixed in equal parts. The buffer solution was one of rapid inversion with a pH of about 1.4. The buffer and sucrose solutions were prepared according to Berthet (1960). It was found that the pH varied slightly from that mentioned by Berthet, but did not affect the calculation of temperature as a separate constant of inversion K'T had to be calculated instead of using the values given by Berthet. For this purpose a portion of this solution was poured into three small screw top bottles (volume 30 cc) and placed in each of the constant temperature rooms at $5^{o}C$ and $10^{o}C$. The third bottle was deposited in the deep freeze at $-20^{o}C$. The remainder of the solution was pipetted into 36 glass tubes (14 cm long, 7 mm external diameter, and a 0.9 mm thick wall); each tube was filled to about four-fifths of its volume and sealed by a rubber bung. Thus 36 tubes were put into a freezing mixture contained in a thermos flask, transported to the sample area and placed in position. Collection of tubes from the field was made on a specified date and the angle of rotation of the solution measured. The mean temperature was calculated using formulae I and II above.

(c) Measurement of temperature under bark, inside log, and between log and ground

The logs in the study area were found to be in three stages of decay (i) recently fallen logs with wood quite hard and bark firmly attached, (ii) wood soft, easily sawn with bark separated, and (iii) wood which could be crumbled by hand or broke into fragments when sawn. The centipedes only inhabited logs in categories (ii) and (iii).

The logs in the sample area varied in length and diameter. Twelve logs of varying diameters (4, 6, 8, 10, 12, 14 and 16 cm of each of the two specified stages of decay were selected at random on the sample area. In each log three glass tubes containing an equal mixture of buffer and sucrose solution were placed horizontally, under bark, in wood, and beneath log (Fig.4) and ground as shown Fig.5. The tube in wood was placed approximately in the centre by carefully chiselling out a triangular block of wood of the same length. Any crevices formed when replacing this triangular block of wood were packed with powdered wood. The bark under which the tube was placed was gently anchored to stakes to prevent displacement by wind or animals.

(d) Results

The difference in the mean temperatures between logs of the decay stages (ii) and (iii) during the commencement of

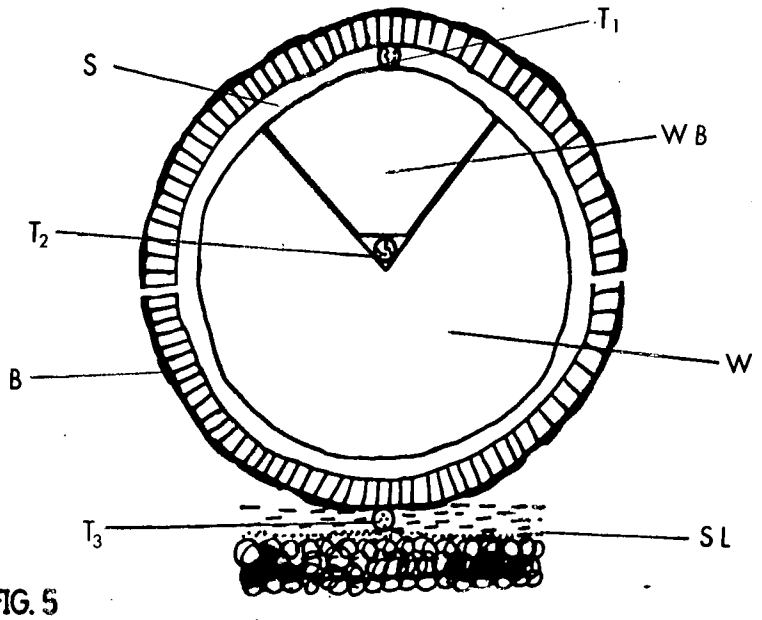


FIG. 5

T.S. OF LOG/SOIL SHOWING POSITION OF TEMPERATURE INTEGRATORS

Key to Figures 4 and 5:- S = space caused by decay, B = bark, T_1, T_2, T_3 = temperature integrators, W = wood, SL = soil layer, WB = triangular block of wood.

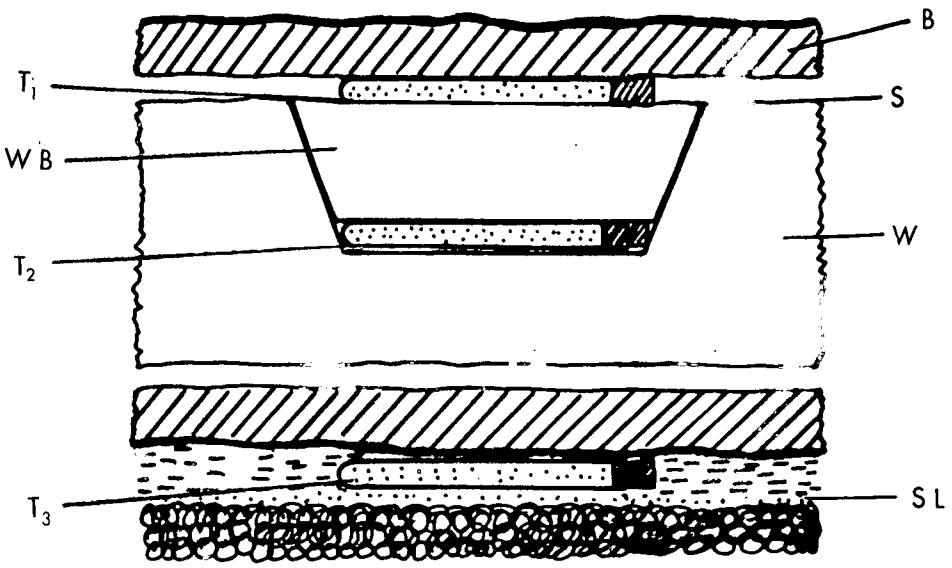


FIG. 4

V.L.S. OF LOG/SOIL(diagrammatic)SHOWING TEMPERATURE INTEGRATORS IN SITU

the period of study were found not to be significantly different and therefore during the latter stages served as useful checks one against the other. Figure 6 shows the mean temperatures for one year under bark in wood and between log and ground. Table 1 shows that the bark temperatures were slightly higher than wood, or log and ground between July and early to mid-September (1966) and again increased in the spring and the summer of the following year. The ground was warmer than logs during the winter. Thus an autumn inversion occurred in early to mid-September with a spring inversion in March. The observed inversion times resemble those noted by Macfadyen (1956) in air/soil studies in the Dell in Wytham Woods, Berkshire. Healey (1967) recorded temperature changes in surface layers and soil of moorland in Cefn Bryn, South Wales, and observed an inversion of temperature in February and mid-September.

(e) Discussion

Temperature is one of the important physical factors affecting distribution and activity of centipedes (Chapter III). Several workers have determined the mean temperature of a number of environments by using maximum and minimum thermometers, thermographs, thermocouples, thermistors and the rate of inversion of saccharose with temperature. Macfadyen (1956 and 1951), Crabb and Smith (1953), Coutts (1955), Healey (1967), and Delaney (1953) recorded mean soil temperatures using thermistors. Temperature

Table 1.

Mean temperature of the microhabitat

Period 1966-67	Temperature °C Ground/ log	In wood	Under bark
20-7-66 10-8-66	10.46	10.51	10.63
10-8-66 25-8-66	12.02	12.13	12.24
25-8-66 10-9-66	12.11	12.18	12.13
10-9-66 25-9-66	12.60	12.60	12.24
25-9-66 12-10-66	10.55	10.42	10.34
12-10-66 2-11-66	10.18	9.90	9.85
2-11-66 2-12-66	8.14	7.38	6.70
2-12-66 3-1-67	5.49	4.81	4.68
3-1-67 2-2-67	5.13	5.16	5.26
2-2-67 6-3-67	6.64	6.59	6.75
6-3-67 1-4-67	6.99	7.13	7.31
1-4-67 1-5-67	7.87	8.17	8.53
1-5-67 15-5-67	9.07	9.31	9.87
15-5-67 1-6-67	10.34	10.54	10.74
1-6-67 15-6-67	11.35	11.51	11.71
15-6-67 30-6-67	11.25	11.55	11.69
30-6-67 14-7-67	12.19	12.41	12.53
14-7-67 31-7-67	12.03	12.14	12.22
31-7-67 15-8-67	11.78	11.84	11.98

Meteorological records at W. Hartlepool

Period 1966-67	Rainfall in cms	Air temperature in °C (ht.33ft)
1966		
March	1.2	6.9
April	8.5	6.3
May	3.8	11.0
June	6.7	14.2
July	5.2	14.5
August	10.4	14.3
September	2.5	14.1
October	10.4	10.5
November	7.3	6.3
December	4.9	4.9
1967		
January	2.5	4.3
February	4.4	6.1
March	3.6	7.5
April	3.1	8.1
May	7.1	9.6
June	5.0	13.2
July	6.2	16.1
August	6.2	15.3

FIG. 6. MEAN TEMPERATURES UNDER BARK, IN WOOD, AND UNDER LOG AND GROUND.

FIG. 7. MEAN MONTHLY TEMPERATURE OF MICROHABITAT.

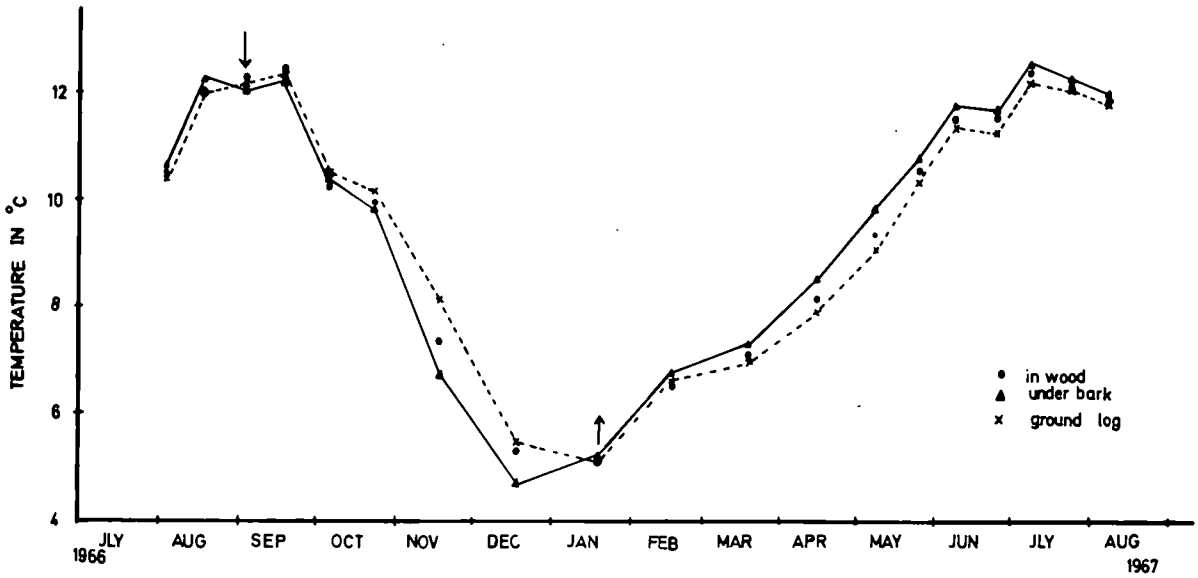


FIG.6 MEAN TEMPERATURES UNDER BARK, IN WOOD, AND UNDER LOG AND GROUND.

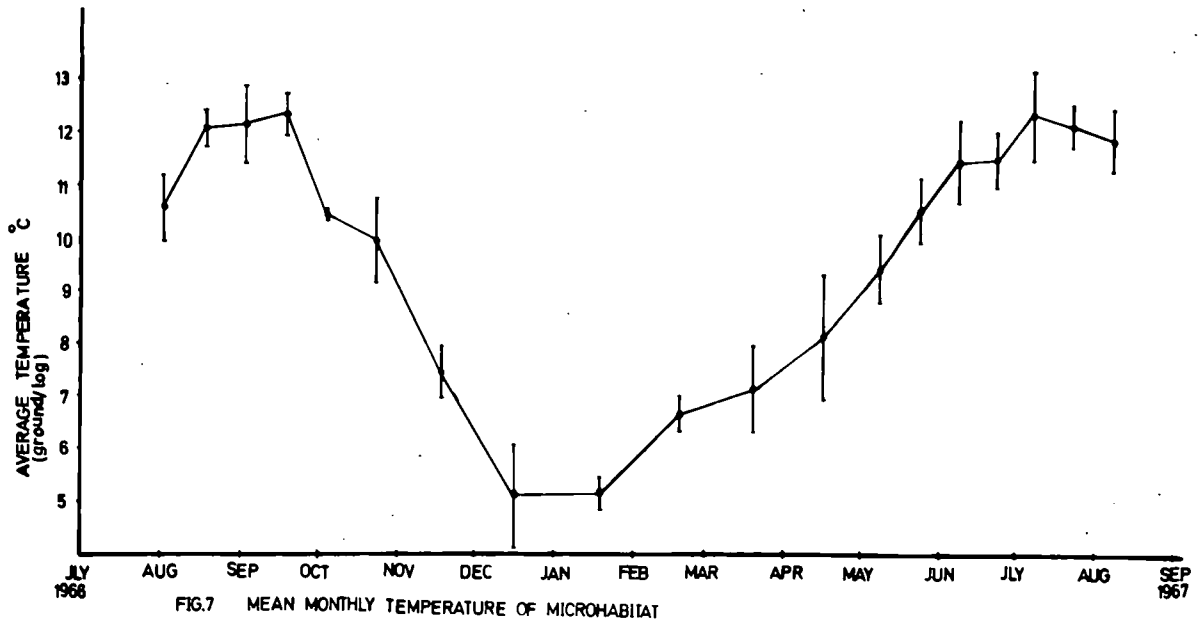


FIG.7 MEAN MONTHLY TEMPERATURE OF MICROHABITAT

readings observed in or on Sitka spruce and mountain pine by Haarlöv and Petersen (1952) indicated temperatures important to wood-boring insects. Berthet's method possesses certain advantages because biological reactions have a coefficient of temperature of the same order of magnitude as the inversion of sucrose and the cost of operation of this method is low. The average monthly figures for rainfall (cm) and air temperatures in degrees centigrade are included in Table 1 with temperatures of the microhabitat. The variations in field temperatures as measured by the inversion technique parallel the fluctuation of air temperatures recorded at the meteorological station, West Hartlepool. The temperatures measured under log agree very closely with the temperatures recorded in litter by Bolton (1968 pers. comm.) for the same sample area. The maximum mean temperature of the microhabitat in summer was 12.4°C while the lowest (4.8°C) recorded in the winter for wood. The temperature measured was presumably affected by the vegetal cover (trees, shrubs and forbs), moisture content of the clayey soil, as well as that of the logs and the litter. The accumulation of litter by the end of autumn accompanied by rainfall probably affected considerably the fall in temperature. The vegetation exerts not only a direct influence on log and ground temperatures but an indirect influence on other factors affecting temperature such as depth, porosity or permeability, colour of organic debris and the duration of the snow. Figure 7 shows the average mean

temperature experienced by L. crassipes and L. forficatus which were used in conjunction with the metabolic data to compute field respiration rates.

CHAPTER II

Instar determination of Lithobius crassipes and L. forficatus and the development of stadia of L. crassipes.

(i) Instar determination in L. crassipes and L. forficatus

(a) Terminology used in the description of stadia

Eason (1964), working with L. variegatus in particular, proposed a scheme of stadial classification for Lithobiomorpha which he stated should serve as a reliable guide to the development of British species. This scheme indicates that the majority of species will possess eight developmental stadia. However, Verhoeff (1925), using slightly different criteria to Eason, described twelve developmental stadia in L. forficatus and eight in L. curtipes (a species closely related to L. crassipes). In the present study the problem was to reconcile the two classifications.

The instars of L. forficatus described by Verhoeff (1925) comprise larval stadia 1 to 4, a larva media and a further seven stadia termed in order of appearance, status agenitalis, status immaturus, status prematurus, status pseudomaturus primus, status pseudomaturus secundus, status maturus junior and status maturus senior. L. curtipes also described by Verhoeff (1925) possessed larval stadia 1 to 4 followed by status agenitalis, immature stage, premature stage, pseudomaturus stage and a mature stage. Eason broadly classified the lithobiid developmental stadia into (a) a larval stage and (b) a post larval stage. The larval stage is a group of four stadia mainly characterised by limb development whereas the post larval stage, basically a replica of the adult, is a group of four post larval stadia progressively increasing in

structure and morphological characters. It should be noted that development of genitalia predominates in the post larval stage. Thus the development of the centipede is one of limb development followed by the development of genitalia.

As demonstrated in the next section a study of L. forficatus showed that its developmental stadia would fit the Eason classification. Eason's (1964) scheme was adopted and the Verhoeff equivalents are shown in Table 2, as are the simpler terms proposed by Brolemann (1930). The terminology used is compatible with the two divisions of Brolemann, adopted by Roberts (1957). The stadia of L. curtipes described by Verhoeff (1925) fitted the present scheme without modification (Table 1) and L. crassipes was found to possess the same number of stadia as L. curtipes.

(b) Determination of stadia

In this study the morphological criteria given by Verhoeff (1925) for L. forficatus and L. curtipes (closely related to L. crassipes) were used as a guide to the determination of stadia according to Eason's (1964) scheme. However, morphological characters alone were not adequate for complete separation of stadia and it was deemed necessary to resort to linear measurements. The following measurements were made on both L. forficatus and L. crassipes.

(1) The entire length of the centipede from the anterior end of the cephalic shield between the antennae to the outer

Table 2. The terminology used in the determination of stadia of L. crassipes and L. forficatus.

Instars of lithobiids described by Verhoeff (1925)		Terminology used (Eason (1964))	Terminology of Brolemann (1930)
L. curtipes	L. forficatus		
Larval stadium 1	Larval stadium 1	Larval stadium 1	Anamorph stage
Larval stadium 2	Larval stadium 2	Larval stadium 2	
Larval stadium 3	Larval stadium 3	Larval stadium 3	
Larval stadium 4	Larval stadium 4 Larva media	Larval stadium 4	
Status agenitalis	Status agenitalis	Post larval stadium I	Epimorph stage
Immature stage	Status immaturus	Post larval stadium II	
Premature stage	Status prematurus	Post larval stadium III	
Pseudomaturus stage	Status pseudomaturus primus Status pseudomaturus secundus	Post larval stadium IV	
Mature stage	Status maturus junior Status maturus senior	Adults	

margin of the telson.

(2) The greatest width of the first trunk segment.

(3) The greatest width of the cephalic shield taken posterior to the ocelli and anterior to the termination of the marginal ridge, here referred to as head width.

(4) The width of the coxosternite within the outer margins of the femeroids of the forcipule.

Body length has frequently been used as a means of separating arthropod larval instars [Ford (1917), Strickland (1939) and Salt and Hollick (1944)]. Verhoeff (1925) used this measurement for L. forficatus and L. curtipes in addition to morphological criteria but the present author found this linear dimension to be most unreliable in separating the stadia of both L. forficatus and L. crassipes, as were the greatest width of the first trunk segment and the width of the coxosternite within the outer margins of the femeroids of the forcipule.

Gadd (1947), Jonasson (1955) and Fernando (1963) working with Xyleborus fornicatus (Eichoff), Chironomus antracinus (Zch.) and Attems haemorrhoidalis (F) respectively, successfully separated instars on the basis of head width. Head width proved successful in both species under study. In the case of L. forficatus eight stadia were readily distinguished and in conjunction with morphological criteria allowed Verhoeff's stadia to be grouped

according to Eason's (1964) scheme (Table 2).

Larva media observed by Verhoeff did not occur amongst the specimens collected. This stadium is most probably a transitory phase occurring before the larval centipede moults to the first post larval stadium. The rare larva media was best grouped with larva 4 as it was mainly concerned with limb development. In practice pseudomaturus primus and secundus were difficult to separate on morphological characters and were grouped as post larval stadia IV. On similar grounds status maturus junior and senior were collectively termed adults.

In the case of L. crassipes where previous stadial descriptions were not available the following procedure was adopted. Head widths of larvae were measured only from living larvae, as preserved specimens (70% alcohol) were liable to become distorted, making accurate measurement impossible. The 349 larvae used were those obtained from random sampling.

Figure 8 shows the obtained results in the form of a histogram. The percentage frequency of head width measurements clearly delimits seven peaks which represent seven stadia. In view of the short duration of the first larval stadium (Eason 1964) not a single specimen was obtained in the field samples and this stadium is not represented in Figure 8. Thus the first three peaks represent larval stadia 2-4 while the subsequent ones are post larval stadia I-IV. A graphical analysis of head width versus the cumulative

FIG. 8. HISTOGRAM SHOWING SEVEN PEAKS, EACH PEAK REPRESENTING A STADIUM (L. CRASSIPES).

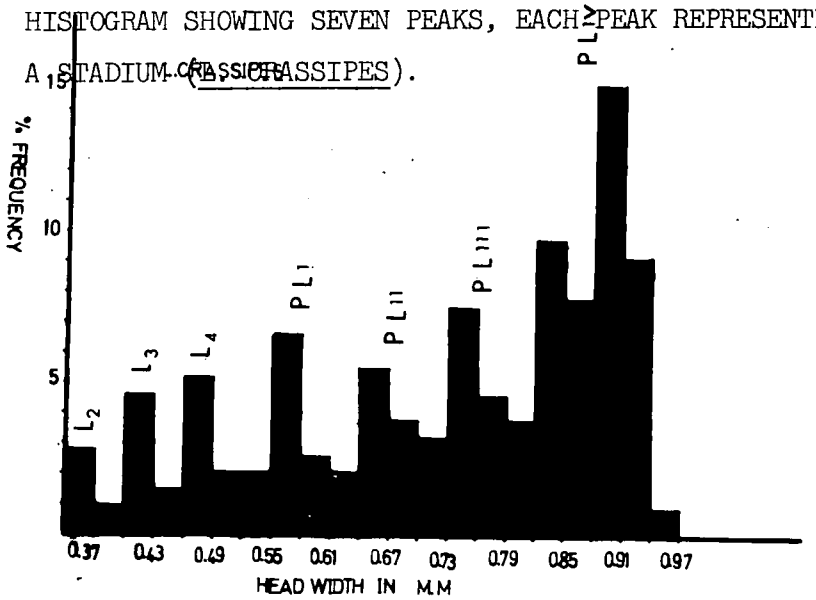
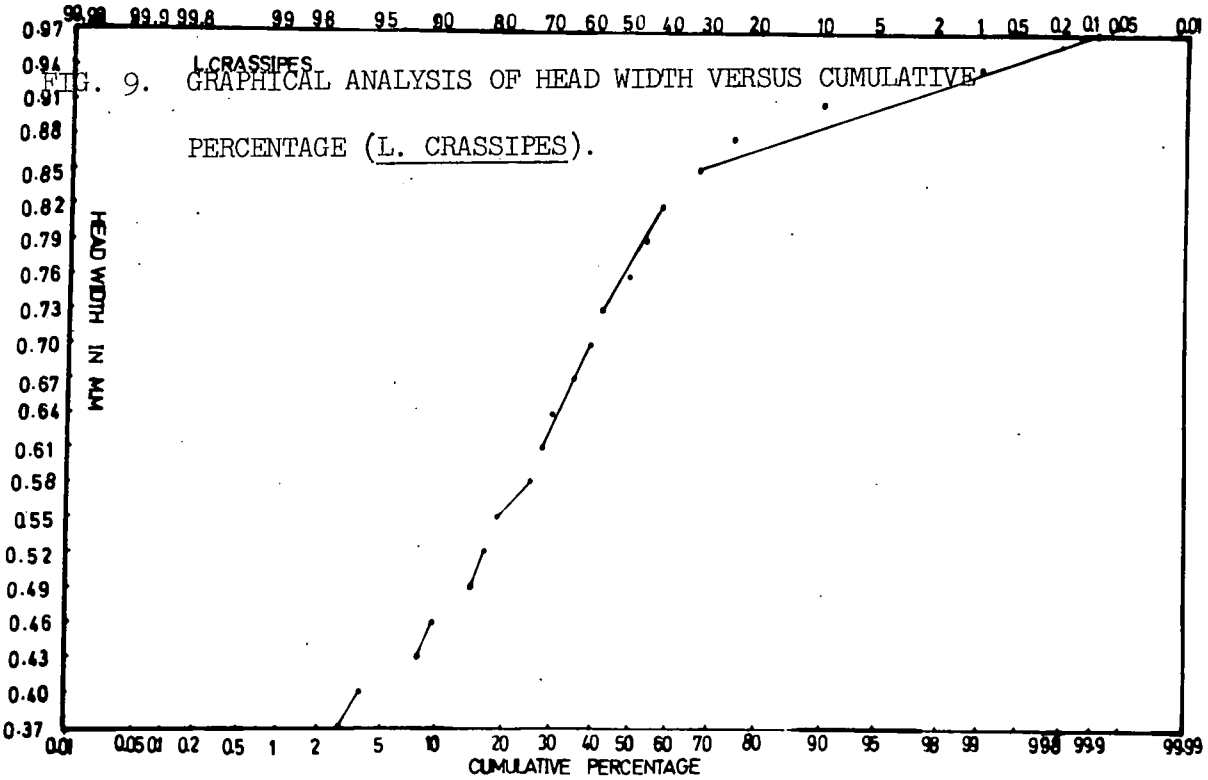


FIG. 9. GRAPHICAL ANALYSIS OF HEAD WIDTH VERSUS CUMULATIVE PERCENTAGE (L. CRASSIPES).



collections. Similar explanations for the form of histogram shown in Figure 8 have been made by Gadd (1947) and Jonasson (1955) for the short duration of some of the instar stages in larval development of Xyleborus fornicatus (Eichoff) and Chironomus antracinus (Zch.) respectively.

(ii) Developmental stadia of L. crassipes (L. Koch)

The development of L. crassipes from larval stage to adult involves a significant change in head width and morphological characters such as limbs, antennae, ocelli and external genitalia. During larval development the formation of limbs predominates while in the post larval stadia development of genitalia appears to be the main feature. It should be noted that in L. crassipes the forcipular teeth and ridges on maxillae do not change during development. The progressive change from one instar to another takes place with the moulting of the centipede. In L. forficatus development is similar with the young centipede gradually attaining the adult stage as a result of moulting between stadia.

(a) First larval stadium (L_1)

Specimens were not found in the course of sampling or collections. It is presumed to have a form similar to other lithobiomorph larvae which possess seven pairs of legs, two ocelli, twelve antennal segments and forcipular teeth 2 + 2. Two pairs of incipient limb buds may be present.

L. CRASSIPES

FIG. 11. 2ND LARVAL STADIUM (L_2)

FIG. 14. 3RD LARVAL STADIUM (L_3)

FIG. 16. 4TH LARVAL STADIUM (L_4)

FIG. 18. 1ST POST LARVAL STADIUM (PL I)

(MAGNIFICATION - x 14)

(b) Second larval stadium (L_2) (Fig. 10 and 11).

A head width between 0.37 mm - 0.40 mm. Antenna with usually 14 segments. Two ocelli on each side of head. Forcipular teeth 2 + 2 and distinct. Stigmata present on 5th segment; well developed limbs on 1st to 8th trunk segments. The future 9th and 10th limbs in the form of buds. Characteristic chitinised ridges on maxilla I occur throughout development. Limbs consist of coxa, trochanter, prefemur, femur, tibia, tarsus and metatarsus ending in an apical claw. Spines present on limbs. Forcipules present. Mandibles well developed.

(c) Third larval stadium (L_3) (Fig. 12, 13 and 14).

A head width between 0.43 mm - 0.46 mm. Antenna usually of 15 segments. Forcipular teeth 2 + 2. Two ocelli on each side of head, a developing third ocellus may occur. Limbs: 10 pairs well developed with coxa and a six segmented telopodite. Stigmata present on 5th and 8th segments. Limb buds on 11th and 12th trunk segments.

(d) Fourth larval stadium (L_4) (Fig. 15 and 16).

A head width between 0.49 mm - 0.52 mm. Antenna usually with 16 segments. Forcipular teeth 2 + 2. Four ocelli on each side of head. Twelve pairs of well developed, segmented limbs with distinct spines. Segments 13, 14 and 15 each bear a pair of limb buds. Stigmata on 5th, 8th and 10th trunk segments.

FIG. 10. VENTRAL VIEW OF THE RIGHT HALF OF THE HEAD OF LARVA 2.

FIG. 12. VENTRAL VIEW OF THE POSTERIOR EXTREMITY OF LARVA 3.

FIG. 13. VENTRAL VIEW OF THE HEAD OF LARVA 3.

FIG. 15. ANTENNA AND VENTRAL VIEW OF THE ANTERIOR EXTREMITY OF HEAD OF LARVA 4.

FIG. 17. VENTRAL VIEW OF THE POSTERIOR EXTREMITY OF POST LARVAL STADIUM I.

FIG. 19. VENTRAL VIEW OF THE POSTERIOR EXTREMITY OF POST LARVAL STADIUM II FEMALE.

FIG. 20. VENTRAL VIEW OF THE POSTERIOR EXTREMITY OF POST LARVAL STADIUM II MALE.

FIG. 21. VENTRAL VIEW OF THE POSTERIOR EXTREMITY OF POST LARVAL STADIUM III MALE.

FIG. 22. VENTRAL VIEW OF THE POSTERIOR EXTREMITY OF POST LARVAL STADIUM III FEMALE.

FIG. 23. VENTRAL VIEW OF THE POSTERIOR EXTREMITY OF POST LARVAL STADIUM IV FEMALE

FIG. 24. VENTRAL VIEW OF THE POSTERIOR EXTREMITY OF POST LARVAL STADIUM IV MALE.

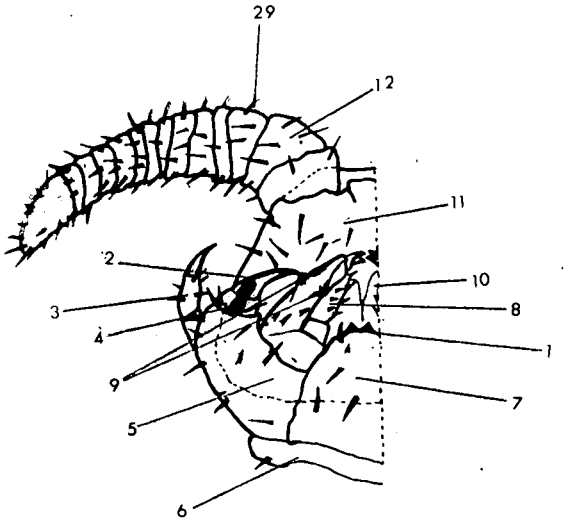


FIG. 10

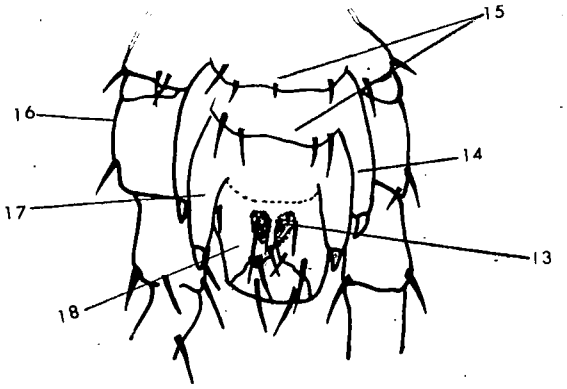


FIG. 12

MAG. 10x

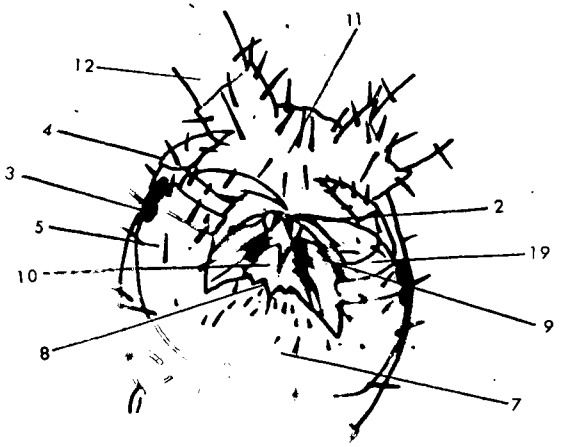


FIG. 13

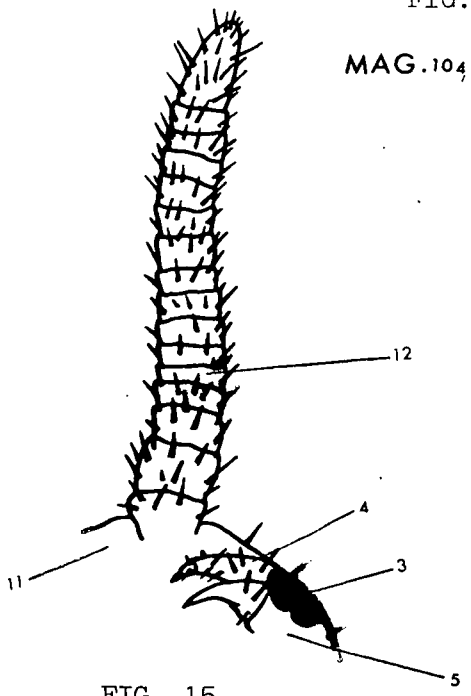


FIG. 15

(e) First post larval stadium (PL I) (Fig. 17 and 18).

