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The biology of spider populations in alder woodland (with an emphasis on the energy dynamics of robertus lividus (Theridiidae) and meta segmentata (Argio Pidae)

T.A. Geyer

THE BIOLOGY OF SPIDER POPULATIONS IN ALDER WOODLAND

(WITH AN EMPHASIS ON THE ENERGY DYNAMICS OF

ROBERTUS LIVIDUS (THERIDIIDAE) AND META SEGMENTATA (ARGIO PIDAE)

by

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'No single measurement is intrinsically

significant.   All measurements derive their interest

from their context and the richness of predictive

generalizations that can be produced from them'

L. B. Slobodkin on 'Energy in Animal Ecology' (1962).

ACKNOWLEDGMENTS

ABSTRACT

A survey of a spider community in alder woodland was carried out between 1967 and 1969. From the information on distribution, abundance, and standing states of spiders, two species were selected for an energetics study.

Robertus lividus and Meta segmentata, having different ecological characteristics, were used to evaluate the flow of energy (A) through spider populations. The energy assimilated (A) was estimated from the sum of net production (P) and respiration (R). Such estimates depend from the outset on reliable data on numbers of individuals, for which purpose appropriate sampling methods were devised.

Survivorship and individual growth curves, which were constructed from density and individual biomass at each census, were used to estimate net production. Calorific equivalents were obtained with a miniature bomb calorimeter.

A constantly recording device measured specific metabolic rates at given temperatures. By regression analysis, these rates were related to field temperatures. An oxy-calorific value was then used in conjunction with population biomass at each census, to estimate calories expended during maintenance metabolism.

SUMMARY

1. In a general survey of the spider community in alder woodland (area about 0.36ha), 49 species were found representing 8 families.

2. A lateral, repellent type of extractor was used for removing spiders from the ground zone. A modified use of the sweep net, referred to as 'bagging', removed spiders from most of the foliage.

3. With very few exceptions, species typical of the ground zone are found at all times of the year. Species in the layers above frequently have a marked seasonal distribution.

4. Robertus lividus (Theridiidae) and Meta segmentata (Argiopidae) were selected for a detailed energetics study. The young of both spiders could be separated from those of other species, while all stages appeared to be adequately sampled.

5. In an order of numerical dominance for the ground zone, R.lividus ranked No.5. In terms of mean monthly biomass, the population of adult M.segmentata was the most prominent in the field layer.

6. An overlap of generations occurred in R.lividus, all stages of which were found throughout the year. Eggs of the main cohort in M.segmentata hatched in May and development was completed by the beginning of October, when cocoons were constructed.

7. Both species appeared to have 5 instars after emergence from the egg. Development time after hatching varied between 6 and 9 months in R.lividus, while the period for M.segmentata was between 5 and 6 months.

8. The spatial patterns of R.lividus were described by Taylor's Power Law. Early instars were aggregated while adults were solitary or randomly distributed. Aggregations of emergent spiders in the argiopid species gave way to a regular distribution in later stages, coinciding with seasonal development of the vegetation.

9. Biocontent of spider material was determined for both species and for some woodland representatives. Values ranged between 5.2 and 6.4 Kcals/g dry weight (ash free).
Significant differences were detected between males and females (adults of all species).
In general, calorific values increased with age, with newly moulted females of M.segmentata having about the same biocontent per gram as spent females.
Eggs yield the highest values, 6.001Kcals/g in R.lividus, and 6.377 Kcals/g in M.segmentata.

10. Respiratory rates (μ O_2/mg wet wt/hr) were temperature dependent with an average Q_{10} of 2.7 and 3.0 for R.lividus and M.segmentata, respectively. The temperature range was between $5^{o}C$ and $15^{o}C$.

In the former species, respiratory energy turnover came to $2.7 \text{Kcals/m}^2/\text{annum}$, compared with 1.0 and 1.4 $\text{Kcals/m}^2/\text{annum}$ in M.segmentata.

11. Production (P_g) in R.lividus was estimated from the survivorship curve of a mean 'cohort', the members of which were regarded as discrete individuals (V) passing through the population.

   In M.segmentata, population density (N) on each sampling occasion, multiplied by individual growth rates, provided estimates of production (P_g).

12. Growth of the mortality fractions (E) were taken into account and together with moult loss (ML) contributed to total production (P).

   Neither excretion (U) nor webs used to ensnare prey, were investigated as components of production.

   Total production (P) amounted to 1.8 $\text{Kcals/m}^2/\text{annum}$ in R.lividus, and 0.88 (1968) and 0.95 (1969) $\text{Kcals/m}^2/\text{annum}$ in M.segmentata.

13. Assimilation (A) was estimated from the sum of R + P.

   In the theridiid species, a mean standing crop of 0.224 $\text{Kcals/m}^2/\text{annum}$ assimilated 4.5 $\text{Kcals/m}^2/\text{annum}$.

   In M.segmentata, standing crops of 0.203 and 0.281 $\text{Kcals/m}^2/\text{annum}$ had a total energy turnover of 1.9 and 2.4 $\text{Kcals/m}^2/\text{annum}$, respectively.

14. The P/R ratios were between 67% and 85%. Mean net production efficiencies (P/A) came to 40% in R.lividus and to 40% and 46% in the argiopid species.

15. The relation between annual respiration and production in the two species is described by the regression equation (McNeill and Lawton 1970) for short-lived poikilotherms.

16. Reproductive efficiencies and breeding success were apparently related to differences in modes of life. Egg production (P_r) in R.lividus accounted for only 6% of total production (P). This contrasts with about 30% in M.segmentata.

17. Monthly mean densities in the whole study area ranged between 502 and 965 spiders per $metre^2$. The largest contribution came from the ground zone which amounted to about 4/5 of monthly totals.

18. Monthly standing crop of the spider community ranged between 117 (February) and 292 mg dry weight per $metre^2$. These values were equivalent to 0.65 and 1.7 $Kcals/metre^2$.

19. Density and standing crop declined markedly from the ground zone to the upper canopy. Mean monthly standing crop (per metre) for the litter layer was 0.67 Kcals, 0.29 Kcals for the field layer, 0.11 Kcals in the lower canopy, and 0.02 Kcals at the highest levels.

20. Average monthly biomass for the whole spider community amounted to 1.1 Kcals per $metre^2$.

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INTRODUCTION

Energy from solar radiation, albeit a minute fraction, is made available to heterotrophic organisms by autotrophic forms. Lindemann (1942) visualized a transfer of energy from one trophic level to the next by applying the Laws of Thermodynamics within the context of the ecosystem. Hence,

Solar energy → autotrophs or → primary → secondary
                 primary producers   consumers   consumers

The very existence of an animal within an ecosystem is determined by its ability to assimilate some of the available energy. At whatever level of organization, whether it be the individual animal, the species population, or trophic level, energy enters in the food consumed (C) minus the rejected portion (FU). At least part of this energy is lost as heat of respiration (R) during maintenance metabolism, while the remainder is used to accumulate organic material (P) through growth or reproduction. Hence, energy flow or total assimilated energy (A) is represented by

$$A = C - FU \quad \text{and} \quad A = R + P$$

There are three main approaches to the study of ecological energetics (Engelmann 1966). First,

physiological studies which are concerned with the individual organism and relate to feeding characteristics (C) and respiration (R). Turnbull (1962) estimated the quantity of food consumed by the spider, <u>Linyphia</u> <u>triangularis</u>. Itô (1964) and Miyashita (1969) have investigated respiratory energy loss in lycosid spiders. The second approach has been designated the 'Bornebusch' method, which in the modern context, seeks to compare energy flow between species populations. Finally, there is the trophic-dynamic approach which utilizes Lindemann's (1942) model of energy relations within whole communities (Slobodkin 1962). The second method was the approach adopted in the present study.

While the bio-energetics of primary consumers in terrestrial ecosystems have been the subject of several investigations, notably by Smalley (1960), Wiegert (1964) and Saito (1965, 1967), there is a paucity of data on predatory invertebrates. Recently, estimates for the latter group have been obtained for an elaterid beetle (Dutton 1968), for centipedes of the genus <u>Lithobius</u> (Whignarajah 1968), and a carabid beetle (Manga 1970).

Spiders appear to differ from most secondary consumers in that they are present within many ecosystems in large numbers and represent numerous species. This raises the problem of selecting appropriate species for an energetics study. Although the taxonomy of spiders

in Britain is well documented (Locket and Millidge 1951, 1953), detailed and systematic ecological studies on spiders have been undertaken in only two ecosystems. Duffey (1962, 1956) has described the community of spiders in limestone grassland, while Cherrett (1961) investigated spiders associated with moorlands. The studies of Turnbull (1960) and Luczak (1963) on woodland spiders, those of oak and pine, respectively, were of a qualitative rather than a quantitative nature. Gabbutt (1956) restricted his observations to spiders of oak litter.

The bio-energetics of spider populations have received scant attention. While Breymeyer (1967) and Kajak (1967) have published data on the biological productivity of spiders in a meadow ecosystem, their studies were of a preliminary nature and, therefore, were far from complete.

The purpose of the present work is two-fold. Firstly, to provide a description of the structure of a spider community in an alder wood. Data on life-histories, seasonal distribution, density and standing crop, were used to prepare the way for the next objective. This second and main objective is the evaluation of the role of two species of spiders in promoting energy flow within a woodland ecosystem.

There are insufficient data on the energetics of spiders to speculate on the significance of the results in the context of the whole ecosystem. However, differences in energy flow take account of adaptations to different modes of life. It was also possible in the present study to relate the data to some of the existing information on the bio-energetics of terrestrial invertebrates as a whole.

CHAPTER ONE

THE STUDY AREA

(a)   Location and weather

The investigation was carried out in an area of about 2ha within Wynyard Estate (grid ref.424287) which is 15 miles south-east of Durham City in North-East England.

The site is about 67 metres above sea level (O.D.).

Boulder clay has covered many parts with impeded drainage and a water table rarely more than 20cm below the surface.   The soil was acidic with values of pH mainly between 4.0 and 6.0.

The average rainfall for the immediate area surrounding Durham is in the range of 70 to 79cm, with average air temperatures of $8.2^{o}C$. (weather reports of Durham and Hartlepool).

In 1967, when sampling commenced, temperatures were higher $(8.6^{o}C)$ than in 1968 and 1969.   All three years experienced slightly higher rainfall than the average.   A mild and dry spring occurred in 1968.   However, summer temperatures were lower (July mean $13.1^{o}C$) than in 1969 (July mean $15.9^{o}C$) and there was considerably less sunshine. The autumn of 1968 was very mild, with the first ground frost in December.

(b) Vegetation

General views of the sample area are shown in Figures 1 and 2.

A mixture of alder and birch covers the area although conifer plantations are seen over much of the Estate and belong to the Forestry Commission.

A permanently moist soil supported quite a rich bryophyte flora comprising _Lophocollea heterophyla_ Schrad. and species of _Pellia_ and _Fissidens_, typical woodland mosses (Dixon 1955) such as _Mnium hornum_ L, _Hypnum cupressiforme_ Hedw., _Dicranella heteromalla_ Schp., and _Thuidium tamariscinum_ B. & S.

Grass was often much in evidence especially where there was surface clay, _Deschampsia caespitosa_ Beauv., _Holcus lanatus_ L., and _H.mollis_ L., and _Poa trivialis_ L. Dog's mercury (_Mercurialis perennis_ L.) and rose-bay willow herb (_Chamaenerion angustifolium_ L.Scop.) formed extensive patches. The outstanding plant associations were bramble (_Rubus fruticosus_ L. _sensulato_), bracken (_Pteridium aquilinum_ L.) and male fern (_Dryopteris felix-mas_ L.) The occasional briar (_Rosa canina_ L.), hawthorn (_Crataegus monogyna_ Jacq.) and hazel (_Corylus avellana_ L.) also occurred.

The main trees were alder (_Alnus_ sp.) and birch (_Betula_ sp.). Part of the litter was derived from a clump of sycamore (_Acer pseudoplatanus_ L.). Complete documentation of the flora is given by Hughes (1970).

Fig.1. Study area in winter (above) with soil sample

removed (below)

Fig.2. Study area in summer (left) with dense vegetation of field layer (right) showing sampling box in position.

(c) Field temperatures

Where metabolic studies are involved, a record
of temperatures is important since laboratory data may have
to be adjusted to accord as far as is possible with field
conditions.

Berthet's (1960) technique had previously
been used by Bolton (1968) and Whignarajah (1968) to measure
temperature in the study area. However, the difference
between the chemical method and maximum-minimum thermometers,
 compared over a six month period, was consistently small,
i.e. within 1.5°C. In view of this, it was considered
adequate to record temperatures by means of thermometers.

One max-min thermometer was buried in
litter to record temperatures in the ground zone, while
another, in the fork of a tree at about 2M above the ground,
provided data on air temperatures for the field layer.

Results

Mean monthly temperatures, from readings taken
as frequently as possible, are given in Table 3. When these
are presented graphically for data from 1967-1968, character-
istic inversions are seen.

The readings from October to about April are
slightly above those recorded by Durham Observatory. This
is explained by the topography and vegetation. First, the

Fig.3. Monthly mean temperatures (°C) of the study area

(● beneath litter in the ground zone; o field layer).
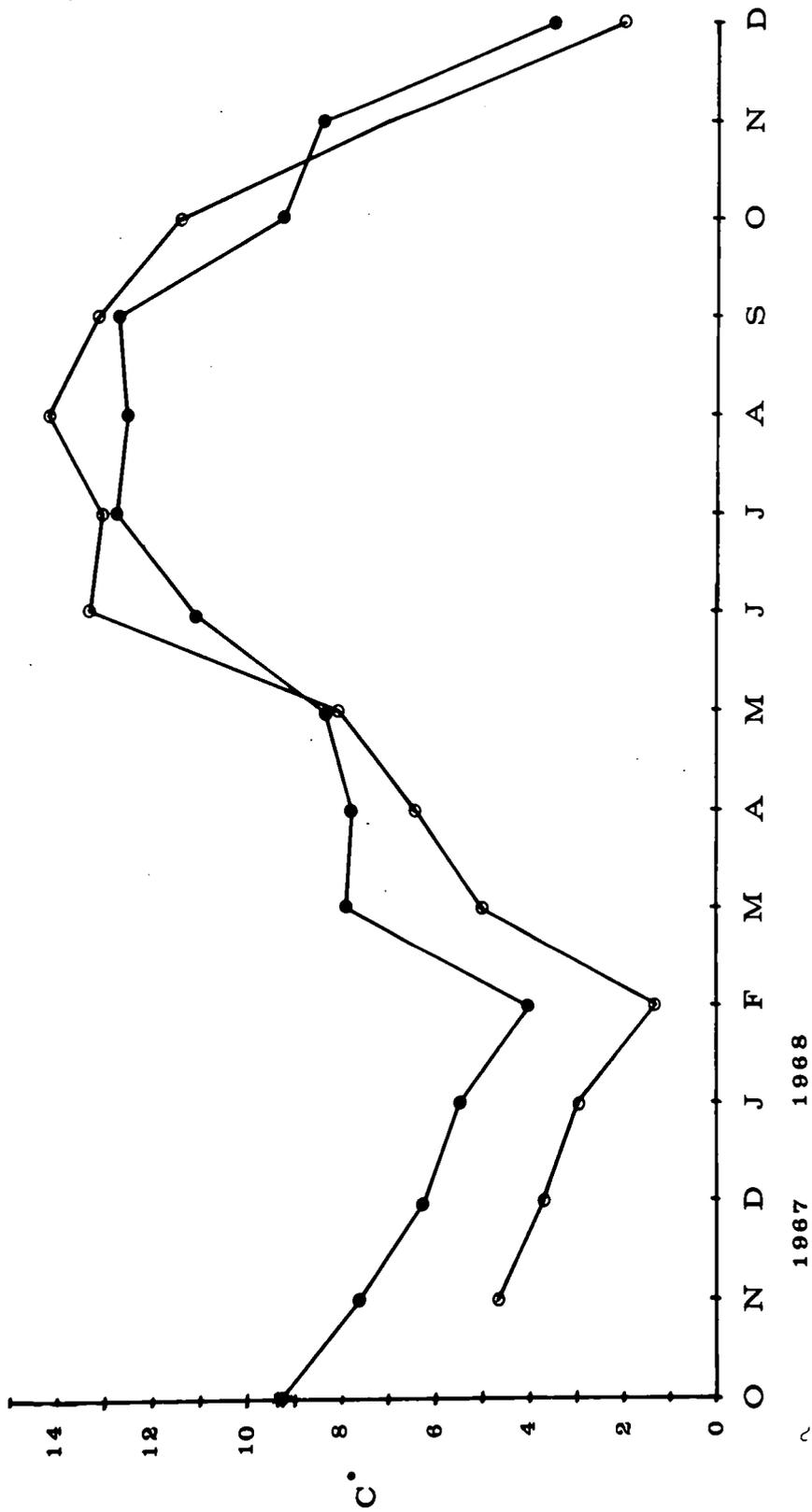
site was on a gradient which faced south-west. Second, vegetal covering reduces heat loss (Russell 1950). In the summer, inversions occurred between the inside and outside of the wood. Air temperatures then were slightly lower under the tree canopy.

(d) Site characteristics and the spider fauna

The site constitutes part of a woodland formation and represents a semi-natural association of alder and birch (Tansley 1954). It is conveniently described in terms of Elton and Miller's (1954) classification of site characteristics. A plan of the main vegetal areas is given in Figure 4. The area in which sampling took place amounted to 0.36ha.

1. <u>Sub-soil and rock</u>. In the study area this stratum is comprised of boulder clay penetrated by the larger roots of the canopy layers. This was not sampled specifically because there was no indication that spiders occurred here. Where the boulder clay came near to the surface, part of it became incorporated in the turves removed for sampling.

2. <u>Topsoil</u>. This was equivalent to the A_o to B horizons of some pedologists (Russell 1950). In some areas it comprised a clay loam while in others it was peaty, having a loose texture and contained the fibrous roots of fern and bracken. It was well penetrated by the tunnels

Fig.4. Main vegetal areas in the study site

A = alder trees

B = birch trees

O = oak tree

S = sycamore trees

b = bramble

f = fern

g = grass

m = dog's mercury

n

O

B   b

B

B   B

b   B

A

B   A   b   g   b

b   g

m

f   b   A

A   A

A   b   A

f   A

b

A   f   A

b   b

b   A

f   A

b   A   b

f

S   b   A   f   b   b

S

ditch

ride

scale
20 M
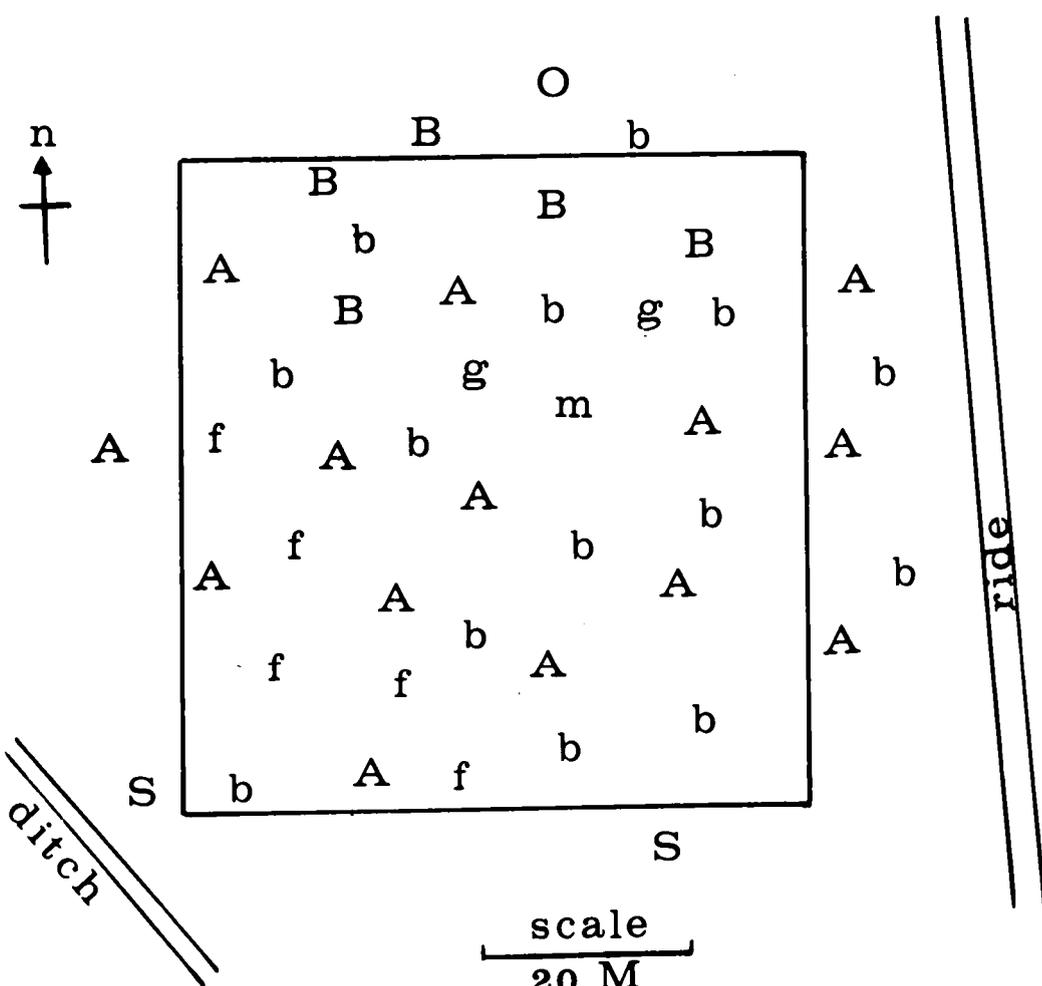
of voles and shrews. The immature stages of many spiders were found in these peaty areas. The thickness of the top soil varied from about 3 to 15cm. A lateral extractor of the type originated and used by Duffey (1962) was constructed to remove the spiders from this layer as well as from the ground zone.

3. **Ground zone.** This included the surface litter which could be brushed away by hand, the relatively rich bryophyte flora and forbs not exceeding 15cm in height. The litter accumulated from September onwards and reached a maximum in December, and then declined steadily over the spring and summer.

As Elton (1954) says, this layer is probably the narrowest in depth but is the most complex. As well as being the home of the ground living spiders, all organisms must at some time be involved in the energy relationships of this layer'..... by their activity in life which bring many species to the ground if only as transients ...' for example, spiders descending to lay their cocoons in litter like Meta segmentata mengei in the early summer, and Meta segmentata in the Autumn together with Helophora insignis, Linyphia triangularis and a host of smaller species of Linyphiids. Also found are the over-wintering stages of Xysticus cristatus, the young and males of Meta segmentata mengei, the sub-adults and adults of Lepthyphantes

alacris, and a very large number of young belonging mainly to the Theridiidae and Linyphiidae.

Except for the winter months there must be a continual rain of excretory products of spiders, cast off webs, the dismembered fragments of insect prey, exuviae, and the actual bodies of spiders dying through imperfect ecdyses, infection or senility. In the spring and autumn vast numbers of cocoons, once white but then yellow and frass filled, are left behind by a mass exodus of emergent spiders as they disperse for other layers.

4. Field layer (usually below 1.8 metres). The vegetation here may be divided into low and high levels, the former dominated during the open phase by grass and dog's mercury (Mercurialis perennis L.) and the latter by bracken (Pteridium aquilinum L.) and bramble (Rubus fruticosus L. sensu lato) which by late summer achieves an overall dominance.

The field layer emerges from the ground zone in April and May and the high level plant species gradually occlude those below. This stratum is penetrated by the trunks of trees and dense outgrowths of alder twigs, providing almost unlimited niches for spiders to live in.

This is the main feeding layer for many spiders and several major families are represented, namely, the Clubionidae, Thomisidae, Agelenidae, Theridiidae,

Tetragnathidae, Argiopidae and Linyphiidae. The field layer is invaded from below in March when immature stages disperse leaving behind glistening lines of web which stretch from the base of tree trunks to the upper canopy. In April and May additional invasions of the emergent foliage in this layer may come from the low canopy or from within the field layer itself. Theridion pallens, Trachynella nudipalpis, Cornicularia cuspidata and Dismodicus bifrons, although at no time found in the ground zone, make their appearance in large numbers. They probably over-winter in the crevices of alder bark (Duffey 1969). Clubiona stagnatalis Kulczynski, Porrhoma convexum (Westring) and Linyphia hortensis Sundevall certainly do so, the last named sealing itself within the crevice by a thin sheet of web.

By June, mature Meta segmentata mengei are very much in evidence and by the end of the month return to the ground zone to lay their cocoons. Eggs are laid in the field layer at this time by Clubiona stagnatalis and C.lutescens, Theridion pictum and Linyphia peltata. In most cases the cocoons are to be found between two leaves drawn together or attached to the underneath of a single leaf. Enoplognatha ovata lays cocoons in July. The eggs of all these species appear to have an incubation period of between 4 and 6 weeks.

As <u>Meta segmentata mengei</u> (~~Blackwall~~) makes
its descent to the ground zone, the over-wintering eggs of
<u>Meta segmentata</u> and <u>Linyphia triangularis</u> have hatched.
The young quickly disperse for the field layer and soon
much of the vegetation is covered by their webs. They are
then joined by several species of <u>Lepthyphantes</u> and together
constitute the dominant spiders until the winter.

5. <u>The canopy layer</u>. This reached 12m and was sub-divided
into lower (1.8M - 4M) and upper (4 - 12M) canopies. Alder
and birch formed most of this layer with some sycamore
(<u>Acer pseudoplatanus</u>), hawthorn (<u>Crataegus monogyna</u> Jacq.)
and very small oak (<u>Quercus</u> sp.).

Few spiders were caught here until well into
June, when the canopy became dense. This layer was windswept
for much of the time and rise in temperature lagged behind
the lower layers. By the beginning of October numbers had
fallen steeply. <u>Theridion pallens</u> Blackwall (Turnbull 1960)
was dominant together with <u>Drapetisca socialis</u>, the latter
occurring on the trunks of alder and the main branches.
The males of <u>Meta segmentata</u> were sometimes found, presumably
in search of females. Aeronaut species, both mature and
immature, occurred especially in the spring, late summer and
autumn (Bristowe 1939, Duffey 1956). Numbers were low
inevitably, partly because of the difficulties of sampling.

Table 1.   Species list for Wynyard sample area

A = alder trunk and canopy F = field layer   G = ground zone

1. Clubiona stagnatalis Kulczynski F.
2. C.lutescens Westring F
3. Xysticus cristatus (Clerck) G
4. Lycosa pullata (Clerck) G
5. Hahnia montana (Blackwall) G
6. Theridion pictum (Walckenaer) F
7. T. pallens Blackwall AFG
8. Enoplognatha ovata (Clerck) F
9. Robertus lividus (Blackwall) G
10. Pachygnatha clercki (Sundevall) G
11. Meta segmentata (Clerck) AFG
12. M. segmentata mengei (Blackwall) FG
13. Araneus diadematus (Clerck)
14. Trachynella nudipalpis (Westring) FG
15. Prosopotheca monoceros (Wider) G
16. Cornicularia cuspidata (Blackwall) FG
17. Dicymbium nigrum (Blackwall) FG
18. D. tibiale (Blackwall) G
19. Gongylidium rufipes (Sundevall)
20. Dismodicus bifrons (Blackwall) FG
21. Gonatium rubens (Blackwall) F
22. G. rubellum (Blackwall) FG
23. Oedothorax fuscus (Blackwall) G
24. Tapinocyba pallens (O.P. - Cambridge) G
25. Monocephalus fuscipes (Blackwall) G
26. Micrargus herbigradus (Blackwall) G
27. Savignia frontata (Blackwall) FG
28. Diplocephalus latifrons (O.P. - Cambridge) G
29. Erigone dentipalpis (Wider) FG
30. Porrhomma pygmaeum (Blackwall) G
31. P. convexum (Westring) FG
32. Meioneta rurestris (C.L. Koch) FG
33. Centromerus sylvaticus (Blackwall) G
34. C. dilutus (O.P. - Cambridge) G
35. Oreonetides abnormis (Blackwall) G

Table 1.   (Contd....)

36. Macrargus rufus (Wider) G
37. Bathyphantes nigrinus (Westring) FG
38. Drapetisca socialis (Sundevall) A
39. Bolyphantes luteolus (Blackwall) F
40. Lepthyphantes alacris (Blackwall) FG
41. L. tenuis (Blackwall) G
42. L. zimmermanni Bertkau FG
43. L. cristatus (Menge) FG
44. L. mengei F Kulczynski
45. L. pallidus (O.P. - Cambridge)
46. Helophora insignis (Blackwall) AFG
47. Linyphia triangularis (Clerck) FG
48. L. peltata (Wider) F
49. L. hortensis (Sundevall) F

(nomenclature according to Locket and Millidge 1953)

Addendum

Theridion denticulatum (Walckenaer)

~~Pachygnatha degeeri Sundevall~~

Meta merianae (Scopoli)

CHAPTER TWO

THE SAMPLING PROGRAMME

Introduction

Density refers to the number of individuals per unit area or volume of the habitat and represents an absolute number. Insofar as spiders are concerned, there are comparatively few quantitative estimates in the absolute sense. In the study of energy flow through species populations, as accurate estimates as possible are essential. Relative determinations from general collecting, searching over standard collection times, pitfall traps, sweeping and sticky traps have been used in the analyses of spider populations (Duffey 1956, Merrett 1967, Luczak 1959, 1963, 1966, Turnbull 1960). As Southwood (1966) points out, the important advantage of relative methods is the low cost of data in terms of effort.

Estimates which are claimed to approach absolute values have been obtained by Gabbutt (1956), Duffey (1962), and Cherrett (196) and refer in the main to readily sampled habitats with soil and litter and an essentially low cover of vegetation. Tullgren funnels or lateral extractors were the main types of apparatus used to remove the spider fauna. Breymeyer (1967) hand sorted wandering spiders as a preliminary to a productivity study of wandering spiders in the ground zone.

In woodland there are an enormous number of places in which spiders may be found. As Turnbull (1960) points out, many are hardly accessible. Each feature of the habitat may require its own sampling technique. A further problem is seen when sampling regularly over a long period. This is the major transformation of the vegetation from the winter aspect to that of summer. Changes in litter content and in the density of ground and field layers, the continual succession of new and different plant associations, variations in weather which may alter the texture of the soil, and the problem of accessibility so that all parts of the site have an equal chance of being sampled, make a consistent programme of sampling difficult to operate. Inevitably total density estimates of spiders in a diverse ecosystem such as woodland must include estimates relating to species more easily sampled and so represent absolute numbers, and those which refer to species which are only apparent during periods of pronounced activity.

<u>Robertus lividus</u>, <u>Oreonetides abnormis</u> and some smaller Linyphiids like <u>Micrargus herbigradus</u> which live permanently in the ground zone are probably adequately sampled using the repellant type of extractor. Other species such as <u>Theridion pallens</u>, <u>Clubiona lutescens</u>, and <u>Drapetisca socialis</u>, which may be found virtually in any layer depending on the season, must be represented by

relative estimates of density. The increasing impenetrability of bramble with the approach of late ; summer must affect to some extent the reliability of estimates for a large number of species, such as <u>Meta segmentata</u>, <u>Linyphia triangularis</u> and the much smaller and often immature spiders.

The total estimate of density for species as a whole must be compounded of both absolute and relative numbers, obtained from the application of both relative and absolute techniques for capture. In order to obtain as complete a picture as possible of the spider fauna use was made of a lateral extractor, by sampling units of vegetation, sweeping, sticky traps, and by brushing tree trunks.

(1) <u>Ground Zone</u>

This included those parts of the site earlier referred to as the litter and topsoil (after Elton and Miller 1954).

(a) <u>Size and number of sample units</u>

Duffey (1962) and Cherrett (1961) removed soil samples of $1/16m^2$ in their studies of limestone and moorland spiders, respectively. Numbers of spiders were higher than those previously recorded (e.g. Van der Drift 1951; Gabbutt 1956).

In the present study sample units of $1/16m^2$ were also chosen (25cm x 25cm = $625cm^2$). When smaller

units of $1/20m^2$ were tried, numbers were lower per m^2.
Sample units in excess of $1/16m^2$ led to highly variable
heat gradients within the turves. Furthermore, when
waterlogged during periods of wet weather, large samples
became heavy, were difficult to manipulate, and often broke
up during removal. In fact, it was found that excessively
disturbed soil yielded consistently fewer spiders than those
which remained intact.

Ten sample units were taken each month
from October 1967 to November 1968. This was the maximum
number which could be handled conveniently at any one time.
During 1969 further samples were removed when spiders were
specifically required for calorimetry and respirometry.

(b) <u>Removal of samples</u>

As a thick cover of bramble often covered
the ground it was necessary to displace this in order to
reach the sampling point below. It was found that a box
having the corners and edges made of dexion and having half
inch plywood sides (Fig.5) could be pushed through the
field layer into the soil. The area at the base of the
sampling box was slightly under $1/16m^2$. As it moved down
it effectively pushed aside the taller plants. One of the
advantages was that very few spiders of the field layer were
found with those emerging from soil in the extractor.

The bottom edges of the dexion were honed to produce sharp
cutting edges which severed many of the lower stems.
A large pair of secateurs was able to cut through the
remaining stems and all but the very thick tree roots
which came near to the surface.   A sharp spade could then
be worked round the box to make a turf of $1/16m^2$.   Lifting
the spade also lifted the turf and sampling box which
ensured that the soil kept in one piece.   These were then
laid on a beating tray, the sampling box detached and the
sample unit slipped into a close fitting polythene bag (Fig.5).
This was numbered and the open end securely tied.   Thus no
difficulties of transportation arose and the samples were
placed in the extractor within three hours of removal.

The depth of sample units was almost constant
because the base of the box had narrow but flat pieces of
dexion above the cutting edges which prevented it from
entering the soil more than about 12cm.   Together with
the litter, a turve of about 15cm in depth was finally
removed.

The few spiders escaping from the sample as
it rested on the beating tray were easily caught by a 'pooter'
and deposited within the polythene bag with the sample.
Very occasionally a sample broke up.   This was discarded
and another taken from the same stratum.

(c) Sampling pattern

Heal y (1962) amd Southweed (1966) in reviews on sampling procedure both point out the merits of stratified random sampling. Particularly important considerations are the elimination of personal choice, an adequate coverage of the sample area as a whole, and the location of sites preferred by particular species of spiders. In an energetics study where absolute numbers are required, a species existing in only one or two strata cannot be considered for further intensive study since it may not be adequately sampled. A case in point was Oreonetides abnormis which was virtually confined to the first stratum.

The sampling area as a whole was approximately 0.36ha. It was divided into 4 strata each of 900 metres^2 and having certain plant and soil characteristics :

	Stratum			
	1	2	3	4
Vegetation	alder	sycamore	alder	alder/birch
	bramble	alder	fern	bramble
	grass	bramble	bramble	fern
	Mercurialis	fern	bryophytes	grass
topsoil	clay	clay loam	peat	clay
water table	low	high	high	low

A total of 10 sample units was removed each
month.   Two sample units of $1/16m^2$ from each stratum and
in addition two extra sample units from two other strata.

Sampling points were determined within each
stratum by the shaking of two dice within a box.   The
numbers on the dice referred to the paces taken to select
a sample unit.   The layout of the strata had to follow a
curve to avoid those areas having very different vegetation
e.g. canopy only of sycamore, and experimental plots set
up by colleagues participating in the same programme of
research.   When it was necessary it was usually possible
to remove turves from the very base of trees although these
were often less thick than those obtained elsewhere because
of large roots just beneath the surface.

(d)   Extraction apparatus

The relatively large size of spiders and
their small numbers when compared with Collembola and Acarina,
their greater mobility and highly developed senses (Cherrett
1961, Macfadyen 1962a), call for a large sample size and a
method of extraction which can handle the soil material.
Flotation methods of the kind utilized by Salt and Hollick
(1944) are impracticable with large amounts of organic
debris.   The suction apparatus of Johnson et al (1957)
appears to have a low efficiency with only 76 spiders per m^2.

Macfadyen (1962b) considered that spiders required a 'wet' regime of slow extraction, little draught, and high humidity. Gabbutt (1956) used tullgren funnels and extracted from litter over 3 days but does not state the temperature of the heat source or gradient. Duffey (1962) extracted over 2 days with a temperature of $76^{o}C$ and used a lateral extractor. In a modified form of that extractor, Cherrett (1961) was able to increase the temperature from $31^{o}C$ to $150^{o}C$ over a period of five days and demonstrated the effectiveness of a longer extraction period. Although a high relative humidity prevailed, there were problems of condensation.

Kempson et al (1963) developed a 'dry' bowl extractor which maintained high temperatures and humidity. High efficiencies of between 90 and 100% for microarthropods were claimed. The Kempson apparatus, however, did not appear to be suitable for the removal of live spiders. The only way of obtaining specimens of Robertus lividus for respirometry studies was by continuous extraction.

The lateral extractor of the kind employed by Duffey and Cherrett was decided upon as the best available to remove spiders from soil and litter. One advantage was that deep sample units of about 12cm thick

could be accommodated easily without the need for spiders

to force their way down and through the soil to escape

the heat source. It was interesting to note that

Whignarajah's (1968) extraction material derived from the same

study area but obtained with a tullgren funnel, included very

few small immature spiders. Furthermore, far less debris

had to be removed from the collection bowls than from those

attached to the tullgren apparatus. Spiders were readily

seen in the bowls and Robertus lividus, for example, could

withstand immersion for several hours.

The extractor used in the present study was

made of wood, with an asbestos lining those parts nearest

the heat source (Fig.6). This consisted of resistance

wire from a 1 Kilowatt electric fire which was suspended

between two rows of five 27 x 27cm sample boxes. These,

with their lids, comprised the top unit which could be

removed from a flat base for cleaning purposes. Heating

was controlled by a simmerstat which gave two levels of

heat. A metal grill separated the soil sample from the

heating element on one side, while a gap of 2cm in height

on the opposite side enabled animals to escape into the

collecting bowls. Spiders were unable to pass from one

box to another or to a receptacle attached to another box.

Each collecting receptacle was filled to about 4cm in

Fig.5. Removing soil samples

Beating tray   Sampling box

Polythene bag   Soil sample   spade

Fig.6. Lateral extractor for soil samples

depth with water containing a few drops of detergent to reduce surface tension, together with 0.5ml of formaldehyde as a preservative.

Physical conditions during extraction

The wooden extractor was not able to take the high temperatures produced by Cherrett (1961). An extraction period of 12 or 14 days was found to be sufficient at the temperatures produced by the simmerstat (Figure 7). Information on the heat regime was provided by inserting thermometers through the boxes into the soil. For the first 8 days the simmerstat registered high and as the samples dried out, was turned to 'low' to reduce the fire risk. A temperature gradient of between 40'C and 60'C existed between sites 1 and 4 within the sample boxes.

Cobalt chloride paper (Cherrett 1961) indicated a humidity gradient (Fig.8). However, the relatively high temperatures at sites 1 and 2 led to inconsistent readings after day 4 and 8, respectively.

The sharp drop in R.H. at position 1 was caused by the close proximity of the heat source. The difference in R.H. between sites 2 and 3 was attributed to difference in soil material in the inverted turves. The relatively early fall in R.H.