A head width between 0.55 mm - 0.58 mm. Forcipular teeth 2 + 2. Antenna with 17 segments. Ocelli usually 4, but a developing 5th may occur. Coxal pores 1, 1, 1, 1 (15th, 14th, 13th and 12th legs). Limbs: 15 pairs well developed, segmented with spines. Genitalia without setae, gonopods apparent as protruberances. Sexes cannot be differentiated. Anal glands present. Forcipules, maxillae and mandibles well developed.

(f) Second post larval stadium (PL II) (Fig. 19 and 20).

A head width between 0.61 mm - 0.70 mm. Forcipular teeth 2 + 2. Antenna usually 18 segments. Ocelli: 6 on each side, 1 + 3.2. Coxal pores usually 1, 2, 2, 2. Sexes can be distinguished, male and female gonopods without spurs. In male, gonopod unsegmented, in female gonopod segmented terminating with or without a claw. Setae absent from male gonopod and 1st genital sternite. In female, a single seta on 1st genital sternite gonopod, with one or two setae at the base. Anal glands usually present.

(g) Third post larval stadium (PL III) (Fig. 21 and 22).

A head width between 0.73 mm - 0.82 mm. Forcipular teeth 2 + 2. Antenna usually with 20 segments. Ocelli eight on each side 1+4, 4;3. Coxal pores usually 2, 3, 3, 3, sometimes 2, 2, 3, 3, or 2, 3, 3, 2. Female gonopods with 1 + 1 spurs or 2 + 2 with the internal pair minute. In the female the 1st genital sternite bears 5 or more setae on each side, coxa of each gonopod with

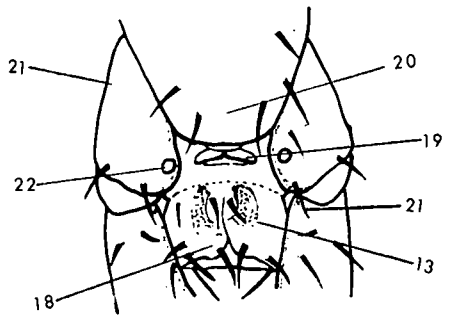


FIG. 17

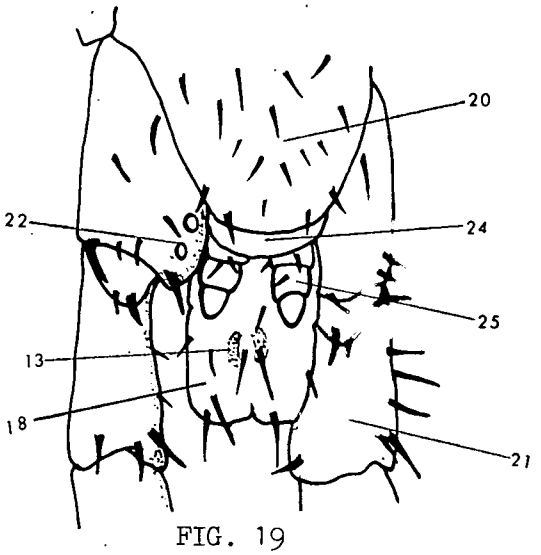


FIG. 19

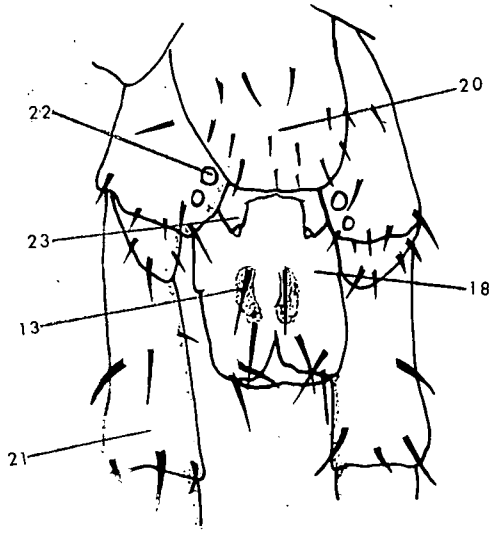


FIG. 20

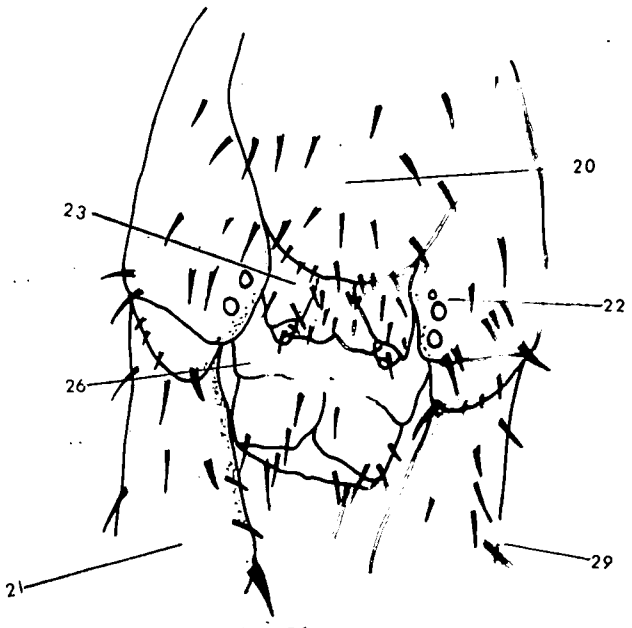


FIG. 21

FIG. 22

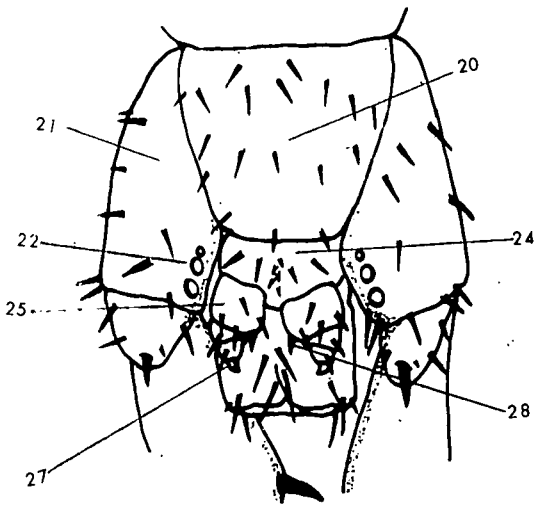
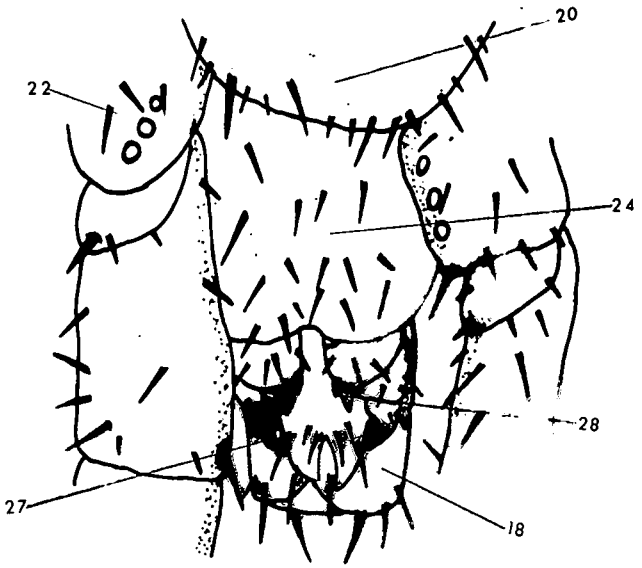


FIG. 23



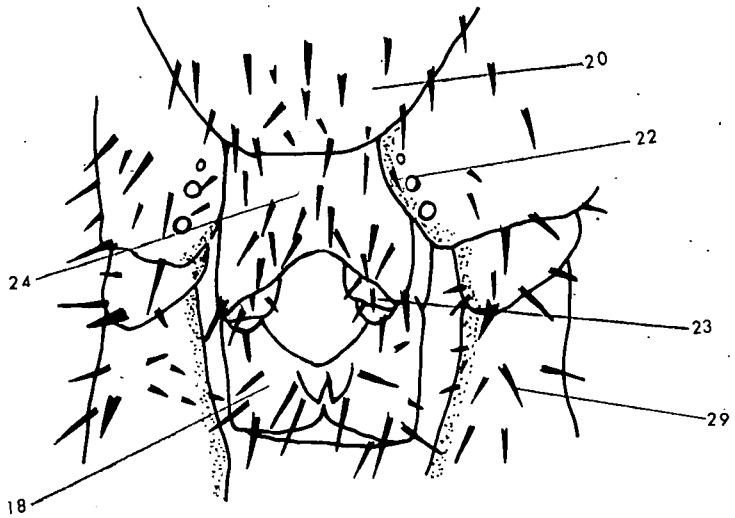


FIG. 24

KEY TO FIGURES (10, 12, 13, 15, 17, 19, 20, 21, 22, 23 and 24)

1. MANDIBLE
2. POISON CLAW OF FORCIPULE
3. OCELLUS
4. MAXILLA II
5. FORCIPULE
6. PLEURITE OF 1ST BODY SEGMENT
7. COXOSTERNITE
8. FORCIPULAR TEETH
9. PROXIMAL ~~CHITINOUS~~ CHITINOUS RIDGES OF MAXILLA I
10. COXAL PROJECTION
11. CLYPEUS
12. ANTENNA WITH SEGMENTS
13. POSITION OF ANAL GLAND
14. LIMB BUD OF DEVELOPING 11TH LIMB
15. STERNITES OF POSTERIAL BODY SEGMENTS
16. THE 10TH LEG
17. LIMB BUD OF DEVELOPING 12TH LIMB
18. ANAL VALVE
19. DEVELOPING GENITALIA
20. STERNITE OF LAST TRUNK SEGMENT (15TH)
21. THE 15TH LEG
22. COXAL PORE
23. GONOPOD MALE

24. 1ST GENITAL STERNITE

25. GONOPOD FEMALE

26. LATERAL PORTION OF 1ST GENITAL STERNITE

27. GONOPOD CLAW

28. SPUR OF GONOPOD

29. SPINE

setae. Male gonopod distinctly articulated, with setae, the 1st genital sternite bears setae. Anal glands absent.

(h) Fourth post larval stadium (PL IV) (Fig. 23 and 24).

A head width between 0.85 mm - 0.97 mm. Forcipular teeth 2 + 2. Antenna usually with 20 segments. Ocelli 9 or 11 on each side with 1+4,3,1 or 1+4,4,2 arrangement. Coxal pores usually 2, 3, 3, 3, but sometimes 2, 3, 4, 3. Female gonopods with 2 + 2 very unequal spurs. Basal and apical articles of gonopods bear setae. In the female the 1st genital sternite with usually 10 to 14 setae on each side. In the male the 1st genital sternite possesses about 10 to 12 setae on each side.

With the above information it was possible to separate the individual stadia of L. forficatus and L. crassipes, make metabolic measurements on each stadium, and apply the information so gained to the field population so as to derive an energy budget for each species population. The remaining chapters are concerned with this aspect.

CHAPTER III

The determination of population density of L. crassipes and L. forficatus

Knowledge of centipede populations is limited. Cole (1946) and Dowdy (1951) estimated population density of chilopods for a restricted period whilst investigating woodland arthropods in the U.S.A. Auerbach (1951), also working in the U.S.A., compared populations of centipedes in prairie and woodland. In S. England Roberts (1957) studied populations of the centipedes L. dubosqui (Bröl.) and L. variegatus (Leach) in mixed beech/oak woodland.

The present study was undertaken to estimate energy flow through two populations of invertebrate predators (L. crassipes and L. forficatus) in a birch/alder woodland in N. England.

(i) Population sampling and extraction of centipedes

(a) General comments

The sample area comprised six grids each with an area of $400m^2$ (20m x 20m). The grids were separated by adjacent paths and each grid was pegged at ten metre intervals into quadrats. Preliminary soil/litter samples of varying diameter and depth were taken in the study area adjacent to the sample area. The results of such sampling aided in determining 1) the abundance of lithobiomorph species, 2) aggregation of species, if any, with different types of vegetation and 3) a suitable sample size for detailed study.

L. crassipes and L. forficatus inhabited the study area in reasonable numbers and it was assumed that a similar situation pertained in the sample area. Aggregation of lithobiid species was not detected within the different types of vegetation, thus indicating that stratified random sampling was a suitable technique for the soil/litter component in the present study (Macfadyen 1962). The positions of the samples were ascertained from a table of random numbers (Snedecor 1950) before sampling began. Over the whole sampling period only one sample was taken from each square meter.

However, in the study area lithobiids were found not only in the litter and soil but also in tree stumps and logs and it was evident that detailed sampling had to be categorised as (1) litter and soil and (2) logs and stumps. The total log volume and stump volume was determined and the calculated log volume per m^2 amounted to 0.46 litres. As the log volume in the sample area was low, log samples were taken on a stratified random basis from the adjacent study area, and the results obtained applied to the sample area. Clearly population estimates for the two categories were calculated in terms of 1) surface area and 2) log volume.

(b)Litter and soil sampling

The sampler was cylindrical (Fig. 25) made of plated steel with a serrated cutting edge (Area = 176 cm^2). A movable cylinder was fitted into the sampler and had a one centimeter square mesh covering at its upper end. Thus a large scale inversion

FIG. 26. THE EXTRACTION APPARATUS.

FIG. 25. CYLINDRICAL SAMPLER WITH MOVABLE INNER CYLINDER.


24
23
22

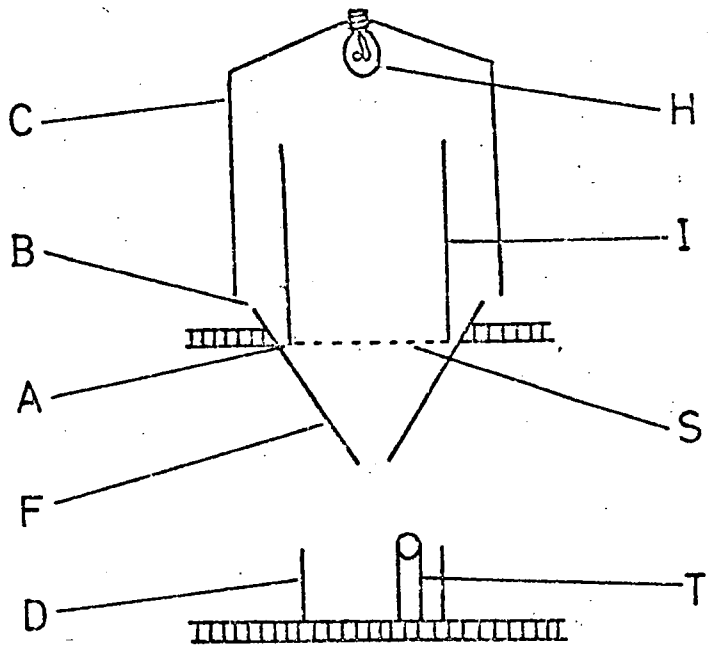


FIG. 27. Section through modified Tullgren funnel showing air passages.

H = heat source, C = cowling, I = inner cylinder, F = funnel, A-B = air passages, D = collecting dish with filter paper, T = test tube with water.

of the sampling tool described by Macfadyen (1962) was adopted. Following sampling the inner cylinder and its contained core was placed in a polythene bag, secured and conveyed to laboratory. The polythene bag was removed and the sample, including the cylinder, placed in the extractor. This procedure ensured against any loss of animals in transit, and held the cores in the same vertical position as in the field. Twenty-four samples, each of 10 cm depth, were taken on each monthly sampling occasion. This depth of core was considered sufficient in that test on cores divided into litter plus 5 cm of soil, and the 7 cm of soil below showed on extraction that lithobiids were restricted to the upper soil layers. This agrees with the findings of Manton (1952) that lithobiids are unable to burrow.

(c) Sampling of logs and stumps

Stratified random samples were taken of logs and stumps in the following stages of decay (i) wood soft, easily sawn, and with bark separated, and (ii) wood which could be crumbled by hand, or broke into fragments when sawn (Chapter 1). It was only in these two stages of log/stump decay that centipedes were found. On each monthly sampling occasion 18 lengths of log (24 cm) randomly chosen from the study area were sawn above a sorting tray and finally placed in polythene bags. It was inevitable that sample volume varied according to log diameter. The lithobiids were extracted from samples by dessication (Dutton

1968). The population of centipedes in logs and stumps was initially calculated on a volume basis but knowledge of log volume/m^2 on the sample area was used to express the results on an areal basis.

(d) Extraction Apparatus

Tullgren extractors and their efficiency have been reviewed by Macfadyen (1953, 1955, 1961 and 1962), Haarlöv (1947 and 1962), Nef (1962) and Murphy (1962). Macfadyen's (1955) results on the extraction of myriapods indicated the suitability of Tullgren funnels for extraction of lithobiids. The apparatus used in the present study was a modified Tullgren funnel extractor incorporating a battery of 24 funnels (Fig.26). The inner cylinder of the sampler (Fig.27) was held in position in the funnel by means of wooden wedges. The cowling adjusted to the required level (after preliminary testing) by allowing it to rest on three wooden blocks (thickness 2 cm). The extractor was housed in a constant temperature room at 25°C. Air passages created as a result of incorporation of wooden blocks eliminated the condensation of moisture on the funnels. The air temperature between the bulb and soil surface was increased (using a variable resistance) until it reached 60°C on the 7th day. During a period of seven days the soil and litter dried completely.

The efficiency of the apparatus was determined by introducing marked animals placed in samples of approximately 6 cm in depth and the results indicating a reasonably high extraction efficiency are shown in Table 3.

Table 3. The efficiency of the extraction apparatus.

GENUS - LITHOBIOMORPHA (L. crassipes, L. forficatus)	Number of animals		% Efficiency
	Introduced	Extracted	
Adults	6	6	100%
Post larval stadium IV	8	7	87.5%
Post larval stadium III	5	5	100%
Post larval stadium II	4	3	75%
Post larval stadium I	4	2	50%
Larva L_4, L_3 and L_2	7	5	71%
TOTAL	34	28	82.3%

During routine sampling the extracted animals were collected in crystallising dishes kept constantly moist by inverting a tube of water on moist filter paper. A few pieces of crushed moist filter paper were distributed in the dish and enabled the animals to hide in the crevices thus formed, thereby preventing damage due to water loss from their body surfaces. Collections from extractors, made every two days, were examined, weighed, and their head widths measured.

(ii) Distribution of L. crassipes and L. forficatus (treat this section with caution)

A comparison of the monthly mean population densities and the variance in the two species (Table 4) showed that in all instances the variance was nearly equal or less than the mean. This phenomenon has been shown by Taylor to obey a power law as represented by the following expression

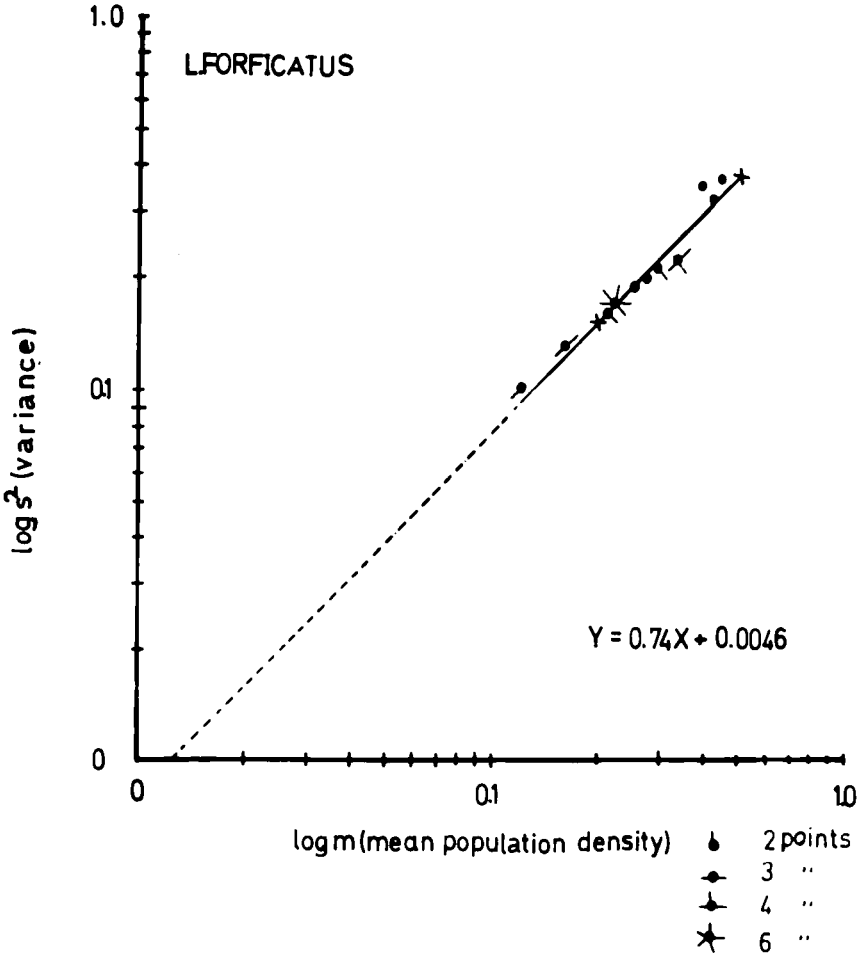
$$S^2 = am^b$$

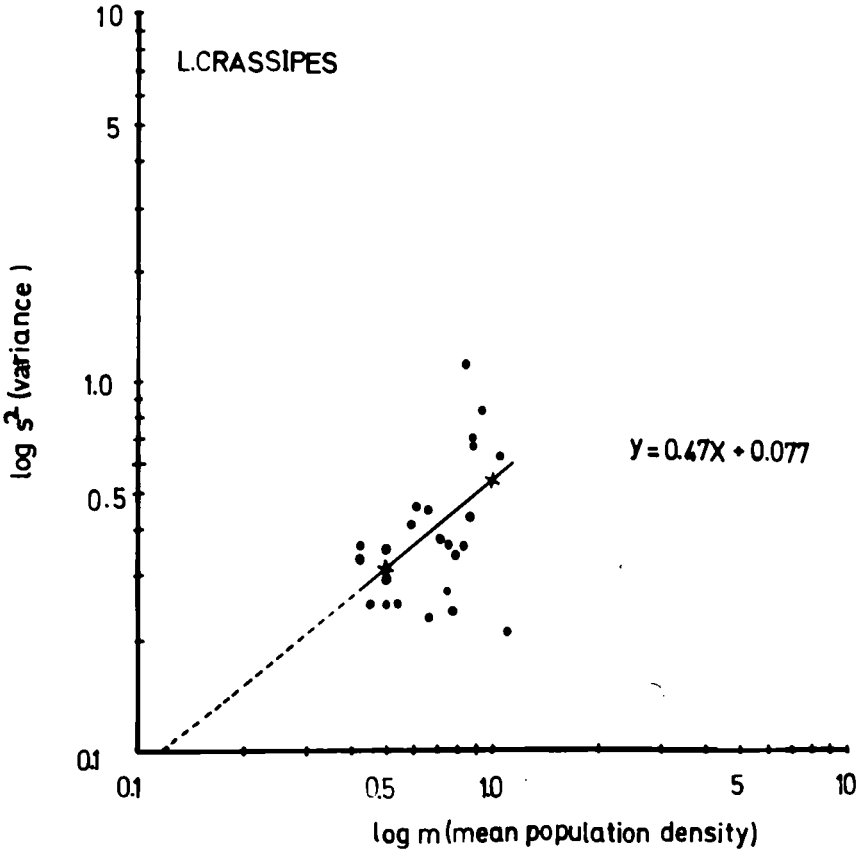
where S^2 = variance, m = mean density, a and b are the population parameters as intercept and regression coefficient respectively. A logarithmic plot of variance versus the mean population density for L. forficatus and L. crassipes (Fig.28 and 29) shows that the regression line in both instances is close to the origin, suggesting that the distribution of the population of the two species is random, and thus justified the use of stratified random sampling in the study.

The behaviour and biology of the centipedes support random distribution. The movement of the lithobiomorphs is rapid when compared with the slow moving millipedes. Eason (1964) has indicated

FIG. 28. LOGARITHMIC PLOT OF VARIANCE VERSUS THE MEAN POPULATION DENSITY OF L. FORFICATUS.

FIG. 29. LOGARITHMIC PLOT OF VARIANCE VERSUS THE MEAN POPULATION DENSITY OF L. CRASSIPES.


L.FORFICATUS
1.0
0.1
0
log s² (variance)
Y = 0.74X + 0.0046
0
0.1
1.0
log m (mean population density)
2 points
3 ''
4 ''
6 ''


L.CRASSIPES
10
5
1.0
0.5
0.1
log s² (variance)
Y = 0.47X + 0.077
0.1
0.5
1.0
5
10
log m (mean population density)

that in the absence of conclusive evidence on the production of eggs and the general behaviour of centipedes that the sexes do not contact in the propagation of the species. Copulation or mating in lithobiids have not been observed. The eggs are laid individually (Verhoeff 1925), and deposited haphazardly, egg laying taking place at intervals of one day or several days (Brocher 1930, and Roberts 1957). The varied diet of lithobiids (Lewis 1965 and Roberts 1957) may contribute to the random distribution of the predator. The absence of adverse climatic conditions during the period of sampling also militated against the possibility of aggregation (Roberts 1957).

Most authorities claim random distribution as rare in nature. The following investigations show that at least some animals are distributed at random within populations. The coccinellid Coccinella 7-punctata (L.) was randomly distributed as observed by Colquhoun (1942). Banks (1954) reported that another coccinellid Adalia 2-punctata (L.) was randomly distributed. Roberts (1957) found L. variegatus distributed randomly at Burley Wood. Auerbach (1951) uses the term "uniformly distributed" for species populations of some centipedes in prairie and woodland. The noteworthy feature, as with the present study, is that all are predators.

(iii) Population densities of L. crassipes and L. forficatus

Table 4 shows the estimated population density per unit area for L. crassipes and L. forficatus in both soil/litter and log/stump habitats. Figures 30, 31, 32 and 33, present the results

Table 4. Monthly population data of L. crassipes and L. forficatus.

	1	2	3	4	5	6	7
MONTH	APRIL	MAY	JUNE	JULY	AUGUST	SEPTEMBER	OCTOBER
Numbers/sq. meter litter L. crassipes	28.3±5.6	32.8±7.8	42.4±6.8	44.7±6.8	40.15±5.9	46.9±7.3	63.3±5.1
Numbers/sq. meter log L. crassipes	0.45±0.16	0.33±0.08	0.65±0.13	0.48±0.10	0.48±0.08	0.57±0.13	0.87±0.16
Total population	28.75 ± 3.45	33.13 ±4.64	43.05 ± 7.75	45.18 ± 5.42	40.63 ± 6.50	47.47 ± 8.07	64.17 ± 8.98
Numbers/sq. meter litter L. forficatus	9.4±3.8	11.9±4.5	16.4±5.1	14.1±5.1	11.9±4.5	18.7±5.4	23.75±6.2
Numbers/sq. meter log L. forficatus	0.26±0.10	0.12±0.04	0.26±0.07	0.24±0.07	0.18±0.05	0.20±0.06	0.32±0.11
Total population	9.66 ± 0.77	12.02 ± 1.08	16.66 ± 1.66	14.34 ± 2.15	12.08 ± 1.08	18.70 ± 1.87	24.07 ± 3.13

Table 4 (continued).

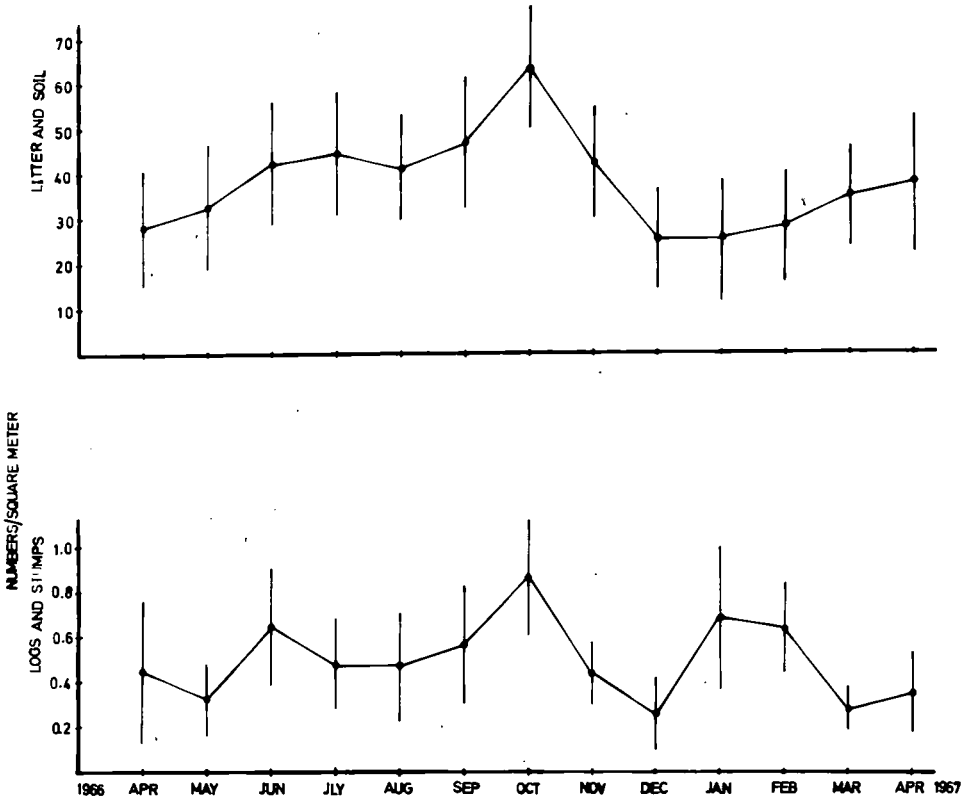
	8	9	10	11	12	13
MONTH	NOVEMBER	DECEMBER	JANUARY	FEBRUARY	MARCH	APRIL
Numbers/sq. meter litter L. crassipes	42.4±6.2	25.4±5.6	25.4±6.8	28.3±6.2	30.5±5.6	32.8±7.9
Numbers/sq. meter log L. crassipes	0.43±0.07	0.26±0.08	0.69±0.16	0.64±0.10	0.28±0.05	0.35±0.09
Total population	42.83 ± 5.14	25.66 ± 3.08	26.09 ± 3.65	17.05 ± 1.87	30.78 ± 3.38	33.15 ± 4.64
Numbers/sq. meter litter L. forficatus	16.4±5.1	9.4±3.9	7.4±3.3	7.4±3.3	9.4±3.9	11.9±4.5
Numbers/sq. meter log L. forficatus	0.14±0.05	0.13±0.05	0.24±0.09	0.18±0.07	0.10±0.03	0.22±0.07
Total population	16.54 ± 1.65	9.53 ± 0.76	7.64 ± 0.61	7.58 ± 0.61	9.50 ± 0.76	12.12 ± 1.09

FIG. 30. POPULATION DENSITY OF L. CRASSIPES IN LITTER AND SOIL.

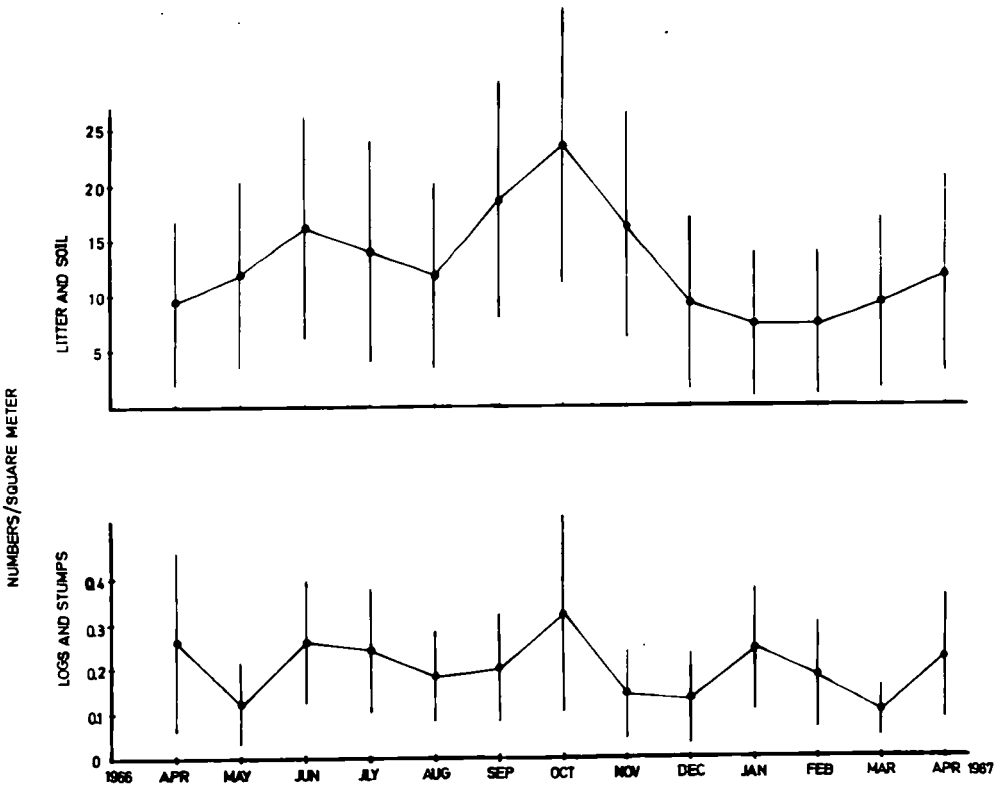
FIG. 31. POPULATION DENSITY OF L. CRASSIPES IN LOG AND STUMPS.

FIG. 32. POPULATION DENSITY OF L. FORFICATUS IN LITTER AND SOIL.

FIG. 33. POPULATION DENSITY OF L. FORFICATUS IN LOG AND STUMPS.



POPULATION OF LCRASSIPES



POPULATION OF LFORFICATUS

FIG. 34. TOTAL POPULATION DENSITY OF L. FORFICATUS.

FIG. 35. TOTAL POPULATION DENSITY OF L. CRASSIPES.

in graphical form. The vertical lines indicate 95% confidence limits of the mean. The extremely low populations in logs and stumps may be attributed to the very small wood volume per m^2 of the sample area. However, the fact that the population fluctuations in each of the microhabitats parallel one another suggests that massive seasonal unidirectional movements between microhabitats did not occur. The total population (Table 4 and Figs. 34 and 35) of L. crassipes reached probable peaks in July and October while in L. forficatus peaks were recorded in June and October. In both species it is probable that the two recorded peaks are real despite wide confidence limits.

This conclusion is supported by the peak production of ova during June and September in L. crassipes and in May and September for L. forficatus.

(iv) Ova production in L. crassipes and L. forficatus

Ova production was studied to show whether any correlation existed with the fluctuation of population of the two species. In nature L. crassipes and L. forficatus lay eggs individually and conceal them in soil and litter. This phenomenon made it impossible to determine the production of eggs in the field. Thus a number of female lithobiids of both species were dissected each month from collections made from the study area.

The ovary was carefully removed from dissected females of L. crassipes. The total number of ova in each ovary was counted and the diameter of individual ova measured. It was convenient

FIG 34

L.FORFICATUS

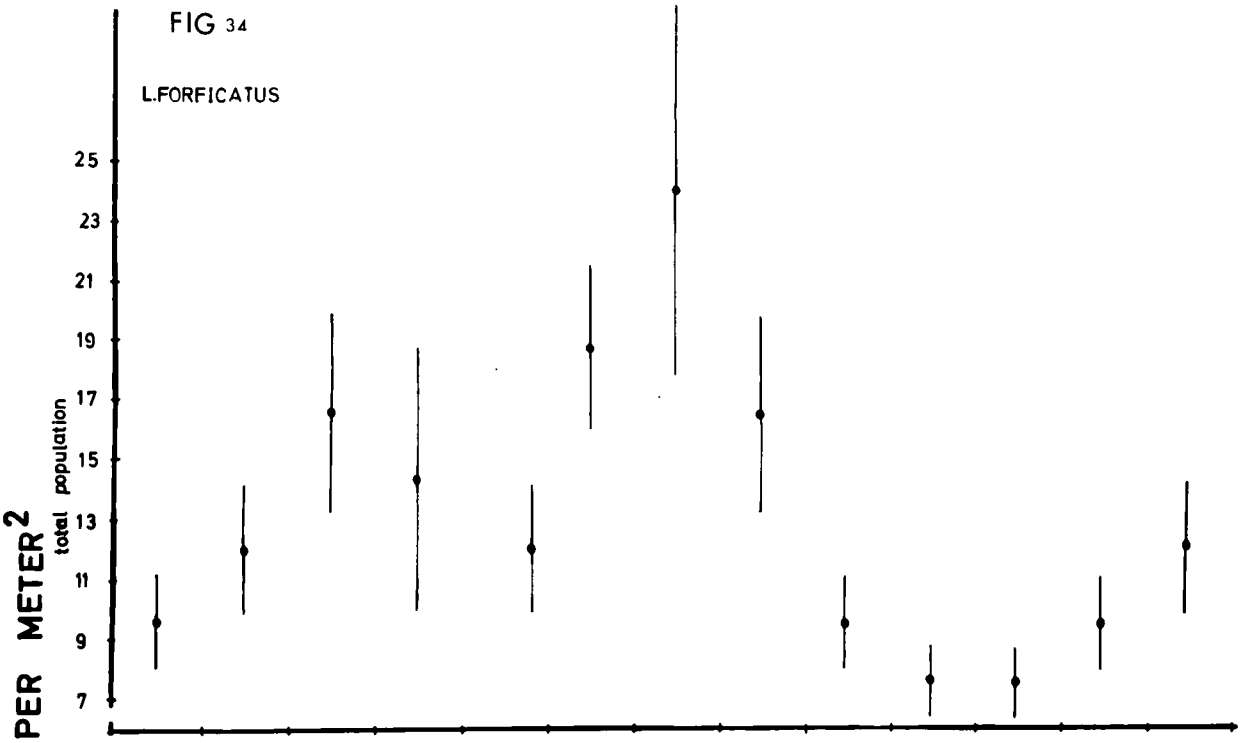
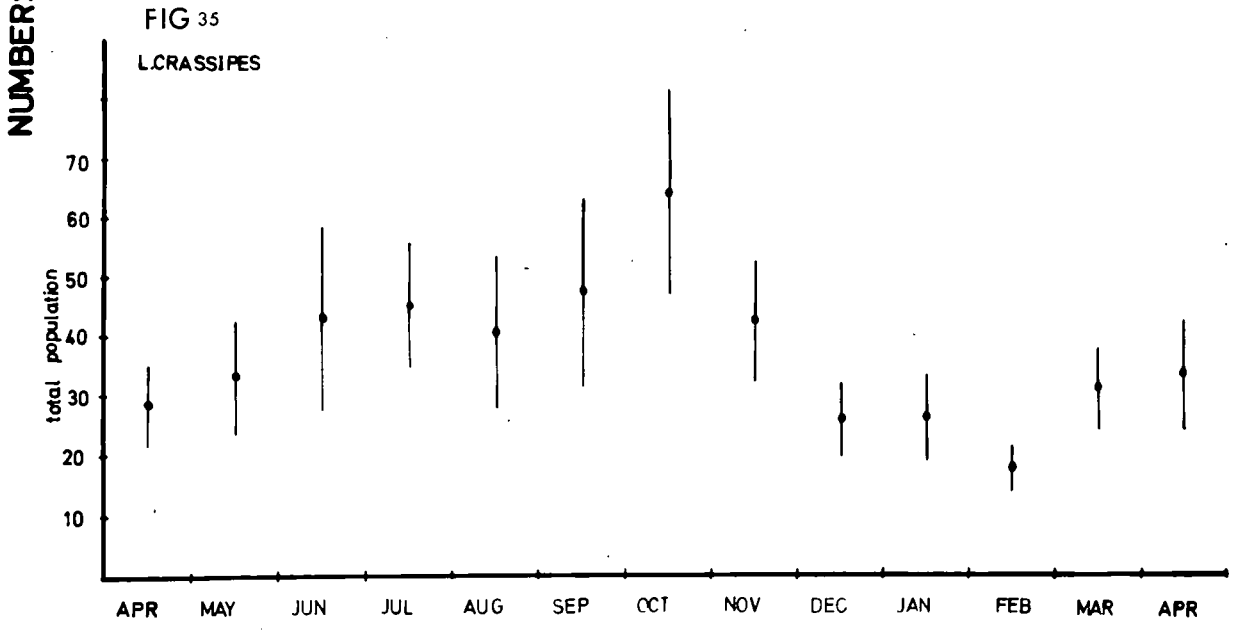


FIG 35

L.CRASSIPES



to grade the ova according to size; large (1.0 mm - 0.60 mm), medium (0.61 mm - 0.30 mm) and small (less than 0.30 mm). The groups large and medium were collectively termed developing ova. The mean number of developing ova per female varied with season; Table 5 and Fig.36 show that in L. crassipes these developing ova increased in number from May to June, decreased in July and August, with an increase in September. A further decrease is apparent from October to January with an increase in March and April of the following year. The standard errors in Fig.36 indicate 95% confidence limits.

Large numbers of ova were found in the ovaries of L. forficatus. It was not practicable to measure all the ova. Thus the live weight of the entire ovary was determined and the largest ova (within a diameter 1.21 mm to 0.69 mm) were measured. The entire ovary was dissected, placed on a filter paper to remove excess moisture and weighed immediately on a microbalance. A correlation between developing egg number and ovary weight can be seen in Table 6. Fig.37 and Table 6 show that the mean weight of the ovary was relatively high in May, gradually decreased in July to gain a significant increase in September. This was followed by a gradual decrease in ova production till February of the following year when a small increase occurred in March and April. Lewis (1965), working with L. forficatus, also showed increased ova production in (a) early summer and (b) autumn. The pattern of ova production was similar in both species of lithobiids. The standard errors in Fig.37 indicate

L. crassipes

Table 5. Mean number of developing ova per female per month.

MONTH	MEAN NUMBER OF DEVELOPING OVA PER FEMALE	STANDARD ERROR OF MEAN
MAY	3.7	± 0.66
JUNE	7.0	± 0.65
JULY	4.1	± 0.74
AUGUST	4.6	± 1.01
SEPTEMBER	10.3	± 0.51
OCTOBER	5.7	± 0.72
NOVEMBER	3.06	± 0.36
DECEMBER	1.80	± 0.50
JANUARY	1.08	± 0.22
FEBRUARY	1.71	± 0.25
MARCH	2.76	± 0.42
APRIL	4.83	± 0.68

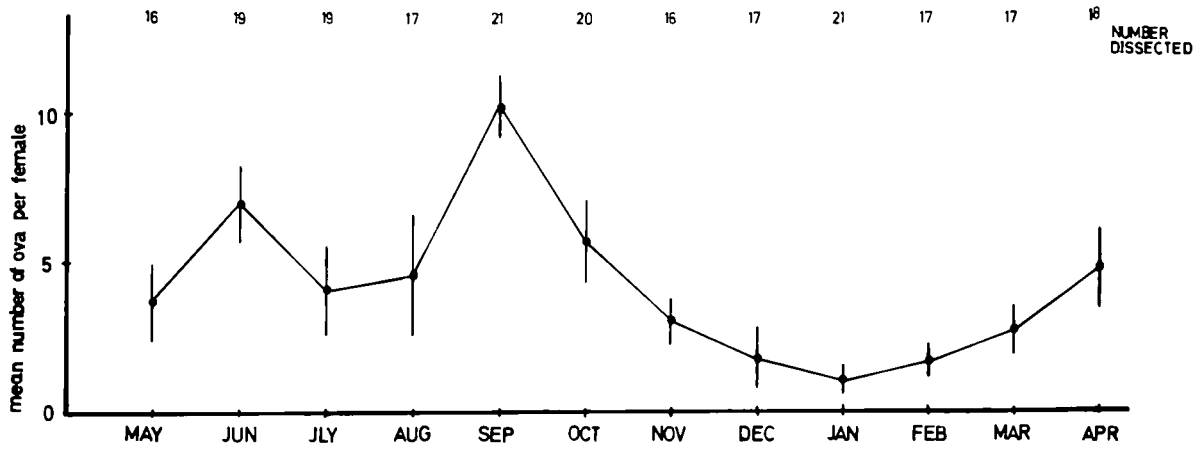
L. forficatus

Table 6. Mean wt. of ovary per female per month.

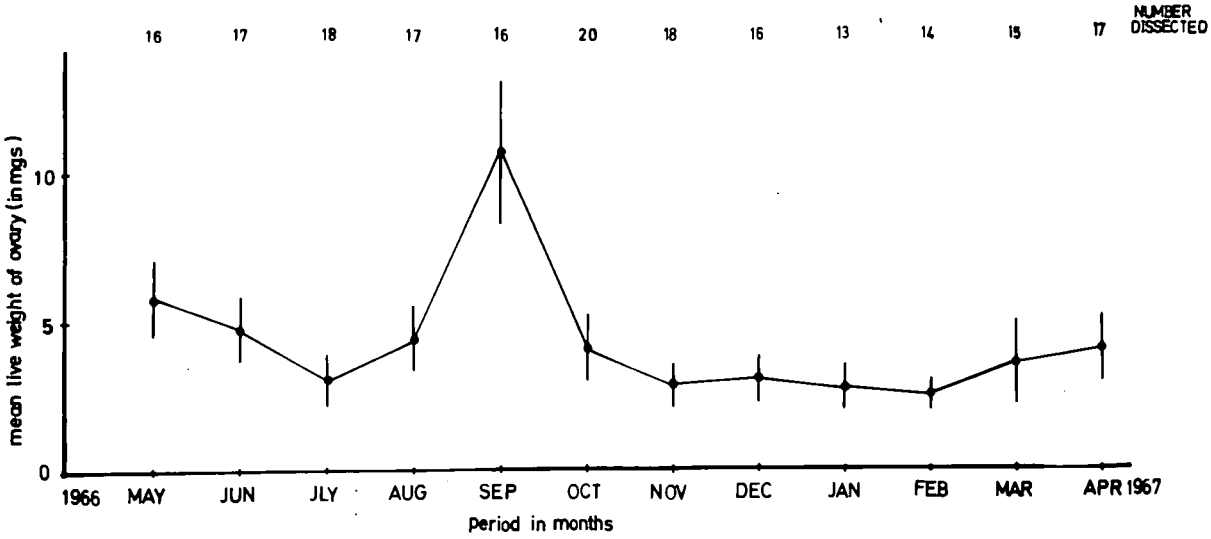
MONTH	MEAN NO. OF LARGE EGGS (1.21mm to 0.69mm)	MEAN WEIGHT OF OVARY PER FEMALE	STANDARD ERROR OF MEAN
MAY	3.8	5.79	± 0.64
JUNE	3.5	4.76	± 0.54
JULY	1.5	3.07	± 0.43
AUGUST	4.2	4.41	± 0.55
SEPTEMBER	13	10.76	± 1.27
OCTOBER	2.5	4.09	± 0.54
NOVEMBER	1.6	2.86	± 0.39
DECEMBER	1.4	3.05	± 0.39
JANUARY	1.3	2.78	± 0.35
FEBRUARY	1.2	2.57	± 0.27
MARCH	2.2	3.56	± 0.52
APRIL	3.5	4.06	± 0.56

FIG. 36. OVA PRODUCTION PER FEMALE OF L. CRASSIPES.

FIG. 37. OVA PRODUCTION PER FEMALE OF L. FORFICATUS.



L.CRASSIPES



L.FORFICATUS

95% confidence limits.

If it is assumed that the decreased number of ova in the ovary is coincident with the discharge of non diapause eggs; then, given suitable conditions, young should appear in early summer or mid-autumn. Eggs laid in late autumn probably over-winter to hatch in the spring of the following year. The hatching of eggs is facilitated by climatic conditions such as temperature and rainfall. The mean field temperature was found to vary between 8°C and 13°C from April to October. As most of the larvae occurred during this period in the field it was assumed that the above range in temperature was suitable for the development of the young. Rainfall was heavy in April and August (Table 1) and preceded the appearance of population peaks of both species. A similar situation was noted by Auerbach (1951) in Peacock prairie and Carle Woods, U.S.A. The population density peaks of L. crassipes and L. forficatus are just out of phase with, but follow, those peaks denoting increased ova production. Thus indicating that the two rises in population density were caused by the addition of young to the existing population. Nevertheless it must be noted that developing ova occurred throughout the year in both species and it is probable that some young are produced whenever conditions are suitable.

Fluctuations of centipede populations in prairie and woodland have been observed by Auerbach (1951); in prairie the peak population periods were May and August whilst in woodland a peak in population density was recorded only for August. These fluctuations

were accompanied by increased rainfall, rise in temperature and probably high relative humidity. The experiments conducted by Auerbach in the laboratory showed that centipedes could not tolerate low relative humidity (35% at 23°C); however in field situations the dense undergrowth etc. and the canopy help to retain moisture in woodland microhabitats and any conclusions on susceptibility of centipedes to humidity must be based on relative humidity studies in the microhabitats themselves. As this aspect of microclimate could not be studied due to unavailability of suitable apparatus, it was assumed that precipitation and temperature were important factors besides predators in affecting the fluctuations of the centipede populations in the sample area.

CHAPTER IV

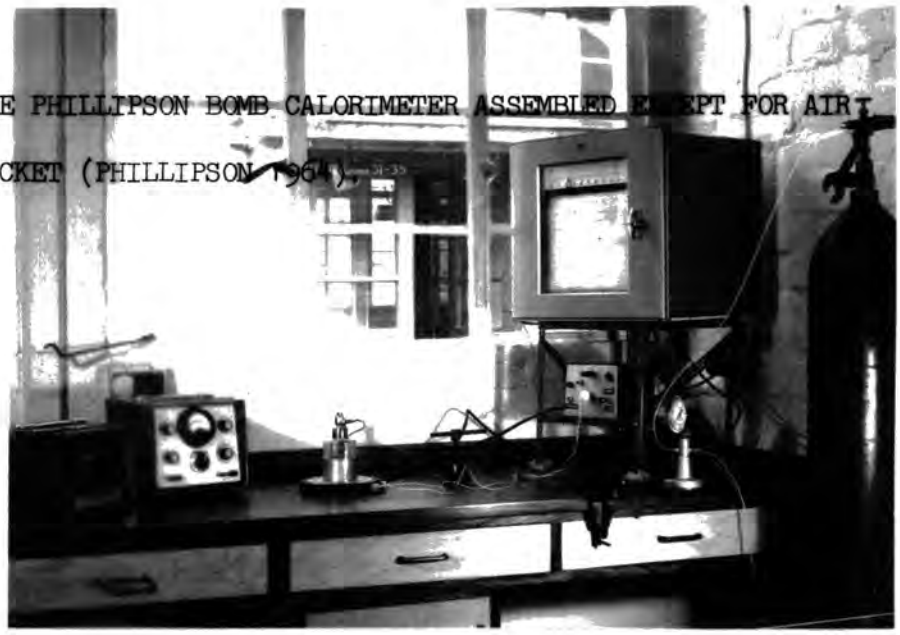
The measurement of calorific content of lithobiid material (L. crassipes and L. forficatus)

(i) Introduction

With the growing interest in ecological energetics many workers have made data of calorific content available. Gere (1956) and Golley (1960) investigated calorific values of the caterpillar Hyphantria cunea and Microtus tissue respectively. Wiegert (1964) listed values for the spittle bug Philaenus spumarius and in 1965 for various orthoptera; Saito (1965) for the isopod Ligidium japonicum and in 1967 for the diplopod Japonaria laminata amigera; Golley and Gentry (1964) for the ant Pogonomyrmex badius and Watson (1966) for the isopods Oniscus asellus and Porcellio scaber. From these studies it was apparent that most calorific values of animal material ranged between 4.0 Kcals/gm and 7.0 Kcals/gm with the exception of Uca species and other crabs (Connell unpublished - Golley 1961) where an average calorific value of 2248 g.cal/g.dry weight was calculated. As an aid to ecological research Golley (1961) compiled the average calorific data for certain plant and animal material. A more recent compilation of calorific values is that of Cummins (1967).

(ii) Method

Phillipson (1964) combusted various biological materials using a miniature bomb calorimeter which was capable of



THE PHILLIPSON BOMB CALORIMETER ASSEMBLED EXCEPT FOR AIR JACKET (PHILLIPSON 1964).

Table 7. Calibration of Miniature Bomb Calorimeter (Phillipson 1964) with Benzoic Acid (6.324 Kcal/gm.)

Sample wt. in mgs.	Ash content	Calorific value (in cals)	Potentiametric reading (mv)	Mv/100 cal.
7.0	nil	45.5328	0.329	0.7225
9.65	-	61.0266	0.450	0.7374
17.41	-	110.1008	0.838	0.7611
14.20	-	89.8008	0.662	0.7372
16.44	-	103.9665	0.770	0.7406
12.02	-	76.0145	0.554	0.7288
8.18	-	51.7303	0.381	0.7364
6.14	-	38.8294	0.286	0.7365
11.44	-	72.3465	0.532	0.7353
6.47	-	40.9163	0.300	0.7332

Mean reading per 100 cal. = 0.73690 $\pm$ S.D. 0.00943
Coefficient of variation = 1.28%

determining calorific values of samples ranging from about 5 mgs to 100 mgs dry weight. The efficiency of the Phillipson bomb calorimeter is well known and its ability to combust very small samples avoids the use of filter substances like benzoic acid (Richman 1958) or millipore membrane as used by Comita and Schindler (1963). The apparatus used in the determination of calorific values of lithobiid material was the Phillipson bomb calorimeter.

The calorific content of L. crassipes and L. forficatus was determined for all stadia of both species. The specimens were collected from the sample area and study area during the year 1966-1967. Most of the calorific determinations were obtained for separate seasons of the year by grouping monthly collections as shown in tables 8 and 9. However, calorific values for post larval stadium I of both species were from annual collections and due to the limited material available for larval stadia (2, 3 and 4) the average annual calorific value for this group was obtained. This averaging appeared to be justified as no real difference in calorific value was shown within the post larval stadium. Lithobiid eggs could not be collected in the field for calorific value determinations as they are laid individually and could not be distinguished from litter and soil. No attempt was made to burn moulted exoskeletons as both species were found to feed on them after ecdysis.

The centipedes collected were vacuum dried at 60°C for 48 hours, finely ground to a powder with an agate pestle and

Table 8. Calorific values of L. crassipes material.

Material L. crassipes	No. of determinations	% ash content (mean)	Kcal/ash free gm	Standard deviation	Coefficient of variation	Period
Adult ♀s	10	3.46	5.750	0.059	1.02	MAR/APR/MAY
Adult ♀s	8	3.58	5.861	0.071	1.25	JUN/JLY/AUG
Adult ♀s	8	3.14	5.831	0.057	0.98	SEP/OCT/NOV
Adult ♀s	8	3.30	5.713	0.056	0.97	DEC/JAN/FEB
Adult ♂s	10	3.68	5.712	0.066	1.16	MAR/APR/MAY
Adult ♂s	10	3.72	5.761	0.086	1.50	JUN/JLY/AUG
Adult ♂s	9	3.47	5.839	0.101	1.74	SEP/OCT/NOV
Adult ♂s	8	2.68	5.645	0.069	1.23	DEC/JAN/FEB
PL IV	4	3.13	5.708	0.092	1.62	MAR/APR/MAY
PL IV	4	3.73	5.789	0.087	1.51	JUN/JLY/AUG
PL IV	4	3.31	5.736	0.126	2.20	SEP/OCT/NOV
PL IV	4	3.11	5.690	0.207	3.64	DEC/JAN/FEB
PL III	4	3.39	5.609	0.065	1.17	MAR/APR/MAY

Table 8 (continued).

Material L. crassipes	No. of determinations	% ash content (mean)	Kcal/ash free gm	Standard deviation	Coefficient of variation	Period
PL III	4	3.54	5.665	0.201	3.54	JUN/JLY/AUG
PL III	4	3.23	5.665	0.102	1.80	SEP/OCT/NOV
PL III	4	3.65	5.588	0.052	0.93	DEC/JAN/FEB
PL II	4	3.21	5.402	0.093	0.86	MAR/APR/MAY
PL II	4	3.12	5.478	0.037	0.68	JUN/JLY/AUG
PL II	4	3.64	5.450	0.036	0.66	SEP/OCT/NOV
PL II	4	3.04	5.355	0.038	0.72	DEC/JAN/FEB
PL I	4	3.21	5.375	0.048	0.89	annual
larva $l_4 + l_3 + l_2$	4	3.60	5.301	0.052	0.96	annual

Table 9. Calorific values of L. forficatus material.

Material L. forficatus	No. of determinations	% ash content (mean)	Kcal/ash free gm	Standard deviation	Coefficient of variation	Period
Adult ♀s	9	3.37	5.760	0.064	1.11	DEC/JAN/FEB
Adult ♀s	9	3.55	5.827	0.106	1.81	MAR/APR/MAY
Adult ♀s	9	3.46	5.943	0.134	2.26	JUN/JLY/AUG
Adult ♀s	9	3.03	5.854	0.134	2.29	SEP/OCT/NOV
Adult ♂s	9	3.29	5.667	0.099	1.74	DEC/JAN/FEB
Adult ♂s	9	3.76	5.744	0.073	1.26	MAR/APR/MAY
Adult ♂s	9	3.26	5.846	0.098	1.68	JUN/JLY/AUG
Adult ♂s	9	2.94	5.870	0.236	4.03	SEP/OCT/NOV
PL IV	4	3.43	5.651	0.095	1.67	DEC/JAN/FEB
PL IV	4	3.32	5.694	0.078	1.31	MAR/APR/MAY
PL IV	4	3.50	5.789	0.101	1.75	JUN/JLY/AUG
PL IV	4	3.22	5.753	0.088	1.54	SEP/OCT/NOV

Table 9 (continued)

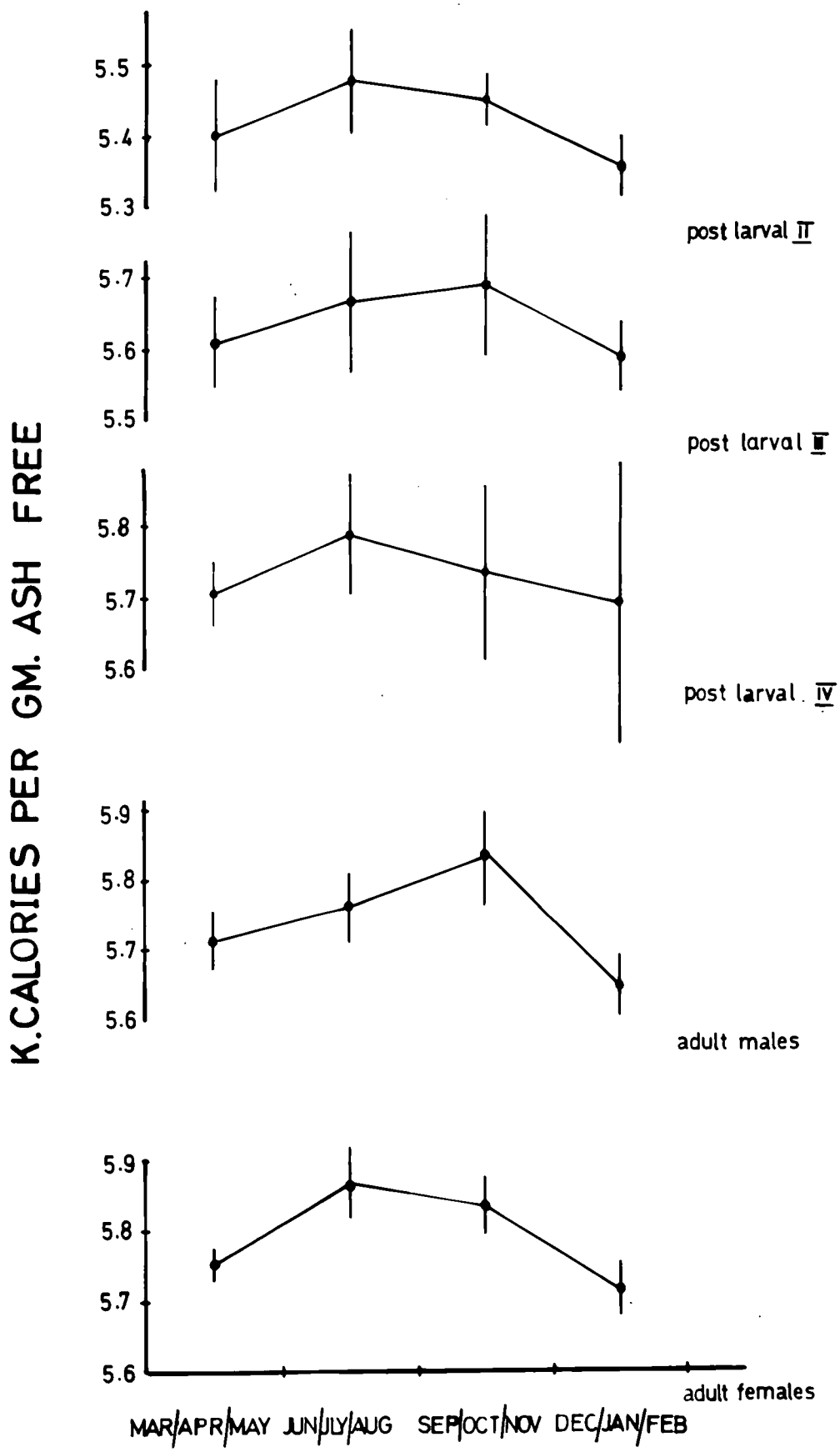
Material L. forficatus	No. of determinations	% ash content (mean)	Kcal/ash free gm	Standard deviation	Coefficient of variation	Period
PL III	4	2.96	5.658	0.079	1.40	DEC/JAN/FEB
PL III	5	3.77	5.671	0.092	1.62	MAR/APR/MAY
PL III	5	3.31	5.755	0.033	0.57	JUN/JLY/AUG
PL III	4	2.86	5.691	0.099	1.76	SEP/OCT/NOV
PL II	4	3.38	5.588	0.063	2.03	DEC/JAN/FEB
PL II	4	3.45	5.627	0.057	1.43	MAR/APR/MAY
PL II	4	3.18	5.696	0.082	1.52	JUN/JLY/AUG
PL II	4	3.38	5.636	0.086	1.13	SEP/OCT/NOV
PL I	4	3.26	5.496	0.096	1.76	annual
larva $l_4 + l_3 + l_2$	4	3.26	5.327	0.082	1.55	annual

mortar, pelleted in a pellet press and stored in a dessicator containing silica gel. The operation of the microbomb calorimeter was described by Phillipson (1964). It was essential to calibrate the bomb before any lithobiid material was burnt. Benzoic acid with a purity of 99.97% and calorific value of 6324 cals per gm was used for this calibration. The pellets ranged from 6.0 mgs to 17.0 mgs, which was approximately the same weight range as the lithobiid pellets used in the bomb calorimeter. The values of ten consecutive benzoic acid combustions (Table 7) gave a mean value of 0.7369 ± 0.00943 mv/100 calories with a coefficient of variation of 1.28%. This calibration figure was used to calculate the calorific values of lithobiid material burned in the bomb calorimeter. The mean calibration value was checked periodically and found to be constant.

The calorific value per unit weight of L. crassipes varied with season. Figure 38 shows that a significant difference in calorific value per unit weight does exist with season in both adult males and females (the vertical lines indicate 95% confidence limits). In the adult females the highest value recorded was in JUN/JLY/AUG and the lowest in DEC/JAN/FEB (Fig.38). The adult males showed an increase in calorific value in SEPT/OCT/NOV and a decrease in DEC/JAN/FEB. However, the annual mean calorific value per unit weight of males and females was approximately the same. In the post larval stadia (II, III and IV) no significant differences in calorific value per unit weight with season were observed either within or between these stadia. As

FIG. 38. CALORIFIC VALUE PER UNIT WEIGHT OF L. CRASSIPES (ADULTS AND DEVELOPING STADIA) WITH SEASON.