Fig.7. Temperature regimes in sample boxes during

a 12-day extraction period.
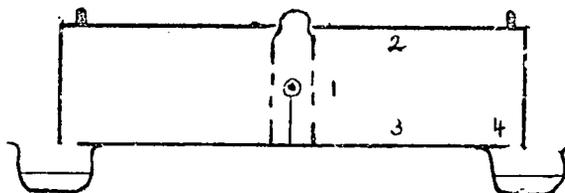
Site within sample box	Range of temperature 'C with simmerstat on	
	low	high
1	58 - 60	80 - 90
2	50 - 54	65 - 70
3	35 - 40	42 - 50
4	22 - 25	25 - 32

Fig.8. Extraction apparatus and humidity

gradients during the extraction period.

        C = collecting dish

        D = direction of draught of air

        E = wire element in pyrex glass tube

        G = grill of wire mesh

        T = ~~thermostat~~ simmerstat with high (h) and low (l)

           levels of heat
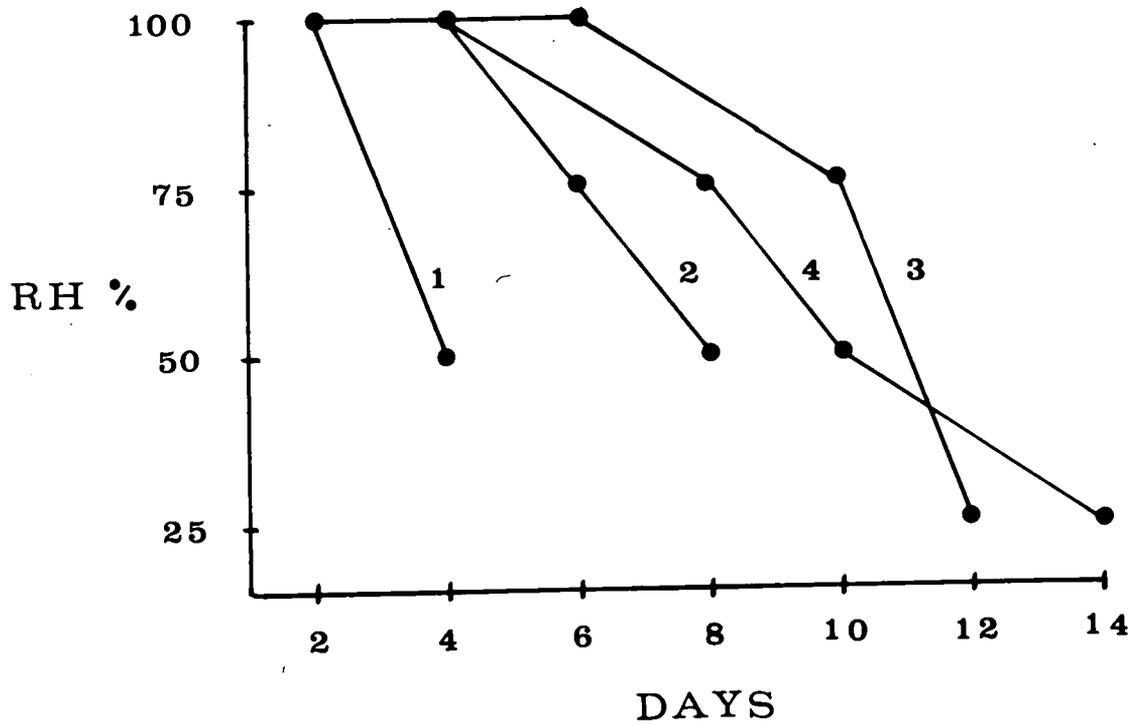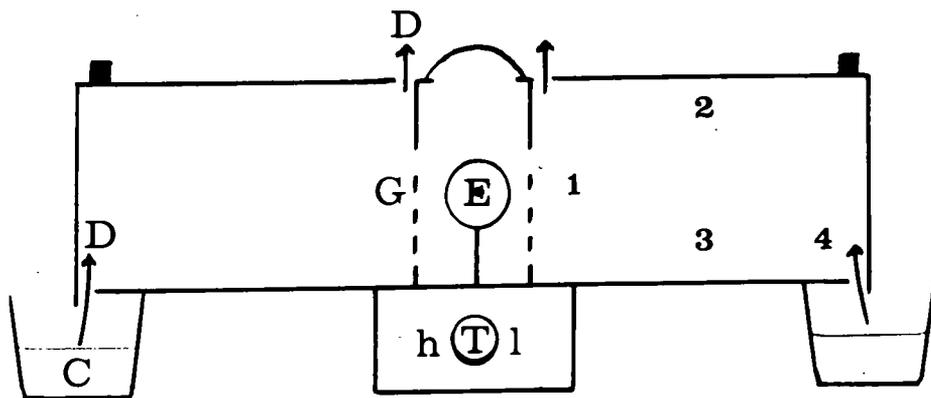
at site 4 within the sample boxes resulted from the incoming draught of air.

Cherrett (1961) had found that draught exclusion resulted in heavy condensation which trapped an appreciable number of small spiders, a factor which was related to a metal construction. Draught was not controlled in the wooden apparatus but its design allowed air to pass through continuously. Most of the free water which was present for the first few days was absorbed by the wood which then dried out. No spiders could be found which had been killed through excessive condensation.

It would appear that the extraction apparatus fulfilled the conditions of a 'wet' regime and a 'slow' extraction. However, a criticism of a long extraction period is that some eggs of spiders might be induced to hatch to give unusually large numbers. Alternatively, as spiders are cannibalistic, numbers might be reduced. Further, spiders may develop within the extractor to a stage beyond that which existed in the field at a given time, e.g. during winter.

The eggs of several species which were cultured during the course of the investigation did not hatch in response to temperature in the short term. For about 7 days at least during a 12 day extraction

period there would probably be sufficient food in the
form of arthropods other than spiders, so that these would
not have to prey specifically on each other.

Since most spiders emerged from the extractor
during the first week, a relatively small proportion would
show appreciable development before they also emerged.

(e) Efficiency of extraction

The numbers of spiders extracted per metre^2
at Wynyard (Table 2) are amongst the highest recorded for
any habitat, although Duffey (1963) found up to 1,496
spiders in Nardus grassland, when a tullgren funnel was
used.

Table 2. Estimates of numbers of spiders per m^2 in the
ground zone of woodland (range indicates minimum
and maximum numbers removed)

Habitat	method of extraction	numbers/m^2	author
Beech forest, Holland	Tullgren funnel	231	Van der Drift (1953)
Oak/Beech, S.W. England	Tullgren funnel	37 - 275	Gabbutt (1956)
Oak, S.E. England	Tullgren funnel	2 - 16	Turnbull (1960)
Alder/Birch N.E. England.	Lateral extractor	445 - 874	present study

Murphy (1955) has pointed out that the highest estimates of the soil meiofauna has risen steadily since the studies of Bornebusch (1930). This is in no small way due to the development of extraction techniques by such investigators as Murphy (1955), Macfadyen (1962a), Duffey (1962) and others, who have turned their attention to the peculiarities of specific groups of arthropods.

There are two possible explanations for a relatively large catchment of spiders. Either, spiders are relatively few but the extraction procedure has a very high efficiency, or spiders are very numerous and despite a low efficiency of extraction, a fair proportion are removed. It is clear that two factors influence the numbers which are caught: the actual number in the field and the efficiency with which they are removed. The former value cannot be known with absolute certainty and in consequence, reliability of numbers can only be based on estimates of efficiency. These estimates in turn are not absolute, and the usual methods for testing efficiency are open to question.

Johnson et al (1957) compared numbers removed by a suction system with those removed by hand and gained an extraction efficiency value of 95%. However, as numbers obtained by both methods were so low, the comparison may not be a fair one. A comparison

between hand sorting and the use of a lateral extractor

yielded no significant difference in numbers removed,

but is only an indication of comparable efficiency

(Cherrett 1961) in a relative sense.

A commonly used method (e.g. Van der Drift

1953, Gabbutt 1956, Cherrett 1961) is to release a known

number of spiders in the extractor after the soil or

litter samples have been rendered barren by heat treatment.

Numbers emerging are compared with those introduced.

Results have not always been consistent (Cherrett 1961)

and Macfadyen (1955) questioned this type of experiment.

However, in the absence of a suitable alternative, this

procedure was adopted with the wooden extractor.

Soil samples which had been in the extractor

for the full extraction period were removed and sprayed

with water to restore their moisture and texture.   After

drying overnight in a warm room to remove excess water,

they were returned to the extractor and a known number

of spiders released onto them.   The experiment was

performed on 3 occasions, the spiders for which were

removed by hand from leaf litter.

The overall efficiency in terms of young

and adult spiders retrieved was about 90% (Table 3).

All were removed within 10 days of the extraction period.

(f) Emergence pattern

The proportions of animals which emerge each day from extraction apparatus are characteristic for particular groups of arthropods (Macfadyen 1962b). A bimodal emergence for spiders was described by Cherrett (1961), with the highest peak occurring at the end of the 5-day extraction period, and arising from the final desiccation of the soil samples. The peak on the first day was attributed to random movements of spiders in response to disturbance.

The wooden extractor used in this investigation produced a lower temperature regime than that of Cherrett, and the period of extraction lasted for up to 12 days instead of 5. Emerging spiders were removed and counted on every other day. Thus there was a maximum of 7 collections over 14 days extraction. The emergence patterns for each month were similar, with the highest number of spiders appearing in the collecting troughs on the day after the soil samples had been placed in the soil extractor. Thereafter, the percentage values fell sharply until about the 8th day when the decline was less rapid (Table 4). The high values of the first collections were the result of disturbance, with subsequent values related to the gradual drying out of the turves. The bimodal curve was the reverse of the one obtained

Table 3. Percentage retrieval as a measure of efficiency

of the extractor

	immature			adult		
Trials	in	out	%	in	out	%
1.	10	8	80	11	11	100
2.	12	12	100	9	8	89
3.	17	12	71	8	8	100
Total	39	32	82	28	27	96

The apparatus appeared to extract young spiders less efficiently than adult spiders. The possible explanations are :

1. Adult spiders are more robust and more mobile than young spiders.

2. During manipulation the more fragile stages are easily damaged.

3. Immature spiders may moult and so become immobilised.

4. Condensation may trap a number of young individuals.

5. Small spiders may fall prey to large spiders.

That the extractor had an acceptable level of efficiency is indicated by the relatively large number of spiders caught when compared with the results of other workers, and by the overall 89% retrieval.

by Cherrett (1961);   numbers declining with time of extraction.

The summer and winter values (Table 4) were similar, with no statistical differences until 10 - 12 days when virtually all spiders had emerged during the summer months by that time.   This is readily explained by the very high water content of soil samples during the winter, which delayed desiccation to the very end of the extraction period.

That the behaviour of spiders may differ seasonally within the extractor was indicated from a comparison of the 'spring' period, with its high proportion of young spiders, and the November-December-January period preceding it.   The difference was highly significant between the first collections (Table 5).   The probable explanation is that young spiders react strongly to both disturbance and increass in ambient temperature.   This phenomenon is readily demonstrated when young spiders, still in the cocoon or communal web, are disturbed. They become very active and disperse throughout the receptacle in which they are contained.   The same response can be induced by transferring newly hatched spiders from a cold (5'C) room to a warm (15'C) room.

Apart from the observations on behaviour in spring of young spiders, which formed a relatively high proportion of those extracted at that time, there were no

obvious differences in rates of emergence between young and adult forms. However, there was a notable sequence in the emergence of certain species. _Meta segmentata_ and other typical field layer species appeared in the collection troughs within a few hours after emplacement of samples. _Robertus lividus,_ both immature and adult, were frequently the only spiders to emerge during the last 2 or 3 days of extraction (Table 6).

Table 4. A comparison between the spider 'emergence patterns' during 'winter' and 'summer'

Extraction days	'Winter' N. D. J. F.		'Summer' A. M. J. J.	
	mean %	2 x S.E.	mean %	2 x S.E.
0 - 2	29.2	9.58	31.5	6.46
2 - 4	19.0	11.61	25.8	3.68
4 - 6	13.8	10.80	16.4	3.54
6 - 8	7.9	7.59	16.5	7.28
8 - 10	12.6	7.82	7.9	2.41
10 - 12	13.4	9.04 *	1.6	1.40
12 - 14	5.0	2.42	0	0

* Difference between means significant at 1% level ('t' test)

Table 5.   A comparison between first collections

(extraction day 2) in 'spring' and 'winter'

	'spring' %		'winter' %
Feb	42.4	Nov	21.4
Mar	40.8	Dec	28.0
April	49.1	Jan	25.2
mean %	44.1	mean %	24.9
2 x S.E.	5.30	2 x S.E.	3.18

Difference between means significant at 0.1% level ('t' test)

Table 6.   The 'emergence patterns' of some species of the

ground zone with the lateral extractor

Days after start of extraction

	2	4	6	8	10	12	14

Meta segmentata

Linyphia triangularis

Lepthyphantes alacris

Dicymbium nigrum

Monocephalus fuscipes

Savignia frontata

Diplocephalus latifrons

Porrhomma pygmaeum

Oreonetides abnormis

Micrargus herbigradus

Robertus lividus

2. The field layer

(a) Method

A wide variety of methods have been used
to expel animals from vegetation (e.g. Southwood 1966).
Those that might have been used for spiders at Wynyard
are summarised as follows :

(1. Direct counting)

(2. Counting webs)

3. Sweeping or beating

4. Wiegert 'cylinder'

5. Chemical knockdown

6. Suction apparatus

The desirability of any of the above has
to be considered in relation to the behaviour of spiders
when disturbed, the nature of the vegetation, and the
object of the sampling programme. The first reaction
of spiders to even a mild disturbance is a rapid with-
drawal to a secure retreat. They may also drop to the
ground or lower levels of vegetation. Bramble in
particular, which constituted much of the field layer,
was often dense, extremely robust, and resisted techniques
like sweeping or the use of Wiegert's cylinder. Furthermore,
as absolute numbers were sought for some species, the method
ultimately selected would have to be used in conjunction
with an appropriate unit of area.

Direct counting of spiders and webs were possible methods. The disadvantages, however, were the small size of many spiders and their ability to conceal themselves in curled edges and axils of leaves and the circinate fern fronds. Some spiders did not always make webs or at least they were not conspicuous, and when they did occur, more than one spider was frequently in residence. After periods of rain or strong winds, webs were often broken or had disappeared.

Suction apparatus, beating or sweeping all led to severe disturbance of the vegetation well beyond the area immediately affected by the appliance or net. Luczak (1959) and Kajak (1967) used sweeping as a quick and effective means of obtaining relative numbers in woodland and meadow, respectively. For absolute numbers these methods are far from ideal.

Chemical knock-down was not considered desirable as a method specifically designed to collect spiders, although the box used by Dempster (in Southwood 1966) which incorporated an anaesthetic would have been suitable were it not for the robustness of bramble.

The most hopeful method which emerged, and the most simple, involved the sweep 'net'. A canvas bag, normally used in sweeping, was placed about 10cm

above the ground beneath the herbage of the field layer.
The leaves and twigs immediately above were cut with
secateurs so that the clippings dropped into the bag,
which was then lifted higher up and the procedure repeated.
Shaking the bag prevented spiders from climbing up the
sides to escape.   The plant debris could be removed and
eventually dried so that numbers of spiders could͵been
related to the biomass of the standing vegetation.
Specimens were either placed in tubes containing ethyl
acetate vapour or, if required alive, in vials with
cotton wool to restrict movement.

(b) Efficiency

The efficiency of the 'bagging' technique
was compared with direct counting and sweeping.   The
investigation consisted of two stages :

1. A small part of vegetation, which could easily be
accommodated in a single sweep, was carefully scrutinized
for spiders.   The number seen was then compared with
numbers caught in the bag after the same piece of vegetation
had been swept with a single lateral and upward movement
of the arm.

The procedure was carried out twenty times
on each of 4 kinds of vegetation, and a comparison of the
numbers obtained are given in Table 7.

Table 7.   Comparison between numbers of spiders seen
           before sweeping and numbers caught in sweep net

Vegetation	numbers seen	numbers in net	% caught of those seen	x^2 (1)	
Bramble	40	26	65	2.97	
Fern	52	26	50	8.67	
Willowherb	50	18	36	15.06	
Grass	54	40	74	2.08	
Total	196	110	(55)	28.78	$p < 0.001$

Table 8.   Comparison between numbers of spiders seen before
           'bagging' and numbers caught in bag

Vegetation	numbers seen	numbers in bag	% seen of those caught	x^2 (1)	
Bramble	36	70	51	10.91	
Fern	40	68	59	7.26	
Willowherb	54	78	69	4.36	
Total	130	216	(59)	22.54	$p < 0.001$

2. Sweeping was then substituted by the bagging technique
already described.   The numbers caught were compared with
those seen beforehand on the vegetation.   These are given
in Table 8 and are based on twenty operations on each of
3 stands of vegetation.

The overall test of homogeneity clearly shows the inadequacy of sweeping, although the deviation from expected numbers in grass was relatively small. As spiders were not easily seen, especially in grass, the numbers directly counted on the vegetation were also gross under-estimates.

The difficulty of actually seeing spiders in even a small group of leaves or twigs is shown in Table 8 where numbers caught by 'bagging' were very much higher. This modified use of the sweep net could not be applied to bramble or fern stems which were rooted to the ground, nor to grass. Since most of the grass was below 15cm in height, it constituted part of the ground zone and was sampled accordingly.

Apart from the exceptions stated already, the 'bagging' technique could be used to sample all herbage in the field layer, including the alder twigs and small branches which grew below 1.8 metres (6'). The inner radius of the canvas bag which was attached to a metal frame was 20cm. Since it formed half a circle, the area was $628cm^2$. The number of bags required to sample a $metre^2$ was 16.

In the latter part of each month 10 samples were taken, 5 along one transect, and another 5 along a transect at right angles to the first.

Approximately 4 paces along a transect separated each sample.
The vegetation did not extend evenly throughout the field
layer and the spaces in between were not taken into account.
As a result, numbers may be over-estimates when expressed
on the basis of a metre^2.   However, there were places
where bramble was so dense that disturbance prior to
sampling, and hence loss of some spiders, was inevitable.

Tree trunks below 1.8 metres were inspected
for webs, each of which was counted as one spider.   The
cross sectional area of each tree was considered to be
equivalent to the area of one bag.   A total of 6 trees
were searched during sampling of the field layer.
From November to April greaseband papers, which are
normally used to restrict the vertical movement of insects
on apple trees, were in position on 6 trees, encircling the
bark at approximately 20 and 100cm above the ground.
Spiders caught on the paper as they emerged from crevices
in the bark in spring were used to estimate numbers
residing on tree trunks during the winter.   In September
and October webs as well as active spiders on the bark
surface were counted.

In every month during 1968, 16 bags or
samples (including the equivalent of 6 tree trunks below
1.8 metres) were used to estimate the number of spiders
per metre^2.

(3) The tree canopy

This was subdivided into 2 layers :
a lower canopy from 1.8 metres to 4m, and an upper canopy
from 4 metres to tree crowns at a height of between 10 - 12
metres. Alder trees only were selected although a few
birch and sycamore projected into the study area.

1. <u>Lower canopy</u>

The foliage in this stratum was sparse
relative to the field layer, but was generally distributed
and covered about 75% of the ground area. The lower
canopy represented an extension upwards of the field
layer since most species found in that layer were also
seen. Much of the vegetation consisted of side shoots
of alder together with the main trunks and branches.

The 'bagging' technique described for
the field layer was used to sample the foliage.
Vegetation which occupied a volume of 2.2×0.24 metres^3,
and corresponding to 4 bags, was removed. Spiders
were separated out from the plant debris and later
identified and counted. In addition, two trunks,
each of which was assumed to have a cross-sectional
area of a bag ($1/16m^2$), were examined for webs and active
spiders in the manner described for the field layer.

Since the total cross-sectional area
(4 bags + 2 tree trunks) of the samples in each month
amounted to $6/16m^2$, the formula used to convert data to
a metre^2 was as follows :

numbers x 2.7 x 0.75 spiders = numbers per metre^2

The removal of leaves and twigs by the
'bagging' method may have altered the environment a little.
It was not known how, and to what extent, destructive
sampling of this kind affected the spider population.

2. Upper canopy

An extending ladder was used to reach this
layer.   As the central trunk of trees only could support
it, sampling was restricted to foliage and branches close
to the ladder.   The highest crowns of trees could not
be reached without scaffolding which, unfortunately,
was not available.

As Turnbull (1960) had discovered, a
beating tray was the most convenient sampling apparatus
for this layer.   A number of criticisms have been
levelled at beating (e.g. Southwood 1966), one of which
is the difficulty of disturbing only those specimens in
the vegetation immediatly above the tray, catching those
that fall, and collecting them before they escape.

The vegetation of alder is not dense if measured in terms of number of leaves per unit volume, particularly at high levels. For example, about 300 leaves of hawthorn were found in a space of 0.25 metres^3, 74 on oak, 25 on birch, and only about 15 on alder. Although these figures are approximate, they reveal large differences in quantity of foliage per unit volume between species of tree. The effect on the spider population can be striking, as was shown in the field layer outside the sample area. Hawthorn and oak accommodated as many as 6 times the numberof spiders per unit volume found in alder.

The dimensions of the beating tray were 100cm x 50cm with a surface area of 0.5 metre^2. The lower parts of the stratum were sampled first and then, progressively, the higher foliage.

By drawing a circle on the ground around each one of 6 trees to mark the circumference of the upper canopy, it was possible to estimate the ground area covered by foliage. A value of 35% was arrived at. The estimated number of spiders in a metre^2 of upper canopy each month was then calculated from 4 samples by using the following formula :

$$\text{mean number per tray} \times 0.35 \times 2 = \text{numbers per metre}^2$$

Webs or active spiders seen on the main trunks were counted in with the numbers collected with the beating tray.

CHAPTER THREE

ANALYSIS OF THE SPIDER COMMUNITY   I

Introduction

An attempt was made to investigate the
characteristics of the whole spider community in quantitative
and qualitative terms.   Information was sought on species
composition, distribution and seasonal abundance, and the
size of the total community in relation to density, biomass,
and biocontent.   From the data it should be possible to
describe the community and so provide a backcloth against
which the status of individual species could be assessed.
The adequacy or otherwise of the sampling programme becomes
apparent as does the suitability of species for an energetics
study.

Fifty-one species were found, belonging
to 37 genera of 8 families (Table 1).   The linyphiid
spiders constituted 73% of total species :

Family	No.of species
Clubionidae	2
Thomisidae	1
Lycosidae	1
Agelenidae	1
Theridiidae	5
Tetragnathidae	1
Argiopidae	4
Linyphiidae	36

1. Ground Zone

(a) Seasonal distribution

Most of the Linphiids were characteristic of the ground zone, the exceptions being Gonatium rubellum and G.rubens, Drapetisca socialis, Bolyphantes luteolus, and species of Linyphia. Lepthyphantes pallidus was the only member of the genus restricted to the ground zone, while Robertus lividus (Theridiidae) was the only non-linyphiid which was totally a ground dweller. Its hammook webs were constructed in the surface litter or within 2cm above it. In the absence of wolf spiders (Lycosidae), its abundance and generally large size would suggest that it occupied the role of an important ground predator.

R.lividus and eight species of linyphiids were found in this zone in relatively large numbers. Their seasonal distribution and respective densities are given in Figs. 9 and 10. With the exception of Porrhomma pygmaeum, Savignia frontata and possibly Tapinocyba pallens all were present throughout the year. According to Locket and Millidge (1953), S.frontata is found all the year, while adults of P.pygmaeum are said to occur in summer. Again, adults of Oreonetides abnormis are present during the winter although reported in late summer and autumn.

Fig.9. Seasonal distribution of some adult spiders

in the ground zone.

Fig.10. Seasonal distribution of some adult

spiders in ground zone.

O N D J F M A M J J A S O N

NUMBERS/M² & NUMBERS/10 SAMPLES

TOTAL
FEMALES
MALES

SAVIGNIA
FRONTATA

ROBERTUS
LIVIDUS

TAPINOCYBA
PALLENS

DIPLOCEPHALUS
LATIFRONS

OREONETIDES
ABNORMIS

MONOCEPHALUS
FUSCIPES
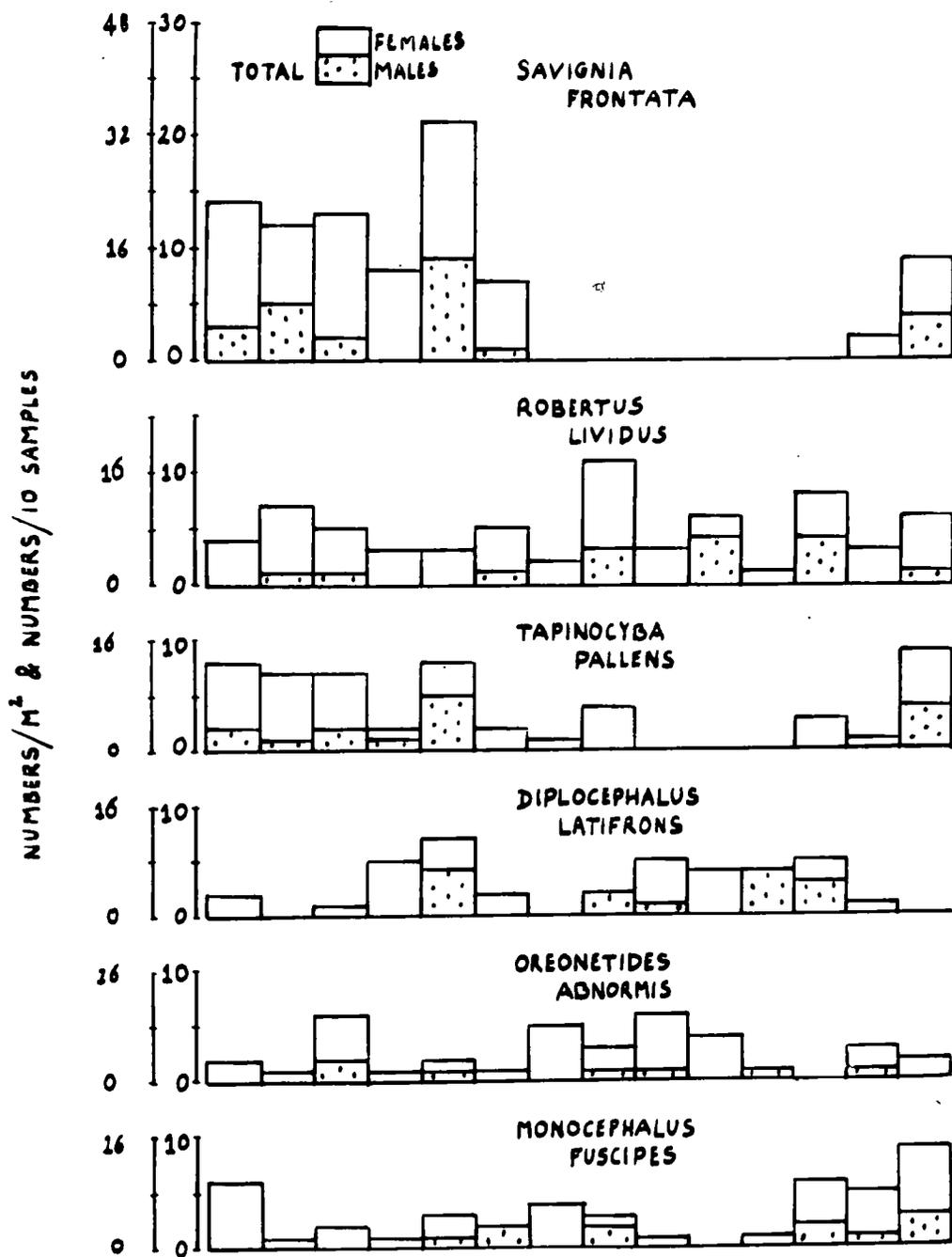
Other ground zone species were either infrequent, e.g. Porrhomma convexum and Centromerus dilutus, or they were not amenable to the sampling operation.

It appears that the conditions of the ground zone enable several species to exist throughout the year. There is evidence that mating and egg production can occur at any time. Spermatophores were present in the palpal organs and epigynes of Micrargus herbigradus and P.pugmaeum in February and March and with the former species, in May, June and July. Mating may have been influenced to some extent by the extractor, but the ability to mate was always present whatever the season. Male spiders were present whenever females were found.

Eggs were laid in the laboratory by O.abnormis and R.lividus caught during February and March. In fact, providing food was present and the temperatures did not fall below about $5^{o}C$, eggs could be laid at any time. The same applied to Micrargus herbigradus, a pair of which laid eggs regularly in the presence of food, from June to August.

The ground zone of woodland is a continuous and abundant source of spiders for the higher strata and for other habitats. The absence of Savignia frontata during the summer months may be explained by its tendency to disperse as an aeronaut. Duffey (1956) records a

substantial exodus by April and a subsequent absence for
a similar period from grass samples at Wytham Woods,
Oxford.

(b)   Numerical dominance

The status of any given species involve
the consideration of as many parameters as possible.
Numerical dominance may be expressed as a percentage of
the total individuals (Luczak 1959) but the problem of
interpretation arises where the total number of individuals
varies for each sampling occasion.

Debauche (1962) defined numerical dominance
as '..... the degree of expansion maintained by a species in
space and time.   The highest numerical dominance occurs
where a species is able to maintain the highest density
with the most uniform distribution of individuals during
the whole annual cycle.'

The state of expansion of a species, or
reverse of aggregation as given in the Disturbance index
of Lexi's (ratio of standard deviation to square root of
mean) is used by Debauche to describe numerical dominance.
This is reflected in the mean and its standard error,
hence

$$E = \frac{M - S}{\sqrt{N}}$$

The mean degree of expansion (D_n) maintained by a species during the annual cycle is, with 12 monthly samples,

$$D_n = \frac{\Sigma E}{12}$$

The sum of D_n may also reflect the receptivity (R) of the habitat towards the community

$$R = \Sigma D_n$$

Numerical dominance (Debauche loc.cit.) was conveniently calculated by computer for the 43 species found in the ground zone. Although monthly mean counts of two or more species may be the same, the variation about the mean will determine the degree of expansion which will be greater when standard deviations are small. A species having one or more individuals in only one sample unit for the month will register a nil expansion, while one with individuals in more thanone sample unit, whatever the number, will be positive.

Results

In Table 9 species in the ground zone are listed in order of numerical dominance. All are quite common in Britain (Locket and Millidge 1951, 1953) but at Wynyard _Micrargus herbigradus_ and _Porrhoma pygmaeum_ are outstanding numerically. The former species is ubiquitous,

also being found in large numbers in moorland areas
(Duffey 1963; Cherrett 1961). P.pygmaeum is not
mentioned by either Cherrett or Duffey (loc.cit.) while
Savignia frontata and Dicymbium nigrum have a more
restricted distribution. Monocephalus fuscipes occupies
10th position in the Wynyard hierarchy but would have
been rated more highly in moorland grassland dominated
by Nardus (Cherrett 1961).

Of those species having a mean dry weight
of exceeding 2mg for an adult individual, Robertus lividus
has the highest mean expansion. This spider also occurs
in a variety of habitats.

There have been so few detailed studies
of numbers of spiders that it is only possible to refer
in a limited way to the same species occurring in other
habitats.

Table 9. Species list in order of numerical dominance

for the ground zone

Species	D_n
<u>Micrargus herbigradus</u>	22.7701
<u>Porrhoma pygmaeum</u>	18.5352
<u>Dicymbium nigrum</u>	7.1368
<u>Savignia frontata</u>	6.7692
<u>Robertus lividus</u>	4.6156
<u>Tapinocyba pallens</u>	2.6424
<u>Diplocephalus latifrons</u>	2.3900
<u>Lepthyphantes alacris</u>	1.9549
<u>Oreonetides abnormis</u>	1.7772
<u>Monoceplalus fuscipes</u>	1.6697
<u>Lepthyphantes cristatus</u>	0.7926
<u>L.pallidus</u>	0.7778
<u>L.zimmermanni</u>	0.7681
<u>Centromerus sylvaticus</u>	0.7143
<u>Helophora insignis</u>	0.7111
<u>Meta segmentata</u>	0.3274
<u>Macrargus rufus</u>	0.2852
<u>Linyphia triangularis</u>	0.2852
<u>Cornicularia cuspidatata</u>	0.1963
<u>Gonatium rubellum</u>	0.1963
<u>Porrhoma convexum</u>	0.1963
<u>Dicymbium tibiale</u>	0.1778
<u>Lepthyphantes tenuis</u>	0.1778
<u>Bathyphantes nigrinus</u>	0.1778
<u>Theridion pallens</u>	0.1154
<u>Trachynella nudipalpis</u>	0.1154
<u>Xysticus cristatus</u>	0.0889
<u>Lycosa pullata</u>	0.0889
<u>Dismodicus bifrons</u>	0.0889

R =   75.8272

Discussion

Only mature stages could be identified
with the exception of <u>Robertus lividus</u>. The order of
numerical dominance can only refer to adults. Some

species may exist in the soil in relatively large numbers during the early stages of development, but seek the upper layers of the habitat at the onset of maturity. The numerical dominance of such species could be an under-estimate.

The forbs of the ground zone grow amongst the lower leaves of the field layer so that a number of 'field layer' species may be trapped within the soil samples. Helophora insignis may be found in leaf litter for two months after leaving the upper foliage. At Wynyard lycosid spiders were mere transients. These spiders are included in the order of dominance but usually have low values.

Apparently the index of numerical dominance proposed by Debauche (1962) has been seldom used. Bolton (1969) uses the Index of Lexis to indicate aggregation in earthworms at Wynyard but does not quantify an order of dominance.

In an energetics study or a population survey where a large number of species may occur as in the Araneida, numerical dominance provides a useful reference point for the species selected for detailed study. Kajak (1967), for example, discusses productivity in named species but does not refer to the spider fauna as a whole in a numerical sense. The likely importance of a species

when compared with its associates may go unnoticed or
may be exaggerated since it may not always be possible
for taxonomic reasons to select a fairly common species
for an energetics study.   Breymeyer (1967) used mean
biomass to describe the status of Trochosa ruricola
in a group of wandering spiders.

Dominance helps provide the background
information on the habitat in relation to species
populations, and as Debauche (loc.cit.) says, 'it is
a means for assessing the degree of occupancy of a
species in the same habitat or between different habitats.'

(c) Seasonal distribution of developmental stages

The density of mature spiders oscillated
only a little during the 14 months (Fig.11).   Peaks of
abundance of the young stages occurred in the autumn.
Minimum numbers were seen in December after which time
there was a progressive increase during the year.

An interesting situation was revealed
when immature stages were subdivided on the basis of
size.   Excluding the young stages of the relatively
large Robertus lividus, immature spiders fell conveniently
into 4 main size groups.   These may approximate to the
4-stage development of most small Linyphiids which were
the largest component in the ground zone.

Fig.11. Monthly densities of mature and immature spiders

(including R.lividus) in the ground zone

GROUND ZONE

IMMATURE SPIDERS

MATURE SPIDERS

NUMBERS / M²
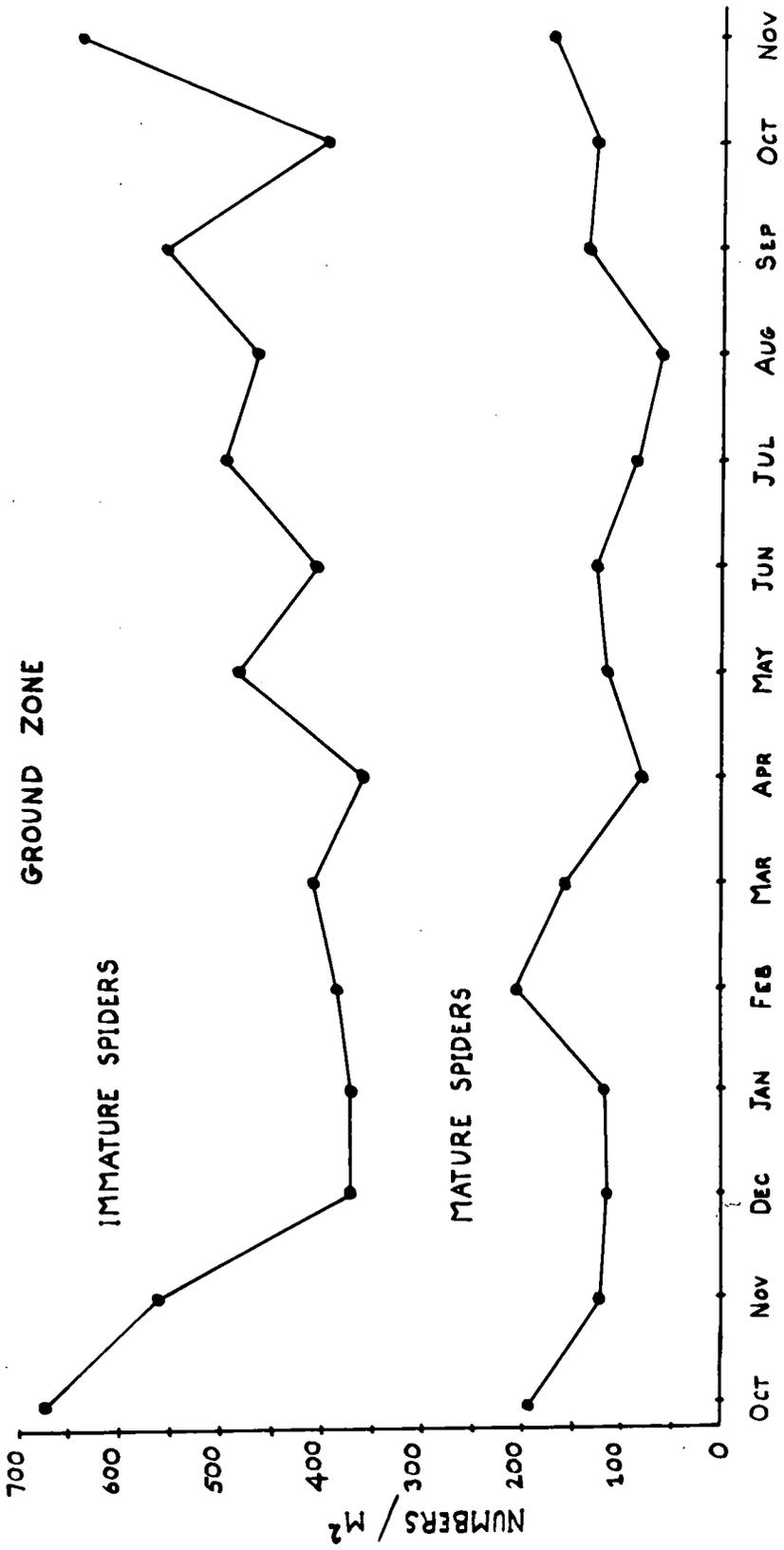
	<u>size groups</u>	(<u>body length in mm</u>)
α	<u>sub-adults</u> (palpal organs apparent, females sclerotinised)	-
A.	<u>small</u>	< 2.0
B	<u>very small</u>	< 1.5
C	<u>minute</u>	< 1.0

Numbers for each size group per m^2 are plotted against months (Fig.12). Group C, the smallest stage and to some extent it represents the young of the smallest species, has a marked periodicity. High late summer and autumn peaks contrast with low winter and spring values.

Group B fluctuates little over the sampling period, the highest peak occurring in November 1967, with lesser peaks in summer. Group A also shows little monthly variation while sub-adults (Group α) reached a maximum density in July to be followed by a diminution until the following March.