L.CRASSIPES


K.CALORIES PER GM. ASH FREE
5.5
5.4
5.3
post larval II
5.7
5.6
5.5
post larval III
5.8
5.7
5.6
post larval IV
5.9
5.8
5.7
5.6
adult males
5.9
5.8
5.7
5.6
adult females
MAR/APR/MAY JUN/JLY/AUG SEP/OCT/NOV DEC/JAN/FEB

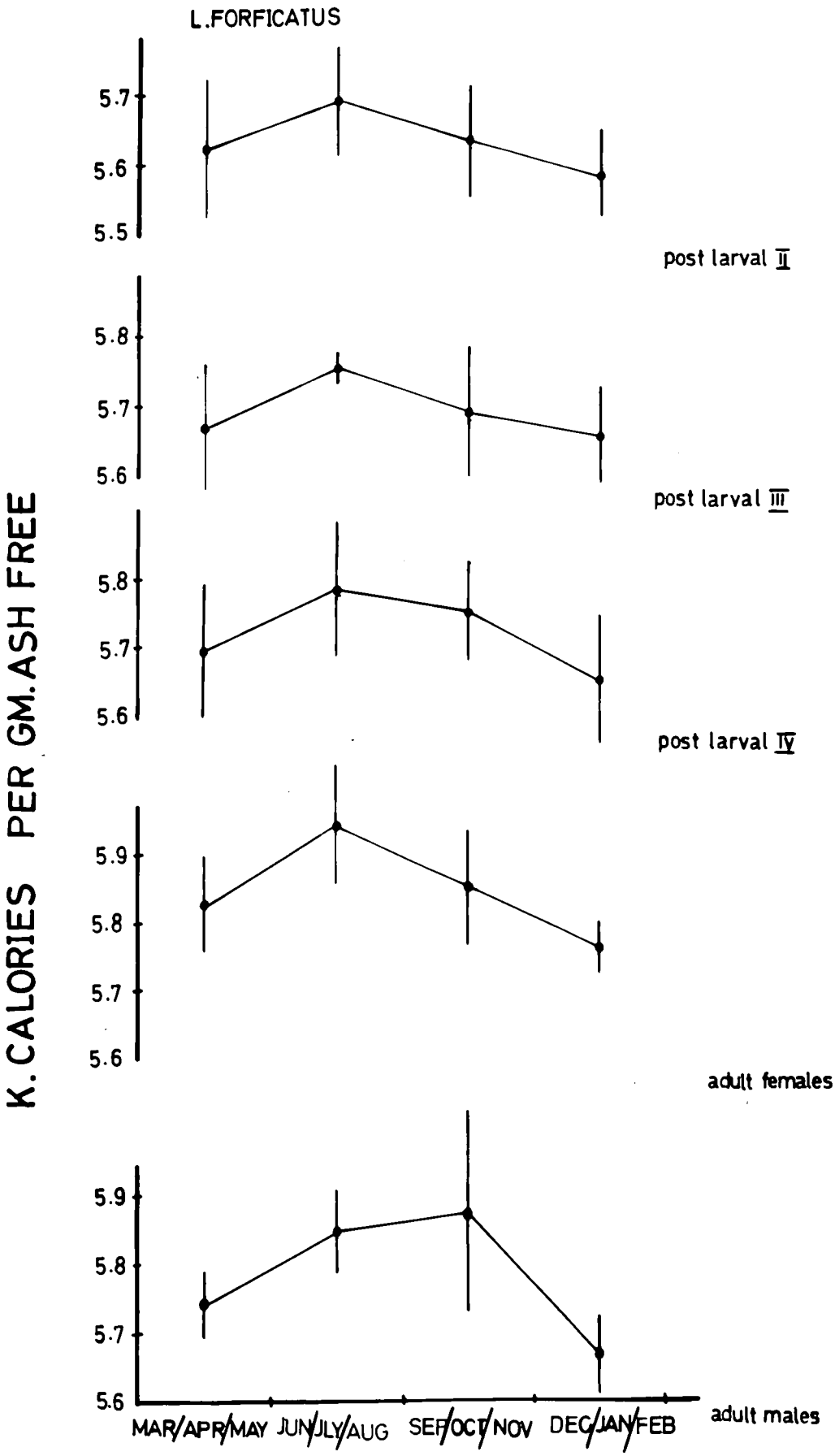
indicated a single value was determined for all larval stadia. Consideration of mean annual calorific values for unit weight for each stadium shows an increase from beginning to end of development.

A similar calorific change was observed with L. forficatus material, however the adult females showed a higher annual mean calorific value per unit weight than males. A recorded minimum for females occurred in JUN/JLY/AUG, and for males in SEP/OCT/NOV. The vertical lines in Figure 39 indicate 95% confidence limits. Though differences in calorific value per unit weight were observed with season in post larval stadia (II, III and IV) these were not significantly different. As in L. crassipes the annual mean calorific value per unit weight increased during development.

(iii) Discussion

In both species the calorific value per unit weight increased with gradual development of larval instars but the percentage ash content remained approximately the same. The only explanation for such calorific differences must be either the production of new tissues with calorific values higher than the earlier tissues; or the storage of materials of high calorific value per unit weight. A similar explanation must hold for seasonal changes within stadia. The seasonal increase in energy value per unit weight in non-adult lithobiids may be associated with overwintering requirements. In adult females the change in calorific content with season is probably linked with the addition of the production of ova

FIG. 39. CALORIFIC VALUE PER UNIT WEIGHT OF L. FORFICATUS (ADULTS AND DEVELOPING STADIA) WITH SEASON.


L.FORFICATUS
K.CALORIES PER GM.ASH FREE
5.7
5.6
5.5
post larval II
5.8
5.7
5.6
post larval III
5.8
5.7
5.6
post larval IV
5.9
5.8
5.7
5.6
adult females
5.9
5.8
5.7
5.6
adult males
MAR/APR/MAY JUN/JLY/AUG SEP/OCT/NOV DEC/JAN/FEB

(Chapter III) while in males it may be coincident with the development of sperm. Lewis (1965) showed that the percentage of sperms in L. forficatus reached a maximum during SEPT/OCT/NOV which is concurrent with the calorific value of the males. It is difficult to correlate differences in calorific content with any specific aspect of the life history of lithobiids, but as the major function of adults during these recorded changes is reproduction the development of reproductive bodies could contribute to this difference. Wiegert (1965) observed "intraspecific variation" in calorific value of Philaenus spumarius adults and larvae with season. The calorific content of both adult females and males of P. spumarius showed similar changes from June to October. In the first instar of P. spumarius the calorific content was the lowest and gradually increased rapidly through nymphal life. A close parallel to the lithobiid situation.

The calorific content per unit weight of lithobiid material was used in conjunction with population data of L. crassipes and L. forficatus to determine the biomass energy content of both species.

CHAPTER V

Population biomass of L. crassipes and L. forficatus

Engelmann (1966) stated that live weight varies with the water content of the animals and hence the need for dry weight determinations for the calculation of biomass in terms of calories per m^2. Hence to evaluate biomass for use in the present population energetics study it was essential to determine a wet weight/dry weight relationship of various lithobiid materials. Amongst others Saito (1965)and Sikora, Hubbel and Paris (1965) used wet weight/dry weight relationships for the isopods L. japonicum and A. vulgare respectively. An invertebrate predator known to illustrate a linear wet weight/dry weight relationship is the polyphagous spider Lycosa pseudoannulata studied by Itô (1964).

The present study deals with the calculation of biomass in cals/m^2 of two invertebrate predators, L. crassipes and L. forficatus using the population data, the regression analysis of live weight/dry weight for all stadia plus the known calorific values in terms of unit weight for each stadium. Collections for the live weight/dry weight determinations were made monthly during a period of two years (1966-1967) from the study area.

(i) Live weight/dry weight relationships of L. crassipes and L. forficatus

All stadia connected with the development of L. forficatus were grouped on the basis of development of limbs and external genitalia. Thus larva 2, 3, 4 and post larval stadium I (Chapter II) were designated as "juveniles" and post larval stadia II, III and IV were termed "juniors".

The mature males and females were grouped as adults. Thus determination of live weight/dry weight regressions were based on these three categories (Fig.40-42). Regression analysis revealed the following equations:-

Juveniles → $y = 3.929x + 0.019$ Fig.40

Juniors → $y = 3.914x + 1.639$ Fig.41

Adults → $y = 3.337x + 13.182$ Fig.42

To avoid lengthy calculations in the conversion of population numbers to population biomass the mean live weight of each category (juveniles, juniors and adults) and the appropriate mean dry weight of each was calculated using the above equations for eventual use with population data expressed in terms of the three size categories. Calorific values obtained for each season and multiplied by dry weight gave the biomass (Table 11) of each category for the season concerned.

The same procedure was adopted for the calculation of biomass of L. crassipes (Table 12). As with L. forficatus mean live weight/dry weight relationships were calculated for each of the three categories: juveniles, juniors and adults. The regressions (Fig.43-44) calculated for live weight versus dry weight were:-

Juveniles → $y = 3.158x + 0.10$ Fig.43

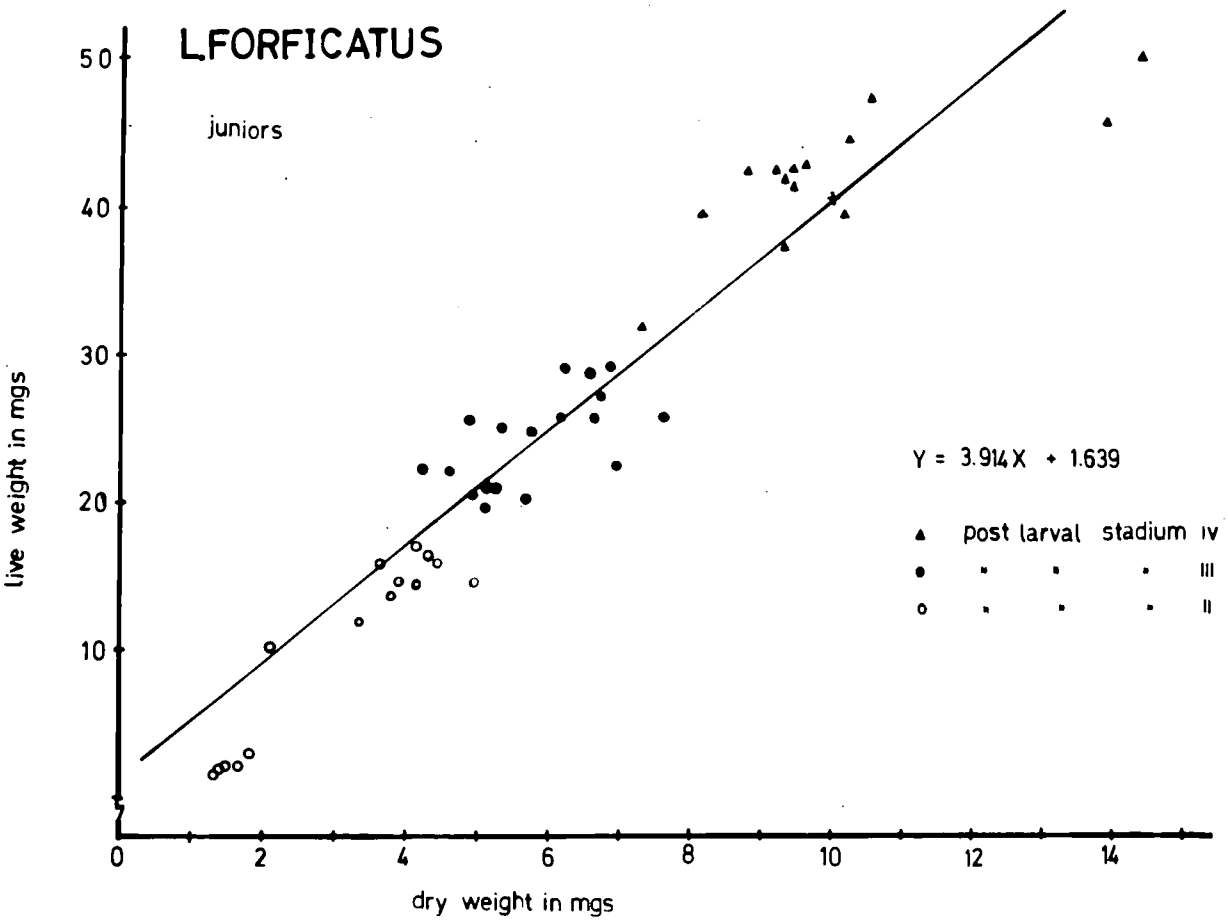
Juniors → $y = 3.335x + 0.406$ Fig.44

Adults → $y = 3.170x + 1.19$ Fig.45

It is evident from these regression equations for L. crassipes and L. forficatus that the water content of each stage

FIG. 41. REGRESSION OF DRY WEIGHT VERSUS LIVE WEIGHT OF L. FORFICATUS JUNIORS.

FIG. 40. REGRESSION OF DRY WEIGHT VERSUS LIVE WEIGHT OF L. FORFICATUS JUVENILES.


L.FORFICATUS
juniors
live weight in mgs
dry weight in mgs
Y = 3.914X + 1.639
post larval stadium IV
III
II

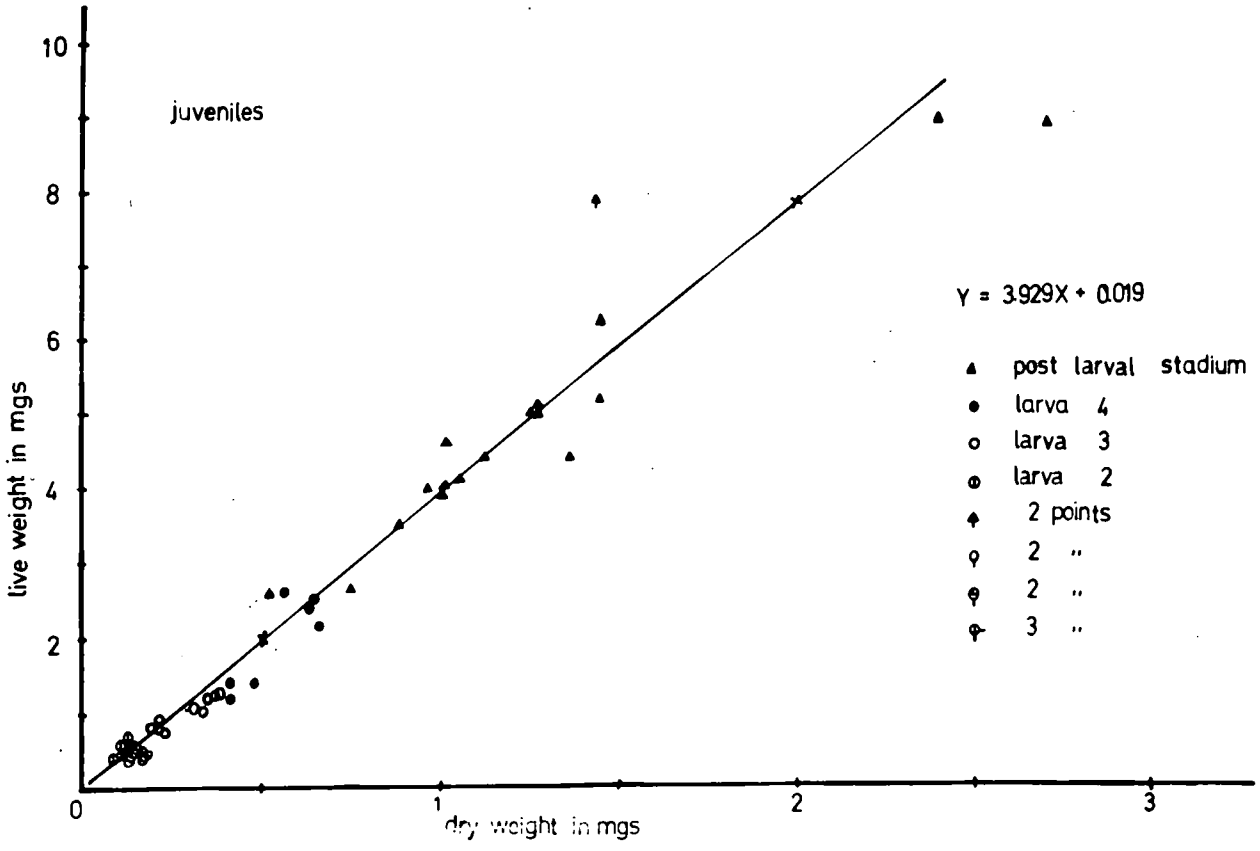
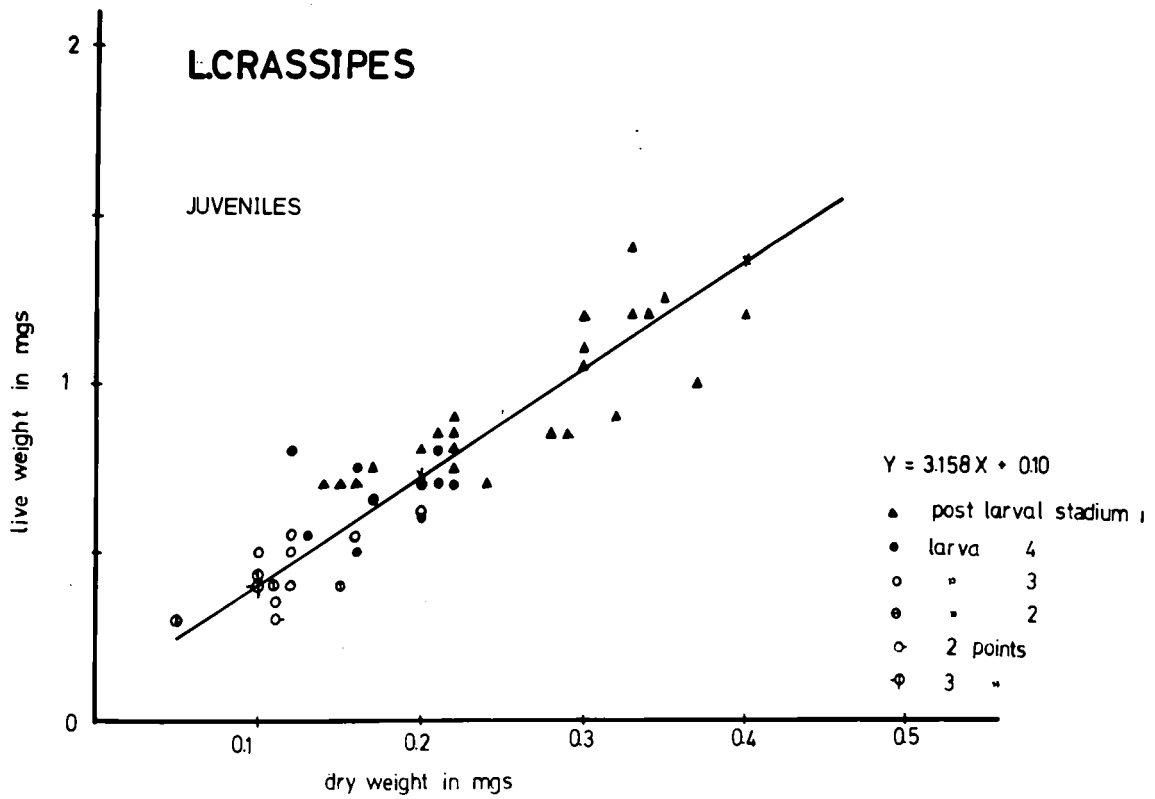

juveniles
live weight in mgs
dry weight in mgs
Y = 3.929X + 0.019
post larval stadium
larva 4
larva 3
larva 2
2 points
2 ,,
2 ,,
3 ,,

FIG. 42. REGRESSION OF DRY WEIGHT VERSUS LIVE WEIGHT OF

L. FORFICATUS ADULTS.

FIG. 43. REGRESSION OF DRY WEIGHT VERSUS LIVE WEIGHT OF

L. CRASSIPES JUNIORS.


L.CRASSIPES
JUVENILES
live weight in mgs
dry weight in mgs
0
1
2
0.1
0.2
0.3
0.4
0.5
Y = 3.158 X + 0.10
post larval stadium
larva 4
" 3
" 2
2 points
3 "

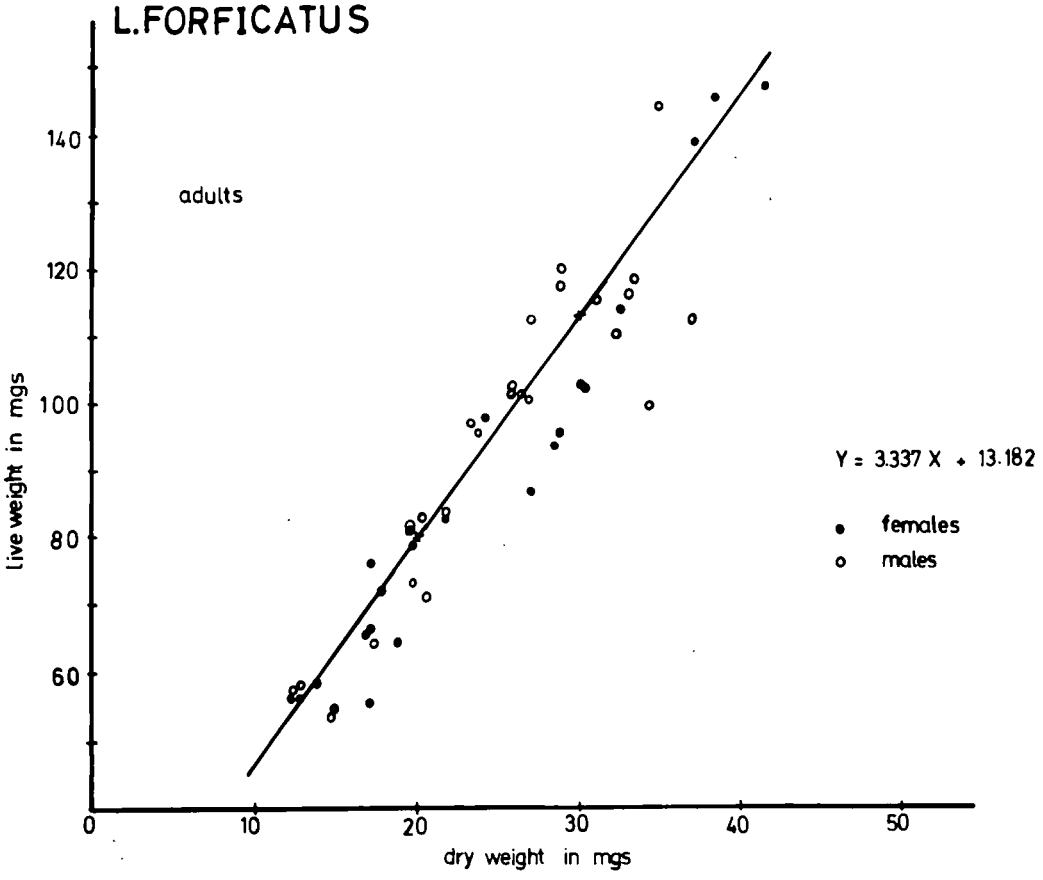
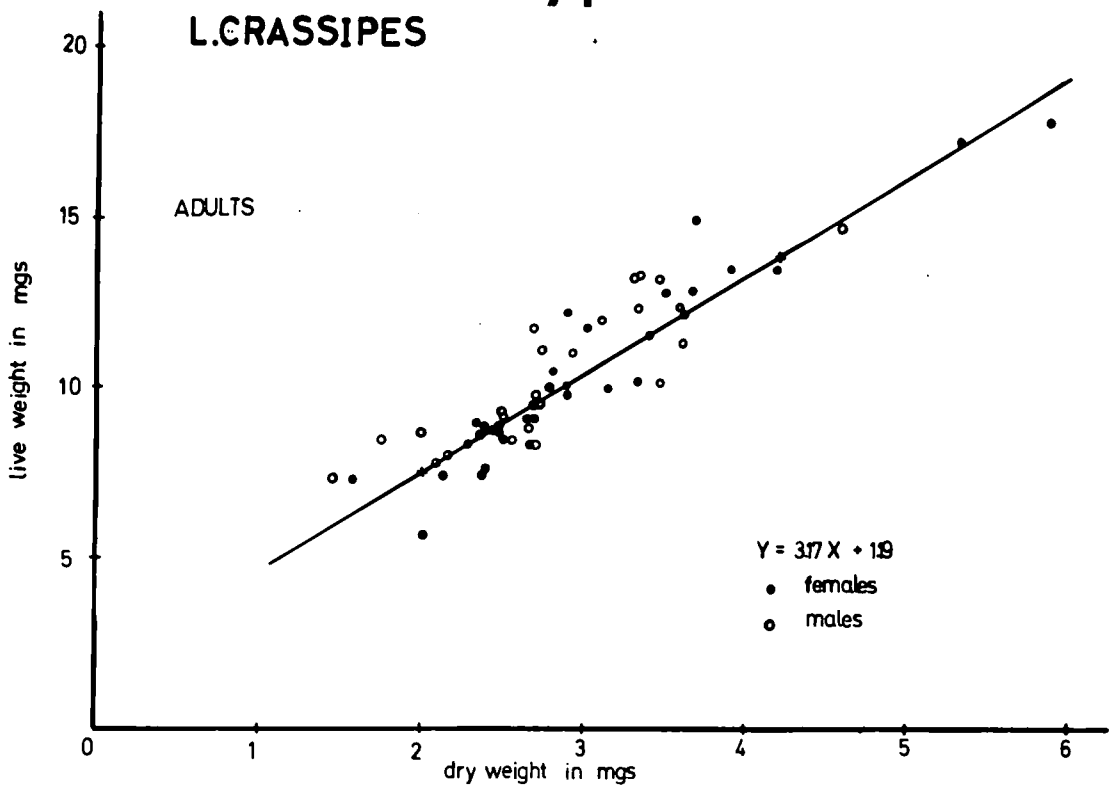
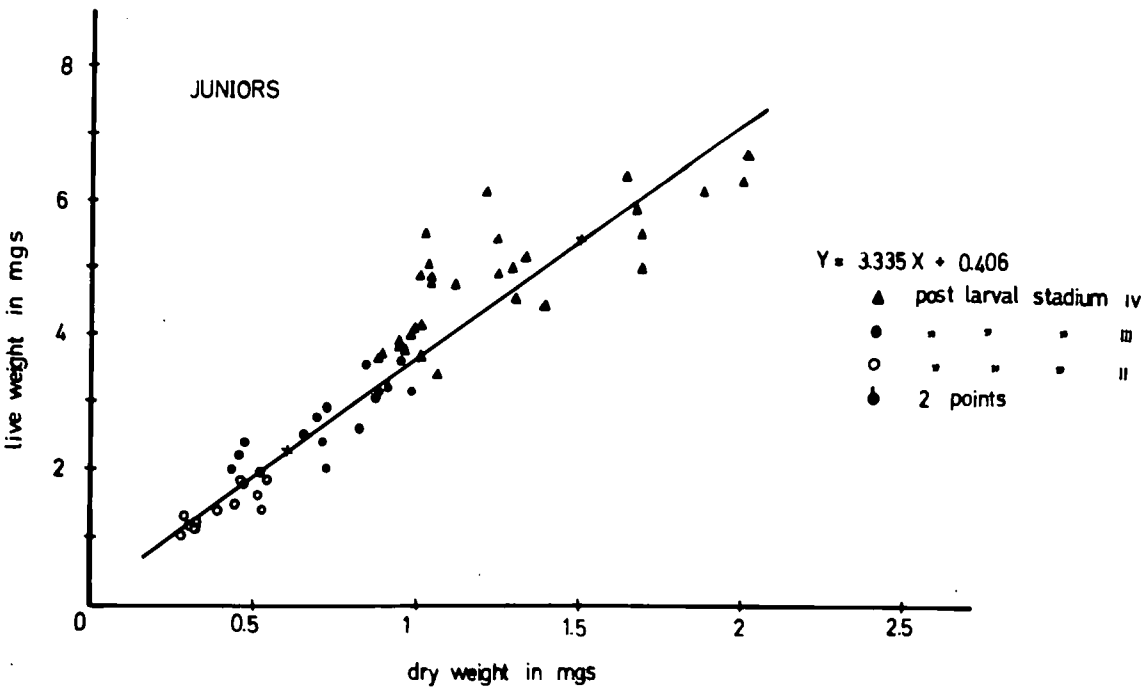

L.FORFICATUS
adults
Live weight in mgs
dry weight in mgs
60
80
100
120
140
0
10
20
30
40
50
Y = 3.337 X + 13.182
females
males

FIG. 45. REGRESSION OF DRY WEIGHT VERSUS LIVE WEIGHT OF L. CRASSIPES ADULTS.

FIG. 44. REGRESSION OF DRY WEIGHT VERSUS LIVE WEIGHT OF L. FORFICATUS JUNIORS.


L.CRASSIPES
ADULTS
live weight in mgs
dry weight in mgs
Y = 3.17 X + 1.9
females
males
0
1
2
3
4
5
6
5
10
15
20


JUNIORS
live weight in mgs
dry weight in mgs
Y = 3.335 X + 0.406
post larval stadium IV
III
II
2 points
0
0.5
1
1.5
2
2.5
2
4
6
8

varies. Thus indicating the need to determine wet weight/dry weight relationship for each of the categories as stressed by Engelmann (1966) for the calculation of population biomass in terms of calories per m^2.

(ii) Population numbers with season

Monthly analysis (Chapter III) of total numbers per m^2 of both species showed no significant difference between adjacent months. The centipedes were present in small numbers and it was necessary to group the recorded monthly figures according to seasons, (Table 10), to discover whether any significant difference in population occurred. Analysis of the variance of the mean population density per season showed the unsuitability of the F-test for showing whether significant differences in population numbers did occur. Significance tests based on non-parametric assumptions were adopted; in particular the formula given by Siegel 1956.

$$\chi^2 = \sum_{i=1}^{r} \sum_{k=1}^{k} \frac{(Oij - Eij)^2}{Eij}$$

where Oij = observed number of cases categorised in the ith row of the jth column.

Eij = number of cases expected Ho in the ith row of the jth.

$\sum_{i=1}^{r} \sum_{j=1}^{k}$ directs on to sum all rows (r) and all columns (k).

Where k = number of columns and r = the number of rows in the contingency table.

Table 10. Total population of L. crassipes and L. forficatus.

PERIOD	L. crassipes Mean nos. per sq.m.	L. forficatus Mean nos. per sq.m.
DEC/JAN/FEB	22.93	8.250
MAR/APR/MAY	30.88	10.393
JUN/JLY/AUG	42.94	14.360
SEPT/OCT/NOV	51.56	19.770

The above formula can be used in conjunction with the null hypothesis. Degrees of freedom being determined by the formula:-

$$df = (r - 1)(k - 1)$$

The rejection region for all values of chi-squared (χ^2) for more than two categories is when Ho (proportion of animals observed) is equal to or less than $\alpha = 0.01$. When comparing χ^2 for two independent samples the value of $\alpha = 0.05$ is the rejection value.

The mean population density/m^2 was determined for each species according to season (k) and used in the above formula to test for significant differences between seasons (DEC/JAN/FEB [winter], MAR/APR/MAY [spring], JUN/JLY/AUG [summer], SEPT/OCT/NOV [autumn]). The χ^2 values are tabulated below:-

Species	χ^2 value	No. of degrees of freedom	Probability level ($\alpha = 0.01$)
L. crassipes	87.32	9	$P < 0.001$
L. forficatus	19.72	6	$P < 0.01$ or $P > 0.001$

The results indicate that statistically significant differences in the population density of each species occur within each year. The distribution of both populations conform to a Poisson distribution. A further analysis using the χ^2-test to compare the population density between seasons (see key to table) was made and Table 13 shows the results.

In L. crassipes statistically significant increases in population density were observed through MAR/APR/MAY, JUN/JLY/AUG and SEPT/OCT/NOV and additions to the population were presumably due

Table 13. Comparison of population density (L. crassipes and L. forficatus) between seasons using χ^2-test.

Species and period	χ^2 value	No. of degrees of freedom	Probability level (α =0.05)
L. crassipes			
I-II	1.90	2	P> 0.05 or< 0.03
II-III	32.52	2	P< 0.001 significant
III-IV	6.57	2	P< 0.05 or > 0.02 significant
II-IV	50.01	2	P< 0.001 significant
I-IV	48.37	2	P< 0.001 significant
L. forficatus			
I-II	2.36	2	P = 0.30 not significant
II-III	0.71	2	P = 0.71 not significant
III-IV	4.09	2	P = 0.10 not significant
I-IV	10.38	2	P = 0.01 or> 0.001 significant
II-IV	5.40	2	P = 0.05 or P< 0.10 just significant

Key. I = DEC/JAN/FEB, II = MAR/APR/MAY
III = JUN/JLY/AUG, IV = SEPT/OCT/NOV

to breeding phenomena (Chapter II). However, during DEC/JAN/FEB mortality clearly exceeded natality resulting in a lower population density. In L. forficatus the increases in population density from MAR/APR/MAY to SEPT/OCT/NOV were barely significant (II-IV, P = 0.05) but the trend is clear. This increase was probably due to breeding whereas the decrease in population from SEPT/OCT/NOV to DEC/JAN/FEB can again be attributed to mortality exceeding natality.

(iii) Calculation of population biomass

Given seasonal population density of juveniles, juniors and adults; and the live weight/dry weight relationship of these three categories, the population biomass can be calculated in terms of dry weight. Tables 11 and 12 show these conversions for L. forficatus and L. crassipes. The pattern of events by season noted in connection with numbers is equally applicable to biomass data within each category. In order to reduce all parameters in the study to a common unit (the calorie) the biomass data was converted to calories using the figures given in Chapter IV.

It is clear that the decrease in biomass of juveniles in JUN/JLY/AUG and the increase for the junior stage during the same period can be attributed to moulting of juveniles to juniors. This increase in junior biomass is due to an increase in the number of juniors and not to an increase in individual weights. On a similar basis the decrease in biomass of juniors of L. crassipes in MAR/APR/MAY was probably due to moulting which caused an increase in the adult

Table 11. Biomass of L. forficatus for the year 1966-1967 (per season) logs and litter.

L. FORFICATUS	Mean nos. per m^2	Mean live wt. in mgs per m^2	Mean dry wt. in mgs per m^2	Cals/m^2 ash free	PERIOD
JUVENILES	3.155	8.212	2.073	10.849	DEC/JAN/ FEB
	3.957	10.300	2.599	13.689	MAR/APR/ MAY
	5.523	14.376	3.628	19.263	JUN/JLY/ AUG
	3.943	10.263	2.590	13.646	SEP/OCT/ NOV
JUNIORS	4.825	124.712	29.838	162.145	DEC/JAN/ FEB
	5.569	143.942	34.438	194.37	MAR/APR/ MAY
	5.620	145.260	34.754	199.029	JUN/JLY/ AUG
	11.939	308.587	73.831	418.993	SEP/OCT/ NOV
ADULTS	0.270	24.352	6.657	36.776	DEC/JAN/ FEB
	0.867	78.197	21.378	119.157	MAR/APR/ MAY
	3.217	290.151	79.325	465.971	JUN/JLY/ AUG
	3.888	350.670	95.870	545.242	SEP/OCT/ NOV

Table 12. Biomass of L. crassipes for the year 1966-1967 (per season) logs and litter.

L. CRASSIPES	Mean nos. per m^2	Mean live wt. in mgs per m^2	Mean dry wt. in mgs per m^2	Cals/m^2 ash free	PERIOD
JUVENILES	3.99	2.881	0.782	4.030	DEC/JAN/ FEB
	9.53	6.881	1.867	9.629	MAR/APR/ MAY
	8.77	6.332	1.718	8.855	JUN/JLY/ AUG
	14.31	10.332	2.805	14.465	SEP/OCT/ NOV
JUNIORS	15.06	52.619	13.931	74.716	DEC/JAN/ FEB
	9.55	33.367	8.834	49.098	MAR/APR/ MAY
	16.73	58.454	15.475	84.620	JUN/JLY/ AUG
	17.51	61.179	16.196	87.889	SEP/OCT/ NOV
ADULTS	3.88	40.876	11.438	63.014	DEC/JAN/ FEB
	11.80	124.313	34.786	198.178	MAR/APR/ MAY
	17.44	183.730	51.413	287.853	JUN/JLY/ AUG
	19.74	207.961	58.198	328.353	SEP/OCT/ NOV

biomass during this same period. Thus the increase in biomass occurring in the categories (juveniles, juniors and adults) can be attributed to either of the two factors; breeding and moulting.

A similar phenomenon was observed for L. forficatus. The decrease in biomass of L. forficatus juveniles in MAR/APR/MAY can be attributed to moulting as can the increase in biomass of juniors during the same period. The decrease in biomass of juniors again correlates with an increase in biomass of the adults during JUN/JLY/AUG. The increase in the juvenile population biomass in L. crassipes and L. forficatus can only be due to breeding as the use of mean weight value per individual effectively eliminates growth effects.

Though migration could be considered to be a factor causing an increase in biomass this is unlikely to have occurred as the larval stadia of the juvenile stage have limited mobility, further there is no reason to suspect that emigration and immigration, even if they did occur, were not equal. Indeed, as both L. crassipes and L. forficatus feed on a variety of foods (Lewis 1965 and Roberts 1957) it is not likely that food shortages are experienced and hence a well recognised cause of immigration is not likely to affect the centipedes. Moreover, most centipedes are relatively immobile at low temperatures (Roberts 1957) and a winter migration when food is more scarce would be improbable. During summer months mean temperatures ranged from 8 to 12^{o}C and conditions were always moist and it is not likely that summer migrations due to climatic conditions occurred.

CHAPTER VI

Respiratory metabolism of lithobiids

The most important parameter in population energetics studies after the determination of population biomass is respiration. A variety of methods have been used for ecological purposes in studying the oxygen consumption of arthropods. Itô (1964) used chemical methods to determine the carbon dioxide produced by the spider Lycosa pseudoannulata and evaluated the oxygen consumption by calculating the respiratory quotient. Berthet (1964) used the Cartesian diver technique to determine the respiratory metabolism of mites at different temperatures. This method also proved successful in the measurement of the oxygen consumption of nematodes and enchytraeids, Nielsen (1961). Qasrawi (1966) measured respiration of the grasshopper Chorthippus parallelus (Zette) with the aid of a Warburg respirometer. Engelmann (1961) obtained respiration data for soil arthropods with a Warburg respirometer and a modification of the Smith and Douglas insect respirometer in a constant temperature water bath. According to Engelmann this latter apparatus was most convenient.

(i) Apparatus

All of the above apparatus can be used to measure the rate of respiration for a limited period only. It has now been recognised in ecological studies that continuous respirometry is a better ecological measurement of respiration. Phillipson (1962) devised a continuously recording respirometer to determine the respiration of the phalangiids Mitopus morio (F) and Leiobunum rotundum (Latr.).

In the present study the Phillipson respirometer (Fig.46) proved convenient when measuring the respiration rates of the two tracheate centipedes L. crassipes and L. forficatus. The working of the Phillipson respirometer has been described (Phillipson 1962); however instead of nichrome electrodes, platinum nichrome electrodes (2.0 inches of platinum wire of 0.5mm diameter fused to end of nichrome) were used, thereby preventing the coating of the electrodes with oxides.

(ii) Method

Respiration was measured at three different temperatures, namely $5^{o}C \pm 0.1$, $10^{o}C \pm 0.1$, and $15^{o}C \pm 0.1$ for both species. The water bath was maintained at the above temperatures by means of an adjustable thermoregulator connected to a cooling unit (Tecam dep. cooler). The entire apparatus was assembled in a $10^{o}C$ constant temperature room during the period of study. Respiration experiments at the three temperatures were conducted on all stadia of both species each month for a period of one year. The centipedes used in the determination of oxygen consumption were either collected from the study area (Wynyard) or in woodland near Durham City each week. The lithobiids collected from the field were acclimatised for a period of three days at the temperature at which the experiment was to be conducted. The animals were kept in beakers containing litter and food found in the habitats. Two acclimatised centipedes of the same species, sex and stadium were introduced into

FIG. 46. CONTINUOUSLY RECORDING RESPIROMETER (PHILLIPSON 1962).

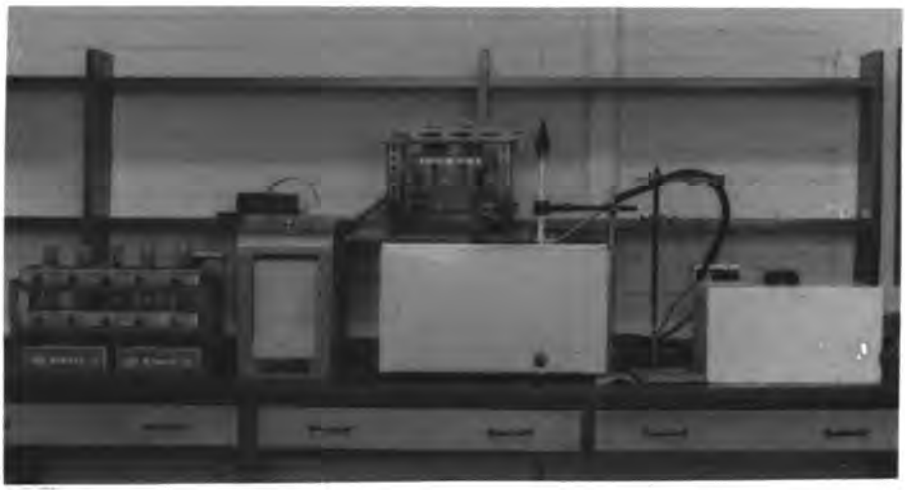


Table 14. Variance analysis of the rates of respiration of L. crassipes significance (F-test).

L. CRASSIPES	Temp. in °C	Mean respiration rate with standard error $mm^3O_2/mg/hr$	Variance	Variance ratio (F)	Level of significance
JUVENILES	5°C	0.193±0.0147	0.00281	12.35	P< 0.01 significant at 1% level
	10°C	0.384±0.00457	0.0347	3.401	P< 0.05 significant at 5% level
	15°C	0.547±0.0029	0.01021		
JUNIORS	5°C	0.0915±0.00457	0.000964	7.064	P< 0.01 significant at 1%level
	10°C	0.188±0.0116	0.00681	1.98	P< 0.05 significant at 5%level
	15°C	0.326±0.01935	0.0135		
ADULTS	5°C	0.075±0.0036	0.00044	2.22	P< 0.05 significant at 5%level
	10°C	0.125±0.0059	0.000979	6.077	P< 0.01 significant at 1%level
	15°C	0.179±0.014	6.077		

each metabolism chamber which was then immersed in a water bath at the required temperature. A relative humidity of 90% was maintained throughout the experiment by the use of damp filter paper. Each experiment lasted for a period of 60 hours and the rate of respiration of the first 24 hours when checked with the second 24 hour period was found not to differ significantly. Nevertheless the lithobiids were allowed to settle in the apparatus for a period of six hours before the measured respiration rates were used in the calculations.

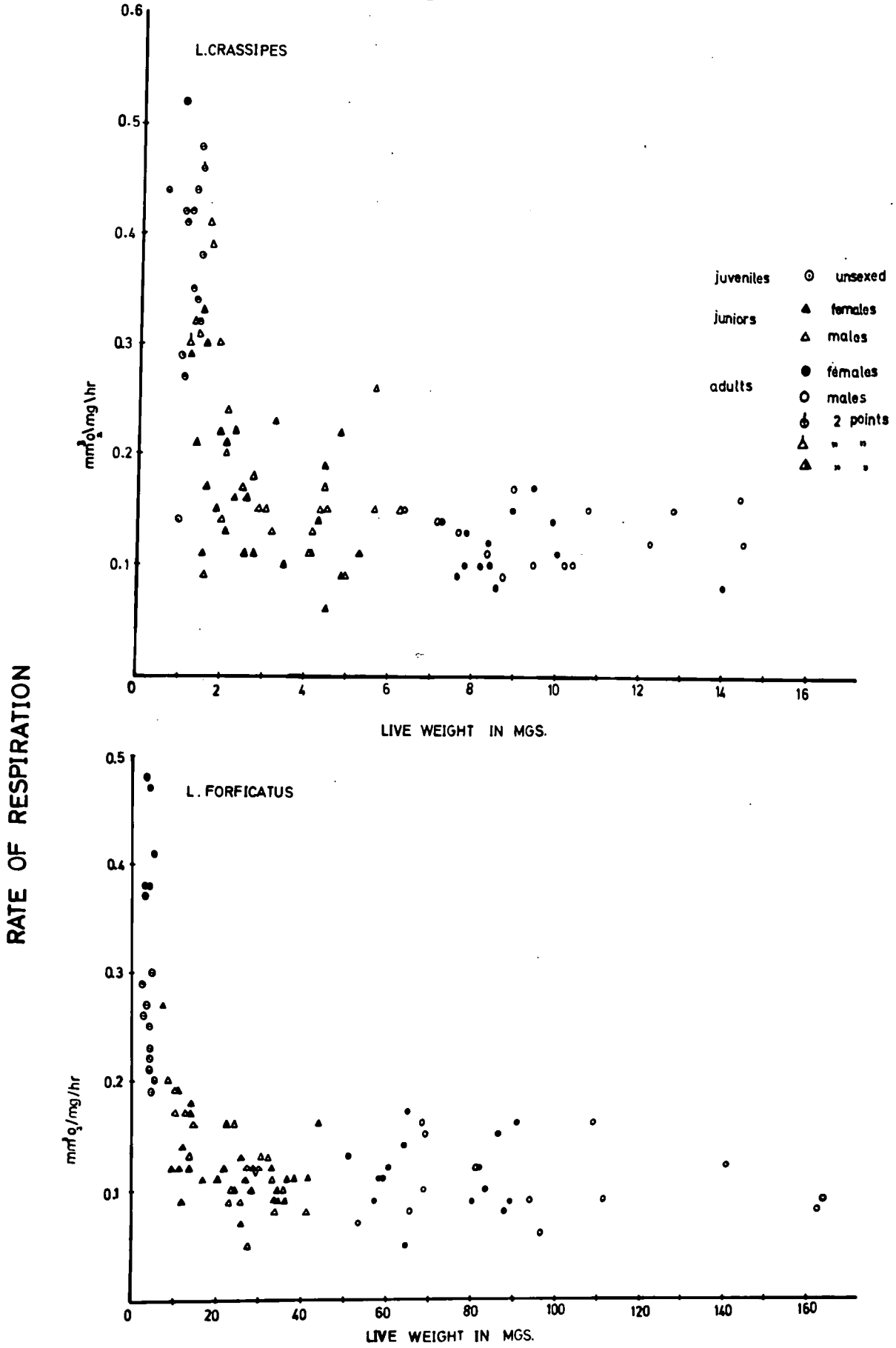
Results

(iii) Respiration of L. crassipes

From the results obtained it was possible to show a relationship between body weight and the rate of respiration. A plot of live weight (Fig.47) versus respiration per unit weight at $10^{\circ}C \pm 0.1$ indicated a typical L-shaped curve as did similar plots for the other two temperatures. For the purpose of combining population and respiration data in the final analysis, the rates of respiration of the stadia were grouped under the three size class categories, juveniles, juniors, and adults. The oxygen consumption per unit weight was lowest in adults and highest in juveniles, a sharp inflection showed in the $10^{\circ}C$ curve at the 2 mg. body weight. The curve obtained followed the pattern shown by Leiobunum rotundum (Phillipson 1963), Oniscus asellus (Phillipson and Watson 1965) and enchytraeids (Nielsen 1961).

The respiration rates of L. crassipes juveniles, juniors

FIG. 47. RELATIONSHIP BETWEEN BODY WEIGHT AND RATE OF RESPIRATION (A) L. CRASSIPES AND (B) L. FORFICATUS.


L.CRASSIPES
RATE OF RESPIRATION
mm³O₂/mg/hr
0.6
0.5
0.4
0.3
0.2
0.1
0
2
4
6
8
10
12
14
16
LIVE WEIGHT IN MGS.
juveniles
unsexed
females
juniors
males
females
adults
males
2 points
L. FORFICATUS
mm³O₂/mg/hr
0.5
0.4
0.3
0.2
0.1
0
20
40
60
80
100
120
140
160
LIVE WEIGHT IN MGS.

and adults obtained at 5°C, 10°C and 15°C are shown in Table 16. The regressions calculated for each stage (Fig.48-50) are:-

Juveniles	$y = 0.0432x - 0.069$	Fig.48
Juniors	$y = 0.0234x - 0.031$	Fig.49
Adults	$y = 0.014x + 0.022$	Fig.50

Figures 48-50 indicate that a definite relationship does exist between oxygen consumption and increase in temperature. The regressions obtained show a similarity to the results of Wiegert (1964) for the spittle bug Philaenus spumarius and Smalley (1960) for the grasshopper Orchelimum fidicinium. The F-test (Bailey 1949 and Snedecor 1950) for significance between temperatures indicated that an increase in temperature (Table 14) caused a statistically significant difference in the increase in oxygen consumption. Significance tests on the mean respiratory rates of adult males and females (Table 15) showed no significant difference at the 5% level. The Q_{10} was calculated between 5°C and 15°C by using the following formula (Prosser and Brown 1962):-

$$Q_{10} = \left(\frac{V_1}{V_2}\right)^{\frac{10}{t_1 - t_2}}$$

where V_1 and V_2 are the rates of reaction at 15°C (t_1) and 5°C (t_2) respectively. The Q_{10} for L. crassipes had a value 2.7.

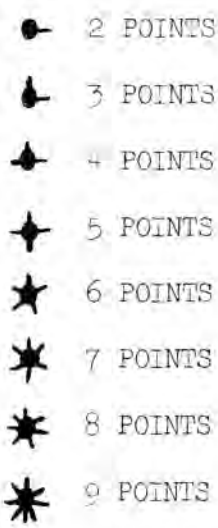
Calculation of field respiration rate per unit weight of L. crassipes

Since laboratory respiratory rates were temperature dependent the field oxygen consumption would vary with season, or

Table 15. Variance analysis of the rates of respiration of L. crassipes adult males and females for significance.

L. CRASSIPES	Temp. in °C	Mean respiration rate with standard error $mm^3 O_2/mg/hr$	Variance	Variance ratio (F)	Level of significance
MALES	5°C	0.071 ± 0.003	0.00022	2.71	P > 0.05 not significant at 5% level
FEMALES		0.079 ± 0.006	0.00061		
MALES	10°C	0.125 ± 0.007	0.0008	1.92	P > 0.05 not significant at 5% level
FEMALES		0.124 ± 0.011	0.0015		
MALES	15°C	0.188 ± 0.017	0.0049	1.44	P > 0.05 not significant at 5% level
FEMALES		0.171 ± 0.014	0.0034		

FIG. 48. REGRESSION OF THE RATE OF RESPIRATION WITH TEMPERATURE OF L. CRASSIPES JUVENILES.



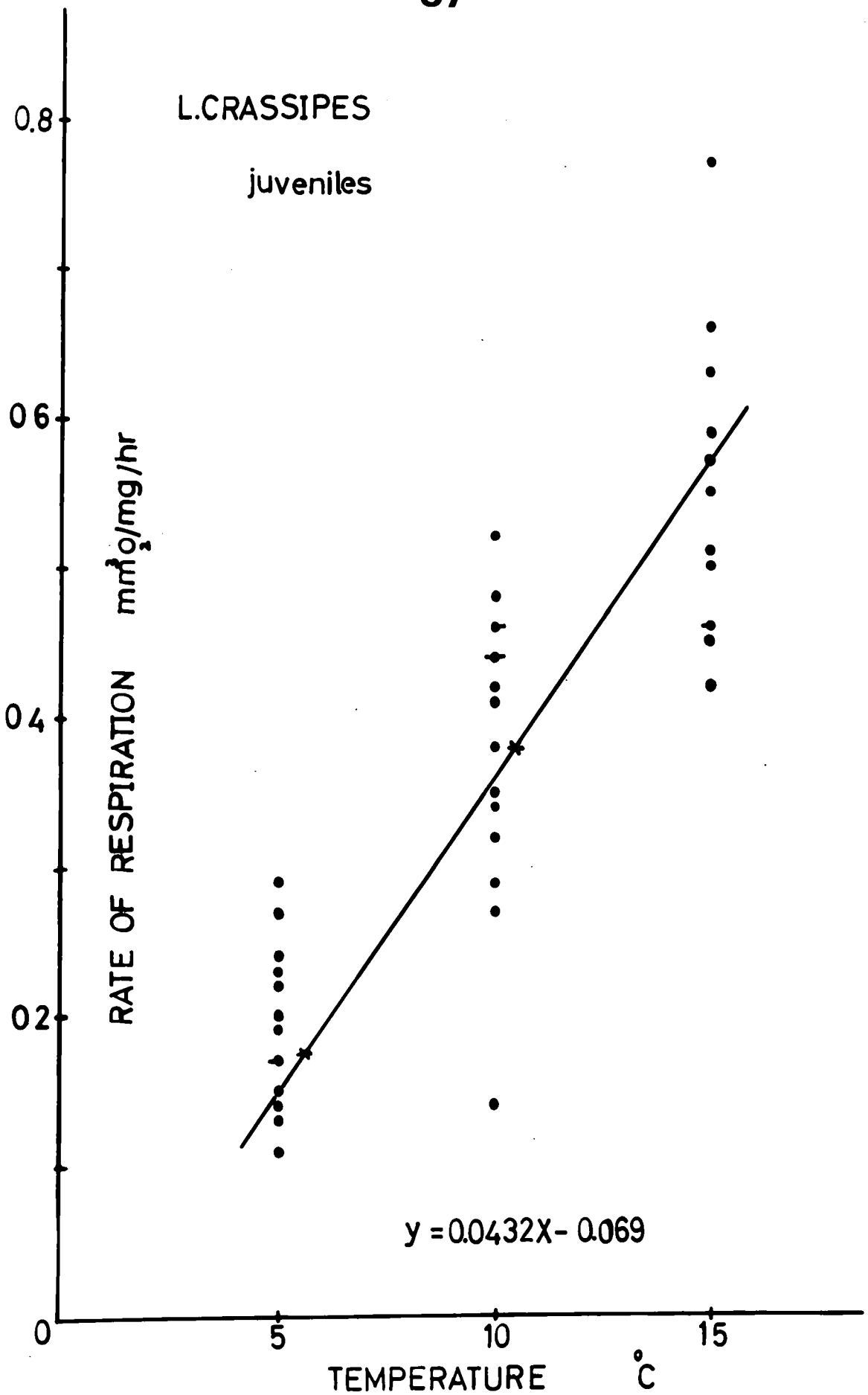

L.CRASSIPES
juveniles
RATE OF RESPIRATION mm³o/mg/hr
0.8
0.6
0.4
0.2
0
y = 0.0432X - 0.069
5
10
15
TEMPERATURE °C

FIG. 49. REGRESSION OF THE RATE OF RESPIRATION WITH TEMPERATURE OF L. CRASSIPES JUNIORS.

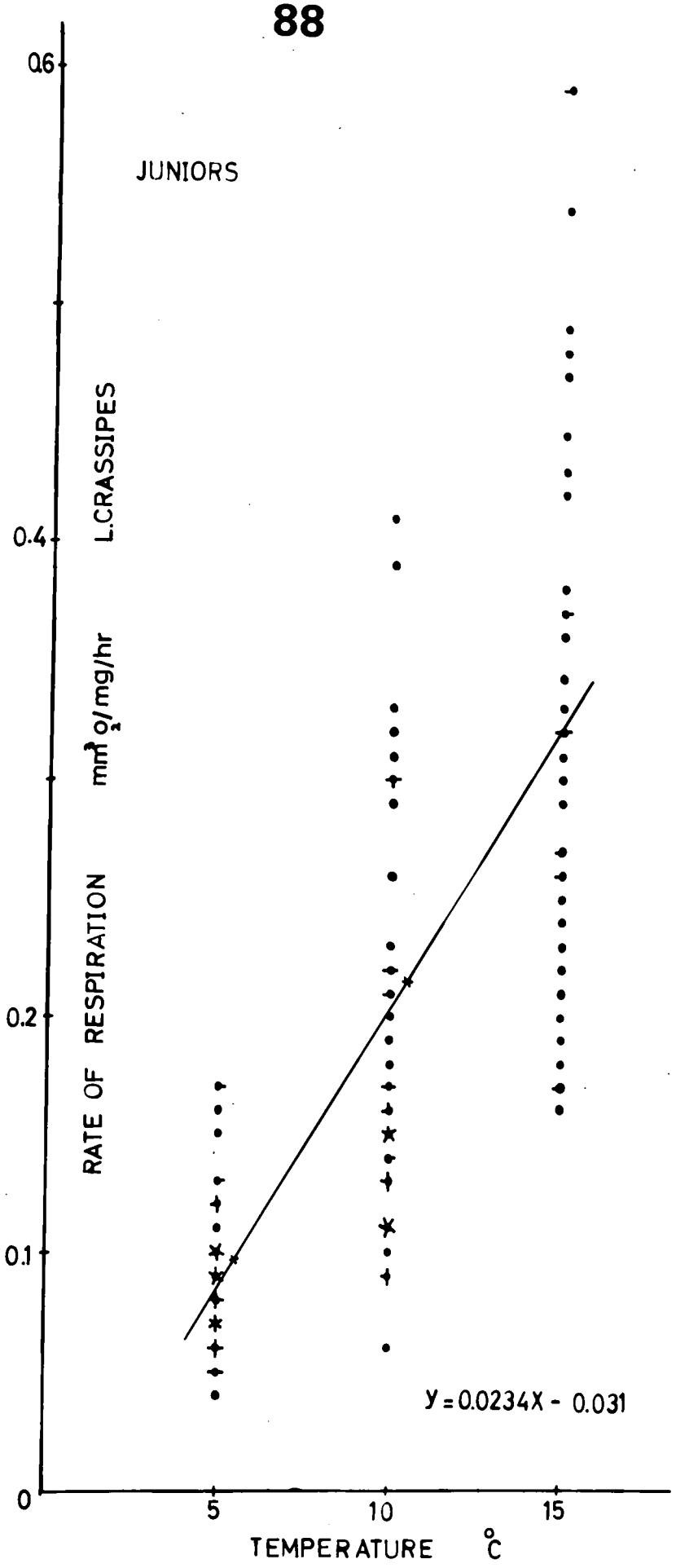
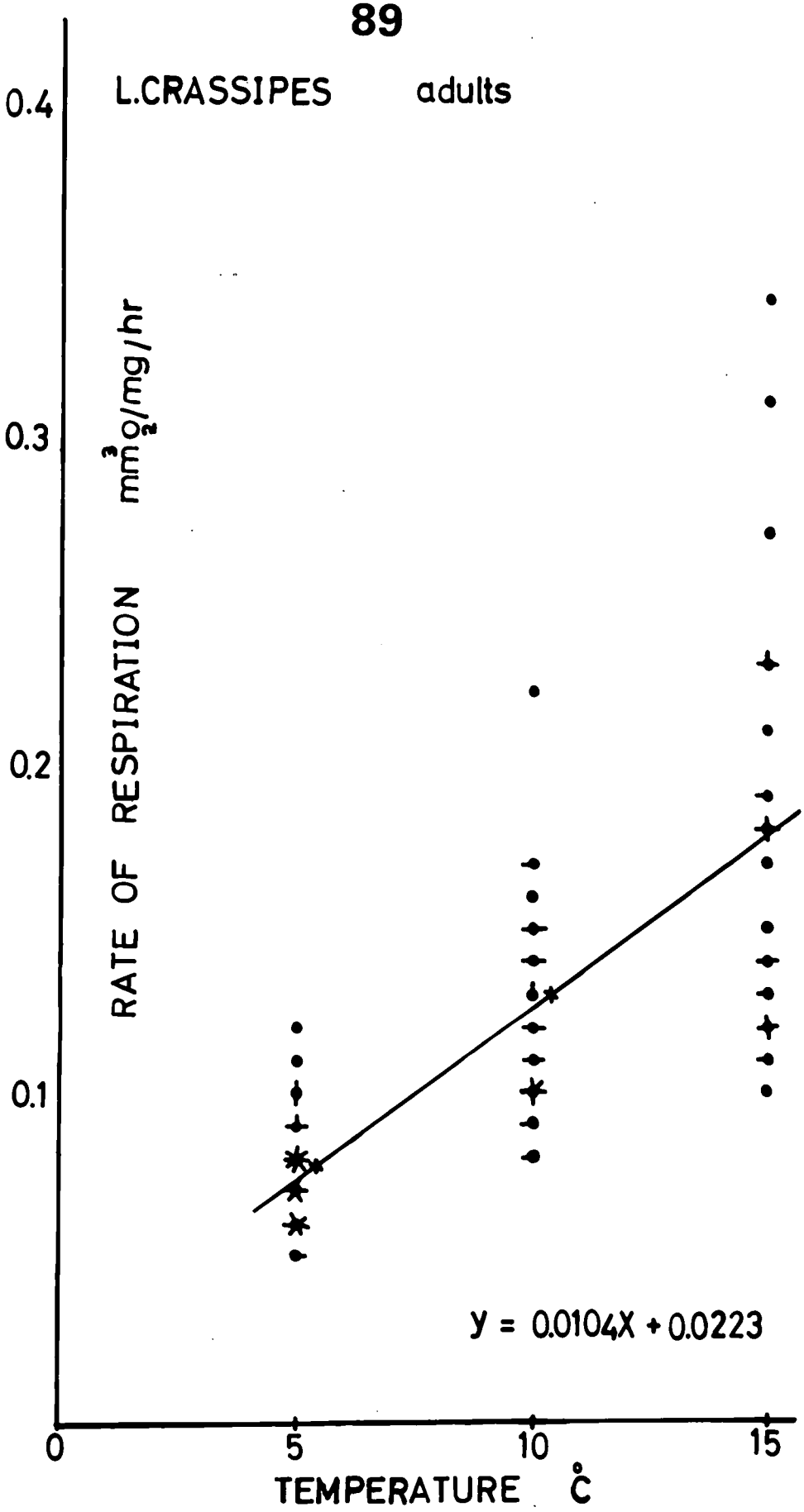

0.6
0.4
0.2
0.1
0
JUNIORS
L.CRASSIPES
RATE OF RESPIRATION mm³ o/mg/hr
y = 0.0234X - 0.031
5
10
15
TEMPERATURE °C

FIG. 50. REGRESSION OF THE RATE OF RESPIRATION WITH TEMPERATURE OF L. CRASSIPES ADULTS.


L.CRASSIPES adults
0.4
0.3
0.2
0.1
0
RATE OF RESPIRATION $mm^3O_2/mg/hr$
y = 0.0104X + 0.0223
5
10
15
TEMPERATURE °C

monthly as the mean field temperature varied monthly (Chapter II). The values obtained for mean field temperatures, using the regressions calculated for juveniles, juniors and adults (Fig.48-50), gave the field respiratory rates per unit weight. Figure 51 shows that the field respiration per unit weight of L. crassipes juveniles, juniors and adults followed the pattern of the field temperature curve (Table 16). Thus the field respiration per unit weight of juveniles, juniors and adults gradually declined from August till a minimum was reached in January and then gradually increased to reach a maximum in July. An increase in the field respiration per unit weight from adults to juveniles was observed for each month.

(v) Respiration of L. forficatus

Figure 47 shows that the relationship between body weight and rate of oxygen consumption per unit weight at $10^{\circ}C \pm 0.1$ of L. forficatus was similar to that of L. crassipes as do the 5 and $15^{\circ}C$ curves. The L-shaped curve at $10^{\circ}C$ showed a change in the rate of oxygen consumption per unit weight with an inflection at a live body weight of 15 mgs. The respiratory rates per unit weight of acclimatised L. forficatus (adults, juniors and juveniles) were found to increase with change in temperature ($5^{\circ}C$, $10^{\circ}C$ and $15^{\circ}C$). The plot of oxygen consumption per unit weight versus temperature is shown in Figures 52, 53 and 54. The regression computed for each category of L. forficatus revealed the following equations:-

Juveniles $y = 0.027x + 0.017$ Fig.52

Table 16. Field respiratory rates of juveniles, juniors and adults of L. crassipes.

Period	Mean temp. °C	Rate of respiration $mm^3O_2/mg/hr$ JUVENILES	Rate of respiration $mm^3O_2/mg/hr$ JUNIORS	Rate of respiration $mm^3O_2/mg/hr$ ADULTS
AUGUST	11.62	0.433	0.241	0.143
SEPTEMBER	11.92	0.446	0.210	0.146
OCTOBER	9.81	0.355	0.198	0.124
NOVEMBER	7.71	0.264	0.149	0.102
DECEMBER	5.50	0.168	0.097	0.079
JANUARY	5.30	0.159	0.093	0.077
FEBRUARY	6.41	0.208	0.119	0.089
MARCH	7.16	0.240	0.136	0.096
APRIL	8.26	0.287	0.162	0.108
MAY	9.98	0.362	0.203	0.126
JUNE	11.47	0.426	0.237	0.142
JULY	12.14	0.455	0.253	0.148

Juniors	$y = 0.0117x + 0.013$	Fig.53
Adults	$y = 0.011x + 0.010$	Fig.54

It is clear that the rate of respiration per unit weight is temperature dependent for each category of L. forficatus. An F-test between 5°C and 10°C and 10°C and 15°C for juniors showed a significant difference at the 5% level. In juveniles a significant difference between 5°C and 10°C was observed (Table 17), but no significance at the 5% level in the respiratory rates between 10°C and 15°C was noted. The only explanation that can be offered is the insufficiency of the number of juveniles used in the measurement of respiration. In L. forficatus adults a significant difference at the 1% level was observed for the respiratory rates per unit weight between 10°C and 15°C, but the absence of a significant difference between 5°C and 10°C could again be due to the insufficiency of adults used in the measurement of respiration at the two temperatures mentioned. Statistical analysis of adult male and female respiratory rates per unit weight (Table 18) at 5°C, 10°C and 15°C showed no significant differences at the 5% level. As this phenomenon was also observed for L. crassipes juniors it was assumed that males and females of juniors of both species showed no difference in their rates of respiration per unit weight. The Q_{10} for L. forficatus had a value of 2.6.