The apparent peaks of young spiders as a whole in June and July are due as much to an increase in sub-adults as an increase in the minute form. From August to November the main contribution was from Group C and to a lesser degree from Group B.

Fig.12. Monthly densities of immature spiders

(excluding _Robertus lividus_)in the

ground zone.

α = sub-adults

A = intermediate stages (1.5 - 2.0mm)

B = intermediate stages

(1.0 - 1.5mm)

C = minute stages ($<$ 1.00mm)

Measurements refer to body length

GROUND ZONE

SIZE GROUPS   IMMATURE SPIDERS
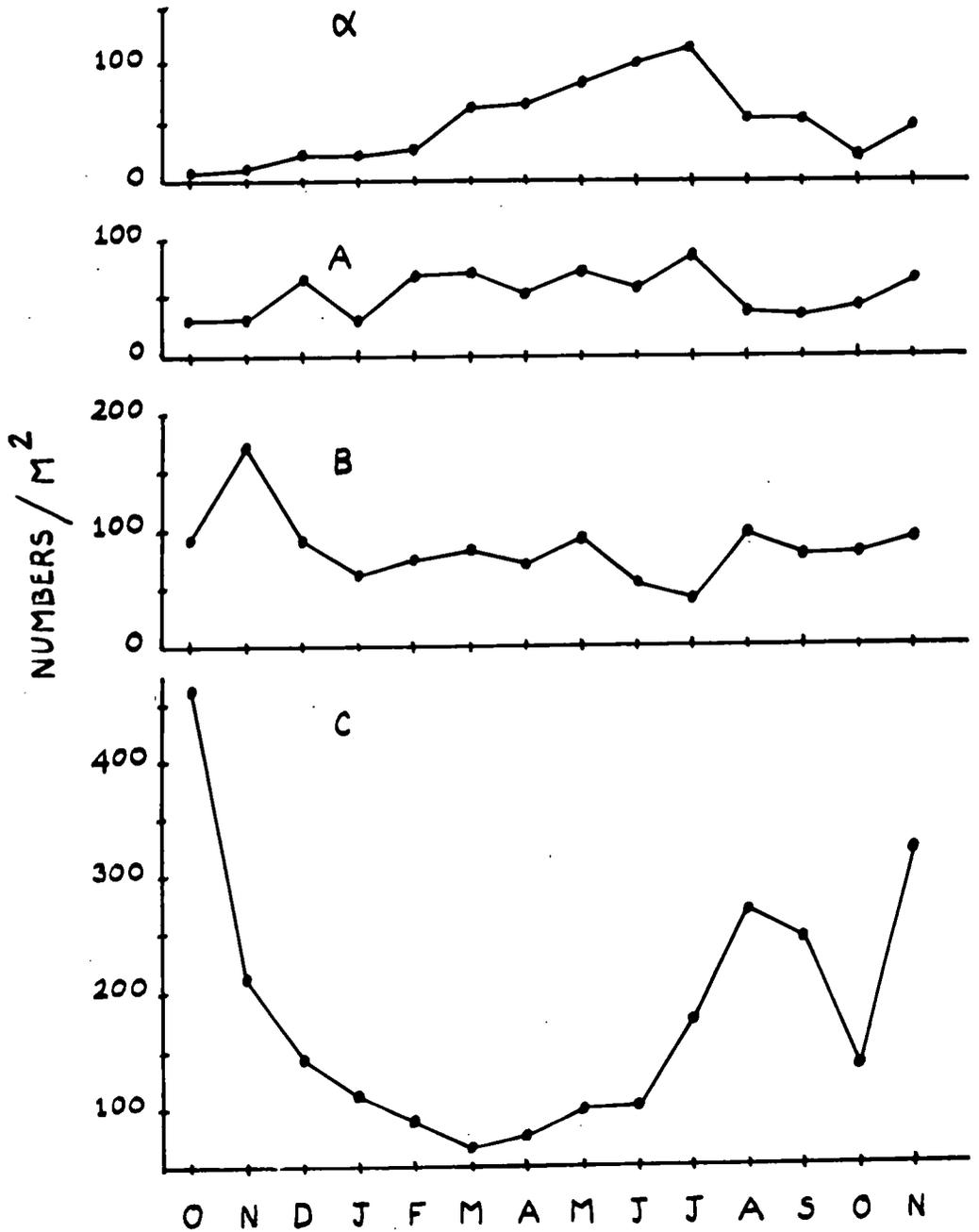
Most authors, e.g. Garbutt (1956, Linyphiids only), Duffey (1956, 1962), and Cherrett (1964, Linyphiids only), record the highest percentage of young spiders in July and August. However, in the light of the Wynyard data two points have to be made on these comparisons.

Firstly, to what extent are the estimates of other authors based on minute immature spiders? It may be that such spiders are not readily removed except by slow extraction with little condensation. If this did not operate, then the autumnal climax of young spiders may have been overlooked. Secondly, the use of percentages as an indication of the abundance of immature and mature spiders may be misleading where total numbers vary substantially over a period of time. Percentages of immature and mature stages implies a dependence of values. An example from the Wynyard data illustrates this point. For July and August the percentage of immature spiders was 86 and 88%, respectively. Although these were the highest, they do not denote the seasonal maxima in numbers per m^2, which amounted to 675 in October 1967 and 643 in November 1968. The unit of comparison is the m^2 which is not based on relative abundance.

It would appear that either the smallest species of the ground zone produce young mainly in the late summer and autumn, or that mortality of the smallest stages is most pronounced during the winter. The picture is complicated, however, by the continuous breeding season. Once a month sampling of the ground zone is too infrequent to reveal the developmental cycles of the smaller species. Considerable overlapping of stages of a species and between several species also occurs. These factors probably account for the consistent numbers in size groups A and B. Certainly, a sampling programme is required for a longer period than 14 months to show any consistent pattern.

The immature component appears to be derived from two main sources :

Group 1

Generally very small or minute species, e.g. <u>Porrhomma pygmaeum</u>, <u>Savignia frontata</u>, <u>Tapinocyba pallens</u>.

Large number of adults which occur mainly from autumn to spring.

Individuals lay few eggs, mostly in the spring. Development completed during the summer, so that adults over-winter.

Group 2

Species often large, e.g. Robertus lividus,
Oreonetides abnormis. Group also includes Micrargus
herbigradus and Dicymbium nigrum.

Number of adults often small, but present
all the year round.

Number of eggs laid by individuals often
large. Males much in evidence during summer months when
mating is followed by oviposition.

Autumnal peak of emergent spiders largely
accounted for by this group. Spiders overwinter at
intermediate instars. Maturity reached by early summer.

The smallest of the immature stages do
not appear to overwinter to any great extent, having
to progress to older instars in order to do so. On
the other hand, there was evidence from the life-history
study of R.lividus that few spiders overwinter as sub-
adults. A high metabolic rate, characteristic for
this stage and for the emergent stage(described later
for R.lividus and Meta segmentata) cannot readily be
maintained during the cold winter months when food is
limited.

2. The field layer

Monthly densities of young and adult spiders are given in Figure 13. Numbers are very low during the winter, but build up considerably during the summer. A peak of abundance of young spiders occurs in July, preceding the peak for adults in September.

(a) Seasonal distribution

Table 9b provides information on species composition of the spider fauna each month during 1967-68. The striking impression is the brief temporal distribution of many adult spiders when compared with species of the ground zone, many of which may be found for several months of the year. Adult Clubiona were only found in June, the life span of some mature male spiders such as Theridion denticulatum and Linyphia hortensis covered one or two weeks, Lepthyphantes tenuis was only found in July, and adults of Meta segmentata mengei were virtually confined to May. In fact, few species were in evidence in substantial numbers as adults, for more than about five weeks.

In the autumn, several large (mean dry wt. 8mg) species were common, Meta segmentata, M.merianae, and Helophora insignis together with the smaller Drapetisca socialis and Lepthyphantes alacris. Eggs were laid from about October onwards shortly after females had dropped

Fig.13. Density of the spider community in the field layer, 1967-68.

FIELD LAYER
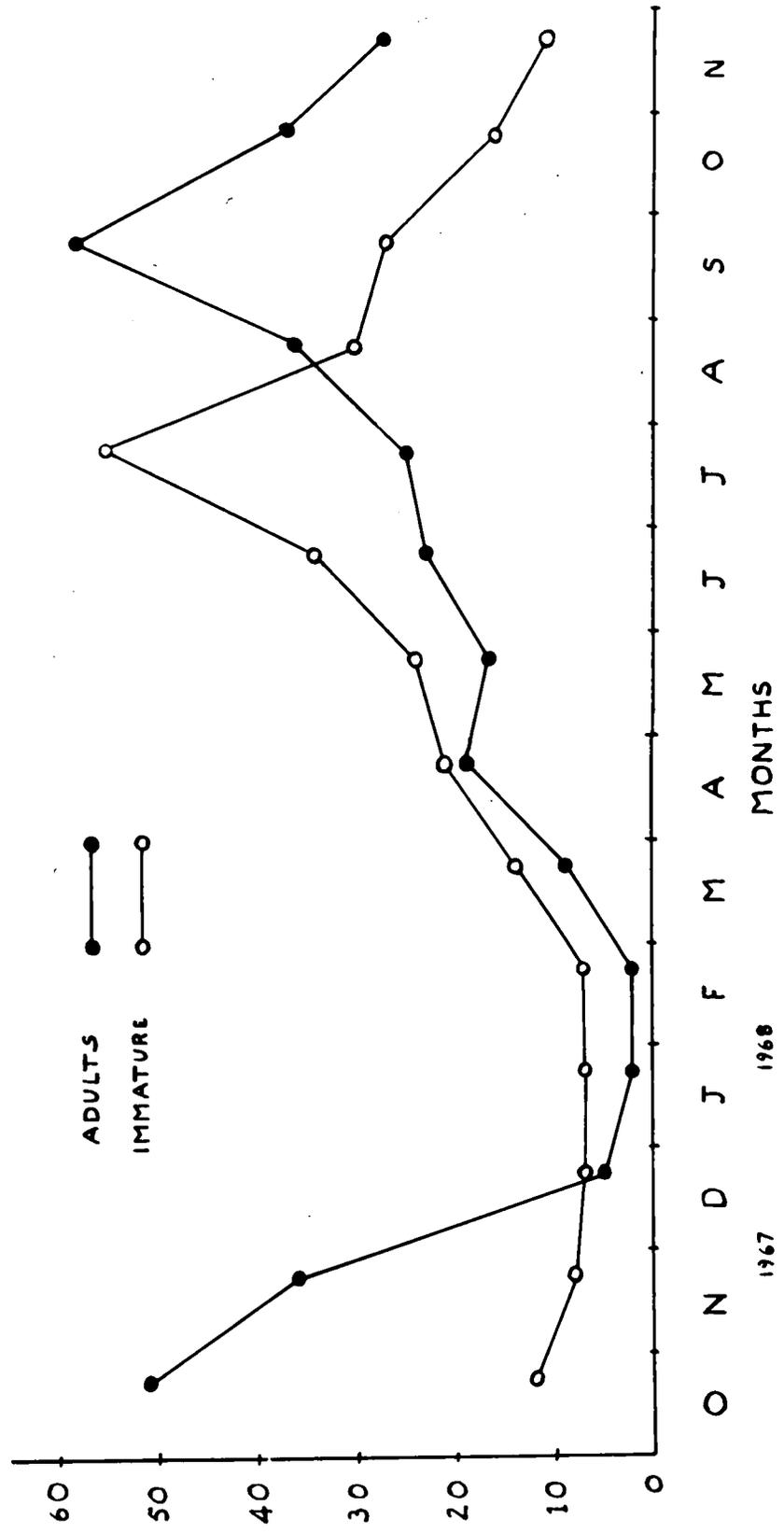
to the litter layer. A number of female L.alacris actually overwintered, and after a period of activity in the spring when they remained in the ground zone, cocoons were constructed.

Immature stages in the late summer and autumn frequently belonged to Theridion denticulatum, M. segmentata mengei, L.hortensis, Trachynella nudipalpis and Cornicularis cuspidata. The remainder included very small developmental stages (< 2mm) of Metaspp., none of which appeared to succeed in overwintering. Fissures in bark and fallen twigs which accumulated in heaps on side shoots of alder trees, provided overwintering sites since all these species were found stuck to the greaseband paper in April and May, or were found during winter in the debris of twigs.

As expected, those species which had overwintered as sub-adults were dominant in the following spring. The smaller spiders with a correspondingly short developmental time were represented by Trachynella nudipalpus and Cornicularia cuspidata. They were then joined or succeeded by Gonatium rubellum, M.segmentata mengei and several others, including Clubiona stagnatalis and C.lutescens, which had been immature during the winter.

From May until August, mature spiders comprised a small (< 40%) proportion of the total population.

The majority of young spiders at this time could be identified to species which were to become dominant in the autumn, namely <u>Meta segmentata</u> and <u>Linyphia triangularis</u>, followed by <u>Gonatium rubellum</u> and <u>Lepthyphantes alacris</u>. These immature stages are largely responsible for the adult peak in September when the proportion of adults rises sharply to 65%.

Thirty one species were found in the field layer representing only 5 families. Diversity was low, especially when compared with Turnbull's (1960) records for a stand of oak in the southern part of England where about 90 species representing 15 families were found. Specimens belonging to the following families were not found in the field layer at Wynyard; Dysderidae Gnaphosidae, Anyphaenidae, Sparassidae, Thomisidae, Salticidae, Lycosidae, Pisauridae, and Agelenidae. In many situations the field layer is extremely rich in species.

(b) <u>Dominance</u>

Sampling the field layer by the bagging technique was time consuming. Hence the numbers of each species in separate 'bags' was not recorded. Without the means and standard deviations the method for describing numerical dominance (Debauche 1962) could not be used. Although numerical dominance can be expressed, the succession of species is a more obvious feature in the field layer than

Table 9b. Monthly species composition and numbers per metre^2 in field layer, 1967/68

Species	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov
Clubiona stagnatalis														
C.lutescens								1	1					
Theridion denticulatum								1	1					
T.ovatum									2	1				
T.pallens	3						1	1	2					
Pachygnatha degeeri	4											1		
Meta segmentata											5	11	3	
M.seg.mengei	1	1	1		1	1	1	2	2				1	
M.merianae	1	5				4	10	3	4				1	3
Trachynella nudipalpis	3					3	3	4	3				2	
Cornicularia cuspidata	1	1												2
Dicymbium nigrum										2				
Gongylidium rufipes														
Dismodicus bifrons							1	2	1					
Gonatium rubens							1		4			2	1	
G.rubellum	4	3									2	4	3	2
Savignia frontata													1	
Erigone dentipalpis	1										1			
Porrhoma pygmaeum	1													
P.convexum							1						1	
Meioneta rurestris	1											2	2	
Bathyphantes nigrinus	3	2										2	4	1
Drapetisca socialis	1										5	7		
Lepthyphantes alacris	19	17									6	13	9	16

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Table 9b. Contd....

Species	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov
L.zimmermanni	1	1							1	4	1			
L.tenuis										14				
L.cristatus	1	1									2			
Helophora insignis	6	5									6	8	7	3
Linyphia triangularis	2										4	8	3	
L.peltata			1	1	1	1			1		1			
L.hortensis									3	2				

Monthly totals:

	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov
Mature spiders	51	36	5	2	2	9	19	14	23	25	36	58	37	27
Immatures	12	8	7	7	7	14	21	24	34	55	30	27	16	11
Total population	63	44	12	9	9	23	40	38	57	80	66	85	53	38

in the ground zone.   Several species are present in the
foliage for brief periods.

A more appropriate indication of status in the
field layer is biomass.   Since the adults of many
species are in existence for short periods, the 'intensity'
of their presence is best expressed as standing crop.
Mean monthly numbers for each species was estimated from
the data in Table 9b, and the values multiplied by
individual dry weights.

Results and discussion

The mean monthly standing crops per m^2, from
December 1967 to November 1968, are given in Table 10.
Only those species whose biomass values are above 1mg
per m^2 are included in the list of dominance.

The abundance of some species, e.g. Lepthyphantes
alacris and L.tenuis raise them high in the order despite
low individual weights.   Otherwise, most species in the
top eight of the list are relatively large.

The use of adults alone restricts the value of
the assessment of dominance.   The coincidence of sampling
with peak densities for some species will influence their
positions.

Table 10. Order of dominance in the field layer based on

mean standing crop (Density from data in Table 9b.)

Species	individual dry wt.(mg)	mean monthly density/m^2	mean monthly standing crop/mg/m^2
Meta segmentata	8.20	6.6	54.12
Linyphia triangularis	4.80	5.0	24.00
Helophora insignis	2.00	6.0	12.00
Lepthyphantes alacris	1.00	11.0	11.00
Meta merianae	4.2	2.0	8.40
Drapetisca socialis	1.0	6.0	6.00
Meta s.mengei	4.4	1.3	5.72
Lepthyphantes tenuis	0.33	4.6	4.62
Trachynella nudipalpis	0.50	4.6	2.30
Gonatium rubellum	0.80	2.4	1.92
Theridion denticulatum	1.20	1.5	1.80
T.ovatum	1.80	1.0	1.80
Clubiona lutescens	1.6	1	1.60
C.stagnatalis	1.4	1	1.40
Bathyphantes nigrinus	0.60	2.3	1.38
Cornicularia cuspidata	0.40	3.0	1.20
Linyphia hortensis	0.80	1.3	1.04
L.peltata	0.50	2.0	1.00

3. The canopy

Qualitative aspects

Parts of the lower canopy were extensions of the field layer. Many species of the latter layer were to be seen at this level. However, numbers were much lower partly because the vegetation was relatively sparse. Conspicuous species were Meta segmentata, Drapetisca socialis and Helophora insignis. Several species appeared to be transients, e.g. Theridion pallens and the young of Clubionidae and Linyphiidae.

Apart from T.pallens, all species found in the upper canopy appeared to be dispersing. The most notable were Savignia frontata, Erigone dentipalpis, Meioneta rurestris and Porrhomma convexium. The webs of D.socialis were frequently in evidence in the crevices of bark. The emergent stage of species of the genus Meta were occasionally found. Large species, or the older developmental stages of such species, were conspicuous by their absence.

4. The selection of species for an energetics study

(a) Identification of developmental stages

About 40 species of spiders were found in the ground zone, of which 30 were typical of this stratum at Wynyard. In the field layer about 10 species were common. This situation raises the problem of selecting appropriate species for an intensive energetics study.

Although adult spiders were identified with relative ease by means of external genitalia, young spiders had few distinguishing characteristics and presented some difficulties in recognition.

A filial connection had to be established between the adult and immature stages to facilitate the construction of a life table. To this end some numerically conspicuous adult spiders from the study area were allowed to lay eggs

from which the young were cultured and examined for identifiable features. Collections of immature stages were then searched for specimens with the same characteristics. Where the number of adult species was low as in the field layer, this approach was fruitful. In the ground zone, however, the large number presented problems of maintaining numerous cultures.

The alternative approach to discover filiations was to sort young spiders into groups on the basis of size, shape of cephalothorax or abdomen, by length in relation to body length, or the position of prominent spines or degree of hairiness. Some specimens could be separated from others because of certain consistent features. An attempt was made to trace particular characteristics from the smallest of the immature stages to the adult. Confirmation of a filial connection was obtained when adults produced young with the same features. The fidelity of certain characters could then be assessed by allowing the emergent stage to develop into the adult form.

Needless to say, a few species only had features which were distinctive and at the same time preserved at every moult. The later instars of *Oreonetides abnormis*, for example, could be identified with reasonable certainty

by the presence of 3 prominent spines in the mid-line of
the cephalothorax, and by the general robustness of the
species.   The earlier or first instars, however, were
not readily separated from the young of other species
in the ground zone, because those identifiable features
of the later stages were not yet apparent.

Status of species

One of the objectives of the present study was
to provide energy budgets for two species of woodland
spiders.   Therefore, the spiders chosen in the sample
area had to be numerically strong to be truly representative.
Biomass may be less important although the activity of a
species may be reflected in its biomass (e.g. Debauche 1962).
At Wynyard, it would have been convenient to
study a lycosid spider, e.g. Lycosa amentata, which had a
well-marked breeding season, recognisable instars and a
synchronised life-history.   It was also easily reared
in the laboratory.   However, results of pitfall trapping
showed it to be present in the wood in very small numbers,
less than 0.05 per metre^2 at the height of summer.   This
spider was not a typical woodland species and occurred as
an occasional intruder.

It was clear that representative species may
not always be the most convenient to study because of
difficulties in establishing a filial connection between stadia.

Practical considerations which included amenability of
all stages to the available sampling methods, and the
numbers available for respirometry and calorific studies,
indicated that <u>R.lividus</u> and <u>M.segmentata</u> could be the
basis of a useful bioenergetics study. One disadvantage
of <u>R.lividus</u> was the overlap of generations.

(b) <u>Robertus lividus</u>

This species was considered a typical ground zone
spider at Wynyard (Fig.14). Its hammock webs occurred
within the litter layer or at the very base of forbs.
In the laboratory immature stages fed on Collembola and
mites as well as on small spiders of other species. The
adults showed a preference for very small winged Diptera.

During the examination of monthly collections of
young spiders of all species, a number were seen to have
4 spines posterior to the fovea (Fig.15). Against the
pale colour of the body these spines were conspicuous,
only occasionally being obscured by suffused pigmentation.
Filiation with the adult spider was revealed when identical
spines, rendered less obvious by the generally dark colour
of the cephalothorax, were found in the same place.

Two female spiders in the spring and three in
the autumn, 1968, produced young all with spines occupying

Fig.14. <u>Robertus lividus</u>, female specimen.

(Body length 6mm)

Fig.15. <u>Robertus lividus</u>, early instar with

4 diagnostic spines in foveal area

(40 x)   Preserved specimen.
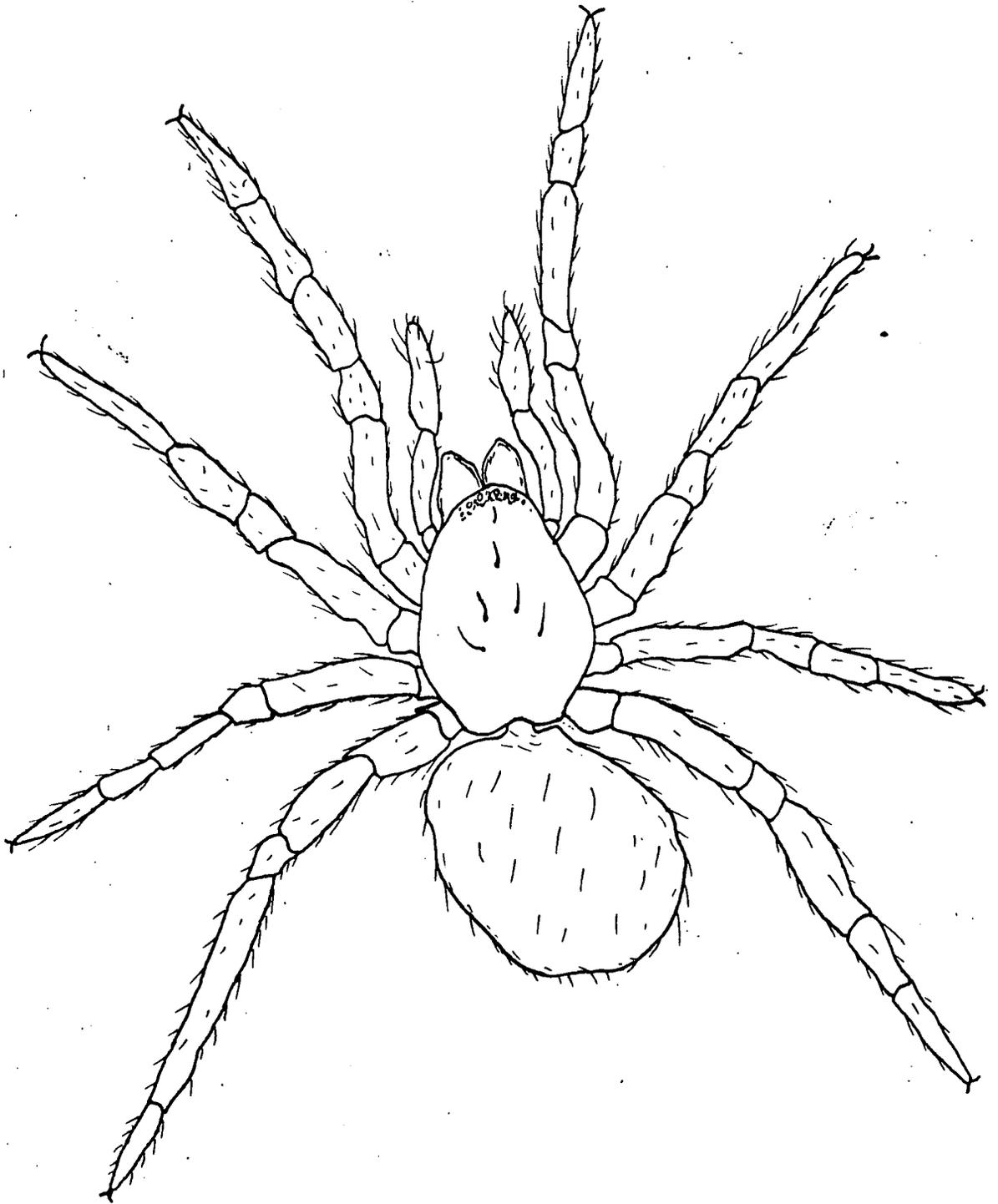
the corners of a trapezium or square. This pattern was
preserved at every instar. The morphology of the pedi-
palps in the male and of the epigyne in the female
(Locket and Millidge 1953) confirmed that the adults
with these spines were R.lividus.

All stages of the spider appeared to be amenable
to the extraction methods used, the apparatus having a
general efficiency of 90% for adult spiders, and 85%
for immature stages.

Robertus lividus turned out to be quite abundant,
and was rated number 5 in the overall order of dominance
in the ground zone (Section 1(b)). When such species as
Meta segmentata and Helophora insignis were excluded from
the list for this stratum the female adults had the highest
individual biomass (mean wet weight = 7mg).

Total density and biomass for the population of
R.lividus was high in relation to the other 40 species
(Table 11). Immature stages constituted between 5 and
34% of the total number of young for all species during
the year. Adult spiders made up 16% of total adult
density in some months. The density of the population
as a whole lay between 6 and 28% of the total during a
calendar year.

Estimates of biomass for the population of R.lividus
varied between 13 and 40% of the total for all species in the
ground zone having a mean of about 25%.

Table 11.   Robertus lividus, numbers and biomass as

percentages of the total spider population

of the ground zone

month	% young	% adults	% total	% biomass mg.
1967				
Oct	12.7	3.5	10.4	17.6
Nov	16.1	8.7	14.6	28.9
Dec	12.6	7.0	11.4	21.2
1968				
Jan	34.0	4.0	26.6	29.1
Feb	24.6	2.4	18.3	22.6
Mar	29.0	5.0	22.8	34.3
Apr	26.8	3.3	27.7	38.1
May	25.1	16.0	23.4	38.8
June	21.3	4.2	17.6	32.5
July	12.8	10.2	12.4	29.5
Aug	5.4	2.5	6.7	13.4
Sept	24.8	9.3	21.7	35.3
Oct	27.8	4.2	23.3	20.0
Nov	23.3	5.3	18.3	31.0

(c) Meta segmentata

The genus Meta was also represented by

M.s.mengei and M.merianae, the young of which were similar

in appearance to those of M.segmentata. However, the

breeding season and period of dominance of the main cohort

of M.segmentata could be described with reasonable certainty.

The main cohort is adult in September and by the

first week in October all females have moved to the ground

zone to lay their eggs. The remaining M.segmentata are

smaller (wet weight rarely exceeding 20mg) and closely

resemble, with their dull abdominal patterns, the few

M.merianae and M.s.mengei.   During the winter, adults

and sub-adults of M.s.segmentata are found in the litter

layer or in heaps of alder twigs.   Since neither M.segmentata

nor M.merianae are found, it appears that they do not over-

winter except as eggs.   In the laboratory M.segmentata and

M.merianae laid their eggs in the autumn.   In the following

May and June, M.s.mengei are adult or soon attain this stage.

In July they disappear and in the laboratory specimens died

after laying eggs.   In the field in May, a mass of young

spiderlings appear, coinciding closely with the emergence

of young M.segmentata in the laboratory.   A second lesser

flush of emergent Meta is found toward the end of June and

in July, corresponding to an emergence of captive specimens

of M.s.mengei and M.merianae.   These spiderlings are readily

separated on the basis of size from those of M.segmentata

which are now at instar 2 or 3, and by the second week of

August become sub-adult.

The life histories of the 3 species of Meta are

summarized in Fig.16.   Although most eggs of M.segmentata

hatch in May, a mild winter may allow some individuals to

emerge in April as apparently happened in 1968.   However,

the main emergence still took place in May.

The only large species to compete numerically with M.segmentata were Helophora insignis and Linyphia triangularis. The young and adults of the latter species were quite distinct from those of M.segmentata. In terms of mean monthly standing crop of adults, per metre^2, this argiopid was well ahead of other species.

Fig.16. A comparison between the life histories of 3 species of spiders of the genus <u>Meta</u>. Columns represent relative abundance of each species.

M. SEGMENTATA 1

M. S. MENGEI 2

M. MERIANAE 3

KEY

EARLY INSTARS
LATE ,,
ADULTS
EGGS

DITTO →

J F M A M J J A S O N D

1

23

CHAPTER FOUR

THE MEASUREMENT OF CALORIFIC CONTENT OF SPIDER

MATERIAL (ROBERTUS LIVIDUS AND META SEGMENTATA)

Introduction

As Odum (1959) pointed out, calorific data are a
more meaningful guide to the function of a species population
when compared with data for numbers or biomass alone. An
important aspect of this is the calorific content of the
body tissue which represents the fate of part of the energy
passing through a population at any given moment in time.
It appears that there has been no previous attempt to measure
the calorific content of spider material. Kajak (1967)
estimated the productivity of 3 species of web spiders
using a calorific equivalent of 5.82 calories to 1 milligram
dry weight of insect tissue (given in Phillipson 1960).
This estimate is open to question because it assumes a close
similarity between insect and arachnid tissue in terms of
biochemistry. No allowance is made for possible differences
in calorific content between age groups of a spider population
and any change in function, i.e. from growth of body tissue
                  a formation of
to/reproductive material. In a comparison between species
the application of an estimate of this kind may conceal
important differences in function at any given time.

Calorific values have been obtained for a number of invertebrates (Slobodkin and Richman 1961), the isopods _Ligidium japonicum_ (Saito 1965), _Oniscus asellus_ and _Porcellio scaber_ (Watson 1966), the spittle bug _Philaenus spumarius_ (Weigert 1964), the ant _Pogonomyrmex badius_ (Golley and Gentry 1964), and the diplopod _Japonaria laminate armigera_ (Saito 1967). More recently Whignarajah (1968) obtained calorific values for the chilopods _Lithobius crassipes_ and _L.forficatus_. For terrestrial invertebrates the values are usually between 4 and 7 kilocalories per gram. A list of calorific values so far obtained has been given by Cummins (1967).

(a) Method

A new and improved version of Phillipson's miniature bomb calorimeter (Phillipson 1964) was used to determine the calorific content of both species of spiders (Fig.17). The instrument is made by J.R. Gentry Instruments (Aiken, S.C., U.S.A.) who claim that samples as small as 1 milligram can be combusted. Calibration involving the use of benzoic acid should give a coefficient of variation of less than 2%. Voltage is directly proportional to temperature change which is measured by thermocouples and recorded by a potentiometer with a 1 millivolt range.

Phillipson (1964) pointed out important advantages of this type of bomb, namely, its ability to handle small quantities of material, and the dispensation of filler substances which may produce misleading calorific values.

The spider material was collected in the field or obtained from the horizontal extractor and within a few hours placed in a vacuum oven at $60^{\circ}C$ for 48 hours. This treatment effectively dried the material to constant dry weight. It was then finely ground in a polished agate pestle and mortar and made into pellets of between 5 and 10 milligrams. Storage over silica gel in a desiccator ensured that the pellets were completely dry and had the effect of hardening them.

Benzoic acid of 97.7% purity was used to make pellets for calibration, the size of these ranging from 8 to 14 milligrams. The combustion of 10 such pellets gave a mean value of 0.5528 ± 0.00938mV/100 calories with a coefficient of variation of 1.68% (Table 12). The mean calibration figure was used to calculate the calorific values of spider material burned in the micro-bomb. At the start of each series of combustions, a pellet of benzoic acid was fired to check the validity of the mean calibration value.

Ash content was somewhat variable because small amounts were scattered within the bomb during combustion. The extent of the error was assessed by burning specimens in a muffle furnace at 400'C. The mean percentage by this method came to 3.89 which approximates to most values obtained with the bomb. However, two important points emerged from this digression: First, any value which is much below the mean of 3.89 represents too low an estimate of ash content. Second, there may be a real difference in ash content in the spider material. In M.segmentata, for example, percentages were in the range of 2.77 and 3.86. The ex ceptional values which were found between 5.26 and 5.92 could be related to spent or newly moulted adult females.

Both Wiegert (1965) and Whignarajah (1968) observed seasonal variations in calorific values as well as differences between instars in arthropods. Meta segmentata was readily available so that the material from all the developmental stages could be burnt separately. In the case of R.lividus, the first 2 instars had to be amalgamated and it was not possible to investigate seasonal variation.

The opportunity was taken to examine the likely range of calorific values in the Araneida. Burnings were made on the adults of Helophora insignis, Linyphia triangularis, and an amalgamation of several small species of Linyphiids.

Table 12.   Calibration of miniature bomb calorimeter

(Phillipson 1964) with benzoic acid (6.324 Kcal/g)

sample wt.mg.	calorific value in cals	potentiometric readings mv	Mv/100 cal
11.420	72.2200	0.394	0.5455
12.745	80.5993	0.440	0.5459
14.505	91.7296	0.500	0.5450
10.825	68.4573	0.393	0.5741
8.320	52.6156	0.293	0.5568
11.440	72.3465	0.395	0.5459
9.690	61.2795	0.339	0.5532
9.195	58.1491	0.318	0.5468
14.080	89.0419	0.500	0.5615
9.690	61.2796	0.339	0.5532

Mean reading per 100cal = 0.5528 $\pm$ S.D. 0.00938

Coefficient of variation 1.69%

Ash content negligible

(b)   Results

Tables 13 and 14 summarise the results of the investigation into biocontent.   Differences between the corresponding stages of the two species, Robertus lividus and Meta segmentata were small and not significant.   Both show an increase in calorific content with stage of development.

While gravid females (>10mg dry wt) of M.segmentata, Helphora insignis, and Linyphia triangularis,

reached or exceeded 6.0Kcal/g dry wt (ash free), the females
of R.lividus varied from 5.58 to 6.07Kcal.

Calorific values for male spiders were about
the same in all species, but were substantially lower than
those of females. Sub-adult males (instar 4) of M.segmentata
appeared to have a slightly higher calorific content than the
mature stage.

Eggs which had been collected shortly after their
extrusion into cocoons had a mean calorific value of 6.000Kcal/g
in R.lividus (based on a single combustion) and 6.377Kcal/g
in M.segmentata. The relatively high values obtained with
eggs possibly arises from a high proportion of lipids
(Davey 1965). In the spitbug, Philaenus leucopthalus,
a value of 6.529Kcal/g dry wt (ash free) had been obtained
(Slobodkin 1962) for eggs.

'Spent' female spiders, i.e. after egg laying,
yielded little more than 5.000Kcal/g in M.segmentata; rather
less than in R.lividus. It is interesting to record here
that females of the last named species frequently survive
if food is available to lay again.

The frass of M.segmentata included the cocoon
with the remnants of spider material within, after the spiders
had dispersed. The high coefficient of variation is
attributed to the fact that in some cocoons, a number of
young spiders had been unable to free themselves, and so

contributed to the calorific value. The lower coefficient

of variation for eggs (0.81) possibly reflects the homogeneous

nature of the material.

As might be expected, cast skins or exuvia

yielded the lowest value, little more than 4.000Kcal/g,

which was based on a single burning.

(c) Discussion

The similarity of biocontent in the species

examined (Table 15) supports the observation by Slobodkin

(1962) that excess calories pass into reproduction rather

than adiposity.

The limitation of time prevented the construction

of large numbers of pellets. Although R.lividus was to be

found at all times of the year, numbers were too few during

some months to make enough pellets for statistical tests

of significance, and so detect seasonal variation. Nonetheless,

the trends in rise or fall of calorific content are clear, and

the results bear out the observations of other investigators

(loc.cit.).

So-called seasonal variation probably arises

from a number of causes. A concomitant increase in biocontent

with development after the egg stage may occur in M.segmentata.

This may be related to changes in feeding conditions or to the

Table 13. Robertus lividus, calorific values (ash free)

Material	Number of pellets	Mean % ash content	Kcal per g.	± S.D.	coeff. of variation
spent ♀	2	3.40	5.392	0.172	3.19
adult ♀	6	4.73	5.716	0.220	3.85
adult ♂	2	4.45	5.550	0.080	1.44
instar 4 ♀	2	3.21	5.540	0.190	3.43
instar 4 ♂	-	-	-	-	-
3	2	3.51	5.519	0.109	1.85
1+2	2	3.29	5.236	0.114	2.18
eggs	1	2.70	6.001	-	-
exuvia mixed	1	4.88	4.071	-	-

Table 14. <u>Meta segmentata</u>, calorific values (ash free)

material	number of pellets	mean % ash content	Kcal per g.	± S.D.	coeff. of variation
spent ♀	3	4.42	5.194	0.101	1.94
gravid ♀	8	3.52	6.294	0.311	4.88
mature ♀	6	5.25	5.495	0.228	4.15
mature ♂	5	3.51	5.359	0.222	4.15
instar 4 ♀	5	3.90	5.560	0.235	4.01
instar 4 ♂	3	2.89	5.630	0.192	4.00
3	3	3.29	5.512	0.270	4.00
2	3	3.20	5.435	0.087	1.60
1	3	3.67	5.205	0.179	3.44
eggs	5	2.55	6.377	0.051	0.81
frass	3	1.69	5.370	0.388	7.22
web	3	2.00	4.892	0.149	3.03
cocoon	3	2.29	5.981	0.190	3.18

Table 15. Calorific values in Kcal/g dry wt (ash free) of some adult woodland spiders

Species	n	females mean	± S.D.	n	males mean	± S.D.
Robertus lividus	6	5.716	0.220	2	5.550	0.080
Meta segmentata	8	6.294	0.311	5	5.359	0.222
Helophora insignis	4	6.296	0.201	3	5.771	0.147
Linyphia triangularis	4	5.931	0.270	3	5.692	0.183
Linyphiid species	4	5.806	0.241	2	5.387	0.119

maturation of gonads and eggs (Wiegert 1964; Whignarajah 1968). The surface law may even apply, if the exoskeleton with a lower calorific content increases with the square, while the soft internal parts increase approximately with the cube, of the linear dimension.

The population at any given moment may not be evenly aged, in which case the females for example may not all be egg bearing. Apparently this was the situation in R.lividus. Variation in the adult females may be explained by the existence in the field of different cohorts in which some females only had reached full term. It had been observed that weight and size of females emerging from the extractor at any given period differed substantially. The largest specimens only had yolk-filled eggs.

Where sampling errors are large, the estimates of population biocontent may not be influenced much by failing to take 'seasonal' or cohort variation into account. However, it is important to be able to record all possible sources of error.