(vi) Calculation of field respiration rate per unit weight of L. forficatus

As the oxygen consumption per unit weight increased with a rise in temperature (5°C, 10°C and 15°C) it was concluded that the

FIG. 52. REGRESSION OF THE RATE OF RESPIRATION WITH TEMPERATURE OF L. FORFICATUS JUVENILES.

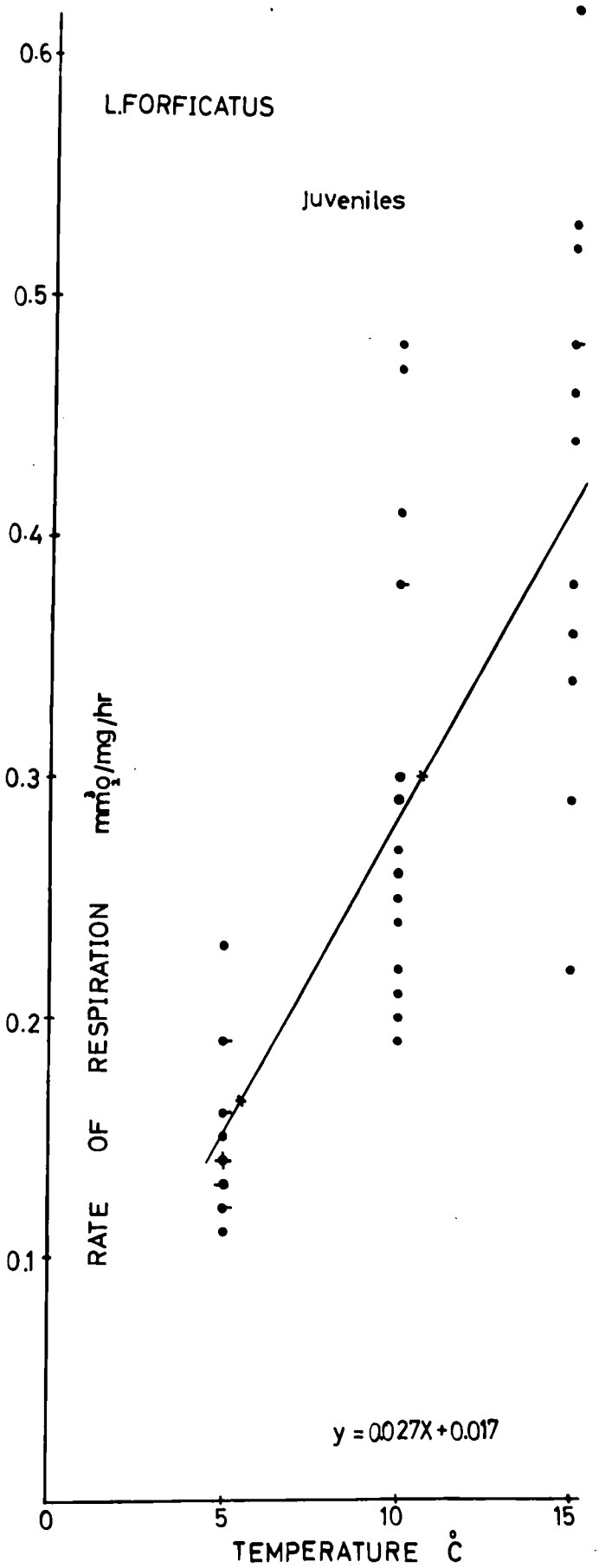

L.FORFICATUS
Juveniles
RATE OF RESPIRATION mm³O₂/mg/hr
0.6
0.5
0.4
0.3
0.2
0.1
y = 0.027X + 0.017
0
5
10
15
TEMPERATURE C°

FIG. 53. REGRESSION OF THE RATE OF RESPIRATION WITH TEMPERATURE OF L. FORFICATUS JUNIORS.

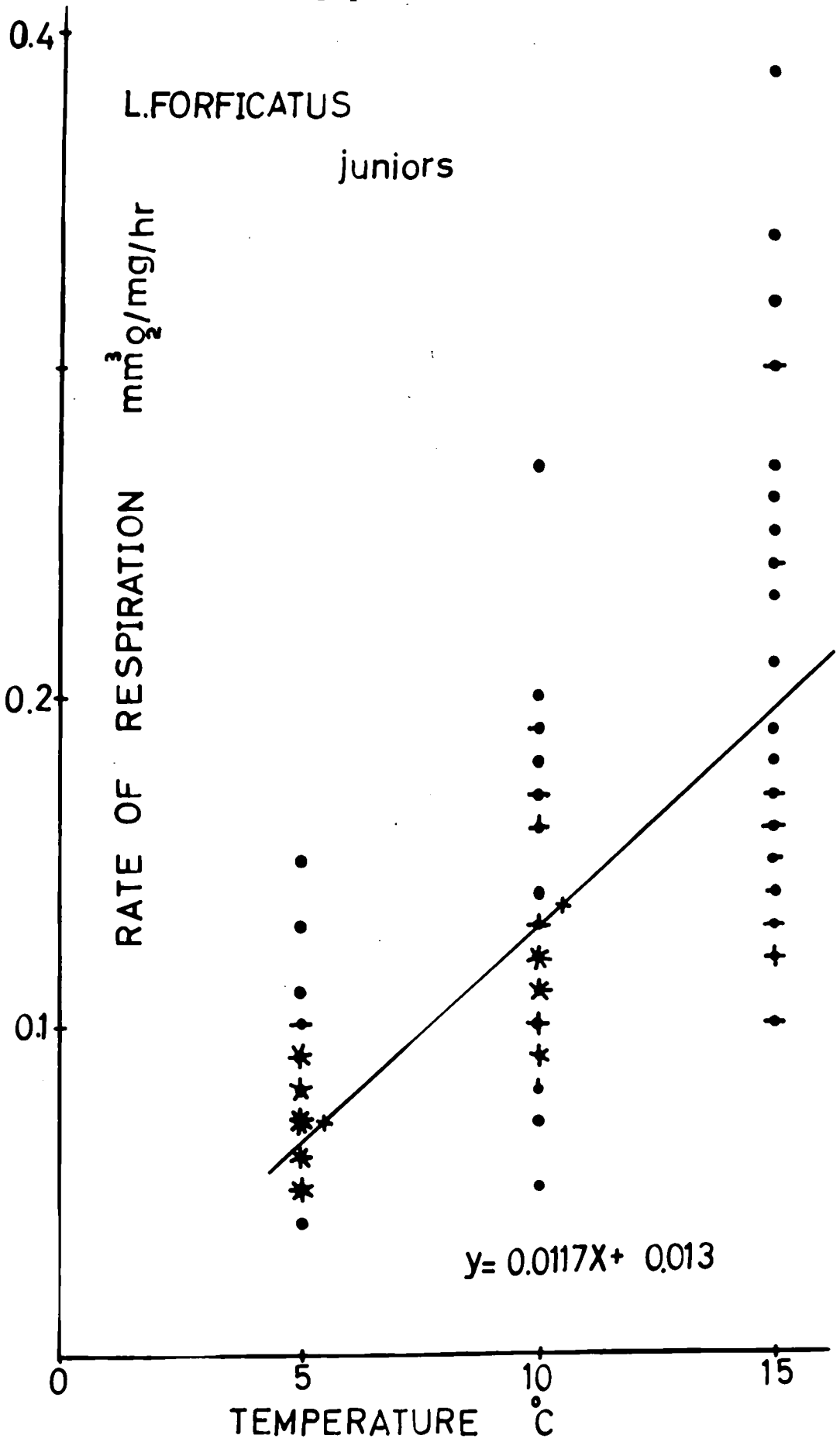

0.4
0.2
0.1
0
L.FORFICATUS
juniors
RATE OF RESPIRATION mm³O₂/mg/hr
y= 0.0117X+ 0.013
5
10
15
TEMPERATURE °C

FIG. 54. REGRESSION OF THE RATE OF RESPIRATION WITH TEMPERATURE OF L. FORFICATUS ADULTS.

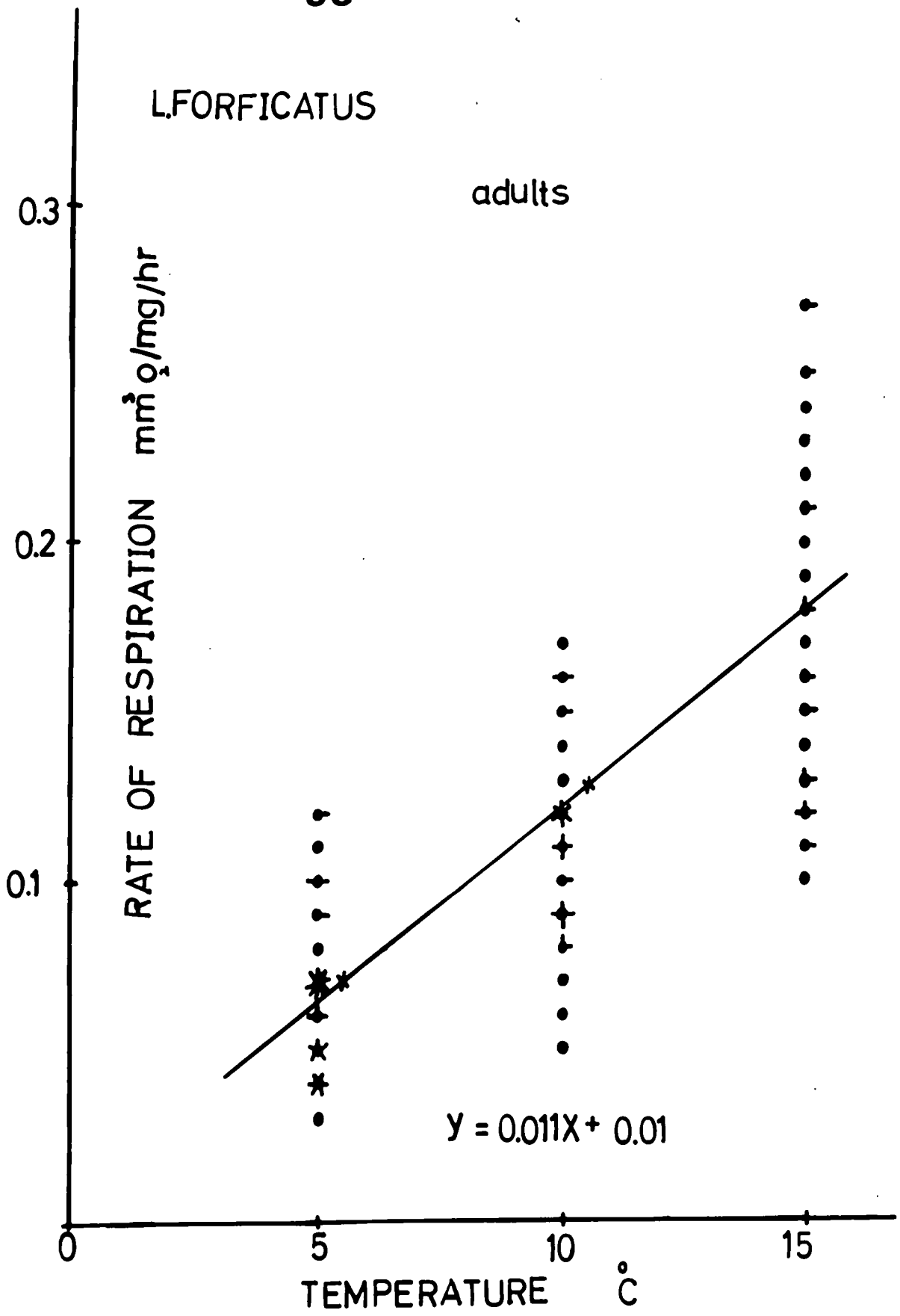
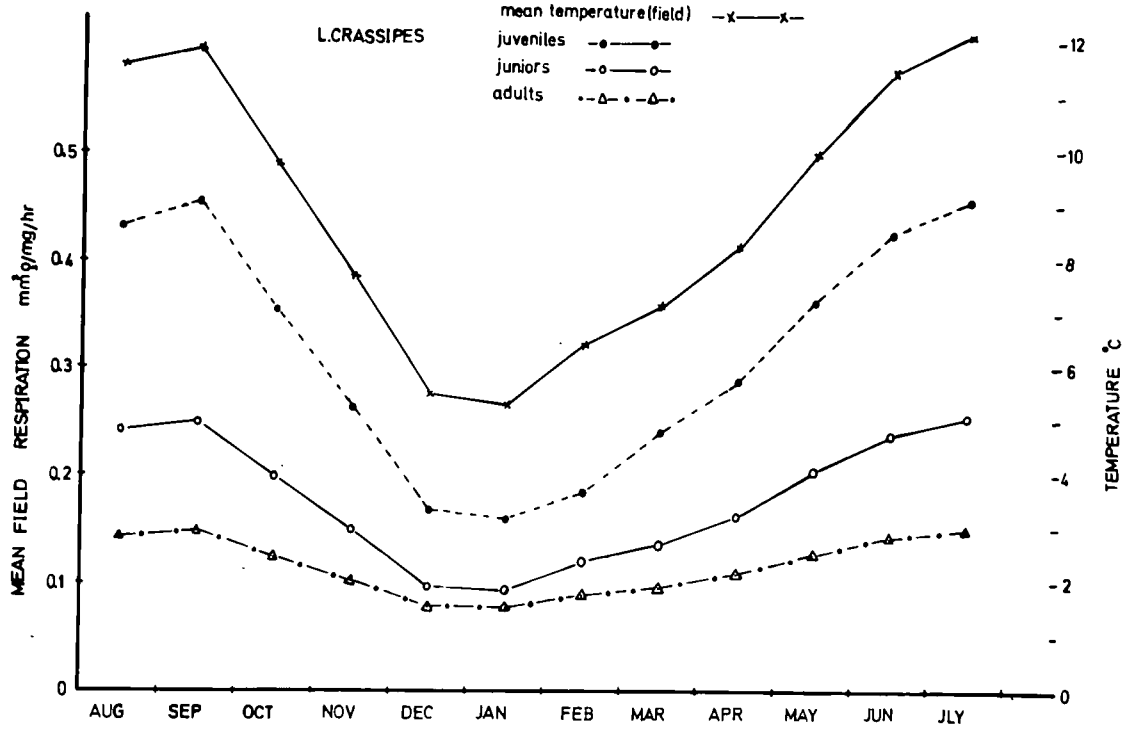

L.FORFICATUS
adults
0.3
0.2
0.1
RATE OF RESPIRATION mm³ o₂/mg/hr
y = 0.011X + 0.01
0
5
10
15
TEMPERATURE °C

FIG. 51. MONTHLY FIELD RESPIRATION PER UNIT LIVE WEIGHT OF L. CRASSIPES JUVENILES, JUNIORS AND ADULTS WITH FIELD TEMPERATURE.

FIG. 55. MONTHLY FIELD RESPIRATION PER UNIT LIVE WEIGHT OF L. FORFICATUS JUVENILES, JUNIORS AND ADULTS WITH FIELD TEMPERATURE.


L.CRASSIPES
mean temperature(field)
juveniles
juniors
adults
MEAN FIELD RESPIRATION mm³g/mg/hr
TEMPERATURE °C
0
0.1
0.2
0.3
0.4
0.5
-2
-4
-6
-8
-10
-12
AUG
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN
JLY

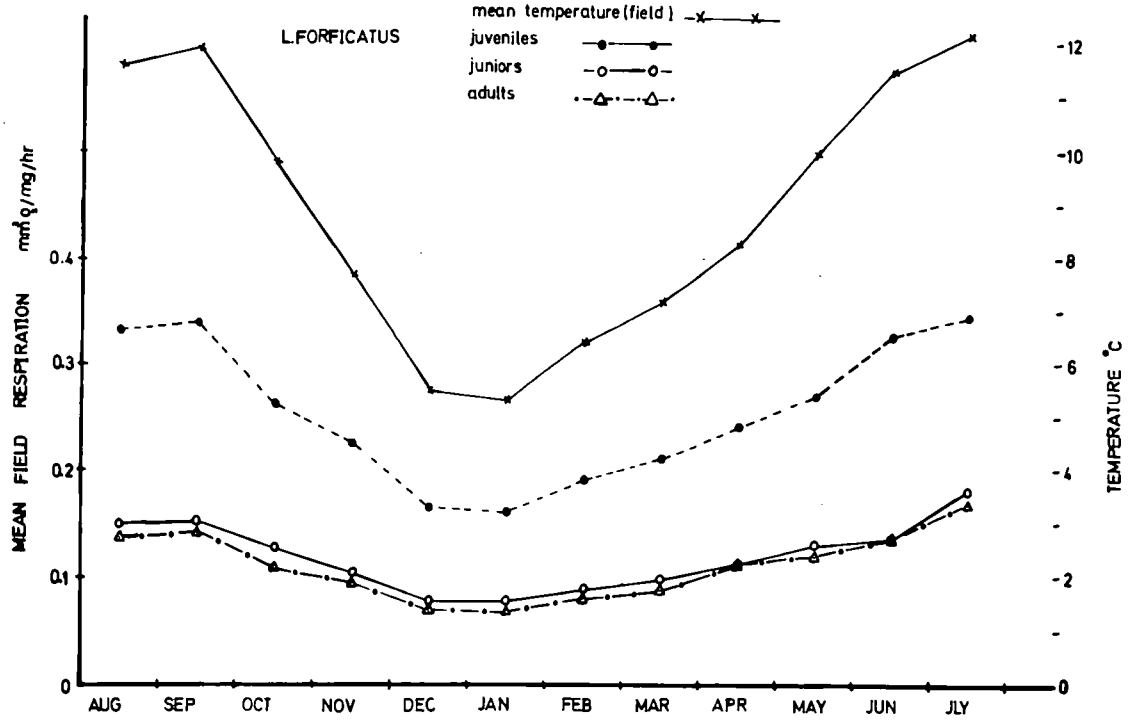

L.FORFICATUS
mean temperature(field)
juveniles
juniors
adults
MEAN FIELD RESPIRATION mm³g/mg/hr
TEMPERATURE °C
0
0.1
0.2
0.3
0.4
-2
-4
-6
-8
-10
-12
AUG
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN
JLY

Table 17. Variance analysis of the rates of respiration of L. forficatus (F-test).

L. FORFICATUS	Temp. in °C	Mean respiratory rate with standard error $mm^3O_2/mg/hr$	Variance	Variance ratio (F)	Level of significance
JUVENILES	5°C	0.149±0.00791	0.00102		
				8.63	P<0.01 significance at 1% level
	10°C	0.307±0.0234	0.0088		
				1.37	P>0.05 not significant at 5% level
	15°C	0.426±0.0032	0.0121		
JUNIORS	5°C	0.074±0.0097	0.00045		
				3.55	P<0.01 significant at 1% level
	10°C	0.125±0.00577	0.0016		
				3.66	P<0.01 significant at 5% level
	15°C	0.191±0.0127	0.00586		
ADULTS	5°C	0.066±0.0067	0.000617		
				1.44	P>0.05 not significant at 5% level
	10°C	0.112±0.0053	0.00087		
				3.01	P<0.01 significant at 1% level
	15°C	0.173±0.00945	0.00268		

Table 18. Variance analysis of the rates of respiration of L. forficatus adults, males and females (F-test).

L. FORFICATUS ADULTS	Temp. in °C	Mean respiration rate with standard error $mm^3O_2/mg/hr$	Variance	Variance ratio (F)	Level of significance
MALES	5°C	0.064±0.0053	0.00054	1.018	P>0.05 not significant at 5% level
FEMALES		0.070±0.0055	0.00053		
MALES	10°C	0.113±0.0067	0.00073	1.479	P>0.05 not significant at 5% level
FEMALES		0.111±0.0082	0.00108		
MALES	15°C	0.187±0.0138	0.00286	1.497	P>0.05 not significant at 5% level
FEMALES		0.159±0.0112	0.00191		

rate of respiration of L. forficatus was temperature dependent. The field respiratory rates for L. forficatus were computed by using the figures obtained for mean field temperature (Chapter II) and from the regression equations. The values of field respiratory rates per unit weight are shown in Table 19. The graphical analysis of these mean field respiratory rates of juveniles, juniors and adults (Fig.55) show that they rise and fall in a manner similar to field temperature fluctuations. Thus the rates of respiration per unit weight of all categories of L. forficatus gradually decrease (Fig.55) from August till a minimum is reached in January and then increase to reach a maximum in July which is coincident with the highest temperature recorded.

The analysis of total field respiration by both species (i.e. where respiration rate per unit weight and population biomass are combined) is given in Chapter VIII.

(vii) Comparison of the rates of respiration using the Phillipson respirometer and the Warburg respirometer

Because of the controversy regarding the use of continuous respirometry and/or short term respirometry in ecological studies it was decided to compare respiration results from the Phillipson respirometer with those from a Warburg respirometer (Umbreit, Burris and Staffer 1949). Both apparatuses are of the constant volume type. Using the Warburg the rate of oxygen consumption was measured at 15°C. The centipedes were acclimatised for a period of three days

Table 19. Field respiratory rates of juveniles, juniors and adults of L. forficatus.

PERIOD	Mean temp. °C	Rate of respiration $mm^3O_2/mg/hr$ JUVENILES	Rate of respiration $mm^3O_2/mg/hr$ JUNIORS	Rate of respiration $mm^3O_2/mg/hr$ ADULTS	
AUGUST	11.62	0.331	0.149	0.138	
SEPTEMBER	11.92	0.339	0.152	0.141	
OCTOBER	9.81	0.282	0.127	0.118	
NOVEMBER	7.71	0.225	0.103	0.095	
DECEMBER	5.50	0.165	0.077	0.071	
JANUARY	5.30	0.160	0.075	0.068	
FEBRUARY	6.41	0.190	0.088	0.081	
MARCH	7.16	0.210	0.097	0.088	
APRIL	8.26	0.240	0.109	0.101	
MAY	9.98	0.269	0.129	0.119	
JUNE	11.47	0.326	0.134	0.136	
JULY	12.14	0.345	0.155	0.143	

and subjected to similar conditions as mentioned for the Phillipson respirometer. Depending upon the body weight of each stadium at least two or more centipedes had to be used in the Warburg flasks. As the smallest flasks available had a volume of 10 m.l. a minimum weight of 25 mgs live weight had to be used in each flask to obtain satisfactory results of the oxygen consumption of each stadium. The oxygen consumption measurements shown below indicate that both apparatuses gave similar results.

Species	Phillipson respirometer $mm^3O_2/mg/hr$	Warburg respirometer $mm^3O_2/mg/hr$
L. crassipes		
Adults	0.179 ± 0.014	0.196 ± 0.0140
Juniors	0.326 ± 0.0193	0.308 ± 0.0292
Juveniles	0.546 ± 0.0029	-
L. forficatus		
Adults	0.173 ± 0.009	0.178 ± 0.021
Juniors	0.191 ± 0.013	0.175 ± 0.021
Juveniles	0.426 ± 0.003	0.345 ± 0.025

A statistical analysis of the rates of respiration for each category, recorded by the two respirometers, showed no significant difference at the 5% level ($P > 0.05$). Attempts to measure the oxygen consumption of juveniles of L. crassipes failed as a total of approximately 30 animals needed to be acclimatised for one Warburg determination. A large number of centipedes within a limited volume led to cannibalism

and these experiments were abandoned. The results from Warburg respirometry were obtained over a period of about 4 hours and would clearly have sufficed in the present study. However, lack of information on respiration rhythms in most animals could lead to difficulties in determining 24 hour rates of respiration and it is clearly of advantage to use a continuously recording respirometer. This is also true in the present study when one recalls the fact that the Warburg required many animals per flask whereas the Phillipson respirometer did not.

(viii) Discussion

The rates of respiration per unit weight of L. crassipes and L. forficatus were temperature dependent, each species having a Q_{10} of 2.6 to 2.7. These findings are quite contrary to the effect of temperature on the metabolism of certain marine invertebrates which show acclimatisation e.g. Actinia equina and Cardium edule (Newell and Northcroft 1967). However, the reproductive behaviour and physiological state of L. crassipes and L. forficatus coincides with increased metabolic activity as well as with temperature and it is difficult to separate the effect of various factors. It is possible that all factors influence, in some way, the metabolic rates of the two centipedes. Nevertheless, the two centipede species did not show acclimatisation phenomena over a period of three days and this period of time was considered sufficient in that the rates of respiration on days four and five were the same. It is clear that in any study of population metabolism researchers must consider the

possibility of acclimatisation in their experimental animals and thus investigate this possibility before correcting laboratory data obtained at constant temperature to field temperature.

CHAPTER VII

Growth and production in L. crassipes and L. forficatus

(i) Introduction

Odum (1959) stated that the term "productivity" is analagous with the phrase "rate of production" and that the rates of energy storage at the consumer and decomposer levels should be referred to as secondary productivity. However, Macfadyen (1948, 1950, 1963 and 1967) noted that the word productivity, which usually denotes the biomass of an organism over a period of time, has led to much confusion and suggests that the word production is more stable. Further, Macfadyen (1967) stated that in an animal population the food which is assimilated (i.e. which is absorbed through the gut wall) could be defined as gross production and that which is built into the body tissue (i.e. not respired) as the net production. Engelmann (1966) also regards production of animal tissue (i.e. assimilation-respiration) as net production, and total assimilation (production + respiration) as gross production. Net production in terms of Lindeman's trophic dynamic concept (1942) is represented by n in the following equation:-

$$\frac{\delta \Delta n}{\delta t} = \lambda n + \lambda n'$$ (where $\frac{\delta \Delta n}{\delta t}$ = rate of change energy content of the standing crop, λn = rate of energy absorbed by standing crop and $\lambda n'$ = rate at which energy is lost which is negative).

Wiegert (1964) defined production as growth or increase of biomass together with the exoskeletal material discarded with each moult in his study of meadow spittle bugs (P. spumarius),

but used the word growth in preference to production in his paper on the grasshoppers (1965) where the energy content of the exoskeleton was excluded. Odum and Smalley (1959) and Smalley (1960) have defined population production as the amount of organic matter or protoplasm added to the population per unit time. Clearly the terms "production" and "productivity" have been used in various senses in the literature.

In the present investigation the increase of biomass per unit time was used to define production of a population of L. crassipes and L. forficatus. The biomass increase per unit time was calculated by measuring the growth rate in terms of dry weight of each individual of each species and applying the results obtained to population data (Chapter III). Biomass was eventually expressed in terms of calories of lithobiid material.

(ii) The measurement of the rate of growth of L. crassipes and L. forficatus

In order to measure growth three quantitative aspects (Simpson, Roe and Lewontin, 1960) have to be considered (a) change of some dimension of the animal with time (b) the relative sizes of two dimensions of a single animal and (c) the third aspect, which is by far the most difficult, is growth concerned with changes in shape. The change in dimension, namely weight, with age of the two species, was found to be suitable for the measurement of growth. It was difficult to correlate any other dimension with growth, as length

could not be measured accurately in live animals, and though the head width of each individual varied, the change was extremely slow with time. A change in head width of the centipedes occurred only when one stadium moulted to the next, but weight changes were noted within individual instars and to allow for this centipede weights were measured monthly to determine the rate of growth with time. Head width was also measured monthly so that individuals could be placed in the appropriate instar, as well as to observe moulting which was accompanied by a significant increase in weight.

Procedure

As it was considered essential to measure growth of L. crassipes and L. forficatus under near natural conditions, growth experiments were conducted in the field (sample area). In order to obtain a regular measurement of growth it was necessary to confine the centipedes by enclosing them in nylon mesh bags. Nylon mesh bags of two sizes, 45 cm by 30 cm and 25 cm by 15 cm and mesh size of 1.0 mm^2 and 0.5 mm^2 respectively were used according to the size of the centipede introduced. The bags were filled with litter from the study area and two centipedes of different sex were placed in the bags before securing them with clips. A total of 54 individuals (14 adults, 30 juniors and 10 juveniles) for each species were experimented with; in the category adults and juniors equal numbers of each sex were introduced into the bags. The juveniles of L. crassipes and L. forficatus, being delicate and pallid, were placed in cylindrical

glass tubes (10 cm by 4 cm) which were filled with litter, the tube ends were covered with nylon mesh (0.5 mm^2) and the whole unit buried in the litter of the sample area. All centipedes introduced into the bags and tubes were undamaged, their weight recorded and head width measured. After a period of one month the bags and tubes were removed from the sample area, conveyed to the laboratory, their contents emptied into a sorting dish and the centipedes collected by disturbing the litter under bright light. Usually dead centipedes were not found in the bags as they had decomposed or been devoured by the survivors. Missing centipedes, presumably due to mortality, were replaced by others of similar head width and approximate weight. Sex and head width were used as distinguishing features when recording monthly weight of individuals, or replacing dead ones. Any water or extraneous matter adhering to the surfaces were removed before weighing. Water was not often seen to adhere to their surfaces since the cuticle was covered by a surface film of lipoid (Blower 1951). The procedure of taking monthly weights and head widths was continued for a period of one year for both species. Moulted centipedes were identified by their violet colour, change in head width, or morphological characters of the new stadium attained.

Results

(iii) The growth rate of L. crassipes

The monthly wet weights of adults, juniors and juveniles of L. crassipes were found to increase from March up to a

maximum in September. A gradual decline was observed from September till a minimum mean wet weight was reached in January with an increase in February and March. The wet weights obtained were converted to dry weights using the appropriate regression equation (Chapter V). The dry weights for each month, which followed the pattern of wet weights, are shown in Tables 20, 21 and 22 for adults, juniors and juveniles respectively. From the dry weights of males and females observed there was evidence to show that the increase in body weight of the female body tissue approximated to that of the male. Further, males and females of similar head width at the end of the breeding season had approximately the same live weight. The growth rate was calculated from monthly dry weights (Tables 20-22 ~~22-24~~) and expressed as increase in mg dry weight/mg/month. The growth rate of each category increased from March to September and decreased till January to increase again in February and March. The growth rate was not constant but found to vary with season.

(iv) Growth rate of L. forficatus

As in L. crassipes the mean wet weights recorded monthly for L. forficatus were converted to dry weights by using the regression equations (Chapter V). The mean dry weights increased from April to reach a maximum in September, gradually declined January to increase again in February and March (Tables 23, 24 and 25). As in L. crassipes there was evidence to show that the increase in dry weights was the same for both sexes of L. forficatus. The growth

Table 20. Growth and rate of production of L. crassipes adults.

PERIOD	Mean dry wt. per month in mgs.	Growth rate per month mg/month/mg	Rate of production per month mg/m^2/month	Rate of production per day mg/m^2/day	Production cals/m^2/day
MARCH	2.084				
APRIL	2.222	+ 0.062	+ 1.3269	+ 0.0942	+ 0.2441
MAY	2.412	+ 0.078	+ 2.7213	+ 0.0877	+ 0.4848
JUNE	2.619	+ 0.086	+ 3.6150	+ 0.1205	+ 0.6746
JULY	2.777	+ 0.060	+ 3.7882	+ 0.1222	+ 0.6839
AUGUST	2.812	+ 0.013	+ 0.6399	+ 0.0206	+ 0.1156
SEPTEMBER	2.894	+ 0.029	+ 1.7381	+ 0.0579	+ 0.3267
OCTOBER	2.815	- 0.027	- 2.0777	- 0.0670	- 0.3781
NOVEMBER	2.645	- 0.060	- 2.1131	- 0.0704	- 0.3971
DECEMBER	2.506	- 0.053	- 1.7744	- 0.0572	- 0.3152
JANUARY	2.329	- 0.071	- 1.4980	- 0.0483	- 0.2663
FEBRUARY	2.380	+ 0.022	+ 0.7175	+ 0.0256	+ 0.1414
MARCH	2.487	+ 0.045	+ 2.1976	+ 0.0709	+ 0.4475

Table 21. Growth and rate of production of L. crassipes juniors.

PERIOD	Mean dry wt. per month in mgs.	Growth rate per month mgs/month/mg	Rate of production per month $mg/m^2/month$	Rate of production per day $mg/m^2/day$	Production $cals/m^2/day$
MARCH	0.6333				
APRIL	0.6803	+ 0.074	+ 0.6332	+ 0.0211	+ 0.1142
MAY	0.7385	+ 0.085	+ 0.7197	+ 0.0232	+ 0.1253
JUNE	0.8252	+ 0.117	+ 1.4987	+ 0.0499	+ 0.2821
JULY	0.8596	+ 0.042	+ 0.6211	+ 0.0200	+ 0.1099
AUGUST	0.8971	+ 0.043	+ 0.7340	+ 0.0237	+ 0.1444
SEPTEMBER	0.9181	+ 0.023	+ 0.4179	+ 0.0139	+ 0.0753
OCTOBER	0.8281	- 0.098	- 1.6699	- 0.0538	- 0.2921
NOVEMBER	0.7829	- 0.054	- 0.6874	- 0.0229	- 0.1247
DECEMBER	0.7779	- 0.013	- 0.1191	- 0.0036	- 0.0940
JANUARY	0.6209	- 0.084	- 1.2450	- 0.0402	- 0.2156
FEBRUARY	0.6668	+ 0.074	+ 0.7326	+ 0.0262	+ 0.1408
MARCH	0.7538	+ 0.130	+ 1.1024	+ 0.0355	+ 0.1917

Table 22. Growth and rate of production of L. crassipes juveniles.

PERIOD	Mean dry wt. per month in mgs.	Growth rate per month mg/month/mg	Rate of production per month mg/m^2/month	Rate of production per day mg/m^2/day	Production cals/m^2/day
MARCH	0.1668				
APRIL	0.2004	+ 0.201	+ 0.4695	+ 0.0156	+ 0.0806
MAY	0.2375	+ 0.185	+ 0.4290	+ 0.0138	+ 0.0715
JUNE	0.2659	+ 0.119	+ 0.3366	+ 0.0112	+ 0.0576
JULY	0.2691	+ 0.001	+ 0.0014	+ 0.00005	+ 0.0003
AUGUST	0.2707	+ 0.006	+ 0.0056	+ 0.0002	+ 0.0007
SEPTEMBER	0.2802	+ 0.035	+ 0.0466	+ 0.0015	+ 0.0053
OCTOBER	0.2691	- 0.039	- 0.1451	- 0.0047	- 0.0245
NOVEMBER	0.2311	- 0.038	- 0.1238	- 0.0041	- 0.0218
DECEMBER	0.1868	- 0.192	- 0.1748	- 0.0056	- 0.0288
JANUARY	0.1510	- 0.192	- 0.0891	- 0.0028	- 0.0144
FEBRUARY	0.1862	+ 0.233	+ 0.2195	+ 0.0078	+ 0.0405
MARCH	0.2197	+ 0.179	+ 0.1661	+ 0.0054	+ 0.0224

Table 23. Growth and rate of production of L. forficatus adults.

PERIOD	Mean dry wt. per month in mgs	Growth rate per month mg/month/mg	Rate of production per month mg/m^2/month	Rate of production per day mg/m^2/day	Production in cals/ m^2/day
MARCH	11.659				
APRIL	11.803	+ 0.0124	+ 0.0397	+ 0.0013	+ 0.0074
MAY	12.145	+ 0.0289	+ 1.7174	+ 0.0572	+ 0.3146
JUNE	12.341	+ 0.0161	+ 0.9778	+ 0.0359	+ 0.1856
JULY	12.624	+ 0.0229	+ 2.7092	+ 0.0874	+ 0.5143
AUGUST	12.759	+ 0.0106	+ 0.6377	+ 0.0206	+ 0.1214
SEPTEMBER	12.978	+ 0.0172	+ 0.9912	+ 0.0330	+ 0.1934
OCTOBER	13.029	- 0.0039	- 0.4603	- 0.0148	- 0.0867
NOVEMBER	12.915	- 0.0089	- 1.0123	- 0.0337	- 0.1975
DECEMBER	12.852	- 0.0048	- 0.0039	- 0.00012	- 0.0007
JANUARY	12.765	- 0.0067	- 0.0297	- 0.00096	- 0.0053
FEBRUARY	12.843	+ 0.0061	-	-	-
MARCH	12.990	+ 0.0114	+ 0.0141	+ 0.00045	+ 0.0026

Table 24. Growth and rate of production of L. forficatus juniors.

PERIOD	Mean dry wt. per month in mgs	Growth rate per month mg/month/mg	Rate of production per month mg/m^2/month	Rate of production per day mg/m^2/day	Production in cals/ m^2/day
MARCH	4.821				
APRIL	5.013	+ 0.0398	+ 1.1727	+ 0.0391	+ 0.2136
MAY	5.256	+ 0.0485	+ 1.4456	+ 0.0466	+ 0.2544
JUNE	5.439	+ 0.0348	+ 1.5320	+ 0.0511	+ 0.2836
JULY	5.532	+ 0.0171	+ 0.5119	+ 0.0165	+ 0.0801
AUGUST	5.618	+ 0.0155	+ 0.4677	+ 0.0151	+ 0.0835
SEPTEMBER	5.785	+ 0.0297	+ 3.0288	+ 0.1009	+ 0.5566
OCTOBER	5.764	- 0.0036	- 0.2688	- 0.0087	- 0.0478
NOVEMBER	5.687	- 0.0133	- 0.5865	- 0.0195	- 0.1074
DECEMBER	5.611	- 0.0134	- 0.7869	- 0.0254	- 0.1383
JANUARY	5.585	- 0.0046	- 0.0017	- 0.00005	- 0.0003
FEBRUARY	5.662	+ 0.0138	+ 0.4209	+ 0.0150	+ 0.0819
MARCH	5.764	+ 0.0184	+ 0.0790	+ 0.0025	+ 0.1393

Table 25. Growth and rate of production of L. forficatus juveniles.

PERIOD	Mean dry wt. per month in mgs.	Growth rate per month mg/month/mg	Rate of production per month mg/m^2/month	Rate of production per day mg/m^2/day	Production in cals/ m^2/day
MARCH	0.687				
APRIL	0.751	+ 0.0899	+ 0.2814	+ 0.0094	0.0491
MAY	0.846	+ 0.1265	+ 0.3981	+ 0.0128	0.0672
JUNE	0.909	+ 0.0745	+ 0.3454	+ 0.0115	0.0603
JULY	0.947	+ 0.0418	+ 0.1305	+ 0.0043	0.0220
AUGUST	0.991	+ 0.0465	+ 0.1454	+ 0.0047	0.0245
SEPTEMBER	1.072	+ 0.0817	+ 0.0035	+ 0.00012	0.0006
OCTOBER	1.036	- 0.0336	- 0.1579	- 0.0051	- 0.0266
NOVEMBER	0.963	- 0.0705	- 0.2169	- 0.0072	- 0.0378
DECEMBER	0.932	- 0.0322	-	-	-
JANUARY	0.912	- 0.0214	- 0.1040	- 0.0034	- 0.0175
FEBRUARY	0.939	+ 0.0296	+ 0.0488	+ 0.0017	+ 0.0091
MARCH	1.014	+ 0.0798	+ 0.1231	+ 0.0039	+ 0.0207

rates of L. forficatus were calculated from the monthly mean dry weights (in mgs)/mg/month. Positive growth occurred from February to September and negative growth from October to January. Growth in L. forficatus was not constant but varied with seasonal changes.

(v) Moulting in L. crassipes and L. forficatus

Moulting in both species was observed during the summer and autumn. Figures 56 and 57 show the marked increase in mean monthly wet weights of L. forficatus when larva 4 moults to post larval stadium I which in turn moults to post larval stadium II. The standard errors indicated represent 95% confidence limits. Thus each moult was accompanied with a significant increase in mean wet weight as well as a head width increase and changes in morphological characters. If it is assumed that larva 4 collected in March develops from eggs hatching in summer or early autumn then the juvenile stage could be completed within a period of one year. In Figure 56, during the period March to October, a gradual increase in mean wet weight was observed with a significant increase in wet weight when moulting occurred, thus wet weight measurements were probably a record of growth and not of the water content of the centipede.

In L. forficatus post larval stadia II, III and IV (Figs. 58, 59 and 60) moulted during the period June to August, and increases in mean live weights were coincident with change in head width and morphological characters. In all post larval stadia monthly mean wet weight increases were observed during the period

FIG. 56. MEAN MONTHLY INCREASE IN LIVE WEIGHT OF L. FORFICATUS FROM LARVAL STADIUM 4 TO POST LARVAL STADIUM I.

FIG. 57. MEAN MONTHLY INCREASE IN LIVE WEIGHT OF L. FORFICATUS FROM POST LARVAL STADIUM I TO POST LARVAL STADIUM II.

FIG. 58. MEAN MONTHLY INCREASE IN LIVE WEIGHT OF L. FORFICATUS FROM POST LARVAL STADIUM II TO POST LARVAL STADIUM III.

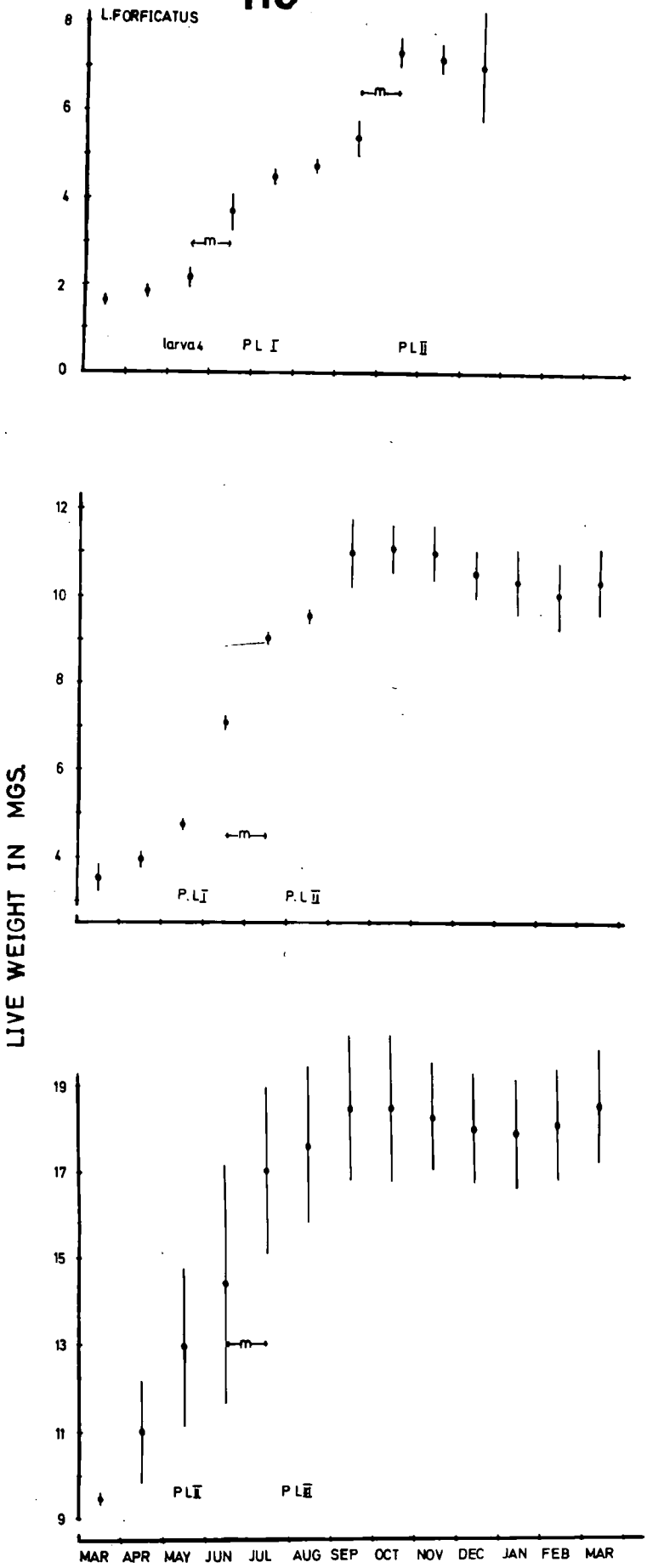

L.FORFICATUS
larva 4
P L I
P L II
P.L I
P.L II
P L III
P L IV
m
LIVE WEIGHT IN MGS.
MAR APR MAY JUN JUL AUG SEP OCT NOV DEC JAN FEB MAR

FIG. 59. MEAN MONTHLY INCREASE IN LIVE WEIGHT OF L. FORFICATUS FROM POST LARVAL STADIUM III TO POST LARVAL STADIUM IV.

FIG. 60. MEAN MONTHLY INCREASE IN LIVE WEIGHT OF L. FORFICATUS FROM POST LARVAL STADIUM IV TO ADULT STAGE.

FIG. 61. MEAN MONTHLY INCREASE IN LIVE WEIGHT OF L. FORFICATUS ADULTS.

March to September/October (see Figures 58, 59 and 60) followed by a gradual decrease in mean wet weight till January and again increasing in weight February/March. The adults that survived for a period of one year moulted once, gaining in weight with the moult and increasing in head width. L. forficatus adults were found to increase in live weight from March to September (Fig. 61), declined in weight till January to increase again in February and March. Thus in all developmental stages of L. forficatus increases in weight were observed in spring, summer and early autumn with a gradual decrease in late autumn and winter.

A similar phenomenon was observed in L. crassipes. Only one stage of the juvenile stadium was used in growth experiments. The post larval stadium I collected in March gradually increased in weight monthly to moult in June/July to post larval stadium II, which continued to increase in weight till November (Fig. 62), decreased from December to February, and increased in March. Moulting from post larval stadia I to II was caused by a significant increase in wet weight together with a change in head width and morphological characters. Post larval stadia II, III and IV (Figs. 63, 64 and 65) showed an increase in mean wet weights from March to September followed by a decrease from October to January to increase again in February and March. Moulting from post larval stadia II to III, III to IV and IV to Adult occurred from June to August and was coincident with a significant increase in mean wet weight together with a change in

FIG.59

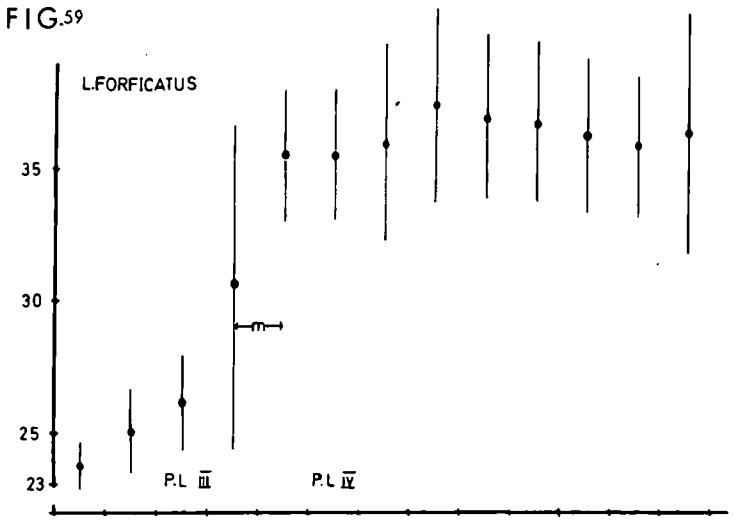
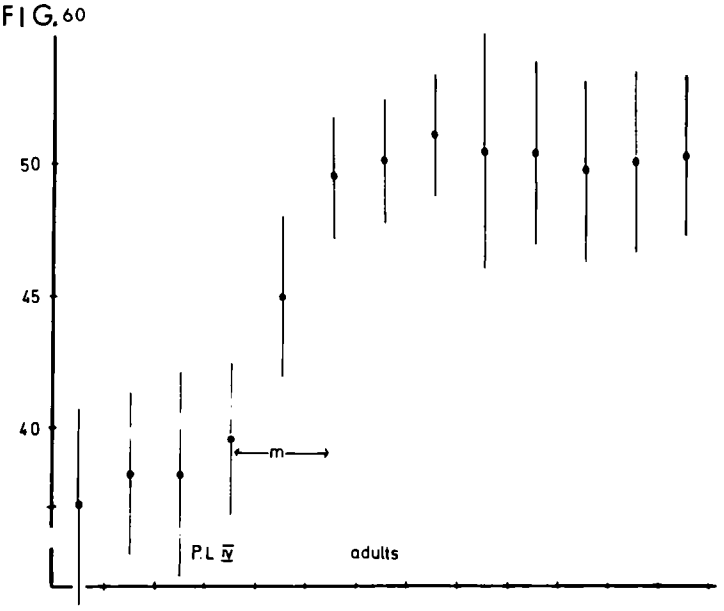


FIG.60



MEAN LIVE WEIGHT IN MGS.

FIG.61

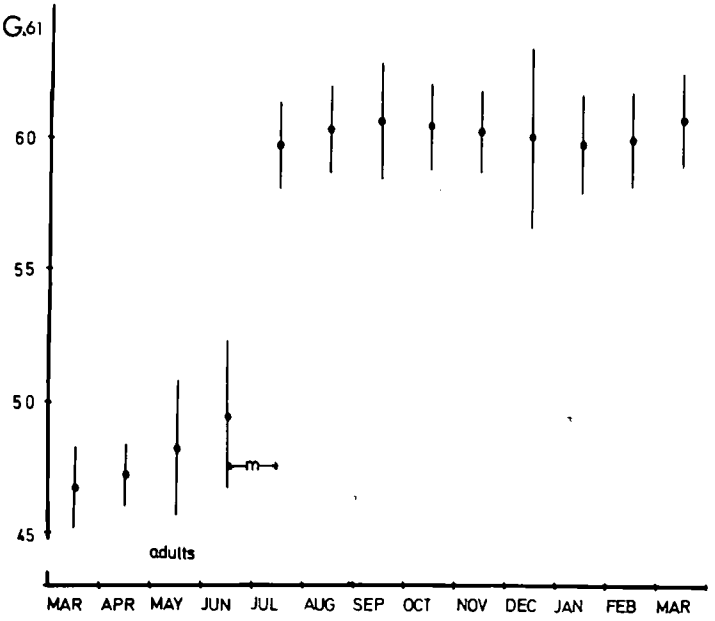


FIG. 62. MEAN MONTHLY INCREASE IN LIVE WEIGHT OF L. CRASSIPES FROM POST LARVAL STADIUM I TO POST LARVAL STADIUM II.

FIG. 63. MEAN MONTHLY INCREASE IN LIVE WEIGHT OF L. CRASSIPES FROM POST LARVAL STADIUM II TO POST LARVAL STADIUM III.

FIG. 64. MEAN MONTHLY INCREASE IN LIVE WEIGHT OF L. CRASSIPES FROM POST LARVAL STADIUM III TO POST LARVAL STADIUM IV.

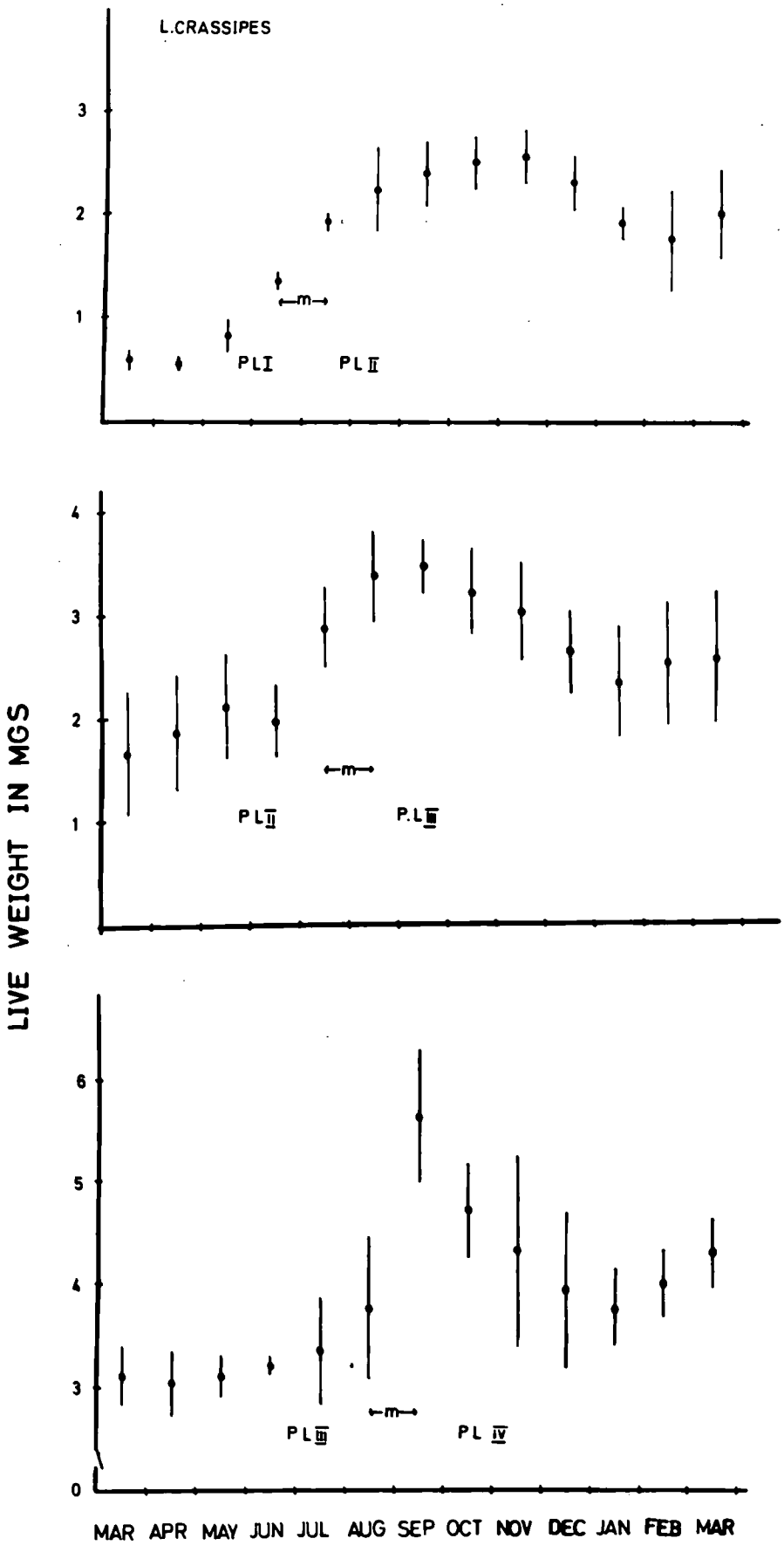
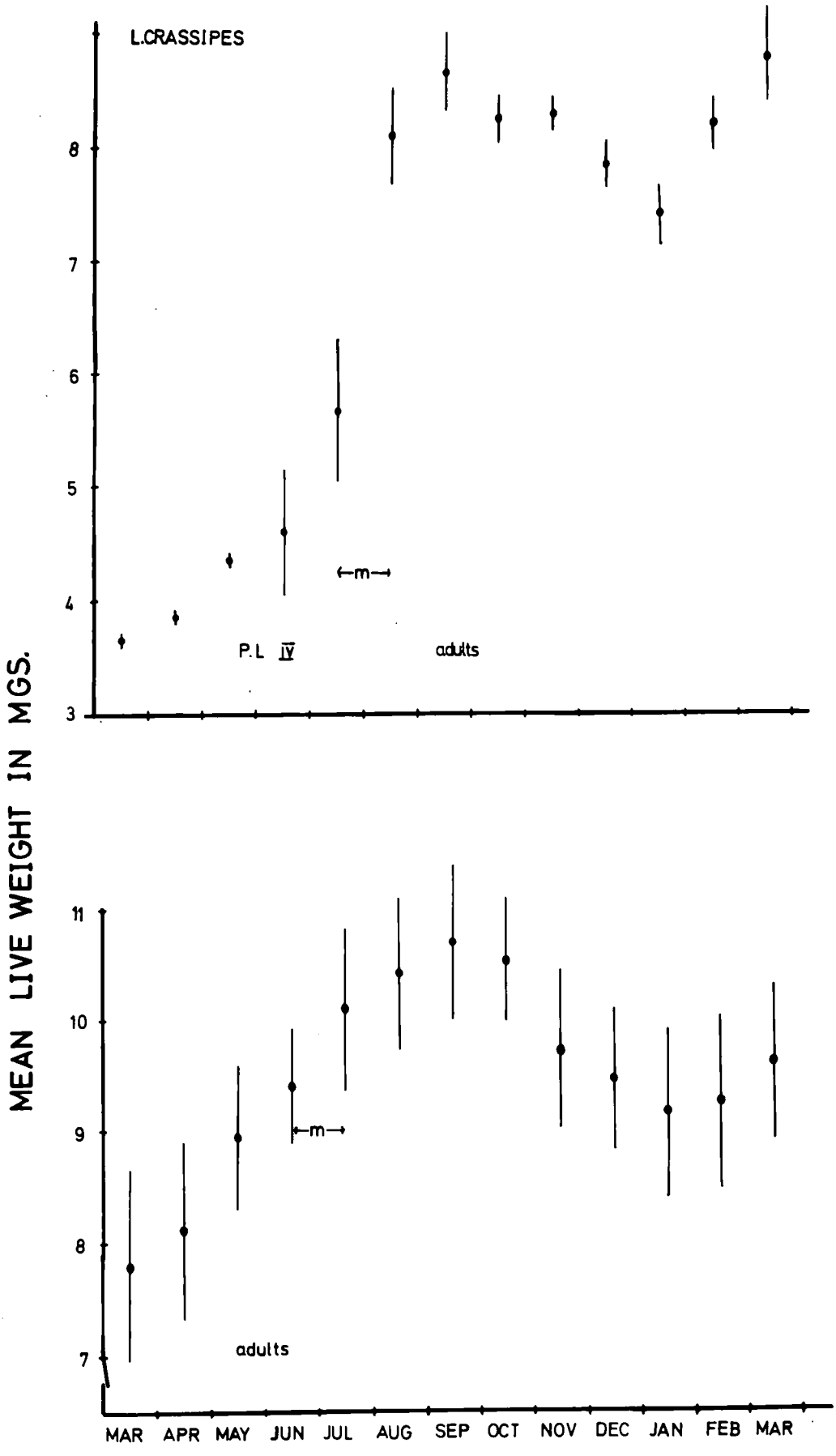

L.CRASSIPES
LIVE WEIGHT IN MGS
PL I
PL II
PL III
PL IV
m
MAR APR MAY JUN JUL AUG SEP OCT NOV DEC JAN FEB MAR

FIG. 64. MEAN MONTHLY INCREASE IN LIVE WEIGHT OF L. CRASSIPES FROM POST LARVAL STADIUM IV TO ADULT STAGE.

FIG. 65. MEAN MONTHLY INCREASE IN LIVE WEIGHT OF L. CRASSIPES ADULTS.


L.CRASSIPES
8
7
6
5
4
3
←m→
P.L IV
adults
MEAN LIVE WEIGHT IN MGS.
11
10
9
8
7
←m→
adults
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN
FEB
MAR

head width. The increase and decrease in mean wet weights followed the pattern of the post larval stadia.

In L. forficatus, larval stadium 4 moulted rapidly to post larval stadium I which in turn moulted to post larval stadium II within a period of six months, thus indicating that the juvenile stage of both species lasts for a period of one year. The rapid development in the juvenile stage is supported by several researchers (Verhoeff 1925, Brocher 1930, and Roberts 1957). The three post larval stadia (II, III and IV) comprising the juniors survived for a period of three years, the adults surviving for a period of about two years, thus making a total life span of five to six years for both species. Eason (1964) has arrived at the same conclusion regarding the life span of lithobiids but without experimental evidence. According to Eason the young lithobiids take two years or more before maturity is reached, after which the adults may survive for a period of three years or so, making a total life span of five to six years. Nevertheless, it is possible that the rate of development may be accelerated during favourable climatic conditions and that the three post larval stadia of the junior stage reach maturity within a period of two years and would then accord with the views of Verhoeff (1925) and Roberts (1957).

(vi) Production in L. crassipes and L. forficatus

Production in theory can be calculated from assimilation and respiration using the formula: P = A - R where

P = production in calories, A = assimilation in calories and R = respiration in calories. This method is rarely used in research and many workers (Teal 1957, Saito 1965, Wiegert 1964 and Smalley 1960) have determined production from detailed population studies based on a supposedly efficient sampling programme. Teal (1957) working with Calopsectra dives (Johannsen) and other Diptera determined production by evaluating mortality between samples from the equation given by Ricker (1946):-

$$Pt = Po\,e^{(k - i)t}$$

where k is the rate of growth or net production, i is the rate of mortality, Po is the weight of the population at time zero, and Pt the weight of the population at time t. Using the figures obtained for mortality, Teal calculated the theoretical population size if no mortality occurred. Production data were obtained by applying the mean calorific value to population numbers at the beginning and the end of each life stage. This method suited rapidly growing populations with a one year life cycle but was not considered suitable for the evaluation of production by lithobiids. Smalley (1960) working with the grasshopper Orchelimum fidicinium estimated production growth per unit weight between sample periods of the survivors and multiplying the mean weight increment during this period by the number of animals surviving at that time. Similarly, Wiegert (1964) determined the growth of the nymphs P. spumarius and in 1965 the growth rates of the grasshoppers using mean dry weights of individuals obtained from population samples.

In the present study the numbers in the population samples were low and it was not considered advisable to determine the growth rate and hence the production of the two species, by using the mean dry weights in the population studies. This is why separate growth experiments were conducted for an accurate estimation of the growth rate of juveniles, juniors and adults of L. crassipes and L. forficatus. The growth rate multiplied by the monthly biomass data (dry weight in mgs) for each category gave the monthly rate of production in mgs/m^2/month. Thus for L. forficatus a positive production was observed from February to September and negative production from October to January following the pattern (Tables 25-27) of growth rates. The absence of production figures for L. forficatus adults and juveniles during the period and December is due to the lack of population data. Using the mean calorific value of L. forficatus juveniles, juniors and adults for each season the production rate was expressed as cals/m^2/day for each category. On a similar basis the production rate of L. crassipes in cals/m^2/day (Tables 22-24) was computed from monthly biomass data for each of the categories concerned.

In both species the growth rates and hence the rate of production followed a similar pattern being affected by seasonal changes. The increase in production with season is coincident with increase in density of L. crassipes and L. forficatus. Since the increase in the production of ova in both species occurs during the

period of positive production it could be assumed that mean dry weights recorded reflected the development of reproductive tissue in the production figures obtained.

CHAPTER VIII

Assimilation and energy flow of L. crassipes and L. forficatus

(i) Assimilation

It is difficult for one worker within a limited period of time to measure accurately all parameters in connection with the population energetics of two species of centipedes. As such the energy of assimilation of L. crassipes and L. forficatus was calculated using the commonly used energy flow equation:-

$$A = R + P$$

This equation can be applied to whole ecosystems, species populations or single individuals. In terms of species populations A = assimilation of energy by the population, R = heat loss as a function of respiration and P = net production of the population as a result of growth. Thus assimilation of both species for each month is the sum of respiration and net production of each month. Tables 26-31 show on a monthly basis the numbers, live weight, dry weight and calorific content/m^2 for each of the three categories of the two species L. crassipes and L. forficatus. Tables 32-37 show the biomass in cals/m^2, respiration, production and assimilation in cals/m^2/day, indicating the rate of energy flow per month for each species. The assimilation being calculated as the sum of respiration plus production. In L. crassipes assimilation/m^2 followed the biomass fluctuations of juniors and juveniles, the same holds for adults excepting October when assimilation/m^2/day decreased despite an increase in biomass. Fluctuations in assimilation/m^2/day in each category of L. forficatus also followed biomass fluctuations except

Table 26. Monthly biomass in cals/m^2 in a population of L. crassipes adults.

PERIOD	Mean nos. per m^2	Mean live wt. (mgs) per m^2	Mean dry wt. (mgs) per m^2	Biomass in calories per m^2 ash free
APRIL	7.260	76.484	21.402	118.287
MAY	11.835	124.682	34.889	192.791
JUNE	14.259	150.218	42.035	235.345
JULY	21.417	225.628	63.137	353.483
AUGUST	16.698	175.913	49.226	275.616
SEPTEMBER	20.331	214.187	59.936	338.196
OCTOBER	26.103	274.995	76.952	434.199
NOVEMBER	11.947	125.862	35.219	198.723
DECEMBER	11.575	121.943	34.123	187.992
JANUARY	7.157	75.398	21.099	116.237
FEBRUARY	11.064	116.559	32.616	179.791
MARCH	16.566	174.523	48.836	274.532

Table 27. Monthly biomass in cals/m^2 in a population of L. crassipes juniors.

PERIOD	Mean nos. per m^2	Mean live wt. (mgs) per m^2	Mean dry wt. (mgs) per m^2	Biomass in calories per m^2 ash free
APRIL	9.560	33.403	8.557	47.688
MAY	9.460	33.053	8.467	47.186
JUNE	14.346	50.125	12.810	72.555
JULY	16.651	58.178	14.790	83.771
AUGUST	19.120	66.805	17.070	96.684
SEPTEMBER	20.332	71.040	18.170	102.061
OCTOBER	19.071	66.634	17.040	95.714
NOVEMBER	14.244	49.768	12.730	71.504
DECEMBER	9.333	32.609	8.352	46.303
JANUARY	16.565	57.878	14.820	82.162
FEBRUARY	11.064	38.657	9.900	54.885
MARCH	9.476	33.109	8.480	47.259

Table 28. Monthly biomass in cals/m^2 in a population of L. crassipes juveniles.