Fig.17. Miniature bomb calorimeter

oxygen cylinder   Potentiometer

Cover for microbomb   'bomb'

switch   electromicrobalance
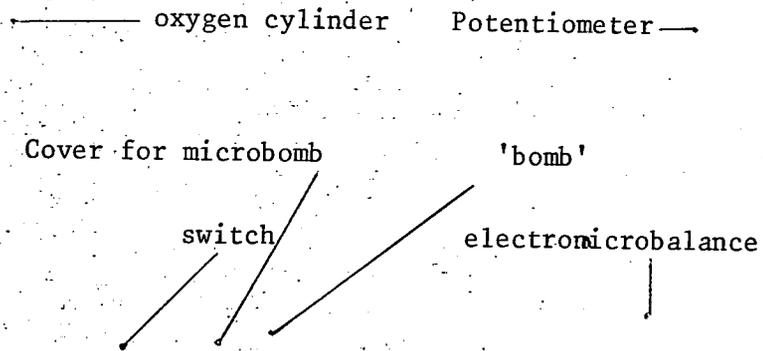
Fig.18. Respirometers (water bath not shown)

Recorder

Relay unit

electrode

Metabolic chamber

electrolyte
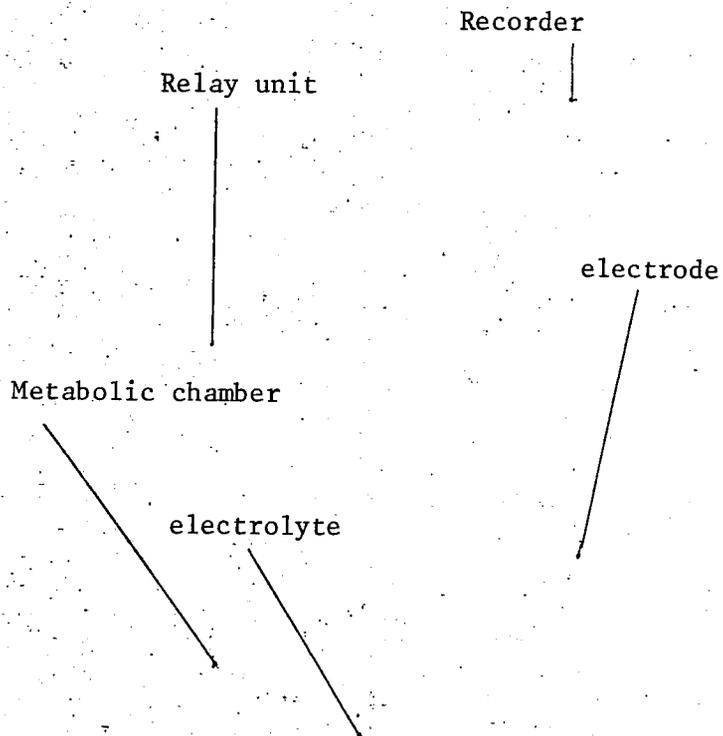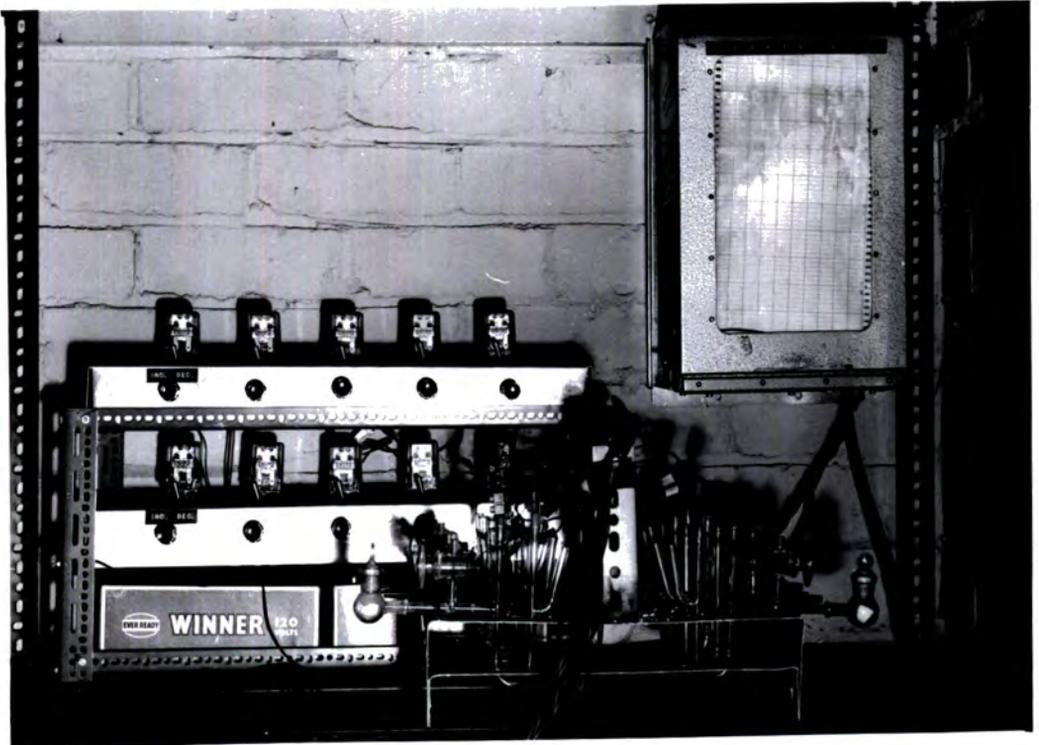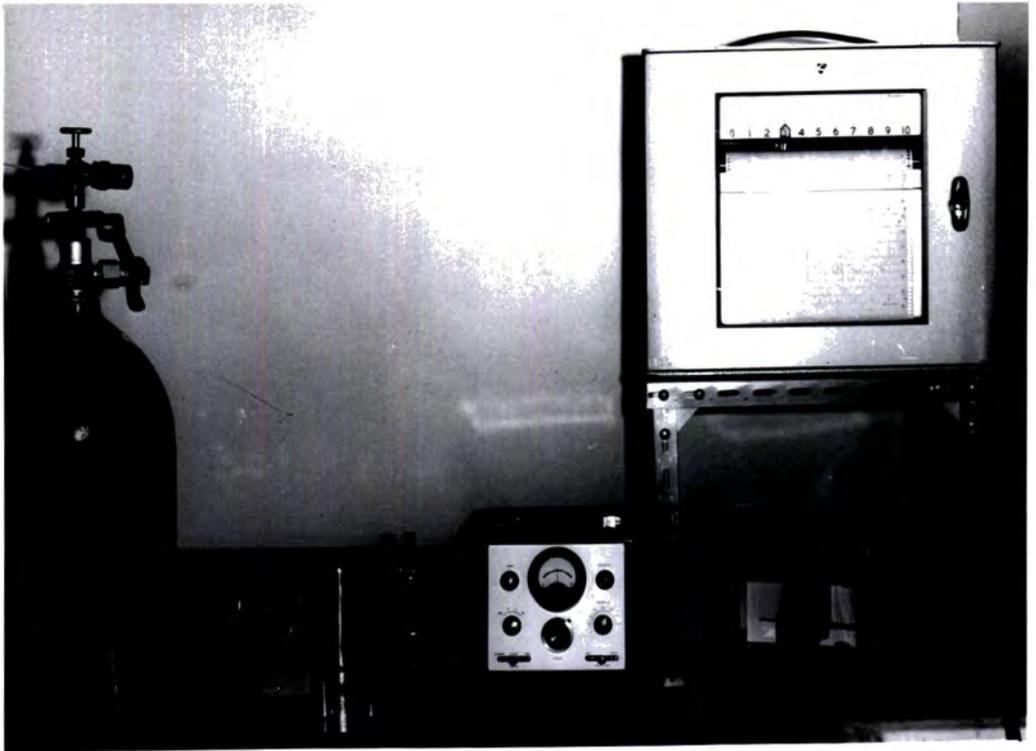
CHAPTER FIVE

RESPIRATION

As much as 70% of assimilated energy may be lost through respiration (Engelmann 1966), which underlines the importance of this parameter in energy flow.

Itô (1964) estimated energy loss through respiration by measuring carbon dioxide production by chemical means.   Starved and replete lycosids were used. With an infra-red gas analyser, Miyashita (1969) investigated the effects of mobility and temperature on lycosids. Diurnal and seasonal changes in metabolic activity were detected by Phillipson (1962) in Opiliones, with an electrolytic continuously recording device.   More recently, Anderson (1970) has described some characteristics of arachnid respiration with particular reference to acclimatization. He used a Gilson differential respirometer.   As diverse as these methods are, all were able to measure gas changes over an extended period.   Where oxygen uptake is not measured directly, estimates can be made from CO_2 production and Q_{10} values.

As Phillipson (1967) points out, the value of these restricted studies on metabolism is that they indicate possible sources of error which could apply to studies on field populations.

(a) <u>Apparatus</u>

The continuously recording respirometer devised by Phillipson (1962) for phalangids was available for the present study (Fig.18). It had already been used with <u>Oniscus asellus</u> (Phillipson and Watson 1965), species of Diploda (Phillipson 1967), an elaterid beetle (Dutton 1968), species of <u>Lithobius</u> (Whignarajah 1968), and the carabid beetle, <u>Nebria brevicollis</u> (Manga 1970).

Results of Warburg respirometry on centipedes were similar to those obtained with the continuously recording device (Whignarajah 1968). Adult specimens of <u>Meta segmentata</u> also gave comparable results (Table 16). However, as with centipedes, only the largest stages could conveniently be investigated by the Warburg method. In any case, change in rate of respiration over the diel would only be apparent with continuously recording apparatus.

Table 16. Comparison between respiratory rates (μ O_2/mg wet wt/hr) in <u>M.segmentata</u> at $15^{o}C$, obtained with the Phillipson's continuously recording apparatus and Warburg units. (N = No.of individuals used). (mean $\pm s$).

	N	Continuously recording	Warburg	
Female	10	0.250 $\pm$ 0.02	0.263 $\pm$ 0.04	n.s.
Male	10	0.230 $\pm$ 0.03	0.284 $\pm$ 0.03	n.s.

(b) <u>Method</u>

Respiration in both species was measured at 5, 10 and 15'C, because monthly mean temperatures in the field were expected to fall mainly within this range.   By calculating regressions for rate of oxygen consumption on temperature for various stages of development, it is possible to estimate energy loss of the population under field temperatures.

Since different techniques were used to collect the two species of spiders, the procedures for preparing them for respirometry were not the same.   The extraction apparatus for soil and litter was the only way by which all stages of <u>R.lividus</u> could be acquired.   As some individuals remained in the extractor at high temperatures for up to 12 days, it was considered advisable to acclimatize them to the operating temperature of the respirometer. Petri dishes at 5', 10' or 15'C with wet filter paper made convenient receptacles.   Food in the form of collembola, mites, and small spiders of other species was provided towards the end of the 7-day acclimatization period.

<u>Meta segmentata</u> were caught in the field by sweeping bag and within 2 hours after capture, placed in the respirometer.

Since both time and numbers of <u>R.lividus</u> were limited, the effects of acclimatization were not investigated.

However, experiments were run at temperatures which approximated to those in the field. For instance, during February the operating temperatures were 5' and 10'C, and during June, at 10' and 15'C. Since M.segmentata were found mainly during the summer months, the bulk of the experiments were carried out at 10 and 15'C.

The water bath which accommodated the respirometer at 5 ± 0.5'C and 10 ± 0.5'C was connected to a Tecam cooling unit having an adjustable thermoregulator. The thermostat of the water bath was used in conjunction with a circulating stream of water from a tap, to maintain a temperature of 15 ± 1'C.

Ten respirometer chambers were used for each run, two of which were without animals and acted as barometers. Individual spiders of both species at instars 4 and 5 were large enough to provide consistent results over 48 hours. The smaller stages were enclosed in pairs or groups of up to 10 spiders of similar weight or sex.

(c) Results

A curvilinear relation apparently exists between body weight and rate of respiration per unit weight (Figs. 19 and 20) in both species. The raw data shown for R.lividus were obtained at 10'C, and at 15'C for M.segmentata. The distribution of points on the graph

Fig.19. R.lividus, relation between live body weight and rate of respiration (μl O_2/mg/hr) at 10^oC.

● early instar and sub-adult female; ⌀ sub-adult male;

◖ adult male; O adult female

R. LIVIDUS

$\mu l\, O_2 / MG / HR$ 10° C.

LIVE BODY WEIGHT (MG).

Fig.20. M.segmentata, relation between live body weight and rate

of respiration ($\mu l \ O_2$/mg/hr) at $15^{o}C$.

● early instar and sub-adult female; ♂ sub-adult male;

♂ adult male; O adult female

M. SEGMENTATA

15° C

μl O₂/MG/HR
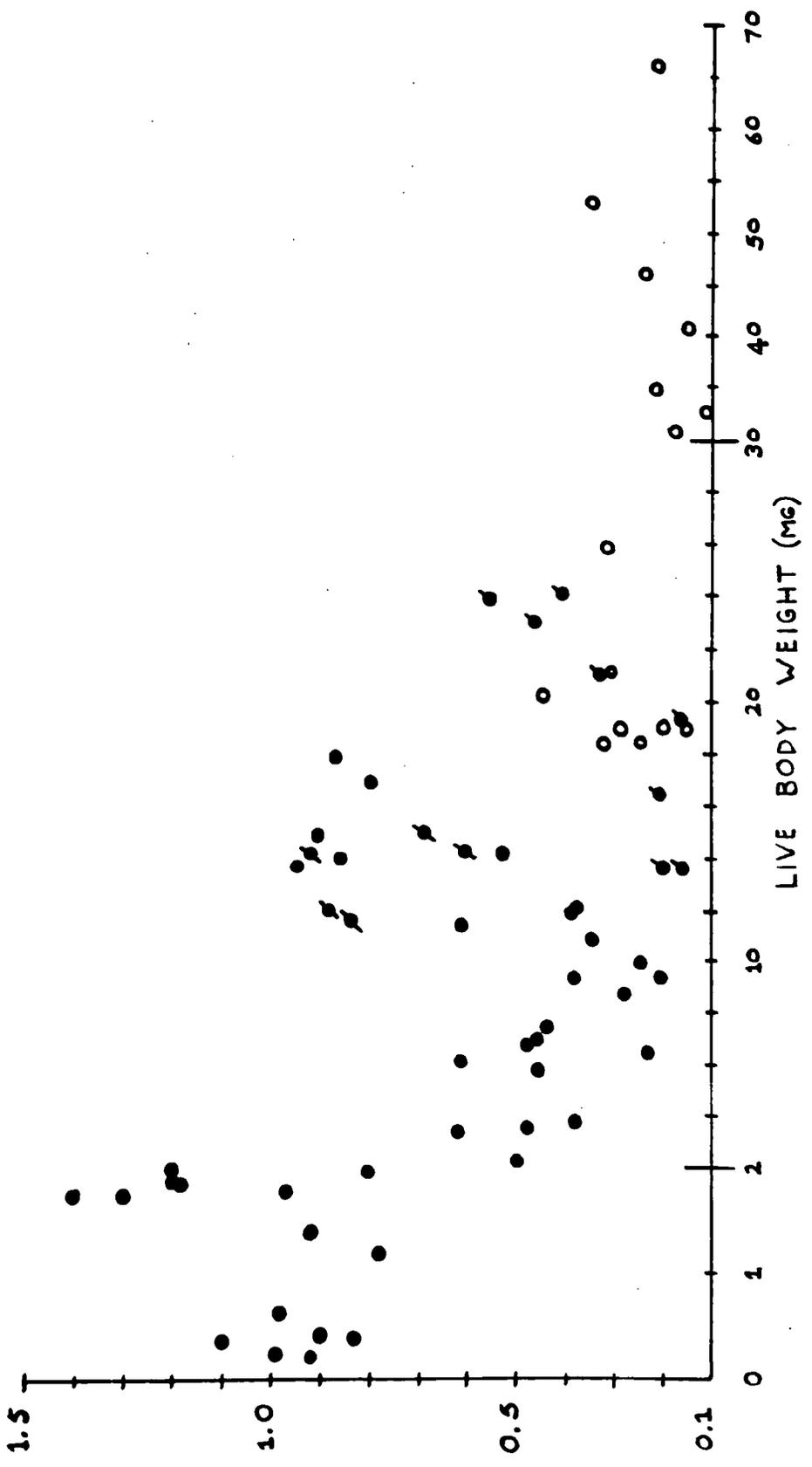
LIVE BODY WEIGHT (MG)

(not shown) at 5'C for the latter species was less clear, partly because few experiments were run at that temperature.

The inflexion of the graph was at about 1mg live body weight in R.lividus. Male spiders at the penultimate stage, however, maintained a relatively high consumption of oxygen. In M.segmentata, the inflexion occurred at about 4mg live body weight. In both species a number of points, which relate to spiders at the sub-adult stage, depart from the general curvilinear pattern.

The results of regression analyses of rate of respiration on temperature are shown in Figs. 21, 22 for R.lividus, and in Figs. 23, 24 for M.segmentata.

The values of Q_{10} were calculated for several stages (Table 17) of both species from the formula (Schmidt-Nielsen 1960) :.

$$M_2 = M_1 \cdot Q_{10}^{(t_2 - t_1)/10}$$

where M_2 and M_1 are the metabolic rates at two temperatures, t_2 and t_1. The mean values for R.lividus and M.segmentata are 2.7 and 3.0, respectively. While metabolic rates usually double for each rise of 10'C, the Q_{10} itself may also be temperature dependent (e.g. Prosser and Brown 1962).

Table 17. Q_{10} values of respiration over 5' to 15'C for

R.lividus and M.segmentata (N = sample size)

R.lividus		N	Q_{10}	M.segmentata			N	Q_{10}
Instars 1+2		17	3.1	live body wt.	0-2mg		36	3.3
	3	17	2.3		2-12		30	2.8
	4	20	2.7	instar 4			30	2.7
female	5	.16	2.2	female 5			30	3.2
male	5	13	3.2	male 5			30	3.2

(d)   Respiration in R.lividus

The mean rates of respiration per unit weight at 5', 10' and 15'C are given in Table 18, and show clearly that oxygen consumption is temperature dependent. With all instars, differences were significant between 5' and 10'C and, with the exception of instar 3, between 10' and 15'C.   In general, the levels of significance were higher between the two lower temperatures than between 10' and 15'C.

Metabolic rate in terms of microlitres of oxygen consumed per unit weight per hour differed significantly between adult males and females at 10' and 15'C, but not at 5'C (Table 19).   The rates for male adults and subadults were about the same, and no real difference was detected between males and females at instar 4.

Variation in rates of respiration within the
diel was not apparent, while seasonal differences were
not investigated.   Although the relation between temperature
and respiratory rates is assumed to be linear, there is a
suggestion in Figs. 21 and 22 of a curvilinear relationship.

(e) Respiration in M.segmentata

In terms of rate of respiration the spiders of
this species could be divided into four main groups (Figs. 23 and 24)
Individuals having a live body weight of less than 2mg
had the highest rates at all three temperatures (Table 20).
An increase in weight from 2 to about 12mg was accompanied
by a decrease in metabolic rate.   A further increase in
weight during the sub-adult stage coincided with a rise
in oxygen consumption per unit weight, which then fell
off as spiders entered the adult stage.

Adult male and female spiders apparently had
similar rates at all three temperature regimes (Table 21).
However, rates for the former were consistently higher.

As with R.lividus, temperature obviously
influences the rate (Table 20) with significant differences
between virtually all temperatures in each of the 4 groups.

Table 18.   <u>Robertus lividus</u>, mean rates of respiration ($\mu l\ O_2$/mg
live wt/hr) with significance of differences
('t' tests) between temperatures

instar	'C	n	mean rate $\pm$ S.E.	level of significance
1 + 2	5	4	0.423 $\pm$ 0.044	
	10	9	1.046 $\pm$ 0.040	$p < 0.001$
	15	5	1.323 $\pm$ 0.116	$p < 0.05$
3	5	5	0.286 $\pm$ 0.027	
	10	7	0.540 $\pm$ 0.038	$p < 0.001$
	15	5	0.658 $\pm$ 0.021	not significant
4	5	3	0.368 $\pm$ 0.031	
	10	9	0.963 $\pm$ 0.027	$p < 0.001$
	15	9	1.213 $\pm$ 0.064	$p < 0.01$
5	5	4	0.232 $\pm$ 0.038	
female	10	7	0.380 $\pm$ 0.033	$p < 0.02$
	15	5	0.521 $\pm$ 0.034	$p < 0.02$
5	5	4	0.368 $\pm$ 0.078	
male	10	4	0.963 $\pm$ 0.072	$p < 0.001$
	15	5	1.213 $\pm$ 0.068	$p < 0.05$

Table 19.   *Robertus lividus*, mean rates of respiration

(μl O_2/mg live wt/hr) of adults with significance

of differences ('t' tests) between sexes

	Temp.'C	mean rate $\pm$ S.E.	level of significance
males		0.368 + 0.078	
	5		not significant
females		0.232 + 0.038	
males		0.963 + 0.072	
	10		$p < 0.001$
females		0.380 + 0.033	
males		1.213 + 0.068	
	15		$p < 0.001$
females		0.521 + 0.034	

Fig.21. <u>R.lividus</u>, regression of rate of respiration

on temperature at instars 1 and 2 (above)

and at instar 3 (below)   (mean ±S.E.)

instars 1 & 2

$\mu L\, O_2 \mid mg \mid hr$

$y = 0.0306 + 0.09\,x$

TEMP °C

instar 3

$\mu L\, O_2 \mid mg \mid hr$

$y = 0.1367 + 0.04\,x$

TEMP °C
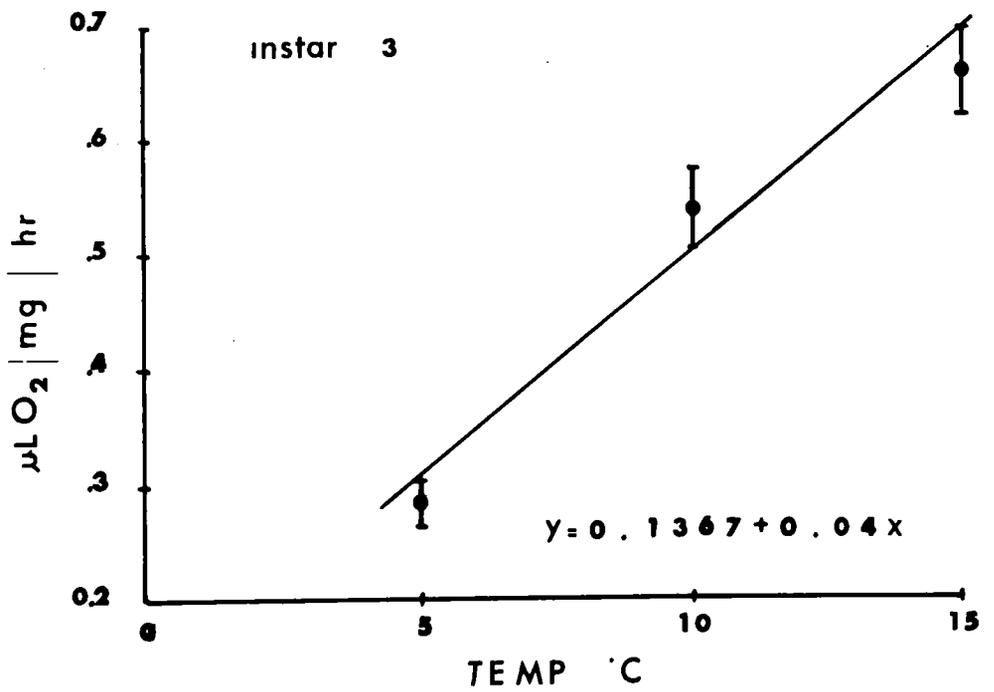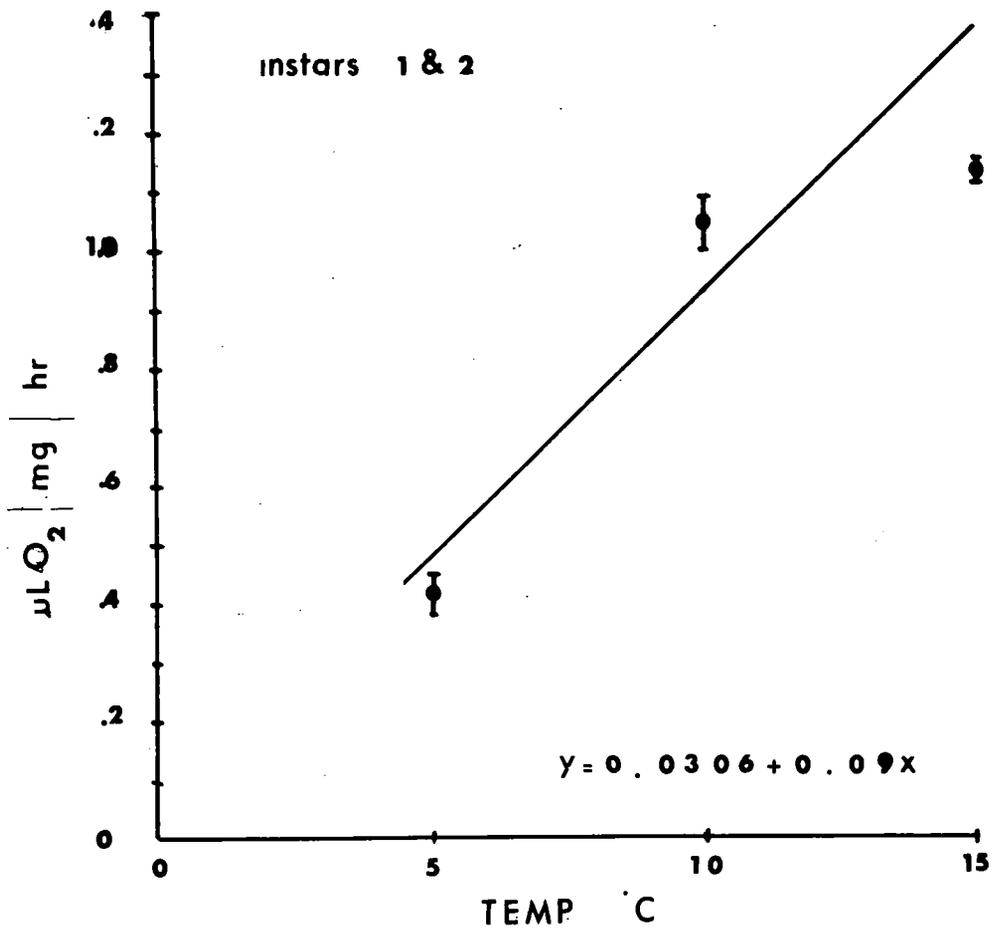
Fig.22.   Robertus lividus, regression of rate of

respiration on temperature for instar 4

(above) and adults (below).   (mean ± S.E)

instar 4

$\mu l\,O_2\,/\,mg\,/\,hr$

$Y = 0.0787 + 0.06x$

TEMP °C

adults

$\mu l\,O_2\,/\,mg\,/\,hr$

♂

$Y = 0.0023 + 0.08x$

♀

$Y = 0.0883 + 0.03x$

TEMP °C
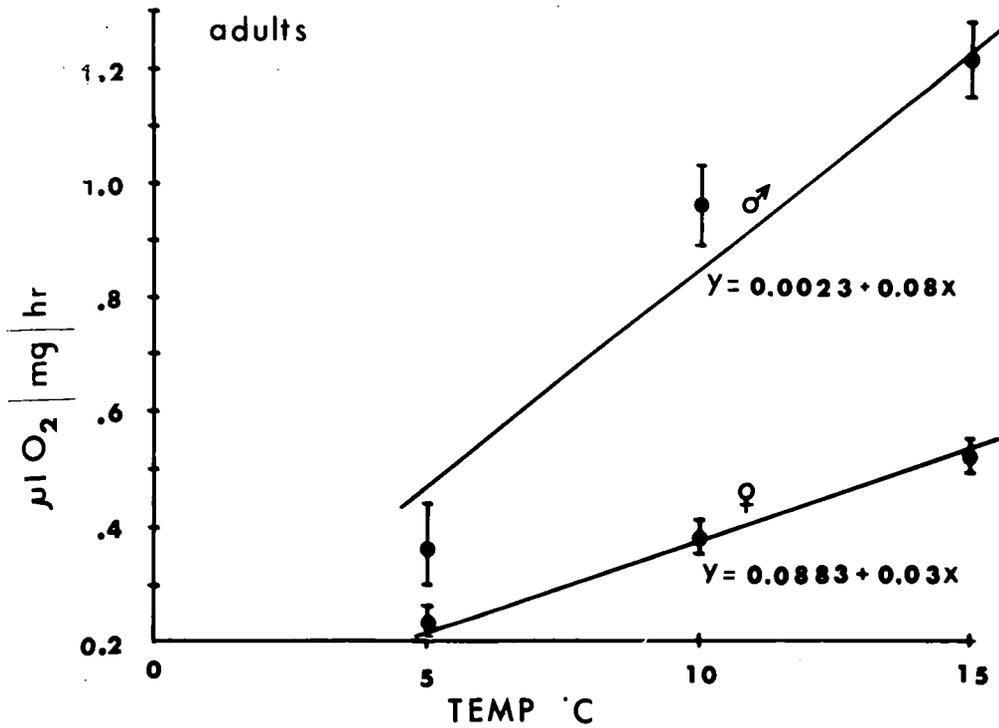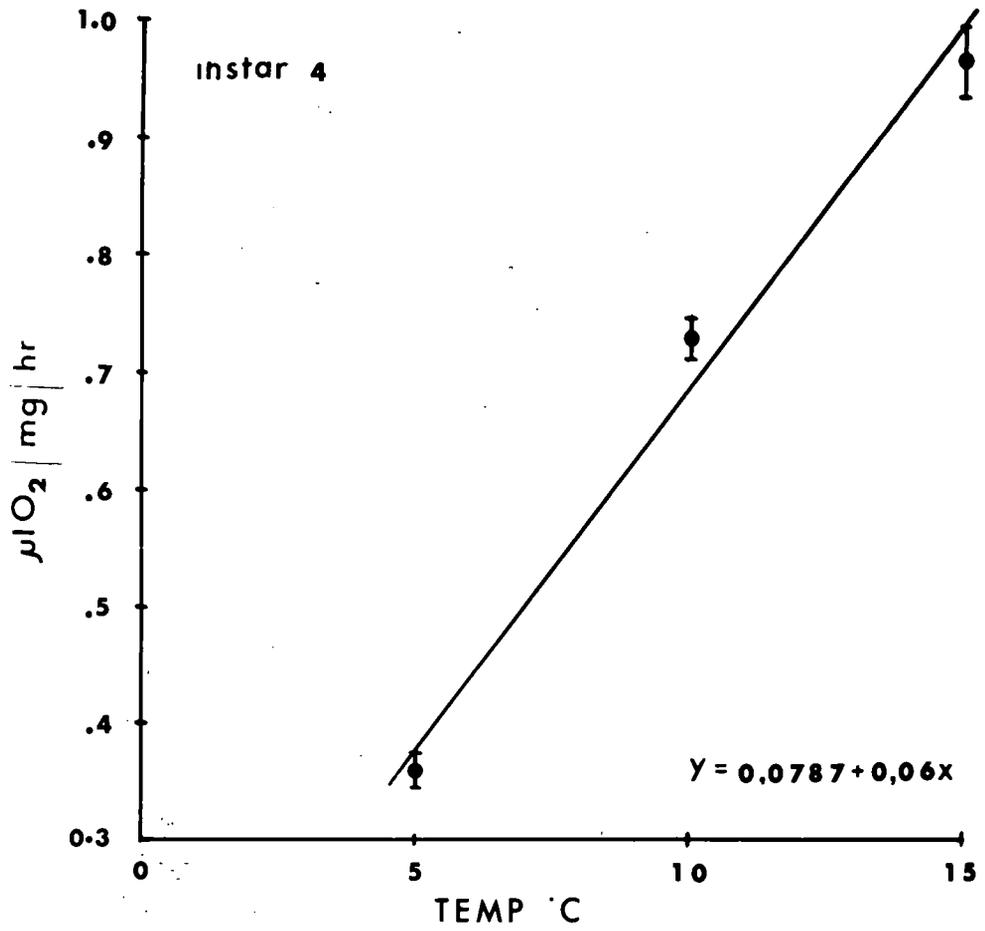
Table 20. <u>Meta segmentata</u>, mean rates of respiration

(μl O_2/mg live wt/hr) with significance of

differences ('t' tests) between temperatures

mg live body wt	n	'C	mean rate $\pm$ S.E.	level of significance
o – 2	8	5	0.238 ± 0.024	
	12	10	0.634 0.035	$p < 0.001$
	16	15	1.028 0.047	$p < 0.001$
2 – 12	3	5	0.141 0.032	
	8	10	0.328 0.039	$p < 0.01$
	18	15	0.396 0.030	not significant
sub-adult	4	5	0.253 0.019	
13 – 18 ♀	5	10	0.573 0.038	$p < 0.001$
11 – 15 ♂	8	15	0.839 0.049	$p < 0.002$
adult	4	5	0.080 0.010	
< 18 ♀	6	10	0.171 0.025	$p < 0.01$
	14	15	0.260 0.022	$p < 0.02$
adult	3	5	0.093 + 0.024	
11=16 ♂	5	10	0.207 0.026	$p < 0.02$
	11	15	0.296 0.040	$p < 0.05$

Table 21. <u>Meta segmentata</u>, mean rates of respiration

$(\mu l \ O_2/mg$ live wt/hr) of adults with

significance of differences ('t' tests)

between sexes

	Temp. 'C	mean rate $\pm$ S.E.	level of significance
males	5	0.093 + 0.024	not significant
females		0.080 + 0.010	
males	10	0.207 + 0.026	not significant
females		0.171 + 0.025	
males	15	0.296 + 0.040	not significant
females		0.260 + 0.022	

Fig.23. <u>M.segmentata</u>, regression of rate of respiration

on temperature for animals with live body

weights up to 2mg (above) and between

2 and 12 mg (below). $(mean \pm S.E.)$
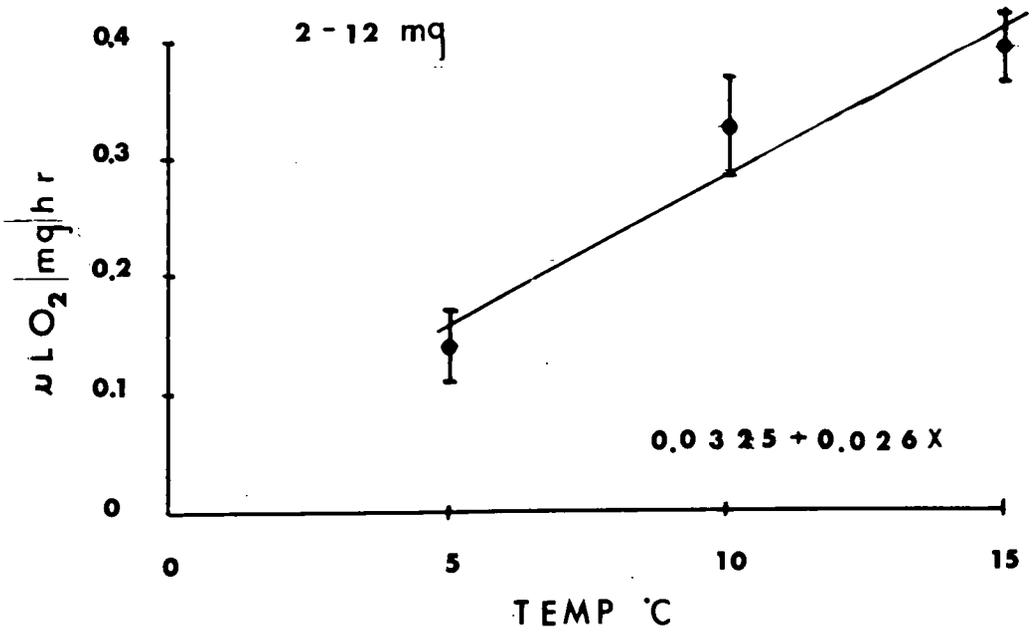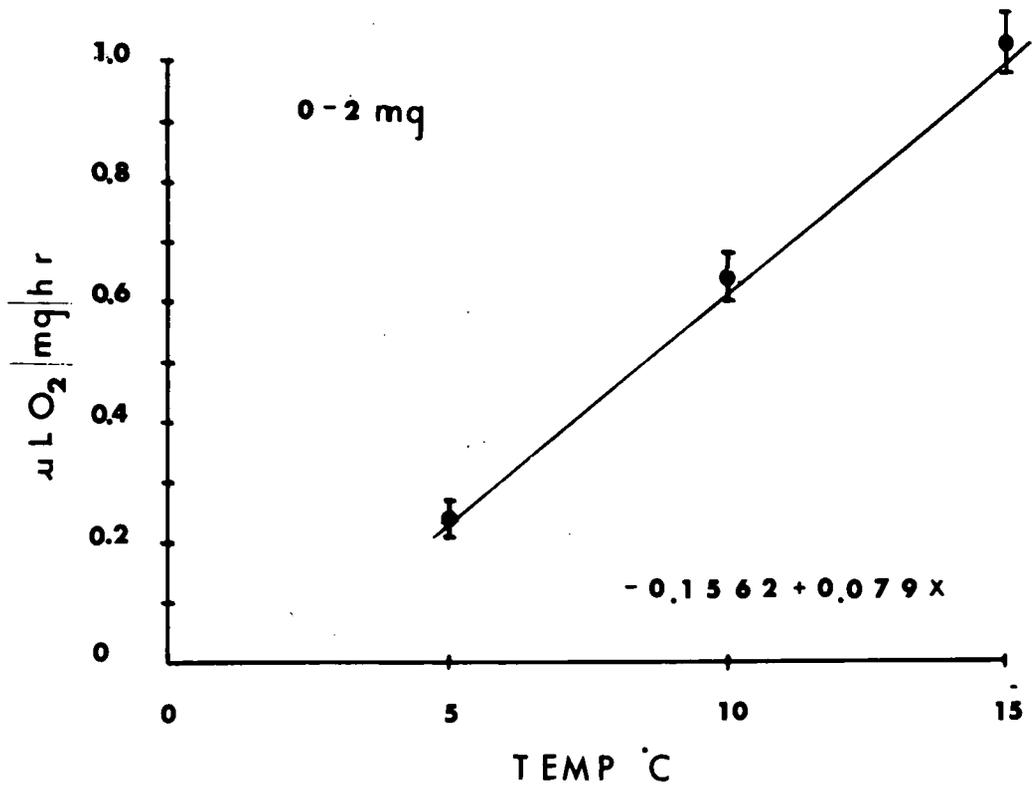
Fig.24. <u>M.segmentata</u>, regression of rate of respiration

on temperature for sub-adults and adults.

(mean ± S.E.)
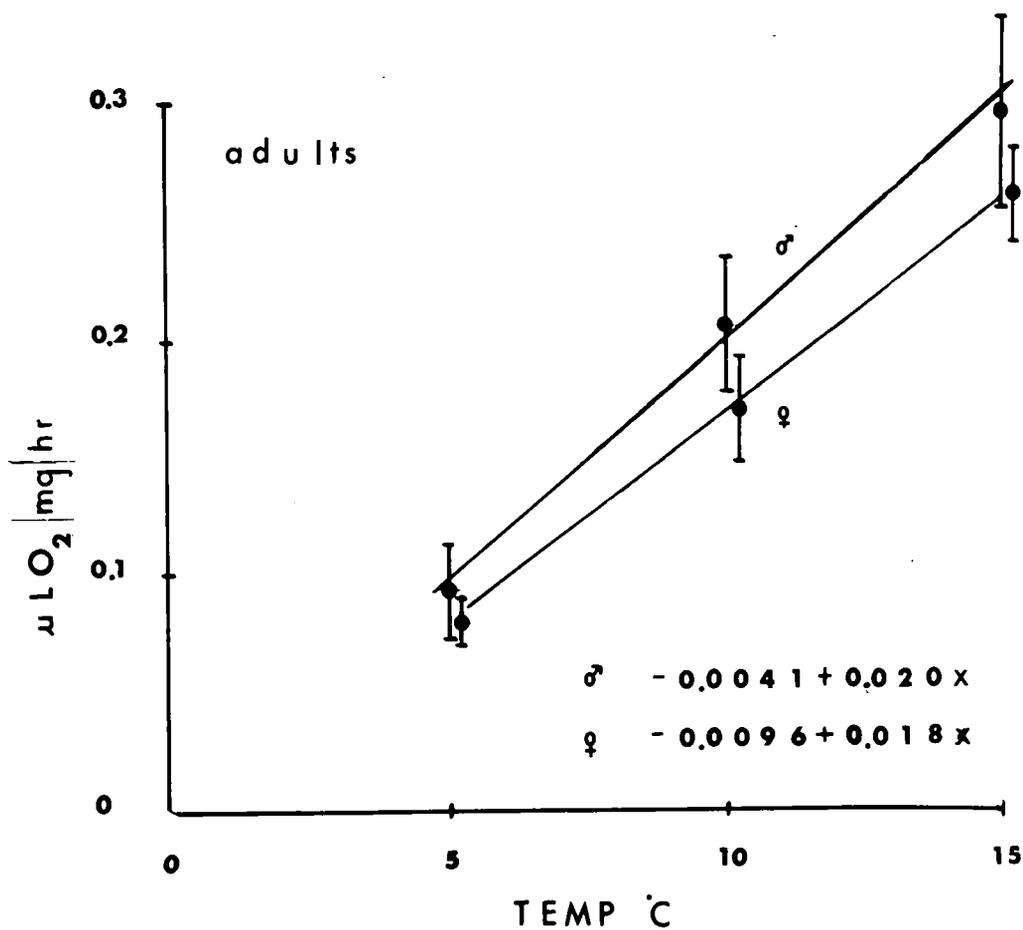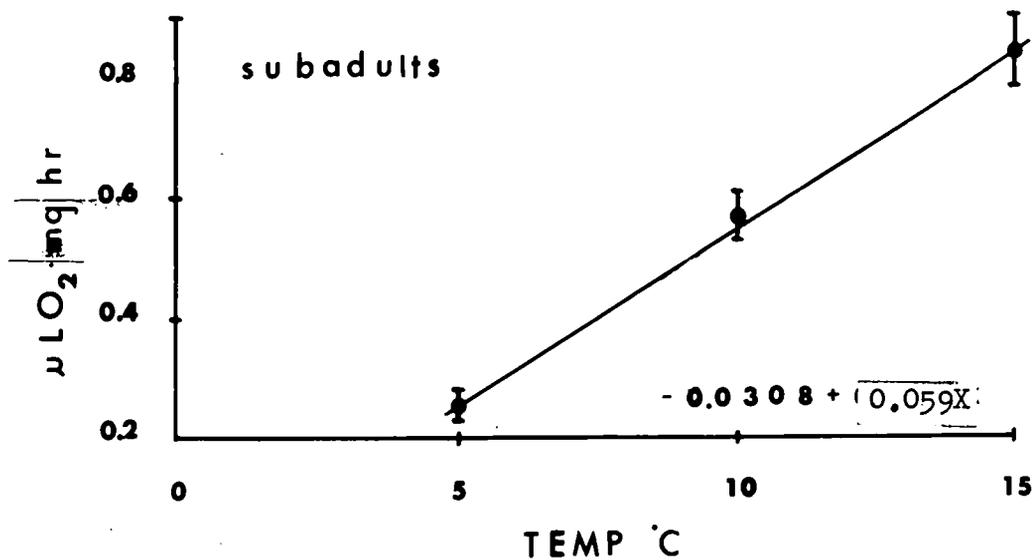
(f) Discussion

The distribution of points on the graphs for
rate of respiration on body weight is similar to that
obtained for Leiobunum rotundum (Phillipson 1963) and
Lithobius crassipes and L.forficatus (Whignarajah 1968).
The implication is that in some arthropods, at least,
the younger stages have a higher metabolic rate per unit
weight than the adults.

Respiration is temperature dependent in agreement
with the results of Anderson (1970), who also found that
oxygen consumption is not independent of even rapid
temperature changes in spiders. Newell and Northcroft
(1967) apparently stand alone on the thesis which states
that a number of poikilotherms are independent of short
term fluctuations in temperature. Tribe and Bowler (1968),
for example, have queried the validity of the experimental
evidence used to support that contention.

At 10'C average weight (gram) specific oxygen
consumption per hour varied between 380 and 1,045 µlitres
in R.lividus, and between 171 and 634 µlitres in M.segmentata.
In the former species, at 15'C, the range was between 521 and
1,323 µlitres, and in the latter, between 260 and 1,028 µlitres.
It seems that the influence of temperature on metabolic rate
is more marked above 10'C in M.segmentata than in R.lividus.

A number of species of spiders are able to reduce oxygen consumption at higher temperatures (Anderson 1970), and this may have occurred in R.lividus. The survival value of compensation in a soil species may be particularly important since desiccation of the litter layer in which its prey presumably lives would often be associated with an increase in temperature.

Specimens of M.segmentata were placed directly in the respirometer after collection in the field. On the other hand, R.lividus were acclimatized at 5', 10' or 15'C to combat the possible effects of heat extraction. According to Anderson (1970), metabolic rates show a particularly large increase at higher temperatures after acclimatization at lower temperatures, a feature which was also noted in male blowflies (Tribe and Bowler 1968). By allowing R.lividus to become acclimatized to the temperature of the respirometer, especially after extraction during the winter when field temperatures are low, the tendency for such large increases in oxygen consumption possibly did not occur.

In general, respiration rates per unit weight at a given temperature were higher in R.lividus than in M.segmentata. However, the rates of increase were more consistent over the three temperature regimes in the latter species. The magnitude of increase in rate of respiration

was less between 10' and 15'C than between 5' and 10'C

in R.lividus.

Sub-adults, i.e. instar 4, of both species have

a higher average weight specific oxygen consumption which

in R.lividus is upheld in adult males.   The reasons for

this phenomenon were not investigated.   However, gonad

development in phalangids is associated with an increase

in oxygen consumption (Phillipson 1963).

Both R.lividus and M.segmentata are web builders,

although the young of the former species may actually seek

out prey.   In the respirometer, partial webs were

constructed by all stages of both species after which

there was no noticeable movement.   Consequently, the values

for oxygen consumption possibly represent 'resting'

metabolism.

CHAPTER SIX

POPULATION DYNAMICS OF <u>ROBERTUS LIVIDUS</u>

1. <u>Instar determination</u>

(a) <u>Introduction</u>

The size of a species may decide the maximum
number of instars a spider may pass through before the
attainment of maturity (Bristow 1958), while the amount
of food consumed may influence the actual number (Deevey 1949,
Miyashita 1968a) as in <u>Lactrodectus mactans</u> (Fabr.)
(Araneae:Theridiidae) and <u>Lycosa T-insignata</u> Boes.(Araneae:
Lycosidae). <u>Linyphia triangularis</u> Clerck (Araneae:
Linyphiidae) moults four times after emergence from the
egg irrespective of the quantity of food supplied
(Turnbull 1962).

Laboratory bred specimens of the large green
lynx spider, <u>Peucetia viridans</u> (Hentz), (Araneae;Oxyopidae),
undergo fewer moults than when living in the field. The
male has 7 or 8 moults while the female has 8 or 9
(Whitcomb 1966).

Dondale (1961) and Whitcomb (1966) found width
of carapace an easily measured structure which served as a
reliable guide to the number of instars, although some
variation and overlapping of size between contiguous instars

was seen in Peucetia viridans (Hentz). However, Miyashita
(1968a) concluded that after the first two instars of
Lycosa T-insignata Boes. carapace width was influenced
too much by the amount of food consumed.

When measurements of part of an insect's body
are plotted for each instar on log paper the mean values
may fall on a straight line. According to Dyar's Law
(Wigglesworth 1950) the slope of the line is about 1.4
and represents a constant geometric growth rate for that
part of the body. Whittaker (1965), for example, applied
this information to head width measurements of Neophilaenus
(Hemiptera;Cercopidae) to corroborate evidence for the
number of instars. There are few published growth
characteristics for spiders. Miyashita (1968a) considered
that increase in carapace width in the lycosid spider did
not follow Dyar's Law. It might be argued, however, that
the few measurements made by him would make it unlikely for
observed values to fit precisely those predicted. Width
of carapace was found to increase slightly after moulting.

(b) Method and Results

It was not possible to separate R.lividus from
other species as they emerged from the soil extraction
apparatus and at the same time make precise measurements.

All material was pickled in 70% alcohol containing a few drops of 1% formalin. This resulted in some shrinkage of the abdomen but the carapace remained unaltered. Pickling without previously subjecting specimens to a relaxing agent like ethyl acetate causes the legs of spiders to curl beneath the body and so made it impracticable to measure such structures as leg segments and sterna. Immature stages had to be examined in spirit which meant that reflection of light rendered head width measurements inaccurate. As a possible indication of stage of development, width of carapace was selected.

Carapace width of all but damaged specimens was measured, the sample consisting of about 800 spiders collected from October 1967 to November 1968, and all definitely Robertus lividus.

A histogram was constructed from measurements made with an occular micrometer and 4 peaks are seen (Fig.25). A plot of cumulative frequency against width of carapace on arithmetic probability paper suggest 4 clear inflexions and so indicate 5 main size groups (Fig.26). The method of Taylor and Lewis (1967) to separate overlapping stages revealed the possible existence of two stages in the first peak of the histogram.

Fig.25. _R.lividus_, a frequency histogram of width of carapace.
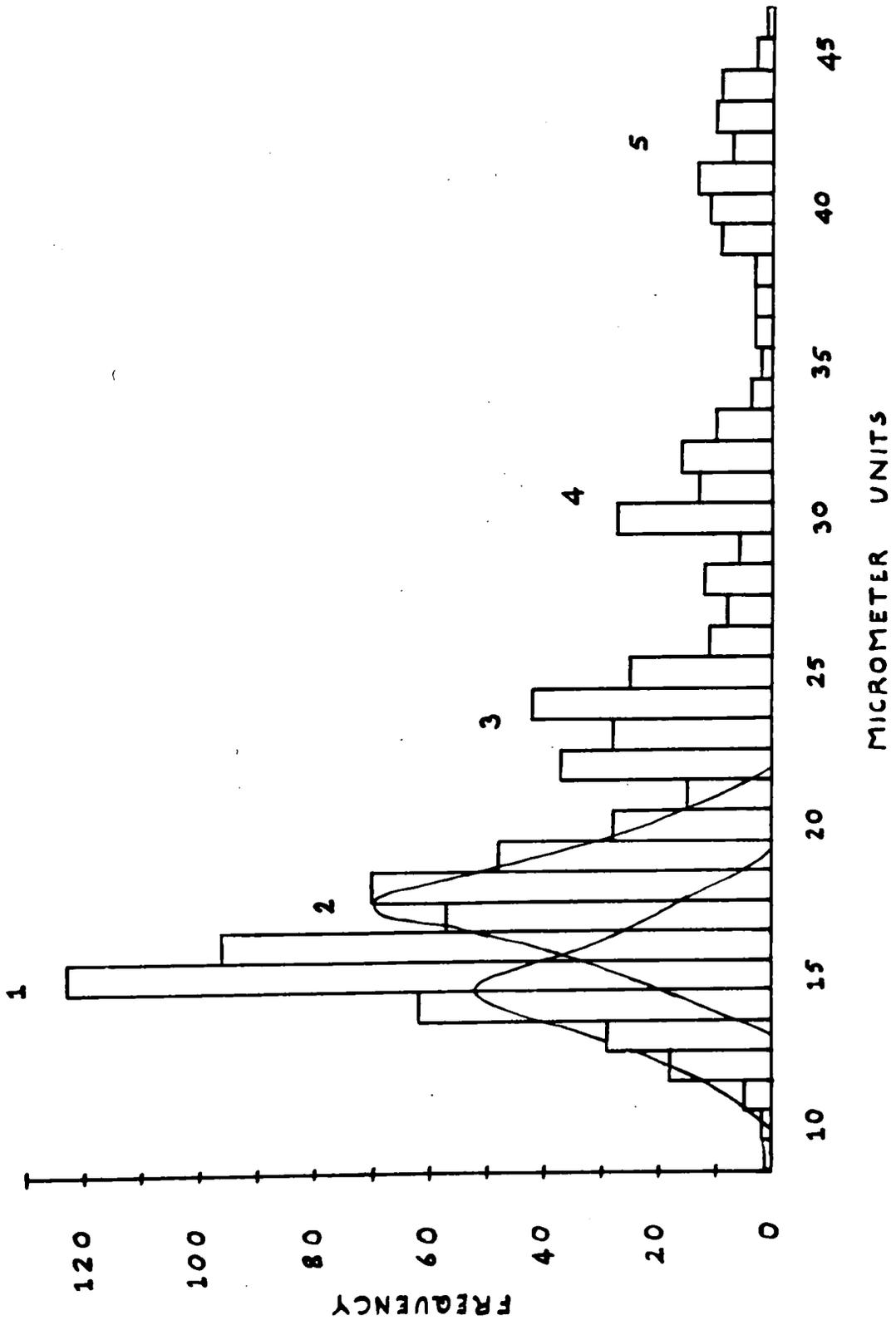
Fig.26. <u>Robertus lividus</u>, cumulative frequency

distribution of carapace width.
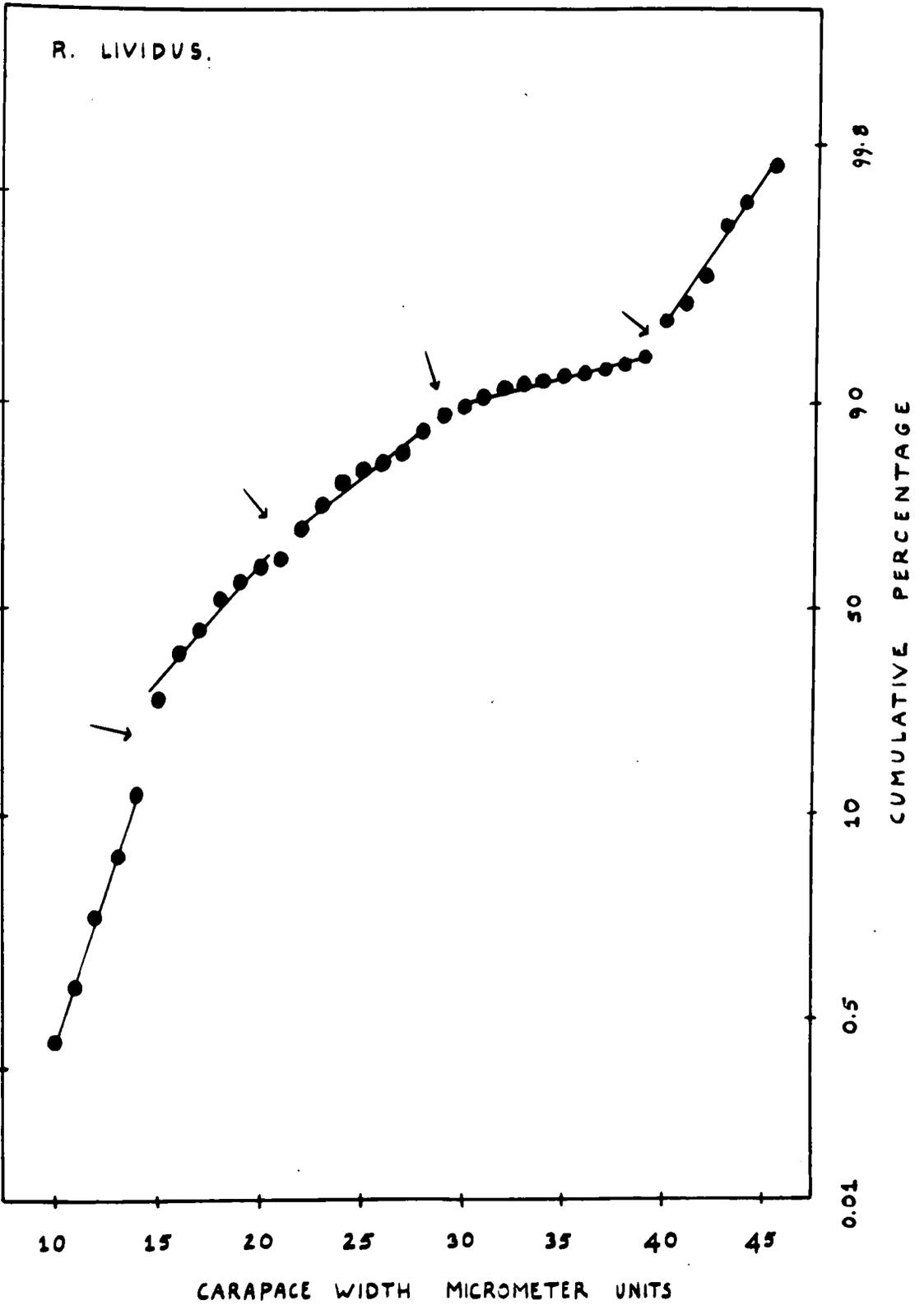
R. LIVIDUS.

That there are 5 instars in the life history of
R.lividus was supported by observations on laboratory specimens.
On completion of ecdysis all had carapace widths within one
standard deviation (determined graphically) for a given peak
on the histogram. Newly hatched spiderlings fed once before
moulting shortly after emerging from the egg. The short
duration of this first instar may explain why it is not
readily discerned on the histogram.

The first peak on the histogram apparently
represents an overlap of first and second instars. The
remaining peaks represent instars 3, 4 and 5. Carapace
width increased between moults but not to an extent which
merged the peaks. Male adults and sub-adults have wider
carapaces than their female counterparts which will explain
the bimodal nature of the peaks for the last 3 instars.

Table 22. Robertus lividus, measurement of carapace width

	instars				
	1	2	3	4	5
mean (micrometer units)	15.2	17.8	24.0	31.1	42.6
mean in mm.	0.47	0.55	0.74	0.95	1.31
standard deviation in mm.	0.06	0.07	0.09	0.07	0.09
Rate of increase		1.17	1.35	1.29	1.37 (mean 1.29)

A regular geometric increase in width of carapace
(Table 22) indicates that instars intermediate to those

Fig.27. Robertus lividus, log. plot of width of

carapace of each instar (straight line)

and corresponding arithmetic plot (curved line).

R. LIVIDUS
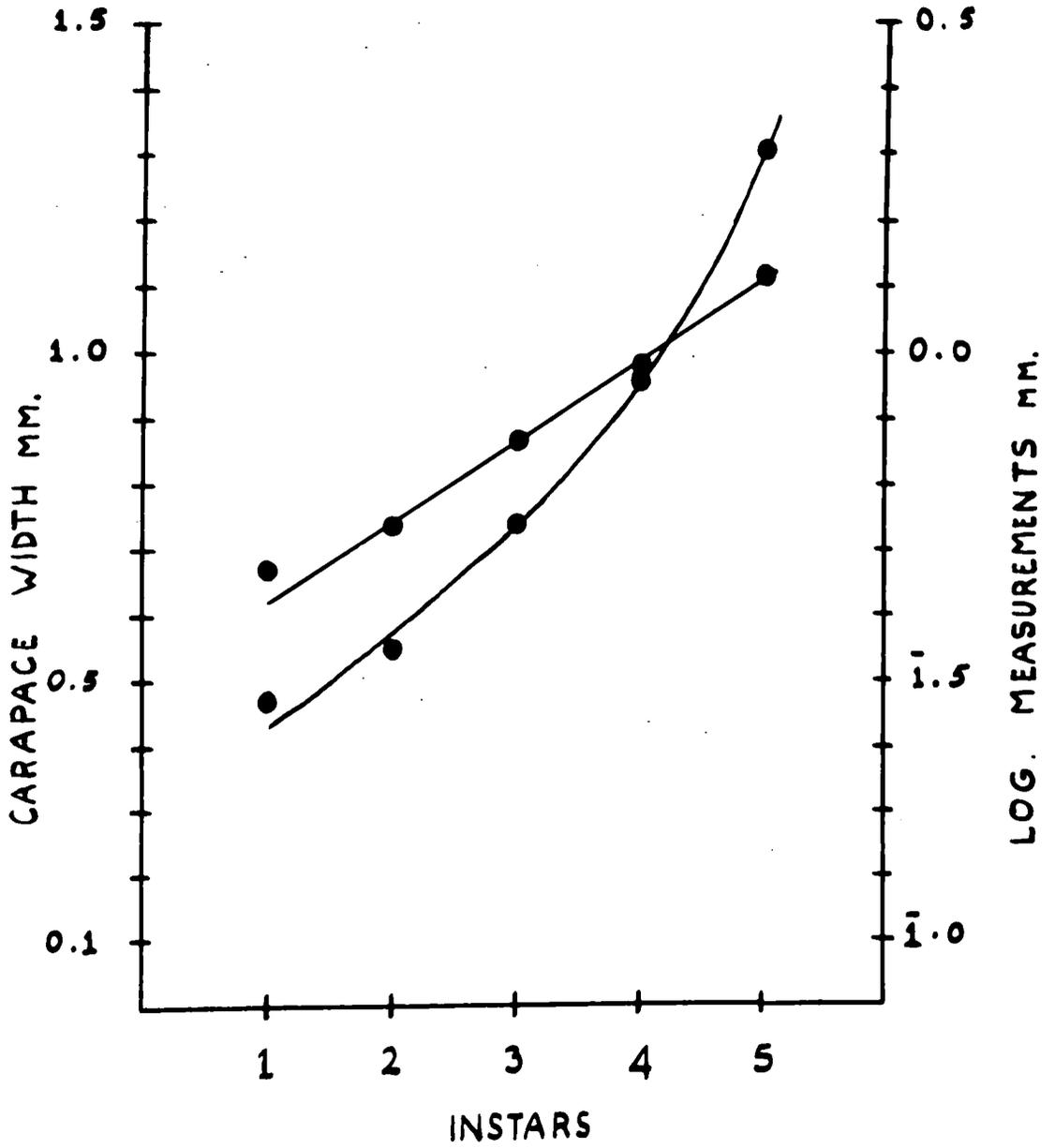
suggested do not exist.   Except for instar 1, used here
to describe the stage which emerges from the egg, logarithms
of mean widths for instars lie close to a straight line
(Fig.27).

(c)   Distribution of instars

The percentage composition of instars is used to
describe the structure of the population throughout the
entire sampling period.   However, when numbers fluctuate,
percentage values may be misleading.   Reference must also
be made to the actual numbers removed from the extractor.

Instar 1

The main periods in which eggs hatch must coincide
closely with the peaks of abundance for instar 1 (Fig.28).
Numbers for this instar may well have been higher were it
not for the short duration of this stage.   In the laboratory
where food was plentiful, spiders passed through this stage
in 5 days at room temperature.   Captive specimens in the
field took between 10 and 15 days to reach instar 2 when
temperatures ranged from 5 to 10'C.

It appears that there was an autumnal hatch in
September 1968 in addition to the earlier hatch which
commenced in January.   According to actual numbers caught
(Table 25), the winter emergence was sustained until March

when numbers ranged between 30 and 35.   Female spiders
which were extracted between July and March readily laid
eggs in captivity if food was plentiful.

Instar 2

        The September peak for instar 1 is followed by
a peak for the second stage in October and November (Fig.28).
An increase also took place from February to March and in
May, most probably as a result of recruitment from winter
and spring hatching.   Numbers then declined until the
following autumn.   A significant difference at the 5% level
occurred between May and June and between August and September,
for numbers of instar 1 + 2 combined.

Instar 3

        The first peak occurred in April after the peak
in March for instar 2 (Fig.28).   The difference in numbers
between the two months was significant.

        A pronounced peak of abundance is seen in July
coinciding with a drastic reduction in numbers of instar 2.
The periods of maxima were generally one month behind those
for instar 2.

Instar 4

        A chi-square test of homogeneity (Appendix 4)
revealed significant seasonal differences.   Numbers were
generally low in winter but increased progressively from
9 to 37 spiders in the autumn.

The first monthly peak occurred in April,
probably from instar 3 individuals which had passed through
at least part of the winter. From then on peaks of abundance
were about a month behind those for instar 3 (Fig.28).

A significant difference was found between numbers
of instar 3 in July and August, which coincided with an
overall increase in instar 4 in the summer and autumn.

Numbers were higher in October and November 1968
than in the corresponding period in the previous year
(Table 25). In 1968 the mean maximum field temperature
reached 15 and 8'C with only 10 ground frosts for the two
months (Durham University Observatory). In 1967 there were
24 ground frosts and with mean maxima of 7'C and 4'C. This
developmental stage seems to be most sensitive to temperature,
and specimens in the laboratory only survived between 10 and
12 days at 5'C.

Instar 5 (adults)

Females of R.lividus were to be found in similar
numbers throughout the year. Males were fewer, only being
conspicuous from May to September. It may be that they exist
for but a short time, since in the laboratory none lived
longer than 14 days at 10'C, and at lower temperatures 3 out
of the 5 specimens observed were moribund after 5 days'
captivity. It is quite likely that some individuals were

Fig.28. Robertus lividus, percentage composition of the population.

Numbers from 1 to 5 refer to instars.

PERCENTAGES

MONTHS 67-68
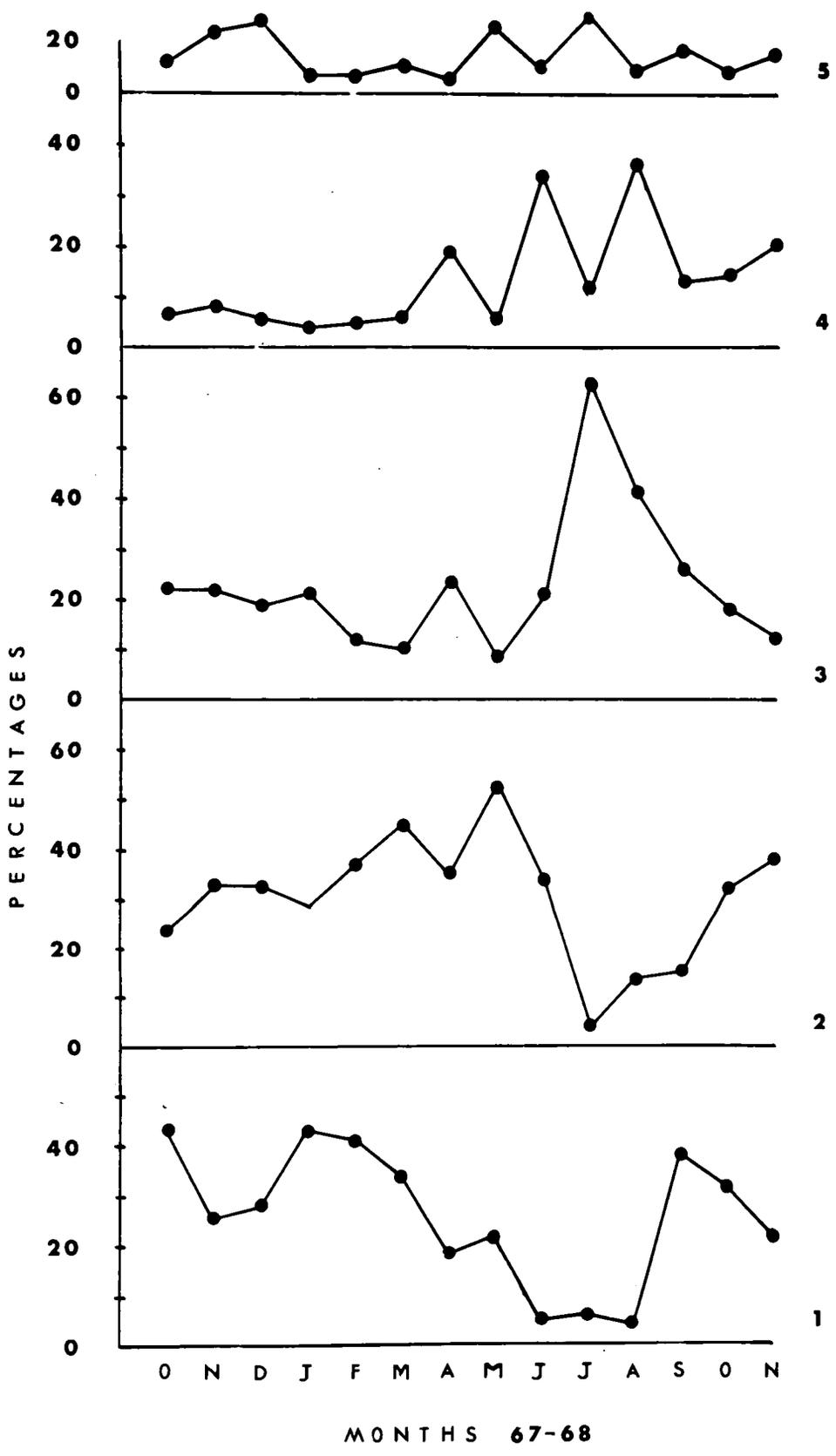
missed by a once-monthly sampling programme.   They did

not appear to feed.

Peaks of abundance for adults (Fig.28) are seen for

May, July and September, about one month behind the peaks for

instar 4.   Seasonal differences (Appendix 4) were not

significant.

Mating was not seen in captivity.   However, in

October 1967 and in November 1968 two females had plugs lodged

in their epigynes, suggesting that mating had occurred at that

time.   It is possible that oviposition in winter and spring

is preceded by mating during the autumn before the male

spiders die out.

2. Life history

Robertus lividus undergoes 4 moults outside the egg,

apparently having 5 developmental stages apart from the egg.

The number and duration of cohorts are obscured by the presence

of every instar on each sampling occasion.   The overlap of

generations seems to be the result of a protracted period of

hatching which extends in the main from September through the

winter to May.

Instar 1 in September becomes instar 2 in October

and November providing temperatures do not fall much below

5°C for very long.   In the laboratory, specimens only

occasionally fed or moved about at that temperature.   At

10 and 15'C all stages were active and female spiders

readily laid eggs. Development of instar 2 continued to instar 3 during the winter months of 1968, leading to a peak of instar 4 in April, and culminating in a peak for adults in May. The duration of this cohort, from September to May, was about 9 months. Eggs laid during the summer would have been mainly responsible for the hatch in September.

The results suggest that typical life cycles are : Instar 1 which emerged in January and February 1968, became instar 2 in February and March, instar 3 in April, sub-adult in June, and finally, adult in July. Some females would then have laid eggs to contribute to the autumnal hatch.

The emergent spiderlings from March to May may well have accounted for the increase in instar 3 in June and July, which eventually became adult in the autumn. Females of this cohort presumably over-wintered with, perhaps, some females of the previous cohort, to lay eggs which hatched from January to May.

There appears to be 3 main cohorts, the details of which are depicted in Table 23. One of the interesting features is the period in which male spiders are particularly in evidence. They are able to inseminate, firstly, those female spiders which appear in early summer, and secondly, those which are about to overwinter.

The longest duration of a cohort from the time of hatching to attainment of the adult condition is about 9 months when the young spiders emerge in September. The cohort of shortest duration is probably the one whose young emerge in spring and mature by September, extending over a period of between 5 and 6 months.

The length of life of adult female spiders under natural conditions is not known. Specimens in the laboratory lived for as long as eight weeks if supplied with food in the form of Drosophila. Cocoons from individuals which had just been extracted contained between 15 and 32 eggs (mean 20). Laboratory fed specimens laid as many as 4 cocoons, with as many as 43 eggs in the first formed. About one third of the spiders extracted in any given month laid eggs shortly after extraction. The remainder, usually smaller in size, required food for at least 10 days before laying eggs at 10'C.

3. Numbers of Robertus lividus

(a) Extraction

Except in 1969 when specimens were required for calorimetric and respiration studies, the sampling programme for the ground zone was not directed specifically at R.lividus. All species were removed, identified, and counted from September 1967 to November 1968. The first month was used to determine the effectiveness of the soil extraction apparatus.

Table 23.   Robertus lividus, possible cohorts based on

extraction data and monthly composition of instars

month	first cohort	second cohort	third cohort
1967			
Aug	eggs		
Sept	1		
Oct	2		
Nov	2/3		
Dec	3	eggs	
1968			
Jan	3	1	
Feb	3	1/2	
Mar	3/4	2	eggs
Apr	4	3	1
May	5	3/4	2
Jun	Mating	4	3
Jul	eggs	5	3/4
Aug		eggs	4 } Mating
Sep			5
Oct			
Nov			eggs
Dec			

Details of sampling procedure and extraction are
described in Chapter 2(i).   As specimens emerged from the
extractor they were stored in 70% alcohol.   It was possible
to separate R.lividus from other species (Chapter 3(i)) and to
describe details of development and population structure.

The efficiency of extraction of the spider community
in the ground zone was estimated to be 89% (Chapter 2(i)).

During April and May 1969 the efficiency was checked using
specimens of R.lividus only.   Soil samples from the study area
were subjected to the usual 12 days' heat treatment, after which
they were moistened and all R.lividus were returned to the
extractor.   The numbers of spiders which emerged were compared
with those introduced.   The results are given in Table 24.
The percentage efficiency of 91% was similar to the one obtained
using several species.

Actual numbers of every instar extracted are given
in Table 25.   They represent monthly totals derived from 10
sample units, each of $1/16$ metre^2.

When multiplied by 1.6, actual numbers are converted
to numbers per metre^2.   Since numbers for every sample unit
were recorded (Appendix 3), 95% confidence limits were
calculated for each sampling occasion (Table 26).

Wide confidence limits result from the large
variances, and it is clear that the population was aggregated.

Table 24.   Robertus lividus, percentage retrieval as a measure
of efficiency of the extractor

| instars | | | instars | | | | |
| 1 | + | 2 | 3 | + | 4 | adult females | |
in		out	in		out	in	out
(1)							
15		12	5		5	3	3
(2)							
8		7	6		5	3	3
	83%			91%		100%	

Table 25.   Robertus lividus, actual numbers extracted from

monthly samples, each of which consisted of

10 sample units of 1/16 metre^2

month	1	2	3	4	male	female	total
1967							
Oct	21	12	11	1	0	4	49
Nov	15	20	13	5	1	6	60
Dec	10	12	7	2	1	4	36
1968							
Jan	35	24	17	3	0	3	82
Feb	34	30	10	4	0	3	81
Mar	30	40	9	5	1	4	89
Apr	11	22	15	12	0	2	62
May	19	46	7	4	3	8	87
Jun	3	20	12	20	0	3	58
Jul	3	2	29	5	4	3	46
Aug	1	3	9	8	0	1	22
Sep	36	14	24	12	4	4	94
Oct	23	23	13	10	0	3	72
Nov	16	28	9	15	1	5	74

Table 26.   Robertus lividus, total population density per

metre^2, based on numbers emerging from extractor

month	young	adult	Total $\pm$ 95% confidence limits
1967			
Oct	72.0	6.4	78.4 $\pm$ 28.8
Nov	84.8	11.2	96.0 $\pm$ 56.0
Dec	49.6	8.0	57.6 $\pm$ 30.0
1968			
Jan	126.4	4.8	131.2 $\pm$ 36.8
Feb	124.8	4.8	129.6 $\pm$ 60.8
Mar	134.4	8.0	142.4 $\pm$ 70.4
Apr	96.0	3.2	99.2 $\pm$ 17.1
May	121.6	17.6	139.2 $\pm$ 52.8
Jun	88.0	4.8	92.8 $\pm$ 41.6
Jul	62.4	11.2	73.6 $\pm$ 17.1
Aug	33.6	1.6	35.2 $\pm$ 22.4
Sep	137.6	12.8	150.4 $\pm$ 116.8
Oct	110.4	4.8	115.2 $\pm$ 55.2
Nov	108.8	9.6	118.4 $\pm$ 24.0

(b) Homogeneity of data

As ten sample units were taken, ten sites were effectively investigated for R.lividus over a 14 months period. It is possible that the data were drawn from different populations with 'between-sample' variation significantly greater than the variation within the samples. An analysis of variance was carried out to compare these two effects.

Since the population as a whole was aggregated with variances much larger than the means (Table 26), monthly values were transformed to logarithms. Some sample units yielded no spiders so log (N + 1) was used, where N is the number of spiders extracted from a particular sample unit.

The sample units were removed from 10 sites each month during the 14 months' extraction period. The results of the analysis of variance are summarised in Table 27.

Table 27.

source of variation	Sum of squares	Degrees of freedom	Mean squares	Variation ratio
Between sites	1.756	9.00	0.089	1.089
Residual	10.699	130.00	0.082	
Total	12.455	139.00		

The 5% level of the F ratio is 1.88 which is larger than the ratio of 1.09 obtained from the population data.

It may be assumed, therefore, that there was no specific
variation between the sites. In fact, the samples were
drawn, apparently, from an area over which R.lividus was
generally distributed, the same spatial patterns existing
at every site.

(c) Changes in numbers extracted

Numbers of each instar as well as total numbers
per unit area are given in Tables 25 and 26

The significance of monthly differences were
calculated using 't' tests for instars 1 + 2, combined,
and instar 3. Since Taylor's 'PowerLaw' indicated aggregation,
numbers per sample unit were transformed to logarithms.
Tabulated values are given in Appendix 1 and 2 (raw data)

The total population differed significantly between
July and August ($p < 0.02$) and between August and September
($p < 0.02$). Numbers of instars 1 + 2 differed between May
and June ($p < 0.05$) and between August and September ($p < 0.02$).
It appeared that as one series of cohorts drew to a close in
summer, another was initiated in September.

Numbers of instar 3 differed significantly between
March and April ($p < 0.05$), June and July ($p < 0.01$) and between
July and August ($p < 0.01$). Spiders which had passed through
the winter as instar 3 developed into instar 4 in the spring.
Spiderlings which emerged in spring and early summer culminated
in a peak for instar 3 in July.

Since instars 4 and 5 (adults) were relatively few, seasonal rather than monthly differences were investigated by chi-square tests. Details are recorded in Appendix 4.

Sub-adults, i.e. instar 4, showed a significant increase from winter, through the summer, to the autumn, during 1968 ($p < 0.001$). Numbers were high shortly after numerical increases in instar 3, particularly during the summer and autumn.

While males were more in evidence during the summer than at any other time, adults as a whole showed no significant differences between seasons ($p < 0.05$).

Total numbers extracted varied between 35 and 142 spiders per metre^2, with the higher value in March and the lowest value in August.

4. Spatial pattern of a population of R.lividus

The pattern of distribution may indicate the extent of coverage of a species within a sample area, the degree of aggregation of individuals, change in distribution with age, and the adequacy of the sampling programme.