PERIOD	Mean nos. per m^2	Mean live wt. (mgs) per m^2	Mean dry wt. (mgs) per m^2	Biomass in calories per m^2 ash free
APRIL	11.920	8.606	2.336	12.064
MAY	11.835	8.544	2.319	11.957
JUNE	14.433	10.421	2.829	14.610
JULY	7.119	5.140	1.395	7.196
AUGUST	4.780	3.451	0.937	4.841
SEPTEMBER	6.799	4.909	1.333	6.871
OCTOBER	18.980	13.703	3.720	19.185
NOVEMBER	16.628	12.005	3.259	16.804
DECEMBER	4.650	3.357	0.911	4.697
JANUARY	2.366	1.708	0.464	1.623
FEBRUARY	4.807	3.471	0.942	4.859
MARCH	4.738	3.421	0.928	4.788

Table 29. Monthly biomass in cals/m^2 in a population of L. forficatus adults.

PERIOD	Mean nos. per m^2	Mean live wt. (mgs) per m^2	Mean dry wt. (mgs)	Biomass in cals/ m^2 ash free
APRIL	0.130	11.725	3.205	17.858
MAY	2.410	217.365	59.425	331.225
JUNE	2.463	222.145	60.733	345.931
JULY	4.798	432.746	118.309	673.884
AUGUST	2.440	220.071	60.165	342.701
SEPTEMBER	2.337	210.781	57.626	325.509
OCTOBER	4.786	431.664	118.013	671.410
NOVEMBER	4.719	425.621	116.361	662.010
DECEMBER	0.033	2.976	0.814	4.496
JANUARY	0.180	16.235	4.438	24.514
FEBRUARY	-	-	-	-
MARCH	0.050	4.509	1.233	6.872

Table 30. Monthly biomass in cals/m^2 in a population of L. forficatus juniors.

PERIOD	Mean nos. per m^2	Mean live wt. (mgs) per m^2	Mean dry wt. (mgs) per m^2	Biomass in calories per m^2 ash free
APRIL	4.765	123.161	29.466	161.039
MAY	4.820	124.582	29.807	162.902
JUNE	7.119	181.442	44.024	244.538
JULY	4.841	125.125	29.936	166.283
AUGUST	4.880	126.133	30.177	167.053
SEPTEMBER	16.491	426.243	101.980	562.286
OCTOBER	12.078	312.180	74.690	411.820
NOVEMBER	7.131	184.315	44.098	243.142
DECEMBER	9.497	245.469	58.729	320.015
JANUARY	0.060	1.551	0.371	2.022
FEBRUARY	4.932	127.477	30.499	166.189
MARCH	7.10	183.514	43.906	239.955

Table 31. Monthly biomass in cals/m^2 in a population of L. forficatus juveniles.

PERIOD	Mean nos. per m^2	Mean live wt. (mgs) per m^2	Mean dry wt. (mgs) per m^2	Biomass in calories per m^2 ash free
APRIL	4.765	12.403	3.131	16.390
MAY	4.790	12.468	3.147	16.476
JUNE	7.059	18.374	4.637	24.272
JULY	4.755	12.377	3.124	16.352
AUGUST	4.760	12.390	3.127	16.368
SEPTEMBER	0.066	0.172	0.043	0.227
OCTOBER	7.156	18.627	4.701	24.609
NOVEMBER	4.684	12.192	3.077	16.108
DECEMBER	-	-	-	-
JANUARY	7.398	19.256	4.860	25.442
FEBRUARY	2.511	6.536	1.649	8.630
MARCH	2.350	6.117	1.543	8.078

in the month of December for the junior stage.

(ii) Energy flow through L. crassipes and L. forficatus

The energy flow through an individual organism, a population or entire ecosystems is governed by the First Law of Thermodynamics which states that whatever quantity of energy enters an organism, exactly the same amount is surrendered by it in some form or other. This is supported from the results of studies of Odum (1956) and Teal (1957) on Silver Springs and Root Spring respectively. In Silver Springs the energy entering the ecosystem and ultimately leaving it was exactly the same, while in Root Spring the discrepancy between the energy entering the ecosystem and leaving the ecosystem was attributed to experimental error.

The fate of the energy entering the centipede populations can be summarised by the equation:-

$$A = R + P$$

when all parameters are given in cals/m^2. In energy flow studies population size at any one time is equivalent to the standing crop and is generally measured in terms of dry weight/m^2 or calories/m^2. The loss of metabolic heat by the standing crop of centipedes was ascertained by measuring the oxygen consumption per unit weight of living tissue and applied to the biomass data. A measure of the energy absorbed by the population for production was determined from growth experiments and expressed in terms of calories per unit weight, and applied to biomass data. The population energy flow for both

species of L. crassipes and L. forficatus can be represented as respiration plus production and is equal to the assimilation or the intake of metabolisable energy. The energy flow of L. crassipes and L. forficatus for each of the categories: adults, juniors and juveniles, is expressed in calories/m^2/day in Tables 32-34, and 35-37 respectively, and must be converted to an annual basis.

In compiling the annual energy budget for both L. crassipes and L. forficatus (Table 38) the energy flow of the mean annual standing crop was expressed in cals/m^2/annum for each category. The parameters of the energy flow equation, namely respiration, production and assimilation in cals/m^2/day shown in Tables 32-37 were converted to cals/m^2/annum. In calculating the energy budget the following conversions were made. Respiration of acclimatised animals at laboratory temperatures (5°C, 10°C and 15°C) were converted to respiratory rates at field temperature, using the regression equations. The results were applied to population data. The oxycalorific value used in the conversion of oxygen consumed by the centipedes to calories was the mean calorific value of glycogen, fat and protein (4.793 Kcals/L.). The failure to consider mortality and egg production in both species would result in an underestimate of total production obtained. As lithobiids fed on moulted exoskeleton it was assumed that loss due to moulting was compensated. The L. crassipes population with a mean standing crop of (Table 38) 321.86 cals/m^2/annum transformed 1268.05 cals/m^2/annum as respiration and 73.56 cals/m^2/annum as production. The assimilation of

Table 32. Energy flow through a population of L. crassipes adults.

PERIOD	Biomass cals/ m^2 ash free	Respiration cals/m^2/day R	Production cals/m^2/day P	Assimilation cals/m^2/day A
APRIL	118.287	0.9502	+ 0.2441	1.1943
MAY	192.791	1.8071	+ 0.4848	2.2919
JUNE	235.345	2.4537	+ 0.6746	3.1283
JULY	353.483	3.8412	+ 0.6839	4.5251
AUGUST	275.616	2.8937	+ 0.1156	3.0093
SEPTEMBER	338.196	3.5953	+ 0.3267	3.9220
OCTOBER	434.199	3.9925	- 0.3781	3.6144
NOVEMBER	198.723	1.4767	- 0.3971	1.0796
DECEMBER	187.992	1.1082	- 0.3152	0.7930
JANUARY	116.237	0.6678	- 0.2663	0.4015
FEBRUARY	179.791	1.1933	+ 0.1414	1.3347
MARCH	274.532	1.9473	+ 0.4475	2.3948
TOTAL		25.9270	1.7619	27.6889

Table 33. Energy flow through a population of L. crassipes juniors.

PERIOD	Biomass cals/ m^2 ash free	Respiration cals/m^2/day R	Production cals/m^2/day P	Assimilation cals/m^2/day A
APRIL	47.688	0.6225	+ 0.1142	0.7367
MAY	47.186	0.7718	+ 0.1253	0.8971
JUNE	72.555	1.3665	+ 0.2821	1.6486
JULY	83.771	1.6932	+ 0.1099	1.8031
AUGUST	96.684	1.8377	+ 0.1444	1.9821
SEPTEMBER	102.061	2.0266	+ 0.0753	2.1019
OCTOBER	95.714	1.5176	- 0.2921	1.2255
NOVEMBER	71.504	0.8530	- 0.1247	0.7283
DECEMBER	46.303	0.3630	- 0.0940	0.2690
JANUARY	82.162	0.6191	- 0.2156	0.4035
FEBRUARY	54.882	0.5292	+ 0.1408	0.6700
MARCH	47.259	0.5179	+ 0.1917	0.7096
TOTAL		12.7181	0.4573	13.1754

Table 34. Energy flow through a population of L. crassipes juveniles.

PERIOD	Biomass cals/ m^2 ash free	Respiration cals/m^2/day R	Production cals/m^2/day P	Assimilation cals/m^2/day A
APRIL	12.064	0.2879	+ 0.0806	0.3685
MAY	11.957	0.3558	+ 0.0715	0.4273
JUNE	14.610	0.5106	+ 0.0576	0.5682
JULY	7.196	0.2690	+ 0.0003	0.2693
AUGUST	4.841	0.1719	+ 0.0007	0.1726
SEPTEMBER	6.871	0.2518	+ 0.0053	0.2571
OCTOBER	19.185	0.5596	- 0.0245	0.5351
NOVEMBER	16.804	0.3646	- 0.0218	0.3428
DECEMBER	4.697	0.0648	- 0.0288	0.0360
JANUARY	1.623	0.0312	- 0.0144	0.0168
FEBRUARY	4.859	0.0831	+ 0.0405	0.1236
MARCH	4.788	0.0944	+ 0.0224	0.1168
TOTAL		3.0447	0.1894	3.2341

Table 35. Energy flow through a population of L. forficatus adults.

PERIOD	Biomass cals/ m^2 ash free	Respiration cals/m^2/day R	Production cals/m^2/day P	Assimilation cals/m^2/day A
APRIL	17.858	0.1362	+ 0.0074	0.1436
MAY	331.225	2.9754	+ 0.3146	3.2900
JUNE	345.931	3.4754	+ 0.1856	3.6610
JULY	673.884	7.1184	+ 0.5143	7.6327
AUGUST	342.701	3.4935	+ 0.1214	3.6149
SEPTEMBER	325.509	3.4187	+ 0.1934	3.6121
OCTOBER	671.410	5.8593	+ 0.0867	5.9460
NOVEMBER	662.010	4.6512	- 0.1975	4.4537
DECEMBER	4.496	0.0243	- 0.0007	0.0236
JANUARY	24.514	0.1269	- 0.0053	0.1216
FEBRUARY	- (nil)	-	-	-
MARCH	6.872	0.0456	+ 0.0026	0.0482
TOTAL		31.3249	1.2225	32.5474

Table 36. Energy flow through a population of L. forficatus juniors.

PERIOD	Biomass cals/ m^2 ash free	Respiration cals/m^2/day R	Production cals/m^2/day P	Assimilation cals/m^2/day A
APRIL	161.039	1.5442	+ 0.2136	1.7578
MAY	162.902	1.8487	+ 0.2544	2.1031
JUNE	244.538	2.7967	+ 0.2836	3.0803
JULY	166.283	2.2306	+ 0.0801	2.3107
AUGUST	167.053	2.1619	+ 0.0835	2.2454
SEPTEMBER	562.286	7.4527	+ 0.5566	8.0093
OCTOBER	411.820	4.5606	- 0.0478	4.5128
NOVEMBER	243.142	2.1838	- 0.1074	2.0764
DECEMBER	320.015	2.1742	- 0.1383	2.0359
JANUARY	2.022	0.1338	- 0.0003	0.1335
FEBRUARY	166.189	1.2904	+ 0.0819	1.3723
MARCH	239.955	2.0476	+ 0.1393	2.1869
TOTAL		30.4252	1.3992	31.8244

Table 37. Energy flow through a population of L. forficatus juveniles.

PERIOD	Biomass cals/ m^2 ash free	Respiration cals/m^2/day R	Production cals/m^2/day P	Assimilation cals/m^2/day A
APRIL	16.390	0.3424	+ 0.0491	0.3915
MAY	16.476	0.3858	+ 0.0672	0.4530
JUNE	24.274	0.6887	+ 0.0603	0.7490
JULY	16.352	0.4912	+ 0.0220	0.5132
AUGUST	16.368	0.4717	+ 0.0245	0.4962
SEPTEMBER	0.227	0.0067	+ 0.0006	0.0073
OCTOBER	24.609	0.6042	- 0.0266	0.5776
NOVEMBER	16.108	0.3155	- 0.0378	0.2777
DECEMBER	-	-	-	-
JANUARY	25.442	0.3544	- 0.0175	0.3369
FEBRUARY	8.630	0.1428	+ 0.0091	0.1519
MARCH	8.078	0.1477	+ 0.0207	0.1684
TOTAL		3.9511	0.1716	4.1227

Table 38. Energy budget of L. crassipes and L. forficatus.

Species	Mean standing crop per annum cals/m^2/annum	Respiration of standing crop cals/m^2/annum	Production of standing crop cals/m^2/annum	Assimilation of standing crop cals/m^2/annum
L. crassipes				
Adults	242.09	788.612	53.893	842.204
Juniors	70.65	386.842	13.909	400.752
Juveniles	9.12	92.600	5.759	98.371
Total	321.86	1268.054	73.561	1341.327
L. forficatus				
Adults	283.86	952.796	37.182	989.989
Juniors	237.27	925.421	42.559	967.980
Juveniles	14.41	120.176	5.219	125.395
Total	535.54	1998.393	84.960	2083.364

the population totalled 1341.33 cals/m^2/annum. In L. forficatus a mean standing crop of 535.54 cals/m^2/annum (Table 38) respired 1998.39 cals/m^2/annum and 84.96 cals/m^2/annum was absorbed by the population for production. The total assimilation of the L. forficatus population amounted to 2083.36 cals/m^2/annum. Population density of L. forficatus was smaller than that of L. crassipes, but upon conversion gave a higher biomass which transformed a greater quantity of energy. In both species the proportion of energy flow through juveniles was low and the major contribution to energy flow in the total population was by adults.

CHAPTER IX

Discussion

(1) Terminology and nomenclature

Macfadyen (1963a) stressed the need for the study of taxonomy in order to distinguish ecological divergence among species, thus avoiding generalisations about biological rôles of certain groups of animals. In the study of the bioenergetics of the centipedes L. crassipes and L. forficatus it was considered essential to make use of all available taxonomic data. Using Verhoeff's classification (1925) it was difficult to define certain stadia of L. forficatus with accuracy. However, the more recent classification of lithobiids by Eason (1964), based on the descriptions of stadia of L. variegatus, was adopted. The life stadia of L. crassipes were unknown, and morphological characters that were known to separate the stadia of L. curtipes (a species related to L. crassipes) and described by Verhoeff (1925) were used successfully. This division of stadia of L. crassipes fitted into the scheme of developmental stadia of lithobiids suggested by Eason and was based on morphological differences in the number of limbs, ocelli, antennae, mouth parts, coxal pores and development of genitalia. The present author was able to correlate stadial development with head width of L. crassipes. The presence of eight stadia for L. crassipes was confirmed graphically by a plot of head width versus cumulative frequency on probability paper. The various stadial groupings were of great value in estimating biomass and population energy flow. Lithobiids, being predators, occurred only in small numbers

in the sample area and it was not practicable to determine energy flow for each individual stadium because of the necessary grouping of the developmental stadia into juveniles and juniors. The population energy flow of each species was thus given for three categories, namely adults, juniors and juveniles.

(ii) Population and breeding

For the purpose of evaluating energy flow through populations, the population density of L. crassipes and L. forficatus inhabiting the sample area (birch/alder woodland) was determined by adopting techniques based on sampling methods reviewed by Macfadyen (1962). The microhabitats of both species (decayed logs, litter, and soil) were sampled in a stratified random manner. The extraction apparatus was designed to reduce as far as possible any mortality occurring in the process of extraction. The apparatus (a modified Tullgren) showed an efficiency of 82.3%, and agreed with the findings (75%) of Macfadyen (1962) for the efficiency of a controlled-draught funnel extractor for lithobiids.

The comparison of mean monthly densities and variance in L. crassipes and L. forficatus (Chapter III) showed in all instances that the variance was nearly equal to or less than the mean, a graphical illustration of these results based on Taylor's Power Law revealed a random distribution. Random distributions are rare in nature but the investigations of Colquhoun (1942) on Coccinella 7-punctata, Banks (1954) on Adalia 2-punctata and Roberts (1957) on L. variegatus

have shown that random distributions do occur in nature. Auerbach (1951) in determining populations of centipedes used the term " uniformly distributed" for species populations in prairie and woodland in the U.S.A. In the above instances, and the present study, the noteworthy feature is that all are predators. As shown in Chapter III the behaviour and biology of centipedes also support random distribution and it could be suggested that low numbers and random distribution are to the benefit of predators in terrestrial habitats.

The population densities of L. crassipes and L. forficatus revealed population peaks in July and October, and June and October respectively. No significant difference was observed between peak populations but evidence from ova production studies support the existence of two peak populations for each species. Ova production reached a maximum in June and September for L. crassipes and May and September for L. forficatus. The increase in population density was assumed to result from the addition of young larvae hatching from non-diapause eggs. Population fluctuations of both species were affected by temperature and rainfall. The influence of climatic conditions on population fluctuations of centipedes in prairie and woodland have been observed by Auerbach (1951) and found to have a similar effect.

(iii) Bomb calorimetry

Golley (1961) and Cummins (1967) have compiled tables of calorific values of biological material. Most of the calorific

values range between 4.0 Kcals/gm to 7.0 K cals/gm. The calorific values of the lithobiid material ranged between 5.0 Kcals/gm and 6.0 Kcals/gm which was in agreement with the range indicated above. Wiegert (1964) observed variations in calorific value with season in P. spumarius larva and adults. As variation in calorific value was suspected in lithobiids, determinations of calorific data were made monthly, grouped according to seasons and subjected to significance tests. Significant differences in calorific value with season were only observed for adult males and females of both species. The maximum calorific value recorded for adult males and females probably corresponded with reproductive activity of both species. The gradual increase in calorific values per unit weight from juveniles to adults in both species was probably due to the production of tissues with higher calorific values than previously.

(iv) Biomass, numbers and population energy flow

Numbers, biomass and energy flow of the two centipede populations are given in Tables 39 and 40. The energy flow is the sum of respiration and production. In L. crassipes the increase and decrease of numbers per m^2 is followed by corresponding fluctuations in biomass and energy flow. The pattern is similar in L. forficatus except during the months of July and October. In July, though the numbers were low in comparison with June, the biomass increased due to a larger proportion of adults,(Tables 29-31), added to the population, probably due to moulting of the post larval stadium IV. In October

Table 39. Numbers, biomass and energy flow per m^2 in a population of *L. crassipes*.

Month	Numbers/m^2	Dry wt. mgs/m^2	Energy flow cals/m^2/day
APRIL	28.74	32.29	2.298
MAY	33.12	77.91	3.663
JUNE	43.04	57.67	5.344
JULY	45.19	79.32	6.597
AUGUST	40.59	67.24	5.164
SEPTEMBER	47.45	79.44	6.281
OCTOBER	64.15	97.71	5.374
NOVEMBER	42.82	51.21	2.150
DECEMBER	25.55	43.38	1.098
JANUARY	26.07	36.37	0.860
FEBRUARY	26.93	43.46	2.129
MARCH	30.77	57.77	3.220

though the biomass increased with numbers (Table 40), total energy flow was slightly lower than September due to an increase in the population of juveniles which despite high respiratory rate per unit weight had low calorific values. Thus in both species numbers and biomass corresponded with energy flow fluctuations except for minor differences in July and October for L. forficatus mentioned above. In a population which possesses a single generation, as seen in the salt marsh grasshopper Orchelimum fidicinium (Smalley 1959), peak energy flow does not correspond with either peak numbers or peak biomass. The peak energy flow of O. fidicinium occurred during a period where the population was composed of a medium number of medium sized nymphs. This phenomenon can be attributed to a single breeding period per annum for the grasshoppers; unlike the centipedes with two peak breeding periods per annum and lengthy life span where the size class composition was fairly stable throughout the year. Clearly, the population impact of lithobiids as measured in terms of energy flow was reflected in numbers and biomass whereas this was clearly not so in the case of O. fidicinium.

(v) Field temperature and respiration

The monthly mean temperature of the microhabitats inhabited by the centipedes was measured by the inversion of saccharose method (Berthet 1960). Mean temperatures thus recorded, and checked with a set of controls from the same microhabitats, showed no significant differences. The temperature was affected by the vegetal

Table 40. Numbers, biomass and energy flow per m^2 in a population of *L. forficatus*.

Month	Numbers/m^2	Dry wt. mgs/m^2	Energy flow cals/m^2/day
APRIL	9.65	35.79	2.293
MAY	12.02	92.38	5.846
JUNE	16.64	109.39	7.490
JULY	14.38	151.37	10.456
AUGUST	12.08	93.46	6.356
SEPTEMBER	18.89	159.65	11.628
OCTOBER	24.00	197.40	11.036
NOVEMBER	16.53	163.52	6.807
DECEMBER	9.52	59.54	2.059
JANUARY	7.63	9.67	0.592
FEBRUARY	7.44	32.14	1.524
MARCH	9.50	46.68	2.399

cover (trees, shrubs and forbs), and the moisture content of the litter and clayey soil. A noteworthy feature was the inversion of temperature between log and log/ground in spring and autumn (Chapter I) which resembled the observed inversion times noted by Macfadyen (1956) in air/soil temperatures in the Dell in Wytham Woods, Berkshire.

The rates of respiration per unit weight varied with size class. Measurement of the rate of respiration per unit weight of acclimatised centipedes L. crassipes and L. forficatus for each of the categories juveniles, juniors and adults at 5°C, 10°C and 15°C showed that the respiration was temperature dependent. The regression equations from the plot of temperature versus rate of respiration per unit weight (Chapter VI) was used in the determination of field respiratory rates at field temperatures. Similar techniques for the determination of oxygen consumption at field temperatures were used by Smalley (1960), Wiegert (1964 and 1965) and Saito (1965). A Q_{10} of 2.6 and 2.7 which is in agreement with Krogh's curve was obtained for L. crassipes and L. forficatus. Berthet (1963) working with 16 species of Oribatid mites within the same range of temperatures recorded Q_{10s} from 2.6 to 5.6 although it should be noted that he was not working with acclimatised animals.

Using the continuous respirometry method of Phillipson (1962) determination of the rates of respiration proved successful for centipedes. The validity of the resulting rates of respiration were checked using a Warburg respirometer. The estimated

field respiration rates followed the fluctuations of field temperature which were also coincident with the pattern of ova production in both species (Chapter III). It was also observed that the period of moulting May to October (Chapter VII) for both species occurred at the time of increased respiratory activity, thus suggesting that the reproductive and physiological state may, in addition to field temperature, have contributed to the respiratory increases noted. Phillipson (1962 and 1963), Phillipson and Watson (1965) and Wiegert (1965) have shown the variability of respiratory rate with size, physiological condition, and season. Phillipson (1967) has stressed the need for continuous respirometry all the year round, for all stages,for accurate estimation of annual respiratory metabolism of species populations. Population respiratory metabolism of L. crassipes and L. forficatus was evaluated on monthly respirometric studies for all stages for a period of one year. The variations in the respiration rates of each category observed at 5°C, 10°C and 15°C may be due to a combination of temperature and physiological condition. Newell and Northcroft (1967) have shown in certain marine invertebrates e.g. Actinia equina and Cardium edule that the effects of temperature on oxygen uptake due to activity are minimised by progressive reduction in the Q_{10} with increase in temperature. This is contrary to the respiratory phenomenon of the centipedes L. crassipes and L. forficatus which were shown despite allowance for acclimatisation to take place to have a Q_{10} of 2.6 and 2.7 over the temperature range

5^{o}-15^{o}C.

(vi) Growth, moulting and life span

In order to assess growth quantitatively, the mean weight of the centipedes were determined with time. The mean weights of the centipedes were found to fluctuate more rapidly with time than length or head width. Length measurements were discarded as a measure of growth as it was difficult to measure the length of live specimens accurately because of the contractibility and flexibility of the species. Besides weight the only other suitable dimension was head width, but the change of head width was observed only when moulting occurred, a phenomenon with long time intervals between moults. The rate of growth of both species was measured as increase in weight per unit weight per month, and followed a similar pattern, increasing from April to September, decreasing from October to January and to increase again in February and March. Thus growth fluctuations of L. crassipes and L. forficatus closely followed the recorded fluctuations in temperature suggesting that the growth of centipedes was affected by temperature. Itô (1964) showed that the invertebrate spider Lycosa pseudoannulata during a period of starvation showed a decrease in the rate of respiration and body weight. Roberts (1957) working with L. variegatus, L. forficatus and L. dubosqui showed that these centipedes left at 2^{o}C, and then subjected to reduced temperatures (2^{o}C to -8^{o}C) became immobile or died depending on the duration of exposure. In

L. crassipes and L. forficatus respiratory metabolism during the winter was low and was accompanied by a negative growth rate indicating restricted activity and possibly starvation.

Moulting in L. crassipes and L. forficatus occurred from May to October. As mentioned in Chapter VII the moulting phenomenon was recognised by a change in head width concurrent with a significant increase in body weight and change in colour of the newly formed exoskeleton. The centipedes fed on the moulted exoskeleton, thus providing evidence that the energy lost as a result of the discarding of the exoskeleton was regained by the animal. The significant increase in body dry weight caused as a result of moulting supported the view that the mean monthly body weights recorded in growth experiments were a measure of growth and not varying water content of the species concerned.

Hypotheses on the duration of instars and the life span of lithobiids given by Verhoeff (1925), Brocher (1930) and Eason (1964) were based on assumptions without any detailed experimental evidence. Verhoeff (1925) predicted a period of three to four years and Eason (1964) a duration of about five to six years for the entire life span of lithobiids. The present study provided evidence to indicate that the juveniles had a total life span of about one year and the juniors a period of one year for each of the three instars. The adults lived for a period of one and a half years

or more; thus the longevity of each of the two species totalled five to six years, agreeing with the prediction of Eason.

(vii) Production, Respiration and Assimilation

The estimated production figures were based on the rate of growth of the three categories of L. crassipes and L. forficatus. The production calculated (73.56 cals/m^2/annum for L. crassipes and 84.96 cals/m^2/annum for L. forficatus) may be termed net production of the population and is equivalent to the net production of Engelmann (1966). Production/respiration ratios in both species ranged between 4-6% indicating that the amount of energy apportioned to growth was low. Engelmann (1966) proposed a relationship between ~~maintenance~~ metabolism (respiration) and net production and obtained the following regression equation:-

$$\text{Log } R = 0.62 + 0.86 \log p$$

(where R represents the number of K calories respired by the population per m^2/annum and p represents the net productivity in Kcals/m^2/annum). When the data of Golley (1960) was incorporated ~~the slope of~~ the regression altered from 0.62 to one of 0.55. The population studies used by Engelmann to obtain the normal regression (log R = 0.62 + 0.86 log p) were on species that had a maximum life span of two years or less. The centipede populations with a species life span of more than two years fit the Engelmann equation for poikilotherms.

Respiration plus production gave the figure for assimilation in the lithobiids and represented the total energy flow

for each species. Following Wiegert (1965) it can be argued that the production (P)/Assimilation (A) ratio was low (5.5% for L. crassipes and 4.1% for L. forficatus) due to the lengthy life span of the centipedes and their being active for most of the year (spring to autumn). In contrast, an invertebrate with a one year generation, P. spumarius (Wiegert 1964), had a P/A ratio of 42% in a small alfalfa field. For grasshoppers, which also possessed a one year life span (Wiegert 1965), the P/A ratio ranged between 35-39%. Oribatid mites (Engelmann 1961) are again active all the year round and have a maximum life span of less than two years and the P/A ratio was 21%. Golley and Gentry (1964) studied the energetics of the harvester ant Pogonomyrmex badius and obtained a low P/A ratio of about 1%. The harvester ant being a small active animal had a high oxygen consumption value and a low annual production value. Since harvester ants like centipedes are active during most of the year and live longer than two years the P/A ratio was low.

(viii) Comparison of energy flow

The average total energy flow of the lithobiids (L. crassipes and L. forficatus) was 1.7 Kcals/m^2/annum. Unfortunately total energy flow figures for other invertebrate carnivores are not available. The lithobiid energy flow was low when compared with the grasshopper O. fidicinium (Smalley 1960) which had a total energy flow of 30.0 Kcals/m^2/annum. The major contribution of grasshoppers was a result of the standing crop being eight times greater and

production thirteen times larger than lithobiids (a mean standing crop of 0.43 Kcals/m^2/year and average production of 0.08 Kcals/m^2/year). The harvester ant P. badius (Golley 1960) exhibits a high energy flow of 31.0 Kcals/m^2/year though its annual production of 0.09 Kcals/m^2/year was similar to lithobiids. The high energy flow of the harvester ant was mainly due to high respiratory metabolism (30.9 Kcals/m^2/year). Respiratory metabolism of the harvester ant was 19 times greater than centipedes (1.6 Kcals/m^2/year) even though the standing crop was much less (50%). The energy flow (0.88 Kcals/m^2/year) of the spittle bug P. spumarius (Wiegert 1964) was lower than the centipedes though production was approximately the same. The annual respiratory metabolism of the lithobiids was slightly higher than spittle bugs even though the standing crop of the lithobiids was 3 times greater. Thus energy flow provides not only a means of comparing entirely different ecosystems (Odum 1968) but also a means of evaluating the relative importance of populations with diverse sizes and rates of metabolism.

Summary

(1) The developmental stadia of L. crassipes hitherto unknown are described. The pattern of development in L. crassipes follows the general lithobiid plan (Eason 1964) with eight developmental stadia. The duration of the instars was determined and the life span of lithobiids was established from experimental data.

(2) The fluctuations in population density of lithobiids were followed over a period of one year in a birch/alder woodland. A relationship between ova production and population density was shown to occur.

(3) Centipedes being predators were found to have a random distribution, thus agreeing with the studies of previous researchers.

(4) Calorific value of lithobiid material varied with season and significant differences in calorific values per unit weight observed for males and females of adults of both species. The calorific value of both species increased from juveniles to reach a maximum in the adult stage (5.3 Kcals - 5.9 Kcals ash free gm for both species).

(5) Biomass determinations were based on regressions obtained from wet weight/dry weight analysis of juveniles, juniors and adults of L. crassipes and L. forficatus. The population biomass showed variations with season for both species. The mean annual biomass being 0.32 Kcals/m^2/annum for L. crassipes and 0.53 Kcals/m^2/annum for L. forficatus.

(6) The rates of respiration per unit weight were found to be temperature

dependent with an average Q_{10} of 2.65 for both species. Knowing field temperatures from direct measurement regressions obtained from the plot of temperature versus respiration, the field respiratory rates of L. crassipes and L. forficatus were determined. The total respiration of both species was expressed as Kcals/m^2/annum (1.26 Kcals/m^2/annum for L. crassipes and 1.99 Kcals/m^2/annum for L. forficatus).

(7) Growth and moulting prevailed during a period when field temperatures gradually increased, suggesting that temperature fluctuations may have contributed towards these phenomena. Production of both species was recorded as Kcals/m^2/annum based on the growth rate (0.07 Kcals/m^2/annum for L. crassipes and 0.85 Kcals/m^2/annum for L. forficatus).

(8) In the calculation of the energy budget for both species assimilation for both species was determined as the sum of respiration and net production. L. crassipes with a mean standing crop of 0.32 Kcals/m^2/annum respired 1.06 Kcals/m^2/annum and assimilated 1.34 Kcals/m^2/annum. L. forficatus with a mean annual standing crop of 0.53 Kcals/m^2/annum, the estimated energy lost from respiration was 1.99 Kcals/m^2/annum with a total assimilation of 2.08 Kcals/m^2/annum.

(9) The production respiration ratio in both species was low indicating that a small amount of energy was apportioned for growth. Centipedes being active animals for most part of the year had a greater

maintenance metabolism. The logarithm of the annual respiration and net production in Kcals/m^2/annum fitted the Engelmann equation (1966) for poikilotherms thus indicating a trend with the data of other researchers.

(10) Numbers, biomass and energy flow patterns of L. crassipes and L. forficatus corresponded with one another. This coincidence is explained on the basis of a fairly stable age composition throughout the year despite the existence of two peak breeding periods annually; the explanation being in the six year life history. The described pattern of fluctuations in numbers, biomass and energy flow contrasts with the patterns exhibited by animals with a one year life cycle.

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Acknowledgements

I am indebted to Dr. J. Phillipson for assistance and advice throughout the period of study. My thanks are also due to Professor D. Barker for facilities in the Department of Zoology, University of Durham. I am grateful to Mr. J. Richardson of the Department of Zoology for assistance in the collection of the centipedes and to Dr. E. H. Eason for the confirmation of the specimens and useful advice.

I wish to thank the members of the Animal Ecology Research Group, University of Oxford, for their kind co-operation during the writing of the thesis. This work was carried out during the tenure of a grant from the University of Ceylon.