Since the physical or chemical factors of a habitat are probably not randomly distributed, aggregation may quite likely arise because one or few factors are determining the performance or survival of the species (Greig-Smith 1964)! On the other hand, eggs laid in clusters will for a short

period produce aggregation in young. Mortality or emigration will tend to reduce it while recruitment will increase it. The female of the species, particularly in spiders, may lead to a localised concentration of males.

(a) Measurement of dispersion

1. The ratio of the variance to the mean may be used as a measure of dispersion, i.e. s^2/m, and is referred to as Blackman's coefficient of dispersion (Greig-Smith 1964). This test assumes equality of mean and variance for a random distribution, a ratio of less than 1 for a regular distribution, and greater than 1 for an aggregated population. The difference between the observed ratio and unity is compared with its standard error and the significance of the difference estimated by a 't' test. Bartlet's modification (quoted in Greig-Smith 1964) of the Blackman formula was used to obtain the standard error, i.e.

$$s = \sqrt{\left(\frac{2}{N-1} \right)}$$

Inspection of the raw data alone on numbers per sample unit indicated definite aggregation for instars 1 + 2, combined. This was in contrast with the pattern for adults. A decrease in aggregation apparently occurred with reduction in density which itself was related to age.

Distribution of instars 1 + 2 departed significantly from random during all months (Table 28) except in July and August. Instar 3 was aggregated for only 2 months while instar 4 + adults did not differ significantly from a random pattern.

Greig-Smith (1964) discusses the criticisms which have been levelled against the variance: mean ratio, in particular, the validity of using small means.

2. Taylor (1961) has pointed out the need for an index which covers all degrees of aggregation so that a single index describes the distribution of a population, and which should also be the same at different population densities.

In the case studies described by Taylor, the variance was related to the mean by a simple power law. That is, the variance is proportional to a fractional power of the mean. The expression is $s^2 = am^b$, where 'a' is a sampling factor dependent on the size of sample used, or it may be a computing factor involving the particular estimate of variance. The parameter 'b' is apparently a true index of aggregation and is typical for a given population. Where 'b' approaches infinity, a population is aggregated, 'b' $\rightarrow$ 1 suggests random distribution, and b $\rightarrow$ 0, indicates a regular distribution.

Table 28. Robertus lividus, coefficients of dispersion

together with significance at 5% level

	instars		
Month	1 + 2	3	4 + 5
1967			
Oct	3.60*	0.19	0.05
Nov	6.74*	0.03	0.08
Dec	5.11*	0.06	0.05
1968			
Jan	10.14*	4.41*	0.03
Feb	8.59*	0.21	0.06
Mar	18.87*	3.40*	1.90
Apr	4.03*	2.00	0.03
May	5.16*	1.90	0.04
June	11.15*	0.05	0.09
July	0.08	0.95	1.76
Aug	0.04	0.06	0.53
Sept	39.52*	0.10	1.87
Oct	5.43*	0.20	1.05
Nov	3.01*	0.03	1.31

* significance from random distribution at 5% level where 't' = 2.160

Variance and mean of density for instars 1 + 2,
3, and 4 + 5, were plotted for each month on double log. paper
(Figs. 29 and 30). Regressions were then calculated for s^2
on m to find the regression coefficients. Ninety five percent
confidence limits, where 't' = 2.201, were attached to the
regression coefficients (Bailey 1959).

The values for 'b' (Table 29) for the 3 groups of
spiders indicate the overall spatial patterns which existed

Fig.29. R.lividus, log. plot of variance against mean

population density at instars 1 plus 2 to

demonstrate the applicability of Taylor's

Power Law (1961).

INSTARS 1 & 2 $S^2 = 1.48 \, m^{1.8}$

VARIANCE (S^2)

MEAN (m)

$\bar{X}, \bar{Y}$
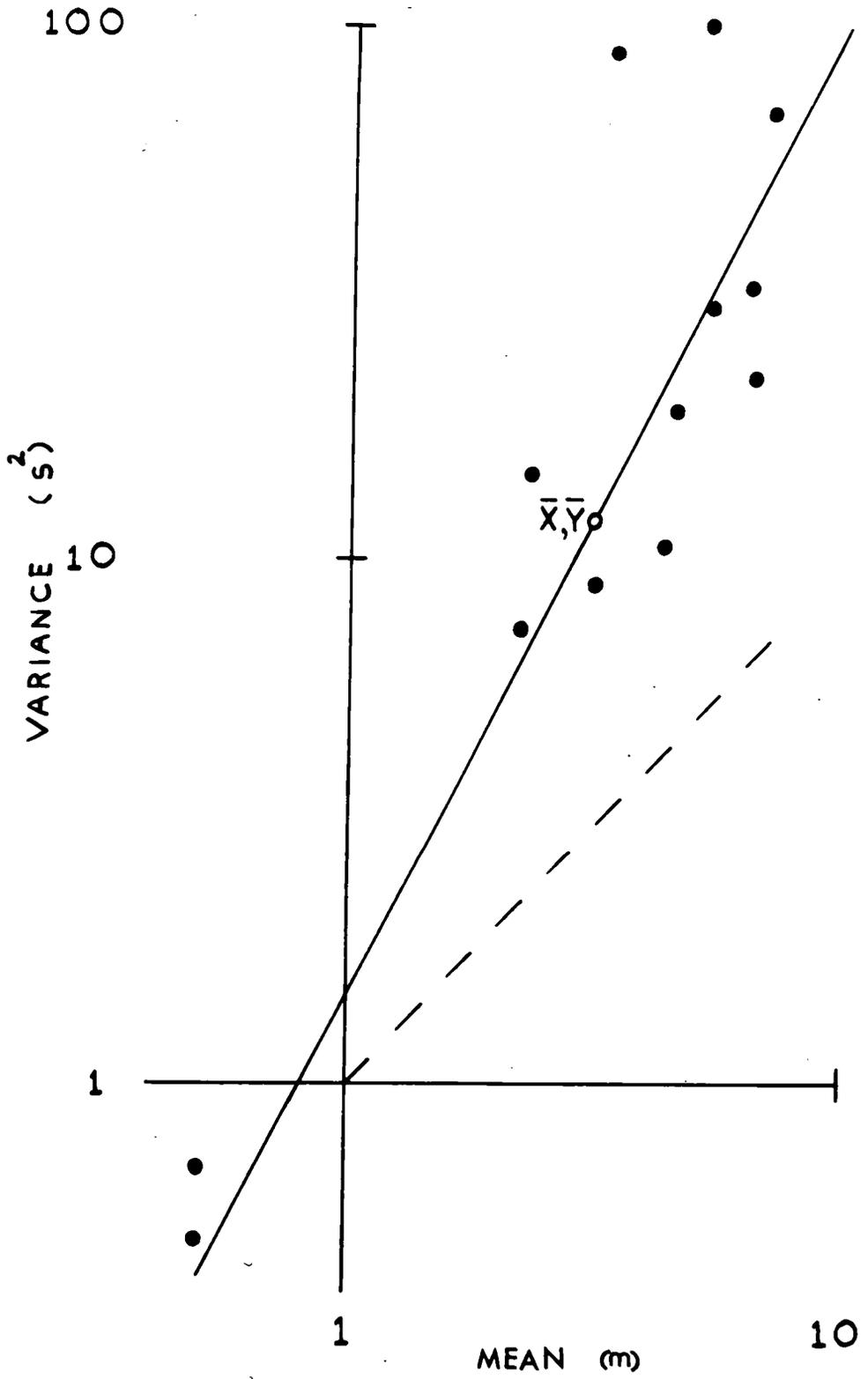
Fig. 30. R. lividus, log. plot of variance against mean

population density at instar 3 (left) and

instars 4 plus 5, to demonstrate the applicability

of Taylor's Power Law (1961).

INSTAR 3

$S^2 = 1.39 \, m^{1.01}$
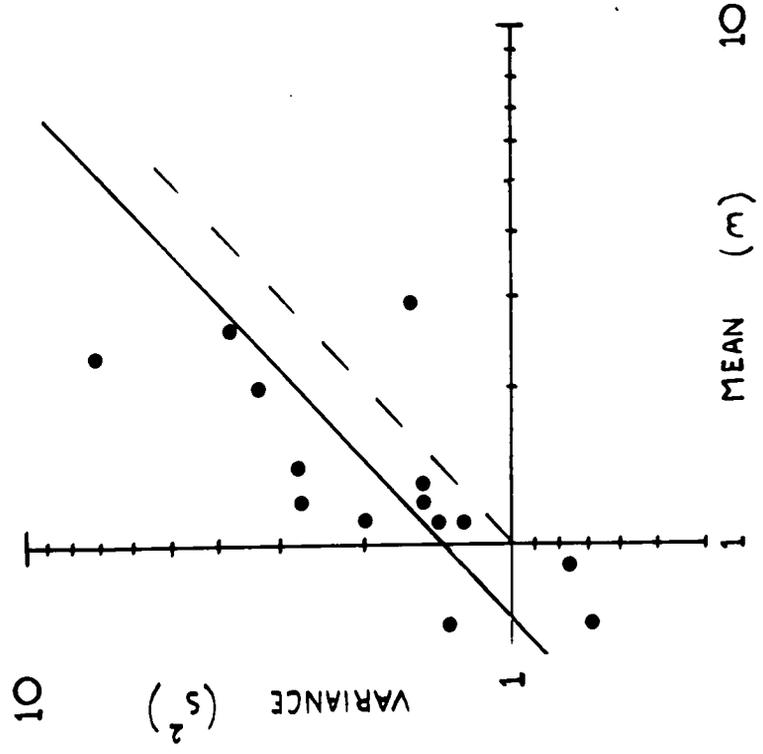
INSTAR 4 & 5

$S^2 = 0.94 \, m^{0.5}$

VARIANCE (s^2)

MEAN (m)
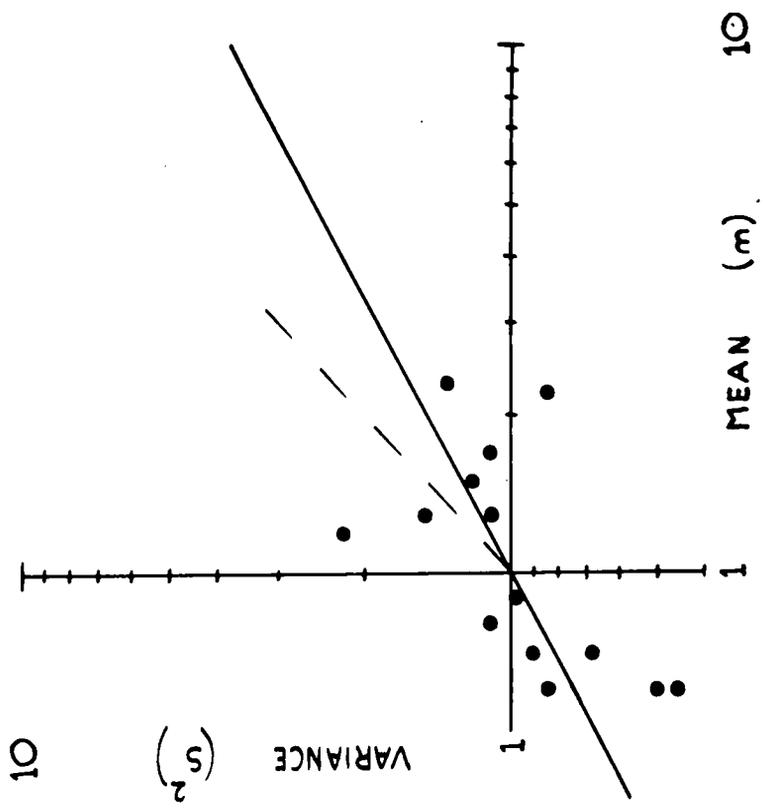
over the sampling period.   The angles of elevation (b = tan β)
of their regression lines are 61', 45', and 26', respectively.

Where $s^2 = am^{1.0}$ or a slope of 45' obtains, a
random distribution is indicated.   The index of 1 is well
outside the 95% confidence limits for instar 1 + 2 (Table 29),
but is included within the limits, which are very wide, for
instar 3.   The 95% limits for instar 4 + 5 just exclude a
random distribution.   The adults are probably solitary.
The values of s^2 are summarised as follows :

Parameters de-transformed :

instars

1 + 2   3   4 + 5

$s^2 = 1.48m^{1.8}$ $s^2 = 1.39m^{1.01}$ $s^2 = 0.94m^{0.5}$

In general terms instars 1 and 2 were highly
aggregated, while instar 3 was randomly distributed.   Instars
4 and 5 were under-dispersed.

Table 29.   <u>Robertus lividus</u>, regression coefficients (b)

calculated from Taylor's Power Law

	Instars		
	1 + 2	3	4 + 5
a (log. intercept)	0.1728	0.1415	−0.0255
b	1.8055	1.0141	0.4982
significance from zero	p < 0.001	p < 0.001	p < 0.05
95% confidence limits	± 0.5331	± 0.4376	± 0.3362

(b) <u>Discussion</u>

Salt and Hollick (1944) applied Blackman's coefficient of dispersion to their wire-worm studies and Whittaker (1959) used it to describe the spatial distribution of moorland Homoptera. Small wire-worms were aggregated initially because eggs were laid in clumps. Older stages had dispersed but in favourable feeding sites new aggregations had arisen.

With <u>R.lividus</u> a characteristic rise in aggregation would be expected if young were actually in the process of hatching. Relatively large numbers of eggs (15 - 33) are laid in a cocoon, and as with many species of spiders, especially those belonging to the Theridiidae, the young may remain in the vicinity of the parent female after hatching.

Healey (1964) used Taylor's Power Law in an interspecific comparison between 2 species of Thrips. Different values of 'b', namely, 2.5154 and 1.4831, resulted

from different breeding habits. However, she was unable to
distinguish between the young stages of the two species.

The Power Law applied to R.lividus. A single index
described the characteristic spatial pattern of each instar.
As the Power Law may break down at very low densities when the
concept of aggregation ($s^2 > m$) is inappropriate (Taylor 1961),
instars 4 and 5 were combined. A distinction seemed unnecessary
in any case, because some individuals were about to become adult,
while a number of adults had just moulted during or prior to
extraction.

There was evidence from the raw data and from laboratory
observations that dispersal from the hatching point did not occur
substantially until the third moult and then, not to any
marked extent. Even at low densities, instar 1 + 2 can have
a variance higher than the mean. The size of sample used,
1/16 metre^2 could still detect some aggregation at instar 3,
as indicated by Blackman's coefficients of dispersion and
Taylor's Power Law. These findings would not be expected
if emigration from the hatching point had been marked.
If new aggregations had arisen, the index of aggregation of
spiders at instar 3 would have been higher. Furthermore,
instar 4 and adults may also have had higher indices.

In the laboratory, adults were not very mobile, only moving across their hammock webs to feed. They may well be relic survivors in the field of former cocoons or 'colonies' founded by solitary females.

The power law can hold good down to low densities of m less than 1 (Taylor 1961). This implies that the population is aggregated at high densities but tends to become regular when density diminishes. This appears to apply to R.lividus where mortality rather than dispersal accounts for declining density. The wide 95% confidence limits of the index of aggregation, 'b', for instar 3, suggest that aggregation breaks down at this stage, i.e. there is a progressive change in degree of aggregation.

According to Blackman's coefficients of dispersion (Table 28), the distribution of instar 3 seemed to resemble that of adults, i.e. under-dispersed. However, despite the variation between some degree of aggregation and under-dispersion, a random distribution is a better description of spatial pattern over a period of time.

CHAPTER SEVEN

POPULATION BIOMASS OR STANDING CROP OF ROBERTUS LIVIDUS

The calulation of standing crop (B) requires information on population density, wet, or preferably, dry weights of individuals, and calorific content which represents the energy necessary to keep the material together.

(i) Population density (N)

   (a) Method

The population data, based on numbers actually extracted, have been discussed. However, the duration in the field of instar 1 is too short for it to be adequately sampled on a once-monthly basis. It may be seen (Table 25) that numbers of this instar were frequently less than those for instar 2. Hence, estimates of biomass for instar 1 will be too low if based on meagre extraction data.

The most likely number of instar 1 for the year beginning October 1967 to September 1968 was estimated by plotting the logarithms of annual totals for each stage against the corresponding instars (Fig.31). A linear relation was established between the observed numbers of spiders at instars 2, 3, 4, and 5. There is close agreement between the observed totals and those calculated from the regression equation, with $p < 0.30$ (Table 30).

Fig.31. Robertus lividus, regression of total numbers (N) extracted on stage of development, which was used to estimate the total density of instar 1 (= stage 2).

$$LOG_e Y = 6.99 - 0.5X$$
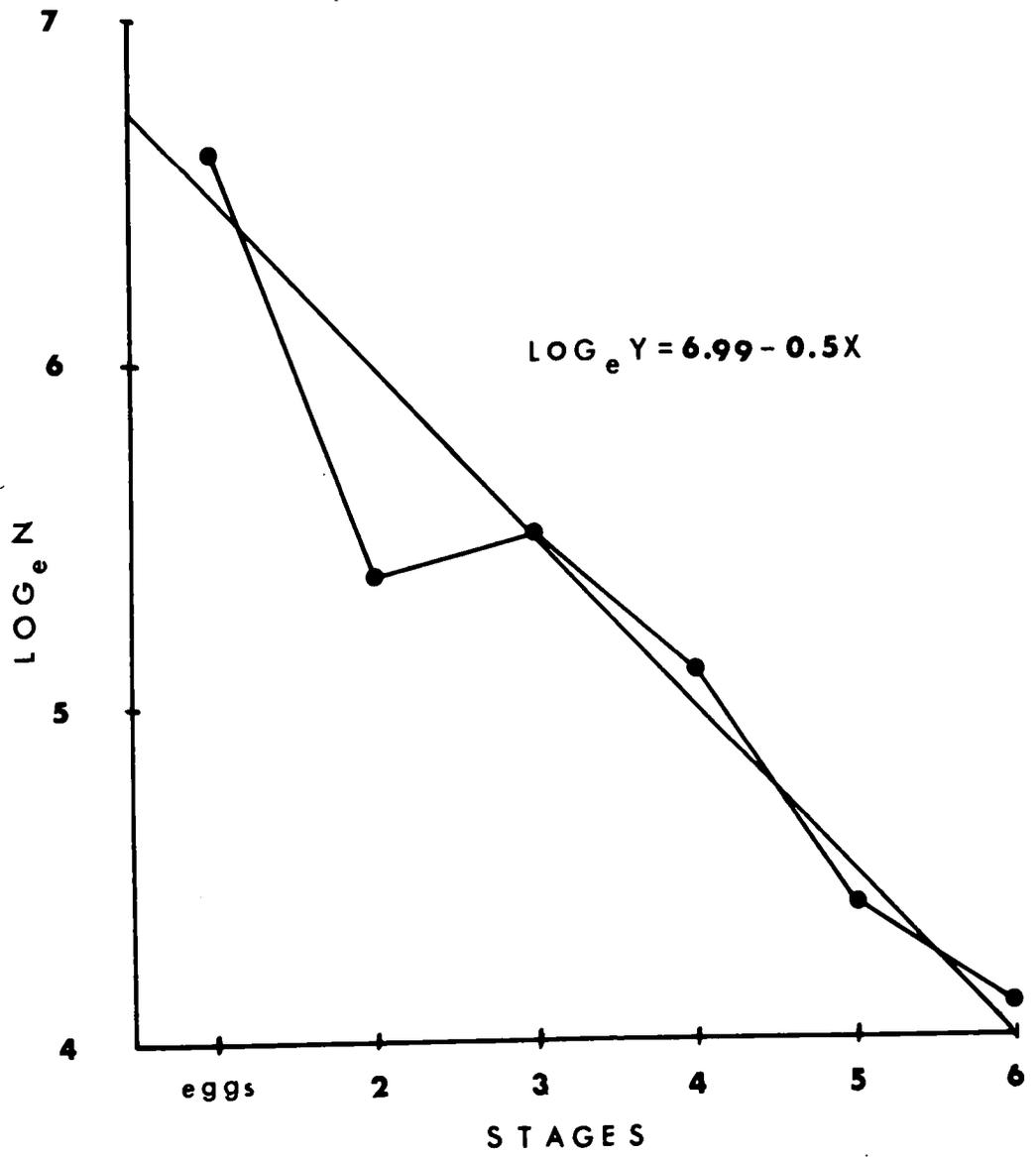
Table 30.   Comparison between numbers extracted (O) and

numbers calculated (ε) from regression equation

(Fig. 31)

Instar	Observed (o)	Expected (ε)	χ^2
2	245	242	0.037
3	163	147	1.742
4	81	89	0.719
5	59	54	0.463

$$\sum \chi^2_{(3)} \quad 2.961 \quad p > 0.30$$

The number of spiders extracted in a given month
will be influenced by their mean duration in the field.

In addition it can be assumed that the number of
instar 1 extracted in a given month was influenced by the
actual number prevailing in the field. The more individuals
there are, the greater the probability that the numbers caught
will be correspondingly high.   On this assumption, monthly
densities for instar 1 were adjusted upwards by multiplying
the monthly total by 1.835.   For example, in October 1967
21 individuals were caught at instar 1, hence the expected
total is

$$21 \times \frac{400}{218} = 38.5 \text{ or } 61.6 \text{ spiders per metre}^2$$

In this way the imbalance in the density of instar 1 was rectified, so improving the estimate of monthly standing crop for this stage.

The monthly totals extracted for all instars are multiplied by 1.6 to adjust them to a metre^2.

(b) Results

Table 31 gives the monthly population densities per metre^2 for a year. Significant differences between monthly extraction figures, together with 95% confidence limits, have been described.

The high population numbers occur in September, and after a brief decline, arise again in January, February, and March when individuals at instar 1 are most numerous. Hatching evidently takes place during these months.

The monthly totals for instar 2 follow closely those of instar 1. From March to May, instar 3 are much in evidence and numbers fluctuate less for this stage than the others. From June to September, sub-adults are more numerous than at other times, having 32 individuals per metre^2, despite a marked decline in the size of the population as a whole.

The numbers of adult spiders are generally low with a maximum of 17.6 spiders per metre^2 in May.

(ii) Standing crop

Estimates of dry body weight could be obtained by weighing specimens which were extracted monthly and stored in 70% alcohol.   During the drying process, the absorbed fluid evaporates.   However, it was shown in Chapter 13(4)that spiders may not only lose up to 40% of their dry body weight during storage, but the loss is highly variable.   In a bioenergetic study, estimates of dry weight need to be as accurate as possible.

Itô (1964) has found a linear relation between wet and dry weight in Lycosa pseudoannulata.   As this applied to R.lividus, dry weights were calculated from the appropriate regression equations.   Furthermore, Engelmann (1966) and Whignarajah (1968) had discovered different regression coefficients between stadia of certain arthropods, separate regression lines were drawn for immature and adult spiders.

(a) Method

During 1969, living specimens of R.lividus, at all stages of development, were removed from the extractor. Width of carapace were used to sort them into instars.   Young stages were weighed on an E.M.B. electromicrobalance, while adults were more conveniently weighed on a Mettler H.16 balance.   The mean live weight for each instar was calculated and 't' tests applied to reveal the significance of the differences between instars.

After drying the specimens in a vacuum oven at 60'C for 48 hours, dry weights were obtained. The regression equations for dry on wet weight could then be calculated.

Table 31. <u>Robertus lividus</u>, monthly population densities per metre^2, 1967-68. (Numbers of instar 1 adjusted)

Month	instars					
	1	2	3.	4	5	Total
1967						
Oct	61.6	19.2	17.6	1.6	6.4	106.4
Nov	44.0	32.0	20.8	8.0	11.2	116.0
Dec	29.3	19.2	11.2	3.2	8.0	70.9
1968						
Jan	102.8	38.4	27.2	4.8	4.8	178.0
Feb	99.8	48.0	16.0	6.4	4.8	175.0
Mar	88.0	64.0	14.4	8.0	8.0	182.4
Apr	32.4	35.2	24.0	19.2	3.2	114.0
May	55.8	73.6	11.2	6.4	17.6	174.6
June	8.8	32.0	19.2	32.0	4.8	96.8
July	8.8	3.2	46.4	8.0	11.2	77.6
Aug	2.9	4.8	14.4	12.8	1.6	36.5
Sept	105.7	22.4	38.4	19.2	12.8	198.5

Table 32.   *Robertus lividus*, relation between dry and wet weights

(from regression equations) together with mean

calorific values

	1	2	3	4	male	female
mean live weight	0.1336	0.2762	0.8453	2.6250	4.8199	7.4000
standard deviation	0.034	0.145	0.274	0.426	0.9897	2.530
mean dry weight	0.0644	0.1129	0.3066	0.9124	1.6363	2.5000
cals/g dry wt ash free	5236	5236	5519	5540	5550	5716

(b)   Results

Table 32 gives the mean live weight for each instar
and the corresponding dry weight.   Differences between instars
were all highly significant.

Figs.32 and 33 show a linear relation between wet and
dry weights.   From the graphs the following regression
equations were obtained for calculating dry weights :

	immature	adult
equation	$Y = 0.0189 + 0.3404X$	$Y = 0.0208 + 0.3352X$
confidence limits	$b \pm 0.0215$	$b \pm 0.1385$
correlation coefficients	0.99	0.95

The population data included numbers of each instar
extracted over 12 months.   Multiplication of the monthly
values by the mean dry weight for each instar provides

Fig.32. R.lividus, regression of dry weight (y) on live weight (x)

for immature spiders.

imm

WET WEIGHT mg

$Y = 0.0189 + 0.3404 X$
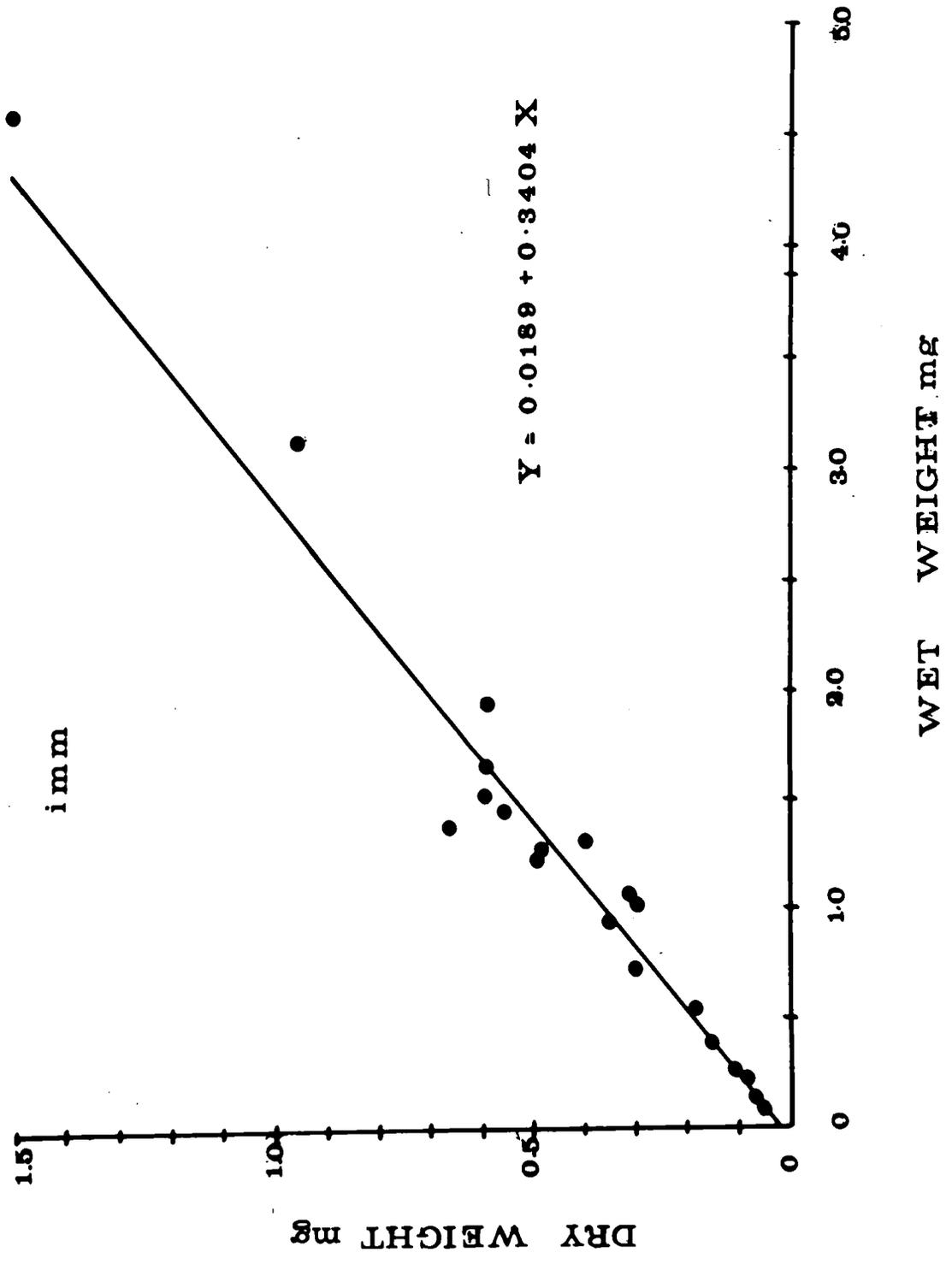
DRY WEIGHT mg

Fig.33.   R.lividus, regression of dry weight (y) on live weight (x)

for mature spiders.

R. LIVIDUS MATURE

Y = 0.0208 + 0.3352X

WET WEIGHT mg

DRY WEIGHT mg
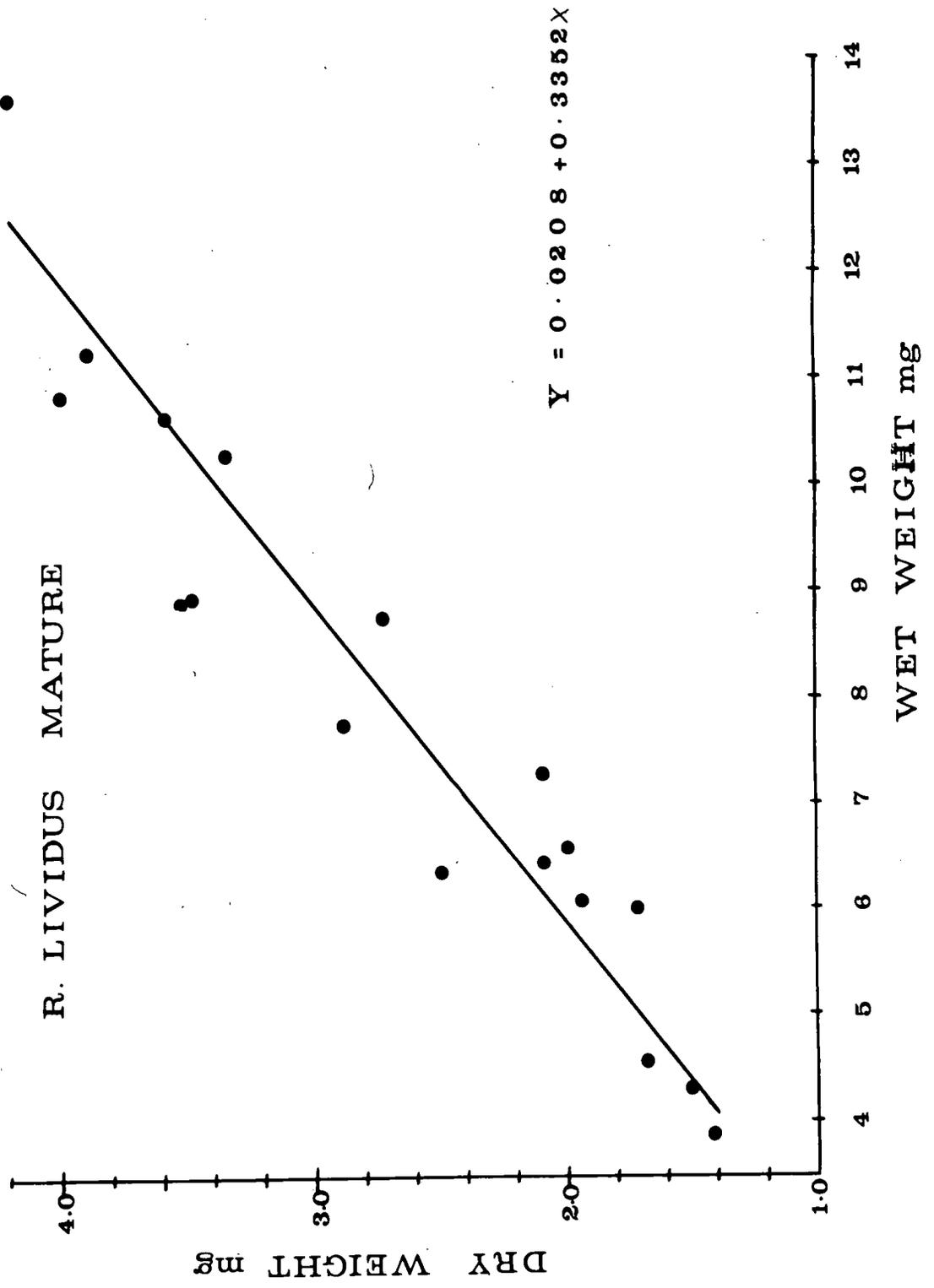
estimates of biomass, which are given in Tables 33-38. The total population biomass is given in Table 39 and is presented graphically in Fig. 35 with total population density.

Standing crop in terms of calories or biocontent was calculated each month by multiplying the mean calorific value of an instar (Chapter 4 (b)) by the total dry weight (Table.40).

(c) <u>Discussion</u>

The contribution of instar 1 to total population biomass was small despite relatively large numbers of individuals. The mean dry body weight was 0.06mg. Only in January, February and September did dry weights exceed 6mg per metre^2, with corresponding calorific value of 30 calories.

As with instar 1, dry weights per unit area were generally low for instar 2. However, the mean body weight had increased by the third instar to produce maxima of 14 and 12mg per metre^2 in July and September. The corresponding biocontent was 78 and 65 calories.

Although numbers were much reduced by the time a particular cohort had reached instar 4, mean body weight had increased to 0.91mg, about three times that of the previous instar. Where a marked increase in density of instar 4 is seen, as in April, June and September, dry weights per metre^2 ranged from 17 to 29mg, equivalent to a maximum of 161 calories.

Adult spiders , and females in particular, made the larger contribution to population biomass. Both mean body weight and calorific content were well above those of other instars. Dry weights per metre^2 were quite consistent with only two pronounced maxima of 24 and 32mg in November and May, respectively. Biocontent reached 183 calories per metre^2 in the latter month.

Mean monthly biomass ($\bar{B}$) of the total population was 41mg per metre^2, equivalent to 223.6 cals. The factors which influenced standing crop were density, mean individual weights, and calorific content which increased with stage of development.

Eggs were not considered in the estimates of monthly standing crop.

Table 33. <u>Robertus lividus</u>, monthly standing crop per metre^2

for instar 1

month	mean density	weight mg		calorific
		wet	dry	equivalents (cals)
1967				
Oct	61.6	8.23	3.97	20.8
Nov	44.0	5.88	2.83	14.8
Dec	29.3	3.91	1.89	9.9
1968				
Jan	102.8	13.73	6.62	34.7
Feb	99.8	13.3	6.43	33.7
Mar	88.0	11.76	5.67	29.7
Apr	32.4	4.33	2.09	10.9
May	55.8	7.45	3.59	19.4
June	8.8	1.18	0.57	3.0
July	8.8	1.18	0.57	3.0
Aug	2.9	0.39	0.19	1.0
Sept	105.7	14.12	6.81	35.7

Table 34. <u>Robertus lividus</u>, monthly standing crop per metre^2

of instar 2

month	mean density	wet	dry	calorific equivalents (cals)
1967				
Oct	19.2	5.30	2.17	11.4
Nov	32.0	8.84	3.61	18.9
Dec	19.2	5.30	2.17	11.4
1968				
Jan	38.4	10.61	4.33	22.7
Feb	48.0	13.26	5.42	28.4
Mar	64.0	17.68	7.23	37.8
Apr	35.2	9.72	3.97	20.8
May	73.6	20.33	8.31	43.5
June	32.0	8.84	3.61	18.9
July	3.2	0.88	0.36	1.9
Aug	4.8	1.32	0.54	2.8
Sept	22.4	6.19	2.53	13.2

Table 35.   <u>Robertus lividus</u>, monthly standing crop per metre^2

of instar 3

| month | mean density | weights mg | | calorific |
		wet	dry	equivalents (cals)
1967				
Oct	17.6	14.88	5.40	29.80
Nov	20.8	17.58	6.38	35.2
Dec	11.2	9.47	3.43	18.9
1968				
Jan	27.2	22.99	8.39	46.3
Feb	16.0	13.52	4.90	27.0
Mar	14.4	12.17	4.41	24.3
April	24.0	20.29	7.36	40.6
May	11.2	9.47	3.43	18.9
June	19.2	16.23	5.89	32.5
July	46.4	39.23	14.23	78.5
Aug	14.4	12.17	4.41	24.3
Sept	38.4	32.46	11.77	65.0

Table 36.   <u>Robertus lividus</u>, monthly standing crop per metre^2

of instar 4

| month | mean density | weights mg | | calorific |
		wet	dry	equivalents (cals)
1967				
Oct	1.6	4.20	1.46	8.1
Nov	8.0	21.00	7.30	40.4
Dec	3.2	8.400	2.92	16.28
1968				
Jan	4.8	12.60	4.38	24.3
Feb	6.4	16.80	5.84	32.3
Mar	8.0	21.00	7.30	40.4
Apr	19.2	50.40	17.52	97.1
May	6.4	16.80	5.84	32.3
June	32.0	84.00	29.20	161.8
July	8.0	21.00	7.30	40.4
Aug	12.8	33.60	11.68	64.7
Sept	19.2	50.40	17.52	97.1

Table 37. <u>Robertus lividus</u>, monthly standing crop per metre^2

of adult male spiders

| month | mean density | weight mg | | calorific |
		wet	dry	equivalents (cals)
1967				
Oct	0	0	0	0
Nov	1.6	7.71	2.62	14.5
Dec	1.6	7.71	2.62	14.5
1968				
Jan	0	0	0	0
Feb	0	0	0	0
Mar	1.6	7.71	2.62	14.5
April	0	0	0	0
May	4.8	23.14	7.85	43.6
June	0	0	0	0
July	4.8	23.14	7.85	43.6
Aug	0	0	0	0
Sept	4.8	23.14	7.85	43.6

Table 38. <u>Robertus lividus</u>, monthly standing crop per metre^2

of adult female spiders

month	mean density	wet	dry	calorific equivalents (cals)
1967				
Oct	6.4	47.36	16.00	91.5
Nov	9.6	71.04	24.00	131.2
Dec	6.4	47.36	16.00	91.5
1968				
Jan	4.8	35.52	12.00	68.6
Feb	4.8	35.52	12.00	68.6
Mar	6.4	47.36	16.00	91.5
Apr	3.2	23.68	8.00	45.7
May	12.8	94.72	32.00	182.9
June	4.8	35.52	12.00	68.6
July	4.8	35.52	12.00	68.6
Aug	1.6	11.84	4.00	22.9
Sept	6.4	47.36	16.00	91.5

Table 39. Robertus lividus, monthly standing crop of young and
adult spiders in mg dry weight per metre^2

month	total density/m^2	standing crop mg young	adult	Total
1967				
Oct	106.4	13.00	16.00	29.00
Nov	116.0	20.12	26.62	46.74
Dec	70.9	10.41	18.62	29.03
1968				
Jan	178.0	23.72	12.00	35.72
Feb	175.0	22.59	12.00	34.59
Mar	182.4	24.61	18.62	43.23
Apr	114.0	30.94	8.00	38.94
May	174.6	21.17	39.85	61.02
June	96.8	39.27	12.00	51.27
July	77.6	22.46	19.85	42.31
Aug	36.5	16.82	4.00	20.82
Sept	198.5	38.63	23.85	62.48

Table 40. Robertus lividus, monthly standing crop in terms of
biocontent (calories per metre^2)

month	total biomass mg	biocontent young	adult	Total
1967				
Oct	29.00	70.1	91.5	161.6
Nov	46.74	85.1	145.7	230.8
Dec	29.03	56.4	106.0	162.4
1968				
Jan	35.72	128.0	68.6	196.6
Feb	34.59	101.4	68.6	170.0
Mar	43.23	132.2	106.0	238.2
Apr	38.94	169.4	45.7	240.1
May	61.02	114.1	226,5	340.6
June	51.27	216.2	68.6	284.8
July	42.31	123.8	112.2	236.0
Aug	20.82	92.8	22.9	115.7
Sept	62.48	211.0	135.1	346.2

CHAPTER EIGHT

ENERGY FLOW IN ROBERTUS LIVIDUS

Introduction

Assimilation, which represents the total energy
entering an individual or species population, has been
estimated from work on food consumption (e.g. Phillipson 1960,
1967; Manga 1970), or from data on respiration and production
(e.g. Saito 1965, Kajak 1967, Whignarajah 1968), i.e.

$$A = C - FU = R + P$$

where C = food consumed, FU = rejecta (faeces and excretion),
R = maintenance metabolism, and P = net production.

It is difficult in a limited time for one worker
to measure all parameters. Hence, in the present study
assimilation or gross production was estimated from the sum
of respiration and net production only. Ideally, the figure
for assimilation in any study should be arrived at by two
independent means (Phillipson 1967).

Energy flow through any organic unit is governed
by the First Law of Thermodynamics which states that all the
energy absorbed by a system must ultimately be surrendered
by it. While respiration in the present study represents
the energy lost in maintaining the spider population, net
production is that amount of energy which is available to

other trophic units before it finally dissipates.

1. Production in R.lividus

Petrusewicz and Macfadyen (1970) defined production as 'The net balance of food transferred to the tissue. of a population during a defined time period,. i.e. net balance between assimilation and respiration', where

$$P = A \div R$$

Production, P, consists of a number of components. There is the accretion through growth (Pg) of somatic material. The formation of reproductive tissue which specifically refers to eggs and sperms but, which in the present context, includes webs of cocoons (Pr).   Net production also covers moulted skins (ML), excretory products and webs for ensnaring prey.   The last two named components were not investigated, hence net production as a whole is

$$P = \sum_{1}^{3} Pg + Pr + ML$$

Symbols after Petrusewicz and Macfadyen (1970).

(i) Production of eggs and cocoons (Pr)

(a) Fecundity

Four captive females were enclosed in the study area during the winter and six during the summer.   Nylon

gauze across the openings of jars which enclosed leaf litter allowed small arthropods from the surrounding debris to enter, but prevented the spiders from escaping. Adult male spiders were placed inside the jars with the females. One cocoon only was constructed by each female although, under laboratory conditions, as many as 4 cocoons were found when food was plentiful. The mean fecundity of spiders under field conditions was 19.8 $\pm$ S.E. 2.7 eggs.

The observed sex ratio in terms of adult spiders removed by the extractor was 14 males : 45 females. The average longevity of adult males is probably short, not exceeding 4 weeks under laboratory conditions. Hence, numbers of males are under-estimates.

The output of eggs per individual amounted to

$$\frac{45}{59} \times 20 = 15.3 \text{ eggs}$$

The population was assumed to be in stable equilibrium, each adult being replaced by one adult in the next generation. Therefore, 93.5% of the eggs laid, i.e.

$$\frac{14.3}{15.3} \times 100 = 93.5\%$$

must have died. The value of 59 surviving adults from October 1967 to September 1968 represented 7% of the eggs

which were originally laid. Hence,

$$\text{total eggs laid} = \frac{93}{7} \times 59 = 784$$

Eggs were treated as if they were discrete individuals having a known duration. During the winter 4 freshly constructed cocoons were placed in the study area. Between 10 and 13 weeks later the young spiders emerged. During the summer in August the incubation time was between 4 and 6 weeks. The mean incubation period was considered to be 2 months ($\bar{t}$), hence 392 eggs were laid.

The individual dry weight of eggs came to 0.0300mg and the calorific content amounted to 6.001 Kcals/g (ash free). This information was used to compute egg production. On the basis of a metre^2, biomass and biocontent came to about 19mg and 113 cals, respectively.

(b) Production of cocoon material

Emergent spiders leave behind the silk cocoon which enveloped the eggs. Since there were 392 eggs laid, which is equivalent to 627 per metre^2, the number of discrete cocoons constructed was

$$\frac{627}{20} = 31.4/m^2$$

The individual weight of cocoons (without spiders and dried over anhydrous $CaCl_2$) came to 1.80mg.   Therefore, contribution to production was 57.6mg, equivalent to 309 cals per metre^2 since there are 5.370Kcal/g of cocoon material.

Table 41 summarises the data on reproductive production (P_r).

Table 41.   <u>Robertus lividus</u>, contribution of reproductive material to production

	N	mean $\pm$ S.E. dry wt mg	numbers/m^2	biomass mg/m^2	biocontent cals/m^2
Eggs	24	0.0300 ± 0.003	627.2	18.8	112.9
Cocoons	6	1.8000 ± 0.060	31.4	57.6	309.3
				76.4	422.2

(ii) <u>Production through growth</u> (Pg)

The parameter, Pg, has been estimated for only a few species of spiders.   In <u>Trochosa ruricola</u> (Breymeyer 1967) developmental stages and breeding season were sufficiently clear to permit a study of a single cohort, so that production of the population could be worked out from a survivorship curve.

In the case of <u>R.lividus</u>, a protracted period of recruitment occurred from September to May.   Low temperatures apparently retarded the development of all stages during December, January and February, as shown by the flattened part of the

population curves in Fig.26. Under laboratory conditions instar 4 individuals were particularly sensitive to temperatures below 10'C, being unable to feed or survive for more than about 4 weeks. From October to March extraction figures for this stage were low. Hence, low temperatures and continual reproduction produced a population with a considerable overlap of generations.

A situation similar to that of R.lividus was found in a population of soil Collembola by Healey (1967). The distribution of numbers of individuals in size classes was used as a survivorship curve and it was assumed that no portion of the population was sampled more than once. On the other hand, a population of continuously reproducing Copepoda was reduced to a single 'cohort' (Winberg et al, cited in Petruswicz and Macfadyen 1970) from information on the physiological length of developmental stages.

The possible methods for estimating production in R.lividus would appear to fall into one of two groups. First, those based on the assumption that each part of the population was sampled only once in a given time period. Second, with information on duration of stages, an attempt can be made to identify particular cohorts or to convert the entire population data to a single 'cohort'.

(a) Construction of a survivorship curve

There were two cohorts which differed substantially in duration. One was initiated in September with adults emerging in May and June, while the other commenced in spring or early summer and was completed by September. From these two cohorts the mean duration of a cohort and its stages could be estimated.

The discrete number of individuals (V_s) at each stage which passed through the population was calculated from the number of spiders $(\overline{N}T)$ extracted over the 12 months sampling period. Since the approximate duration $(\overline{t})$ of each stage is known,

$$V_s = \overline{N}_s \cdot T / \overline{t}_s$$

A survivorship curve could then be drawn from the data in Table 42, together with the individual growth curve to provide a method for estimating production (Fig.34).

(b) Production (Pg)

It was assumed that half the individuals found at two consecutive times (or stages) gained in weight by an amount which was equivalent to the difference in mean weights between the two occasions (Petrusewicz and Macfadyen 1970). Hence,

$$Pg_{Ti} = \frac{N_{Ti} + N_{Tii}}{2} (W_{Tii} - W_{Ti}) = \overline{N}_{Ti} \cdot \Delta W_{Ti}$$

Fig.34. _Robertus lividus_, survivorship and individual growth curves.

INDIVIDUAL DRY WT. mg

2.06

0.91

0.31

0.11
0.06
0.03

MONTHS

7

6

5

4

3

2

1

0

392

218

163

109

54
39
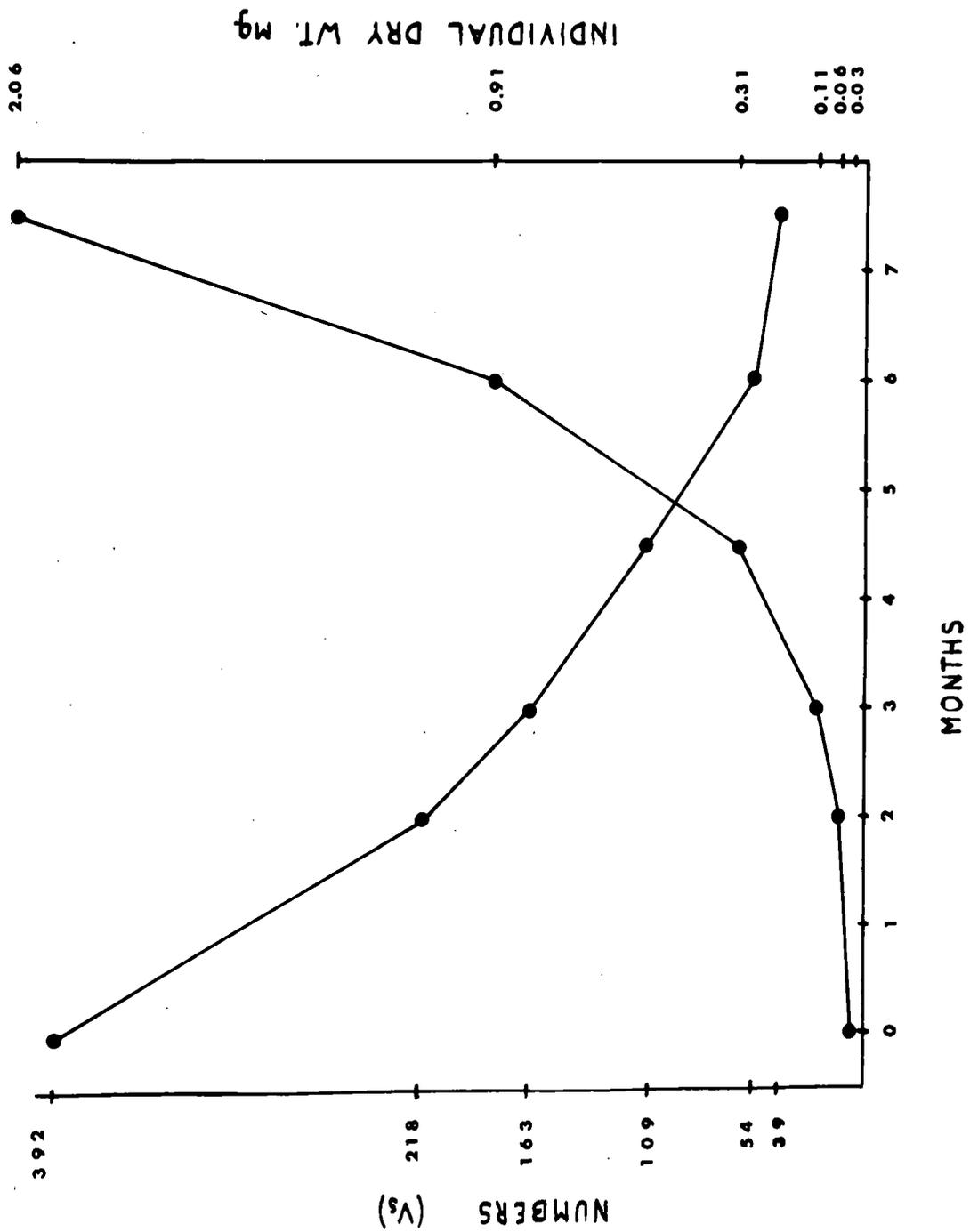
NUMBERS (V_s)

Table 42.   <u>Robertus lividus</u>, actual numbers of stages from the

extractor and numbers (v_s) estimated from mean

duration of stages

	Numbers extracted	cohorts duration in months 'long'	'short'	'mean'	v_s
eggs	784 (estimate)	3	1	2	392
instar 1	218	1	1	1	218
2	245	2	1	1.5	163
3	163	2	1	1.5	109
4	81	2	1	1.5	54
5	59	2	1	1.5	39

Summation of production of all stages or segments of time (k),

gives the total production

$$Pg_T = \sum_{i=1}^{i=k} \bar{N}_{Ti} \cdot \Delta W_{Ti}$$

Since the spiders were extracted from ten sample

units each of $1/16$ metre^2, production figures were adjusted

to a metre^2 (by multiplying them by 1.6).   The results are

given in Table 43.

Table 43.   <u>Robertus lividus</u>, production (Pg) for each stage (K)

for the entire population during October 1967 to

September 1968

'k'	individual dry wt mg	Mean dry wt mg $\bar{N}_{Ti} \cdot \Delta W_{Ti}$	per metre^2 mg	cals
Eggs	0.0300	–	–	–
1	0.0644	10.49	16.79	104.08
2	0.1129	9.21	14.74	76.97
3	0.3066	26.34	42.15	226.37
4	0.9124	49.07	78.51	434.03
5	2.0631	52.93	84.69	474.49
Total		148.04	236.88	1,315.94

(c)   <u>Contribution of mortality fraction</u> ($_E$)

The method, described previously, for computing

production (Pg) accounts for the contributions of survivors

and eliminated individuals.   The estimated proportion

from the mortality fraction was obtained from the differences

in numbers of consecutive stages, multiplied by the average

of their individual weights, i.e. $\Delta N_{T_1} \cdot \bar{W}_{T_1}$.

The mean biocontent (Chapter 4(b)) of consecutive

instars was used to convert dry weight production to

calorific equivalents.

Summation of all stages gives total production

of the whole mortality fraction (E_T).   The formulae used

(Petrusewicz and Macfadyen 1970) are as follows :

$$E_1 = (N_1 - N_2) \; \frac{W_1 + W_2}{2} \; = \triangle N_T \cdot \bar{\bar{W}}_{T_1}$$

hence,

$$E_T = \sum_{i=1}^{i=k} (\triangle N_{T_1} \cdot \bar{W}_1)$$

Estimates of production from eliminated individuals (E) are given in Table 44.

The total for the mortality fraction amounted to 711 cals per metre^2 for the year, 1967-1968. This represents 54% of total production (P_g).

Table 44. **Robertus lividus**, production of mortality fraction per metre^2

instars	$N_1 - N_2$	$\bar{W}_{T_1}$	$\triangle N_{T_1} \cdot \bar{W}_{T_1}$	calories
1	174	0.0472	13.13	68.8
2	55	0.0886	7.79	40.8
3	54	0.2097	18.11	100.0
4	55	0.6095	53.63	297.0
5	15	1.4902	35.76	204.5
		Total	128.42	711.1

(iii) **Production from exuvia** (ML)

All spiders of a particular instar (n_2) will have moulted to reach that stage of development. In addition, it can be assumed that a number of individuals (n_1) at the preceding stage managed to moult before dying. Hence, the mean number ($\bar{n}$) of spiders which moulted was estimated from

$$\bar{n} = \frac{n_1 + n_2}{2}$$

Weights of cast skins were obtained from individuals kept in captivity until they had moulted. After their stage of development had been determined, the exuviae were vacuum dried before weighing.

The number of moults multiplied by the mean dry weight of skins gave the amount of material shed by each instar. Since the calorific value of skins was known (Chapter 4), the equivalent in calories per metre^2 could be estimated (Table 45).

Exuviae from instar 1, had they moulted prior to their emergence from cocoons, would have been included in the estimates for cocoon and contents.

Table 45. Robertus lividus, the contribution of exuviae to population production

Instar	Individuals moulting/ metre^2	mean dry wt. exuviae mg	exuviae per metre^2 mg	calorific equivalent/m^2
1	190	0.0024 ± 0.0003	0.7296	3.0
2	136	0.0119 ± 0.001	2.6054	10.7
3	81	0.0320 ± 0.011	4.1472	17.0
4	46	0.2799 ± 0.021	20.6006	84.5
5				
		Total	28.0828	115.2

(iv) Discussion

A 'mean' survivorship curve was drawn from data which related to more than one cohort. As the mean duration of stages were estimates from observations based on field data it was not possible to define duration very precisely.

A possible alternative approach would have been to plot the main peaks of abundance of each stage for each of the three main cohorts, and so estimate mortality from a regression analysis of numbers on time. This is similar to the technique used by Smalley (1960) with a population of grasshoppers. However, the peaks of abundance for any particular stage of R.lividus may have been derived from individuals belonging to more than one cohort. Furthermore, a constant mortality rate would have to be assumed and that no part of the population was sampled more than once.

Table 46 summarises the data on production. The estimate for the whole of the annual net production is 341mg dry wt which corresponds to 1.853Kcals/metre^2. About 71% of the total calories came from growth and 32% from egg and cocoon production. The main contribution to population production is from female spiders which bear the eggs and so have larger body weights and a relatively high calorific content.

Table 46.   <u>Robertus lividus</u>, components of production

per m^2, 1968

$$\sum_{1}^{3} P = P_g + P_r + ML = \quad Total$$

$$= 237 \quad 76 \quad 28 = \quad 341 \text{ mg dry wt}$$

$$= 1316 \quad 422 \quad 115 = 1853 \text{ calories}$$

The annual estimate of 237mg dry weight per metre^2 (Pg)

for <u>R.lividus</u> differs substantially from the production figure

for <u>T.ruricola</u> (Breymeyer 1967).   This estimate is much

higher than the 141mg recorded for the wolf spider, which

is a larger species and produces over 160 eggs per cocoon.

It may be that the suction device and hand sorting used by

Breymeyer in conjunction with biocenometers yielded

relatively low numbers of spiders.   The subjective nature

of these methods when compared, say, with the lateral

extractor, is open to serious criticism (Petrusewicz and

Macfadyen 1970).

2.   <u>Population maintenance metabolism</u>

(a)   <u>Method</u>

The respiratory data for <u>R.lividus</u> and <u>Meta</u>

<u>segmentata</u>, as well as the data for other species of spiders

(Anderson 1970), clearly show temperature dependence.

Regression equations were calculated, therefore, to describe

rate of respiration on temperature (Table 47).   From monthly

field temperatures for the study area it was possible to

estimate, approximately, field metabolic rates (Table 48).

Daily respiratory rates were multiplied by the oxy-calorific value of 4.8Kcals/litre of oxygen, assuming a mixed respiratory substrate of glycogen, fat and protein, to give energy loss per millegramme live weight.

The monthly mean biomass (mg live weight) was derived from the standing crop (already given) at the beginning and end of each monthly interval. The monthly maintenance metabolism for each instar could then be estimated by multiplying mean biomass by the number of calories lost through respiration per unit weight.

(b) Results

The summation of monthly totals provided the estimate for the annual population metabolism (Tables 49-55) which amounted to 2.74Kcals.

Although low numerically, sub-adult spiders lost 794 calories per m^2 during the year through respiration. This is almost 30% of the total metabolic loss for the population. The higher field temperatures during the summer and their high respiratory rates per unit weight, were mainly responsible. The respiratory energy turnover of adult females, with large individual biomass, is also high.

Adult males had a mean annual standing crop of only 14cals per metre^2, about 1/6 that of females which amounted to 85 calories. However, energy loss per metre^2 of males was only a little under half that for females. The adult male contribution is important despite very low densities.

The maintenance cost of instar 1 was about 10% of the population total. This was partly because of their small biomass and the low temperatures usually prevailing at the time of maximum occurrence.

Discussion

Changes in density, biomass, and metabolism for the population are recorded in Fig.35. The first and second parameters fluctuate more than the field metabolism which has a smooth annual curve.

While population density, consisting of a high proportion of very young stages, is high from January to March, the corresponding biomass is low and maintenance metabolism is at its lowest level. The effect of low field temperatures at this time is clear.

With the development of spiders during the summer, population biomass increased despite diminishing density. Higher temperatures and the increase in standing crop led to an increase in population metabolism.

Density and biomass rose to their respective maxima in September. Large numbers of young spiders appeared while adult females were still relatively numerous. However, the increase in population metabolism is not as pronounced as in June.

It seems that the maintenance cost to the population of young stages is reduced when emergence takes place towards the end of winter. Low temperatures will depress the relatively high specific metabolic rates of these spiders. In turn, this would at least partially offset the effects of shortage of food in winter and when production (Pg) is low. The other appropriate time for hatching is at the end of summer by which time females have reached maturity. There should be sufficient food for all stages to offset the high population maintenance cost.

Other factors like interspecific competition may operate in determining patterns of life-cycles. On the other hand, the fact that a mid-summer emergence does not take place can be explained by the inability of sub-adults to withstand the conditions of overwintering, at least partly because of their high specific metabolism.

Table 47.   Robertus lividus, regression equations for mean

rate of respiration (μl O_2/mg live wt/hr) on

temperature (X)

instar	regressions
1 + 2	0.0306 + 0.09X
3	0.1367 + 0.04X
4	0.0787 + 0.06X
5	
female	0.0883 + 0.03X
male	0.0023 + 0.08X

Table 48.   Robertus lividus, estimates of mean respiratory

rates adjusted to field temperatures

Month	mean field temperature °C	respiration (μl O_2/mg live wt/hr)					
		1	2	3	4	♂	♀
Nov	7.6		0.990	0.441	0.535	0.610	0.316
Dec	6.2		0.864	0.385	0.451	0.498	0.274
Jan	5.5		0.801	0.357	0.409	0.442	0.253
Feb	4.0		0.666	0.297	0.319	0.322	0.208
Mar	7.9		1.017	0.453	0.553	0.634	0.325
Apr	7.8		1.008	0.449	0.547	0.626	0.322
May	8.4		1.062	0.473	0.583	0.674	0.340
June	11.2		1.314	0.585	0.751	0.898	0.424
July	12.8		1.458	0.649	0.847	1.026	0.472
Aug	12.6		1.440	0.641	0.835	1.010	0.466
Sept	12.8		1.458	0.649	0.847	1.026	0.472
Oct	9.3		1.143	0.509	0.637	0.746	0.367

Table 49. Robertus lividus, monthly maintenance metabolism for instar 1

month	mean biomass live wt. mg	respiration (μl O₂/mg live/hr)	respiration (cals/mg live/month)	maintenance (cals/metre²/month)
Nov	7.1	0.990	3.42	23.9
Dec	4.9	0.864	2.98	14.6
Jan	8.8	0.801	2.77	24.4
Feb	13.5	0.666	2.30	31.0
Mar	12.5	1.017	3.51	43.9
Apr	8.0	1.008	3.48	27.8
May	3.9	1.062	3.07	16.6
June	4.3	1.314	4.54	19.5
July	1.2	1.458	5.04	6.0
Aug	0.8	1.440	4.98	3.9
Sept	7.2	1.458	5.04	36.3
Oct	11.1	1.143	3.95	43.8
Total				271.7

Note: respiration header reads "respiration μl O₂/mg live/hr"

Table 50. *Robertus lividus*, monthly maintenance metabolism for instar 2

month	mean biomass live wt mg	respiration (μl O_2/mg live/hr)	respiration (cals/mg live/month)	maintenance (cals/metre^2/month)
Nov	7.1	0.990	3.42	24.3
Dec	7.1	0.864	2.98	21.2
Jan	7.9	0.801	2.77	21.9
Feb	11.9	0.666	2.30	27.4
Mar	15.4	1.017	3.51	54.0
Apr	13.2	1.008	3.48	45.9
May	15.0	1.062	3.07	46.0
June	14.5	1.314	4.54	65.8
July	4.9	1.458	5.04	24.7
Aug	1.1	1.440	4.98	5.5
Sept	3.7	1.458	5.04	18.6
Oct	5.7	1.143	3.95	22.5
			Total	377.8

Table 51.   Robertus lividus, monthly maintenance metabolism for instar 3

month	mean biomass live wt mg	respiration (μl O_2/mg live/hr)	respiration (cals/mg live/month)	maintenance (cals/metre^2/month)
Nov	16.2	0.441	1.52	24.6
Dec	13.5	0.385	1.33	17.9
Jan	16.2	0.357	1.23	19.9
Feb	18.2	0.297	1.03	18.7
Mar	12.8	0.453	1.56	20.0
Apr	16.2	0.449	1.55	25.1
May	14.9	0.473	1.63	24.3
June	12.8	0.585	2.02	25.8
July	27.7	0.649	2.24	62.0
Aug	25.7	0.641	2.21	56.8
Sept	22.3	0.649	2.24	49.9
Oct	23.7	0.509	1.76	41.7
Total				385.6

Table 52. Robertus lividus, monthly maintenance metabolism for instar 4

month	mean biomass live wt mg	respiration (μl O_2/mg live/hr)	respiration (cals/mg live/month)	maintenance (cals/metre^2/month)
Nov	12.6	0.535	1.85	23.3
Dec	14.7	0.451	1.56	22.9
Jan	10.5	0.409	1.41	14.8
Feb	14.7	0.319	1.10	16.2
Mar	18.9	0.553	1.91	36.1
Apr	35.7	0.547	1.89	67.5
May	33.6	0.583	2.01	67.5
June	50.4	0.751	2.59	130.5
July	52.5	0.847	2.93	153.8
Aug	27.3	0.835	2.88	78.6
Sept	42.0	0.847	2.93	123.1
Oct	27.3	0.637	2.20	60.1
Total				794.4

Table 53. Robertus lividus, monthly maintenance metabolism for adult males

month	mean biomass live wt mg	respiration (μl O_2/mg live/hr)	respiration (cals/mg live/month)	maintenance (cals/metre²/month)
Nov	3.3	0.610	2.11	7.0
Dec	7.7	0.498	1.72	13.3
Jan	3.3	0.442	1.53	5.0
Feb	0	0.322	1.11	0
Mar	3.3	0.634	2.19	7.2
Apr	3.3	0.626	2.16	7.1
May	11.6	0.674	2.33	27.0
June	11.6	0.898	3.10	36.0
July	11.6	1.026	3.54	41.1
Aug	11.6	1.010	3.49	40.5
Sept	11.6	1.026	3.54	41.1
Oct	11.6	0.746	2.58	30.0
			Total	255.4

Table 54.   Robertus lividus, monthly maintenance metabolism for adult females

month	mean biomass live wt mg	respiration (μl O_2/mg live/hr)	respiration (cals/mg live/month)	maintenance (cals/metre^2/month)
Nov	59.2	0.316	1.09	64.5
Dec	59.2	0.274	0.95	56.2
Jan	41.4	0.253	0.87	36.0
Feb	35.5	0.208	0.72	25.6
Mar	41.4	0.325	1.12	46.4
Apr	35.5	0.322	1.11	39.4
May	59.2	0.340	1.17	69.3
June	65.1	0.424	1.46	95.0
July	35.5	0.472	1.63	57.9
Aug	23.7	0.466	1.61	38.1
Sept	29.6	0.472	1.63	48.2
Oct	47.4	0.367	1.27	60.2
Total				656.8

Table 55.   Robertus lividus, population maintenance metabolism for each month

| | maintenance ($Cals/metre^2/month$) | | | | | | |
| | instars | | | | | | |
month	1	2	3	4	male	female	Total
Nov	23.9	24.3	24.6	23.3	7.0	64.5	167.6
Dec	14.6	21.2	17.9	22.9	13.3	56.2	146.1
Jan	24.4	21.9	19.9	14.8	5.0	36.0	122.0
Feb	31.0	27.4	18.7	16.2	0	25.6	118.9
Mar	43.9	54.0	20.0	36.1	7.2	46.4	207.6
Apr	27.8	45.9	25.1	67.5	7.2	39.4	212.8
May	16.6	46.0	24.3	67.5	27.0	69.3	250.7
June	19.5	65.8	25.8	130.5	36.0	95.0	372.6
July	6.0	24.7	62.0	153.8	41.1	57.9	344.5
Aug	3.9	5.5	56.8	78.6	40.5	38.1	223.4
Sept	36.3	18.6	49.9	123.1	41.1	48.2	317.2
Oct	43.8	22.5	41.7	60.1	30.0	60.2	258.3
Total	271.7	377.8	385.6	794.4	255.4	656.8	2741.7

Fig.35. Robertus lividus, monthly density, biomass and maintenance

cost of the population.
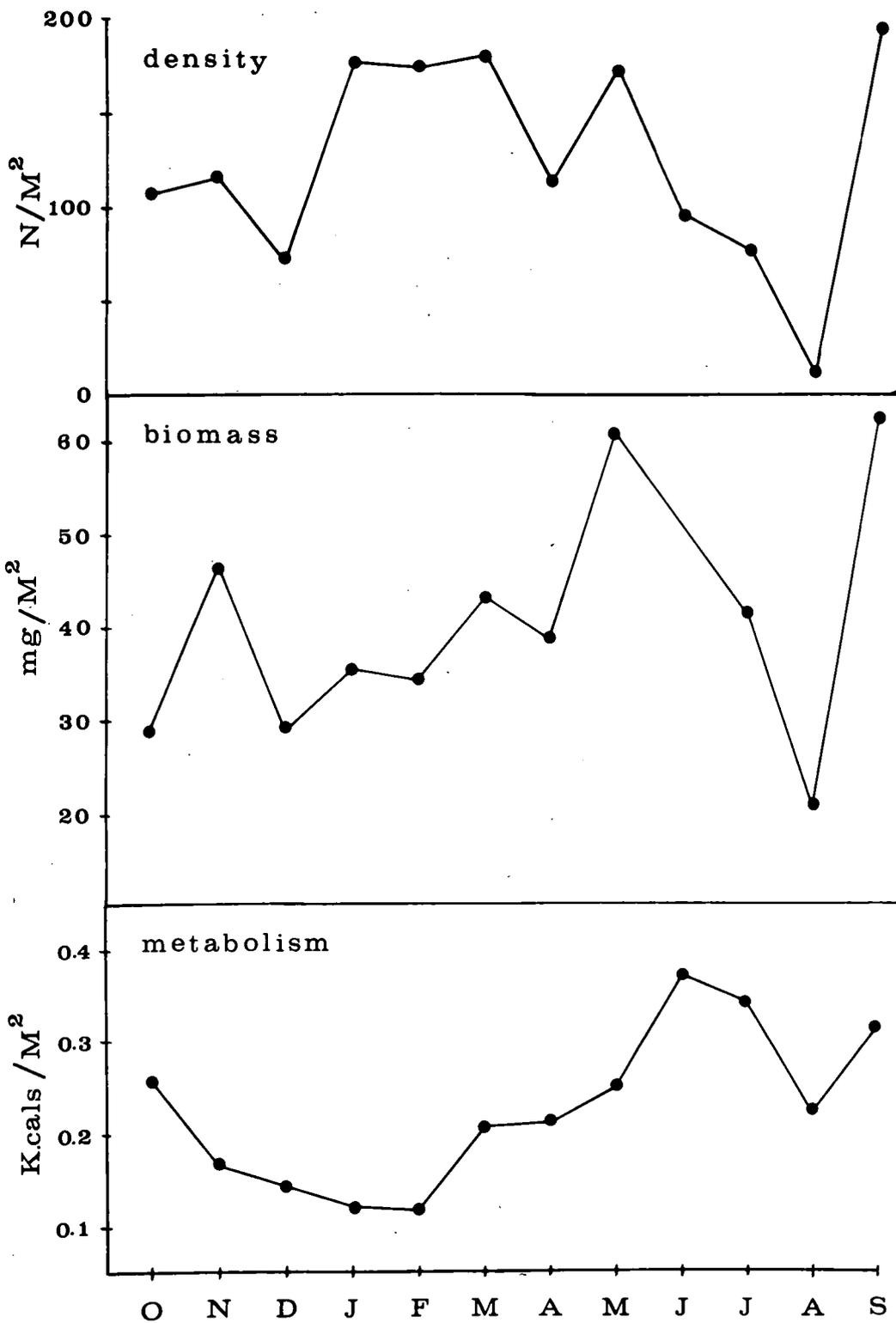
3. Energy flow in R.lividus

In energy flow studies (e.g. Teal 1957) population size at any given time is expressed in millègrammes dry weight or in calories, per metre^2, and is referred to as the standing crop.

The energy absorbed to hold the living material together is equivalent to net production which was derived from survivorship and individual growth curves for a 'mean cohort', and includes the energy of cocoons and exuviae.

The loss of energy through respiration, i.e. maintenance metabolism, was estimated from mean rates (μl O_2/mg live wt/hr) which were adjusted to field temperatures. Respiration in eggs was not considered.

The energy budget for the population of R.lividus is given in Table 56. A mean standing crop of 0.278Kcals/metre^2/year respired 2.742Kcals and retained about 1.853Kcals/metre^2/year. Total assimilation came to 4.59Kcals/metre^2/year. Net population production efficiency was about 40% (Chapter 12(v)).

Table 56. Robertus lividus, energy budget for the population, 1967-1968

stage	mean standing crop cals/m²/annum	respiration of standing crop cals/m²/annum	production of standing crop cals/m²/annum	Assimilation A = R + P cals/m²/annum	% P/A ratio
cocoons + eggs	35	-	422	(422)	-
instar 1	18	292	107	399	27
2	19	378	88	465	19
3	37	386	243	629	39
4	55	794	518	1313	39
Adults 5	114	892	475	1367	34
Total	278	2742	1853	4595	40

CHAPTER NINE

1. Life-history of <u>Meta segmentata</u>

   (a) <u>General comments</u>

Cocoons with eggs were found from the end of September and beginning of October at the base of tree trunks, or in crevices of fallen logs, all of which were in a state of decay.

Eggs hatched at the end of April or during the first half of May. As many as 132 eggs per cocoon were laid although the usual number was less than 100. In the laboratory, spiderlings remained within or around the cocoon for two or three days until disturbed, or when there was a marked rise in temperature. Dispersal then took place and in the field the distance covered was quite considerable with young spiders distributed throughout the field layer and canopy. At this stage they apparently favoured south-facing and sunny aspects.

From about the middle of June, there was a marked tendency for the spiders to congregate in the more sheltered and damp parts which, in fact, constituted the study area. The population figures were influenced initially by this immigration of young spiders.

The life span of <u>M.segmentata</u> (outside the egg) occupied nearly 5 months. In her study of web spiders belonging to the Argiopidae Kajak (1967) records 100 days

for the large <u>Araneus quadratus</u> and 160 days for <u>A.cornutus</u> and <u>Singa hamata</u>. These observations from lowland areas contrast with those of Cherrett (1961) for <u>Meta merianae</u> which overwinter in moorland to lay their eggs in their second summer. Despite the suggestion by Locket and Millidge (195**3**) that <u>M.segmentata</u> also may pass the winter, there was no evidence at Wynyard that this happened.

(b) <u>Developmental stages</u>

The first collections of <u>M.segmentata</u> were made in the autumn of 1967. Eggs were laid in captivity and while some cocoons were retained, others were placed in the study area in nylon mesh bags with litter. Young spiders emerged during April in 1968, while in the field during 1969, emergence was delayed until May. The first spiders to appear have been referred to as instar 1.

<u>Meta segmentata</u> was specifically sampled during 1969. After spiders had been anaesthetised by ethyl acetate vapour, measurements were recorded for width of carapace, length of tibia 1, width of abdomen, and overall length. Live and dry weights of some specimens were also recorded. All measurements were made with an ocular micrometer in a x6 eye-piece which was used in conjunction with a 2/3 objective. It was hoped that a frequency distribution of the data would indicate the number of instars.

With the exception of length of tibia 1, all measurements varied continuously. Although spiders could be placed into 4 groups on the basis of tibia 1, the suggestion of 4 instars was not convincing. Spiders which were known to be male because of swollen pedipalps varied enormously in size, despite the fact that the lengths of tibia 1 were about the same. A linear relation was not found between the possible instars and their mean length of tibia 1, even when logarithms were used. Clearly, the length of this structure did not necessarily increase at every moult.

Cherrett (1961) had found that he could separate satisfactorily the instars of Meta merianae by using a combination of measurements rather than a single one, which on its own may be less sensitive than a 'multivariate' analysis. Accordingly, it was decided to adopt a similar procedure with M.segmentata.

Measurements of tibia 1 were added to the corresponding carapace widths and the combined values plotted against body length. From the distribution of points it was possible to detect 5 groups (Fig.36). The presence of genitalia or swollen pedipalps enabled the sexes to be distinguished as early as the 3rd instar. This discovery was particularly interesting because it not only revealed the possible error in the 'univariate' approach, but also

Fig.36. M.segmentata, the evidence for 5 instars based on body length and length of tibia 1 plus width of carapace. Measurements in micrometer units.

M. SEGMENTATA   POSSIBLE INSTARS

BODY LENGTH (vertical axis, values 200, 80, 60, 40, 20, 100, 80, 60, 40)

TIBIA I PLUS CARAPACE (horizontal axis, values 20, 40, 60, 80, 100, 20, 40, 60, 80, 200, 20)

Instar labels: 1, 2, 3, 4, 5

Legend:
● YOUNG
⟍ YOUNG (SWOLLEN PALPAL ORGANS)
♂ ADULT MALE
○ ADULT FEMALE
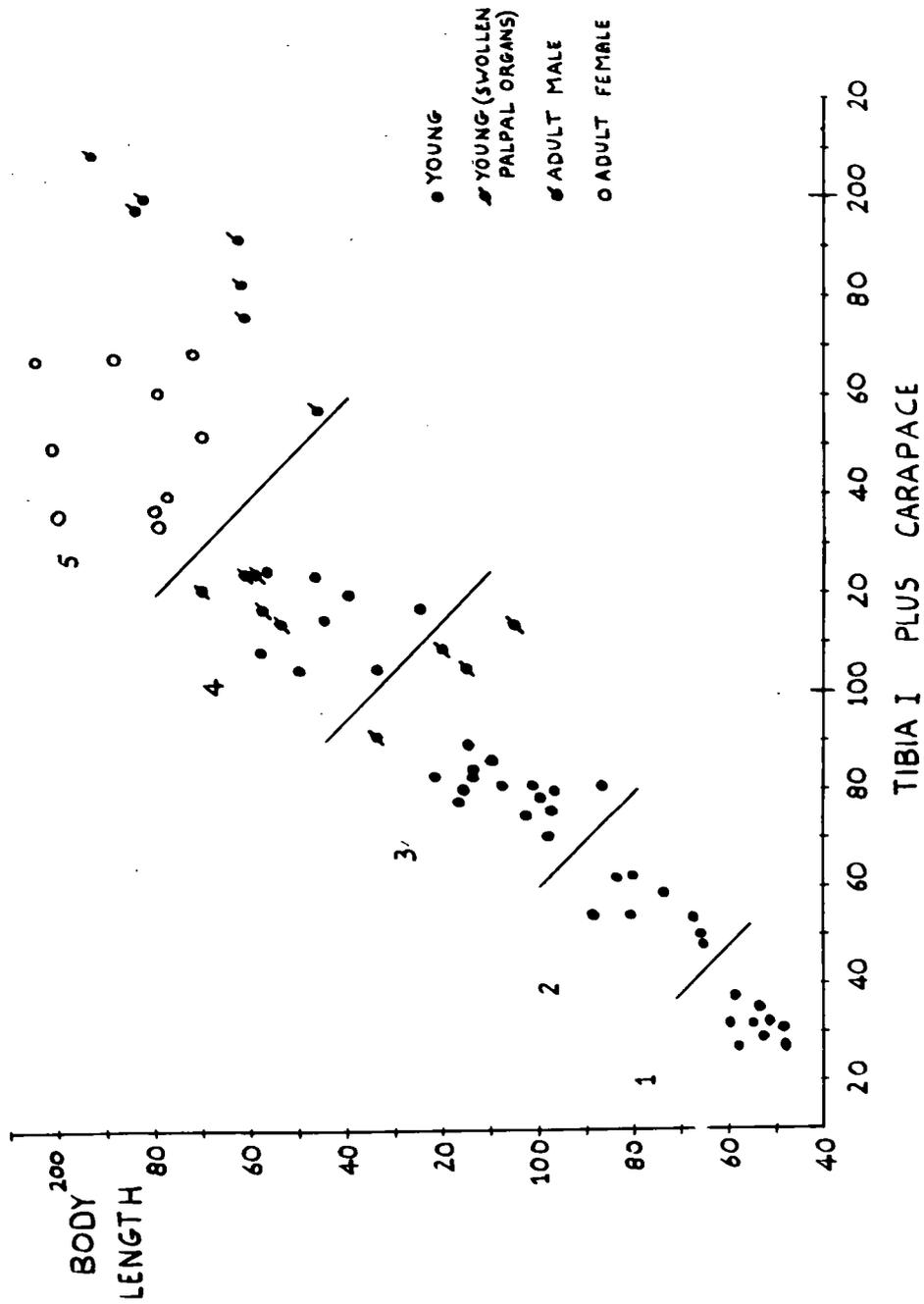
Fig.37. M.segmentata, log. means (length of tibia 1 plus width of carapace) of suggested instars. Measurements in micrometer units.

META SEGMENTATA
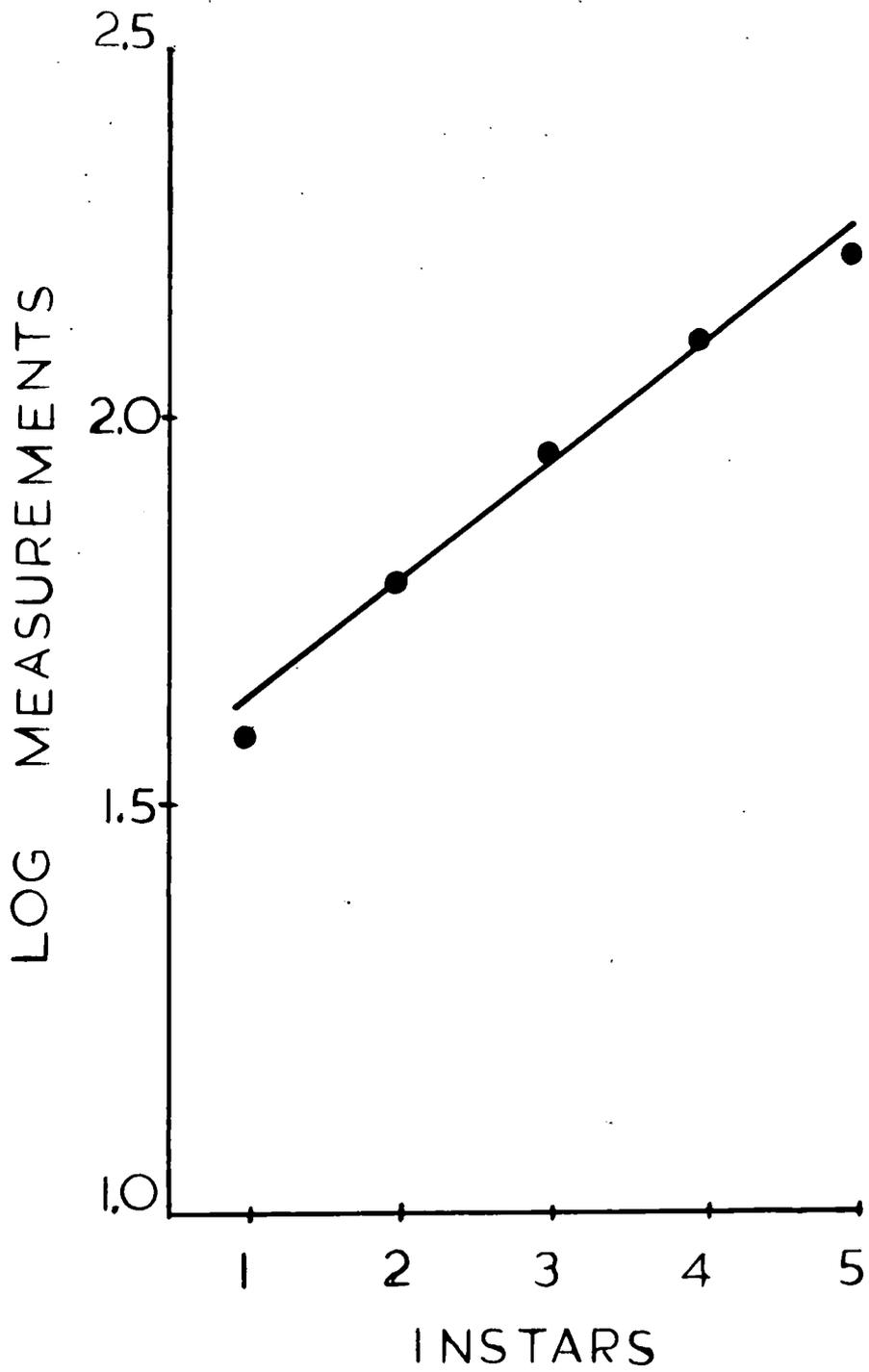
Fig.38. <u>Meta segmentata</u>, mature specimens (above)

in characteristic situation (below).

Fig.39. *Meta segmentata*, instars 1 (right) and 3 (left).
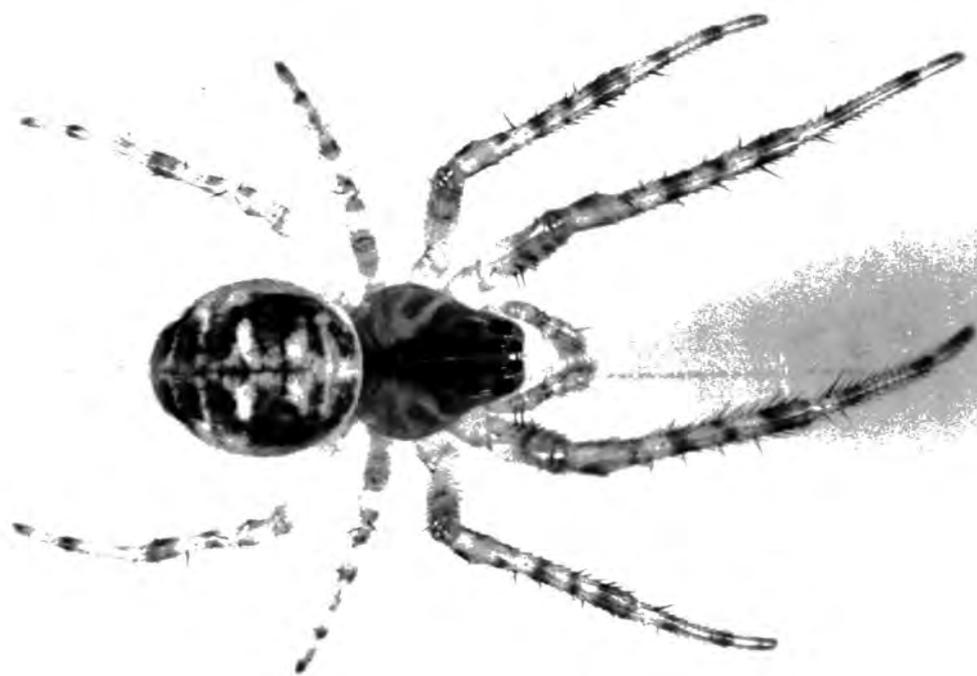
corrected the common assumption that swollen pedipalps can only denote the penultimate stage of development in male spiders.

Further credence is given to the possibility of 5 instars when the log. measurements of tibia 1 plus carapace width are plotted against the appropriate instars (Fig.37).

As far as is known, there are no records of number of instars in M.segmentata. Cherrett (1961) suggested that the closely related M.merianae underwent 7 moults. Blackwall (cited by Comstock 1940) described 5 instars in Epeira calophylla (syn. Zygiella atrica in Locket and Millidge 1953).

Three of the 5 instars are shown in Figs. 38 and 39.

(c)   The duration of instars

Cocoons which had been placed in various parts of the wood were used to indicate the main period of emergence. Of the 22 cocoons observed, 15 were empty by the 14th day of May, 3 more by the 22nd, and 1 more by the 27th. The remaining cocoons produced no spiders and gradually were invaded by a fungus.

Most eggs had hatched by the first half of May. The main cohort from then onwards was very much apparent

by its synchronous development. With reference to length of
tibia 1 and the external genitalia, the percentage composition
of stages revealed a peak for instar 1 in May, 2 in June,
3 in July, 4 in August, and for adults in September (Fig.40).

A more precise picture of duration is presented
by using the technique of Gabbutt (cited by Whittaker), which
was also used successfully by Whittaker (1965) in the study
of moorland Homoptera. If, as in the case of Meta segmentata,
the mean dry weights of spiders caught on each sampling occasion
are plotted against the dates on which sampling had taken place,
a growth curve is produced. The growth taking place in the
species population is represented by changes in the mean
weights between successive samples. The mean dry weight of
a particular sample depends on the proportions of different
developmental stages. When the mean dry weights for each
instar, calculated from specimens already assigned to the
instar during the analysis of developmental stages, is
superimposed on the growth curve, it is possible to estimate
the time lapse between instars. Although this technique
excludes instar 1, the duration of this stage can be
calculated from information on the period of emergence from
cocoons.

The growth curve was constructed from the
mean weights of both sexes (Fig.41). The fact that there
are differences will affect to some extent the estimates

Fig.40. <u>Meta segmentata</u>, percentage composition of instars in the population, 1969.
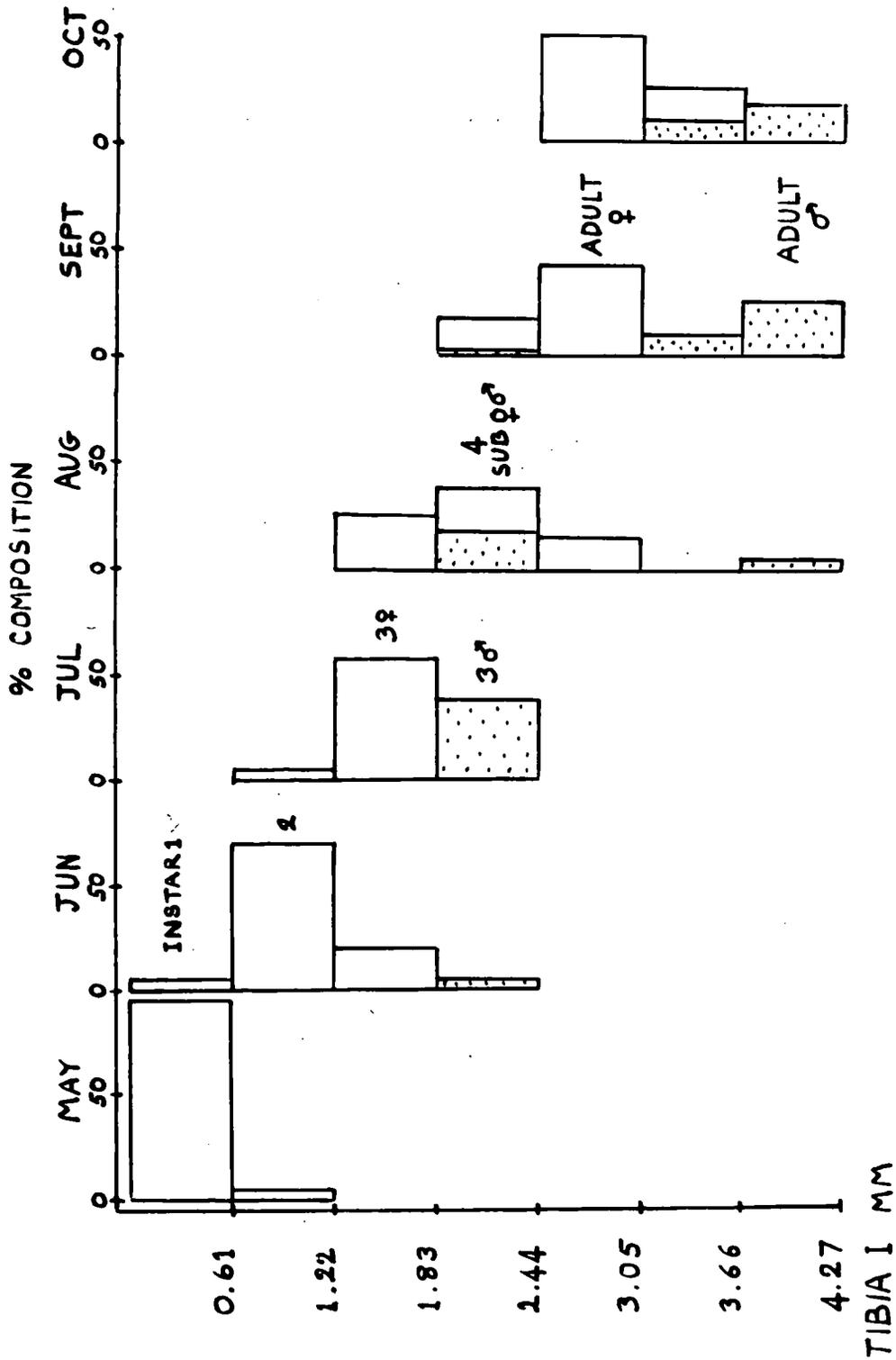
Fig.41. <u>Meta segmentata</u>, duration of instars in the study area. Each point represents the mean dry weight of the population on a sampling date. The horizontal lines are the individual dry weights of instars 2 to 5, projected onto the curve.

META SEGMENTATA
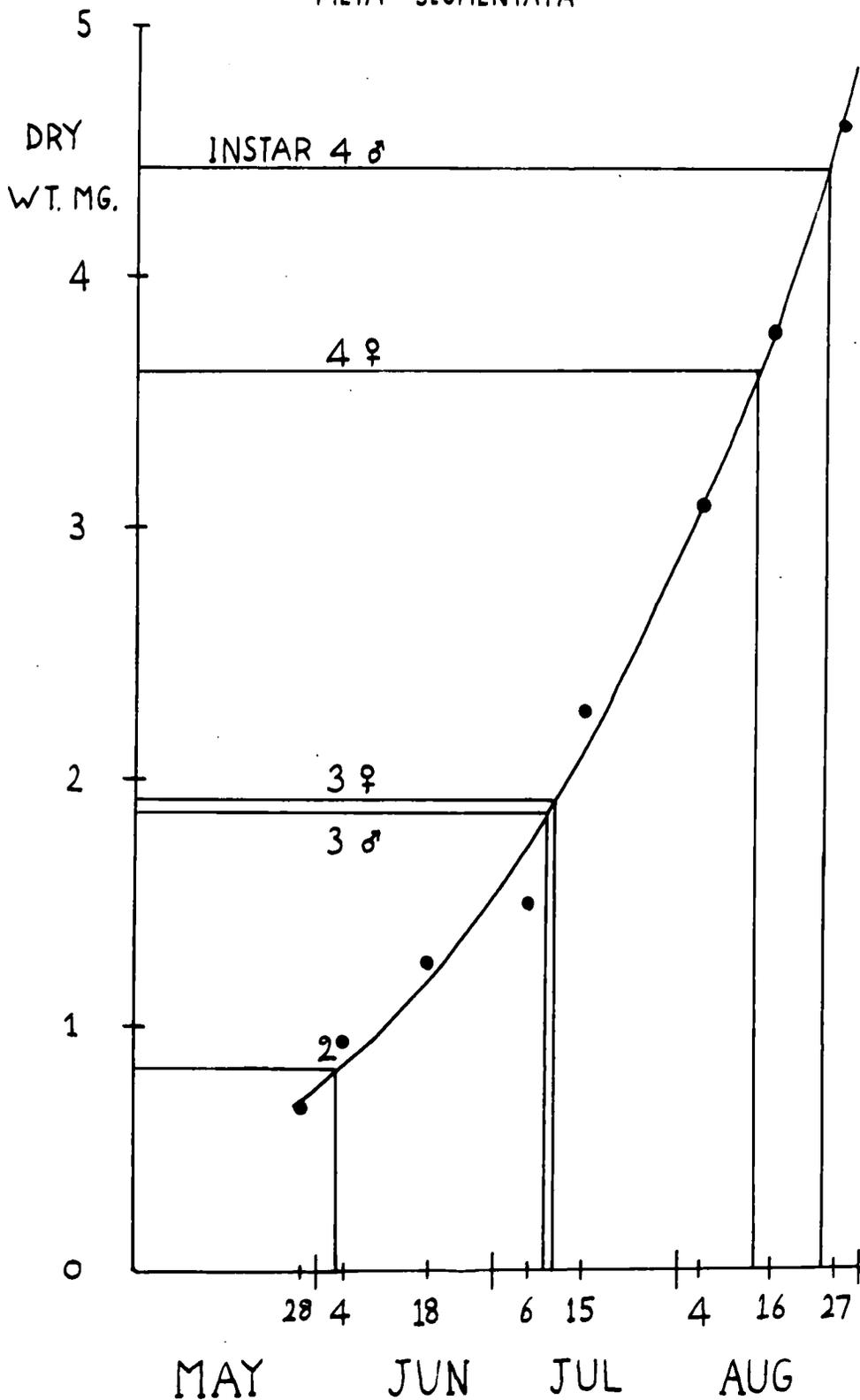
of duration.   However, these differences are small until
the adult stage.

Ideally, two independent methods of calculation
are preferable to one in the estimation of duration.
Whittaker (1965) obtained supporting evidence on the duration
of cercopid nymphs by plotting a series of distribution
curves for each instar at regular intervals of time.
Although it was not possible to implement this procedure
in the present study, it was noted that Whittaker found
very close agreement (to within two days) between the two
methods.

As shown in the previous section, the sexes
could be distinguished from instar 3 onwards.   This meant
that the growth curve for dry weight could also indicate
the duration of adult male and female spiders.   Very few
adult spiders were in evidence in the catch for 27 August.
However, by the next sampling occasion, 13 September,
virtually all specimens were adult.   By drawing a curve
for female spiders, based on observations from August onwards,
it was possible to show that they underwent their final moult
by 10 September.   Male spiders appeared to mature at about
the same time, and from the middle of September they were
invariably seen in the company of females.

The likely duration of instars is set out in Table 57. The overall life span of males and females was about the same, 135 and 139 days after hatching, respectively. Male spiders may have just reached maturity before females and if the time taken by females to lay their eggs in the ground zone is included, then females probably outlived their partners by several days.

By the end of the first week in October the main cohort had disappeared. Freshly constructed cocoons were found from the end of September, accompanied in several cases by the parent female which was much reduced in size and moribund. In October, spiders belonging to the genus Meta consisted of a few M.segmentata, the females of which were much smaller than previous specimens, the occasional M.segmentata mengei, and M.merianae.

Apart from sampling M.segmentata during 1968 to record changes in population density and biomass, no detailed analysis was carried out to establish the duration of instars. Although eggs appeared to hatch in April as well as May, the main cohort persisted further into October than in 1969. The relatively mild winter and spring in 1967-68 may account for the earlier emergence. The wet and cooler summer which followed may explain the longer overall life span. There was no obvious evidence to suggest that there were more than the 5 instars.

Turnbull (1962) had found that unfavourable conditions delay rather than increase the number of moults in Linyphia triangularis.

Table 57.   Meta segmentata, duration in days of instars when calculated from the growth curve, 1969

Instar	mean $\pm$ S.E. dry wt.mg	interval	duration in days
Females			
1	0.1143 $\pm$ 0.0243	estimated from hatching	18
2	0.8257 $\pm$ 0.1320	3 June – 9 July	37
3	1.9284 $\pm$ 0.1617	10 July – 12 Aug	34
4	3.6237 $\pm$ 0.2350	13 Aug – 9 Sept	28
5 adult	6.0713 $\pm$ 0.7416	10 Sept – 24 Sept	15
Gravid	14.6771 $\pm$ 2.0223	25 Sept – 1 Oct	7
		Total	139
Males			
1	0.1143 $\pm$ 0.0243	estimated from hatching	18
2	0.8257 $\pm$ 0.1320	13 June – 9 July	37
3	11.8562 $\pm$ 0.2931	10 July – 25 Aug	47
4	4.4314 $\pm$ 0.4470	26 Aug – 6 Sept	12
5 adult	5.4200 $\pm$ 0.8001	7 Sept – 27 Sept	21
		Total	135

2. Determination of population density

Although Turnbull (1960) and Luczak (1963) have examined the abundance of spiders on vegetation on woodland, there has not so far been any attempt to express numbers in absolute terms. Estimates of energy flow must be related, if possible, to fairly precise estimates of density.

(a) Method of sampling

Details of the bagging technique have been described in Chapter $2(b)$. This modified use of the sweep net employed a canvas bag with a surface area of 628cm^2 at the open end. In the field layer, the number of bags required to sample a metre^2 was 16. In the lower canopy 6 bags were used on each sampling occasion and the number of spiders caught adjusted to a metre^2. Spiders in the upper canopy were sampled by a beating tray and the appropriate adjustment made to convert numbers to a metre^2.

General sampling was carried out once a month to obtain estimates of density of the spider community as a whole. However, collections were made more frequently for M.segmentata.

The area as a whole was a square of about 0.36ha. Three transects running approximately north-south were sited by means of canes. Numbers from dice were used to determine the positions of canes down one side of the square. The

paces taken to reach a particular piece of vegetation along each transect corresponded to the numbers on the dice.

(b) Population density during 1968 and 1969

Tables 58 and 59 show the estimated density per metre^2 for the field layer, lower canopy and upper canopy, with 95% confidence limits for the field layer and study area as a whole.

Spiders appear in all strata in May, but the maxima were seen on the second census. There was a general decline in density with season which in the upper canopy was very apparent. From August onwards, virtually no M.segmentata were seen above the lower canopy.

Although the reduction in numbers was gradual, the trends are clear (Figs. 42 and 43). Significant differences were detectable at various times with the two-sample 't' test, with variances assumed equal. Real differences occurred between 4 June and 10 June (p< 0.01) and between 19 September and 3 October (P< 0.02) in 1968. In 1969, density differed significantly between 6 July and 15 July (p< 0.05) and between total number for August and September (p< 0.01) (2-sample 't' tests).

The gentle decline in density may well have been the result of fairly low mortality rates of instars within the wood. However, the sampling of vegetation with substantial

bramble was difficult. The early instars were small and could easily be missed. Hence the estimates of the young stages may well represent under-estimates. As the spiders develop, their larger size renders them more conspicuous and so allows numbers to be expressed with greater precision.

From May to the beginning of July, spiders move about before settling down. Initially, they disperse over a considerable area. The most favoured sites are those parts of the vegetation having a sunny aspect. From July onwards, with extensive development of the vegetation and generally higher temperatures, spiders appear within the wood in greater numbers. That is, they vacate the edges of the wood and the more exposed areas as they reach instar 3. This feature was noticed during 1968, 1969, and 1970, and appears to be typical. A similar but less pronounced shift in the population was seen in Linyphia triangularis.

Although it is possible that the apparent incursion into the deeper parts of the wood resulted from the emergence of a later cohort, this was discounted because the very young stages of M.segmentata were too few within the wood to account for an upsurge of the later instars. Luczak (1963) has referred to similar shifts in populations of spiders and suggests that inter-specific competition is a cause.

Table 58. <u>Meta segmentata</u>, numbers caught per metre^2 at each

census during 1968, with 95% confidence limits for

the field layer and the population as a whole

Date	field layer	lower canopy	upper canopy	Total
13 May	8 $\pm$ 5.0	3.5	2.0	13.5 $\pm$ 4.2
4 June	17 $\pm$ 11.8	9.7	3.6	29.3 $\pm$ 10.2
10 June	13 $\pm$ 8.3	8.1	1.1	22.2 $\pm$ 8.8
18 July	12 $\pm$ 6.6	3.5	1.6	17.2 $\pm$ 7.1
12 Aug	10 $\pm$ 6.1	6.6	1.2	17.8 $\pm$ 7.0
18 Aug	8 $\pm$ 5.2	5.9	0	13.9 $\pm$ 7.8
1 Sept	11 $\pm$ 6.7	4.4	0.9	16.3 $\pm$ 8.3
7 Sept	9 $\pm$ 7.3	1.5	0	10.5 $\pm$ 8.0
19 Sept	10 $\pm$ 8.7	3.0	0	13.0 $\pm$ 8.9
3 Oct	6 $\pm$ 3.4	3.8	0	9.8 $\pm$ 5.0

Table 59. <u>Meta segmentata</u>, numbers caught per metre^2 at each

census during 1969, with 95% confidence limits for

the field layer and the population as a whole

Date	field layer	lower canopy	upper canopy	Total
29 May	9 $\pm$ 5.4	5.1	1.3	15.4 $\pm$ 9.2
4 June	14 $\pm$ 12.8	7.9	2.9	24.8 $\pm$ 15.0
18 June	12 $\pm$ 7.9	6.0	1.0	19.0 $\pm$ 9.0
6 July	13 $\pm$ 5.2	7.4	3.4	26.8 $\pm$ 9.9
15 July	14 $\pm$ 6.1	6.1	1.6	21.7 $\pm$ 8.4
4 Aug	10 $\pm$ 4.8	4.6	0	14.6 $\pm$ 6.0
27 Aug	9 $\pm$ 6.2	3.6	1.0	13.6 $\pm$ 8.2
13 Sept	7 $\pm$ 8.2	4.8	0	11.8 $\pm$ 8.0
25 Sept	6 $\pm$ 6.0	3.6	0	9.6 $\pm$ 8.0

3. The spatial distribution of <u>M.segmentata</u>

(a) <u>Population movements</u>

Mention has already been made of the shift in the

spider population within the study area. Table 60 presents

the numbers caught near the edge and within the wood.

The trend is clear with more spiders appearing in the vegetation beneath the tree canopy as the season progressed.

The null hypothesis that the distribution of spiders is the same throughout the season has to be rejected, since with a 2 x 2 contingency table, the probability of such an event occurring is less than 0.1 per cent.

Table 60.   Meta segmentata, method used to detect movements

of the population in the study area

1968	May	June	July	August	Sept	Oct
Edge of wood	9	37	9	17	11	3
Within wood	4	14	8	14	29	7
% within wood		32%			62%	

1969						
Edge of wood	10	33	28	11	7	0
Within wood	5	11	20	17	14	2
% within wood		34%			65%	

---

2 x 2 contingency (df = 1) :

	May-July	Aug-Oct	Totals
Edge	a	c	e
Within	b	d	f
Total	g	h	k

After Yate's correction :

1968 $\chi^2 = 13.05$ (p < 0.001)

1969 $\chi^2 = 12.35$ (p < 0.001)

Fig.42. M.segmentata, mean ($\pm$ S.E.) population density per metre^2 on each sampling occasion in 1968.
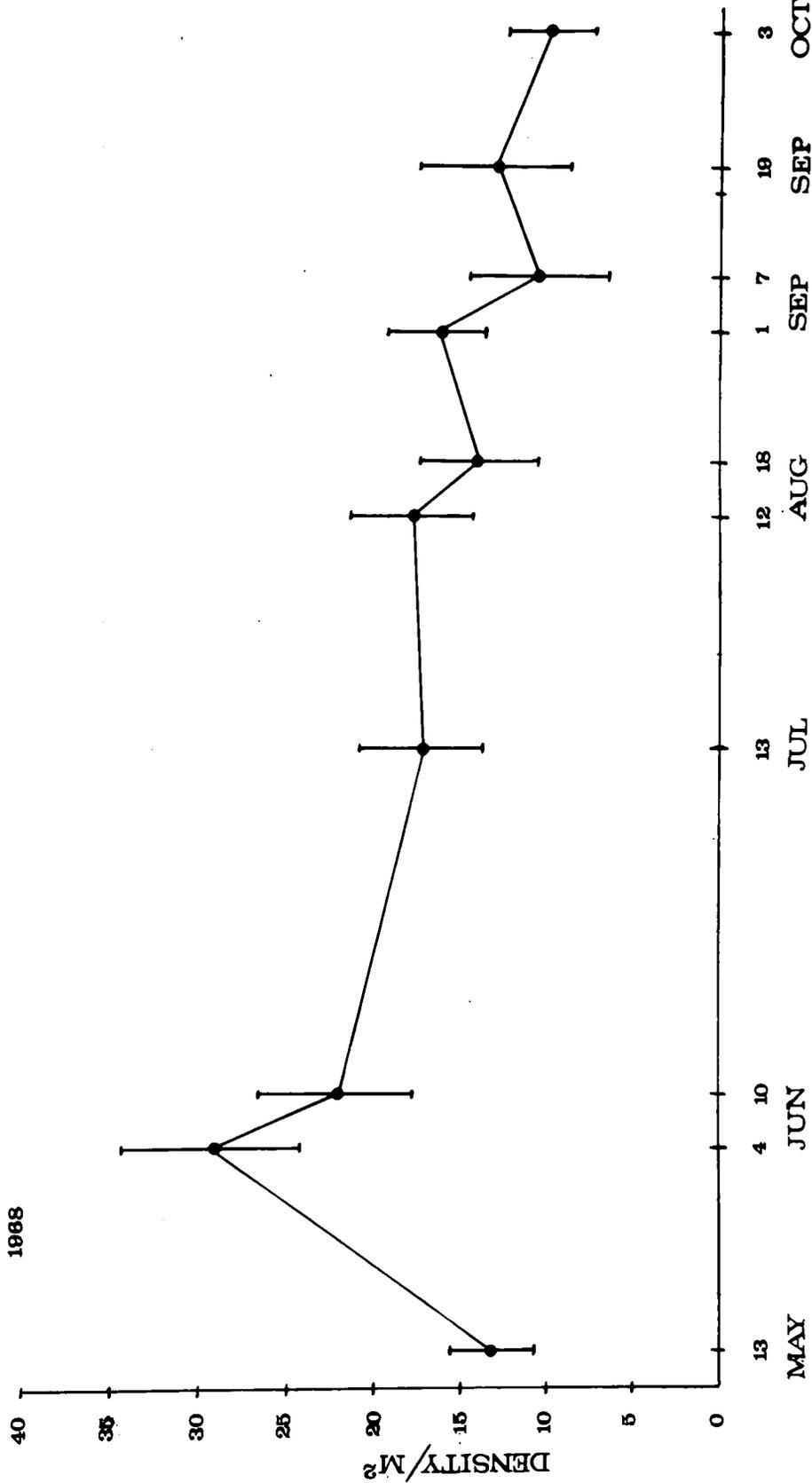
Fig.43. M.segmentata, mean ($\overset{+}{-}$ S.E.) population density
per metre^2 on each sampling occasion in 1969.
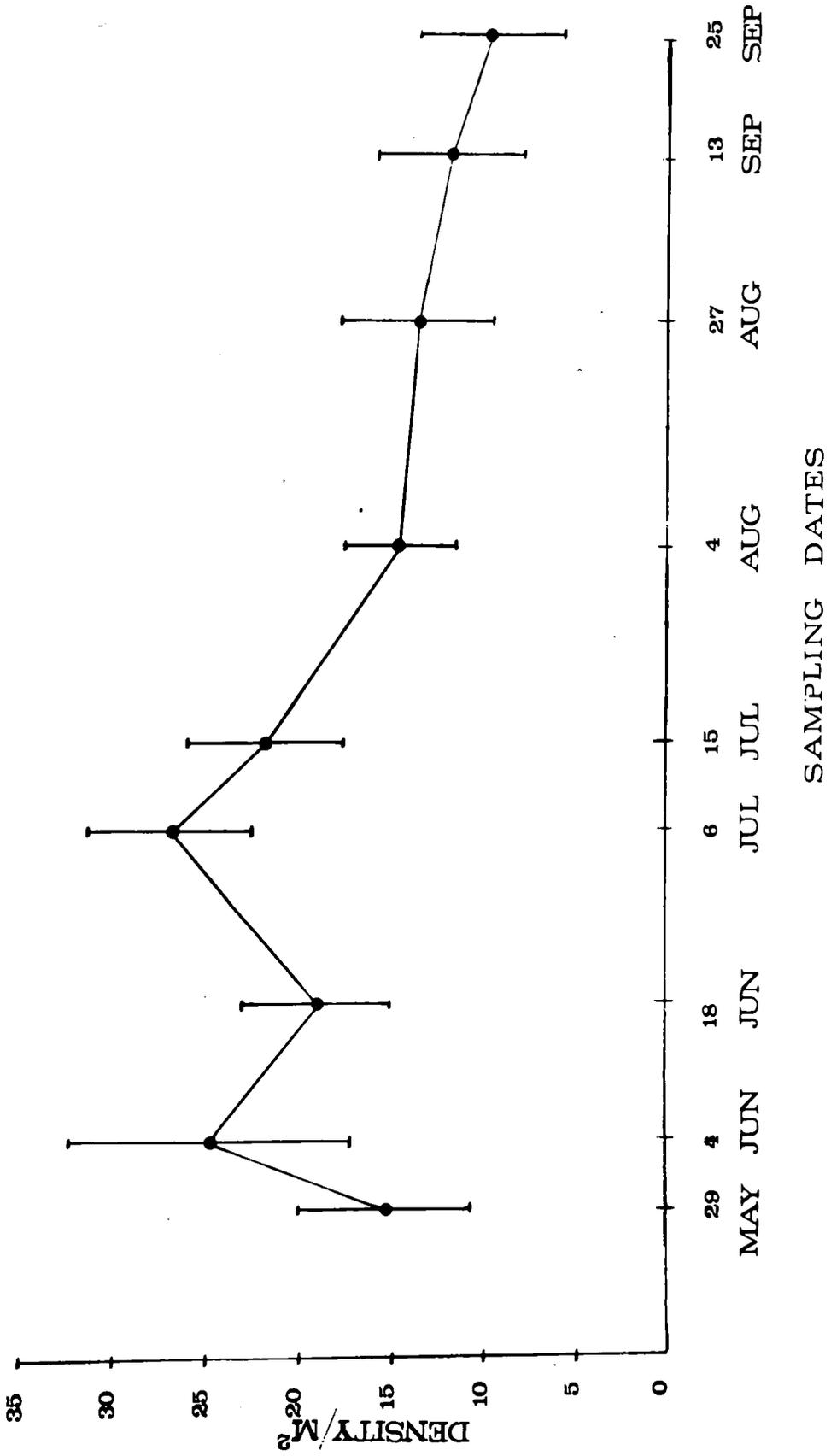
(b) Spatial patterns

Examination of the contents of each sampling bag showed that the spatial pattern within the vegetation also altered. The mean number of spiders per bag altered with time. This aspect was investigated in the field layer only, since numbers in the lower and upper canopy were generally small and any aggregation could be explained simply by the reduced amount of vegetation on which webs could be constructed.

Blackman's coefficient of dispersion was used to measure the spatial distribution of spiders. The mean and variance of numbers of spiders per sample bag are given in Table 61, together with the mean : variance ratio and the significance of its departure from unity.

The population showed a significant degree of aggregation soon after spiders had emerged from cocoons. This can be related to the behaviour of newly hatched spiders and to the fact that the vegetation in May and early June had yet to develop fully. The mean : variance ratio then declined from late June to August so that the population becomes regularly or randomly distributed. This coincided with the maximal development of the field layer and lower canopy.

Aggregation is again detected in September as the spiders become adult and the males actively seek out the females. The result is a localised concentration of male spiders in some areas.

The marked decline in numbers of spiders through mortality led to an under-dispersed adult population in R.lividus. In M.segmentata, on the other hand, the decline in numbers was very gradual and new aggregations of spiders arose, partly at least because male spiders converged on females.

Table 61. Meta segmentata, spatial distribution within the field layer with significance from random distribution

date	mean/bag	variance	mean : var. ratio	value of 't'	significance
1968					
13 May	-	-	-	-	-
4 June	1.060	1.927	1.82	2.24	$p < 0.05$
10 June	0.812	0.963	1.19	0.51	n.s.
18 July	0.750	0.600	0.80	- 0.55	n.s.
12 Aug	0.625	0.517	0.83	- 2.14	n.s.
18 Aug	0.500	0.375	0.75	- 0.68	n.s.
1 Sept	0.687	0.625	0.91	- 0.04	n.s.
7 Sept	0.562	0.729	1.30	3.55	$p < 0.01$
19 Sept	0.625	1.050	1.68	1.86	n.s.
3 Oct	0.375				
1969					
29 May	-	-	-	-	-
4 June	0.875	2.380	2.72	4.72	$p < 0.001$
18 June	0.750	0.867	1.16	- 0.44	n.s.
6 July	0.625	0.383	0.61	- 1.06	n.s.
15 July	0.875	0.517	0.59	- 0.11	n.s.
4 Aug	0.625	0.317	0.51	- 1.35	n.s.
27 Aug	0.562	0.527	0.94	- 0.06	n.s.
13 Sept	0.437	0.929	2.13	3.09	$p < 0.002$
25 Sept	0.400	0.517	1.29	3.53	$p < 0.002$

CHAPTER TEN

POPULATION BIOMASS OF M.SEGMENTATA

The mass of spiders present at a specific instance may be expressed in weight units or in terms of energy content (Petrusewicz and Macfadyen 1970). A record of this standing crop or population biomass provides information on the amount of spider material which is in existence over a period of time. It also indicates the magnitude of any increase or decrease which represent the overall effects of mortality and natality.

Population data, together with live and dry weights and calorific content of spiders, were used to estimate standing crop. Collections of spiders were made at various times when weather conditions were favourable. Wet vegetation made sampling with the sweep net difficult, even though the bagging technique was used. The younger developmental stages adhered to wet plant debris and were difficult to see or handle. Numbers were expressed on the basis of a metre^2.

1. Determination of live and dry weights

(a) Method and results

Spiders which were caught in the sampling bag at each census were weighed live in the laboratory on a Mettler H.16

electrobalance. They were then returned to the study area.

The relation between wet and dry weights was estimated from regression analyses. Spiders which were well outside the study area were weighed before being dried in a vacuum oven at 60'C for 48 hours. The corresponding dry weights were then recorded. The appropriate regression equations were used to estimate dry weights of spiders at each census.

Ito (1964) had found a linear relation between wet and dry weights in the older stages of the wolf spider, Lycosa pseudoannulata. However, it was found that the regression coefficients vary with stage of development in R.lividus. Variation between sexes might also be expected, since adult females in M.segmentata feed regularly, unlike their partners, and bear large numbers of eggs. Accordingly, regressions were calculated separately for the sexes at the adult stage (Figs. 44 and 45). The equations for young stages are recorded in Table 62.

The difference between the estimates of regression coefficients (method described in Bailey 1959) for juveniles in May-June and July-August was significant ($p < 0.05$). The estimates for female and male adult spiders also differed significantly ($p < 0.01$).

Fig.44. M.segmentata, regression of dry weight (y) on weight (x) for adult females.

females

y = -1.15583 + 0.3706 x

WET WT mg

DRY WT mg
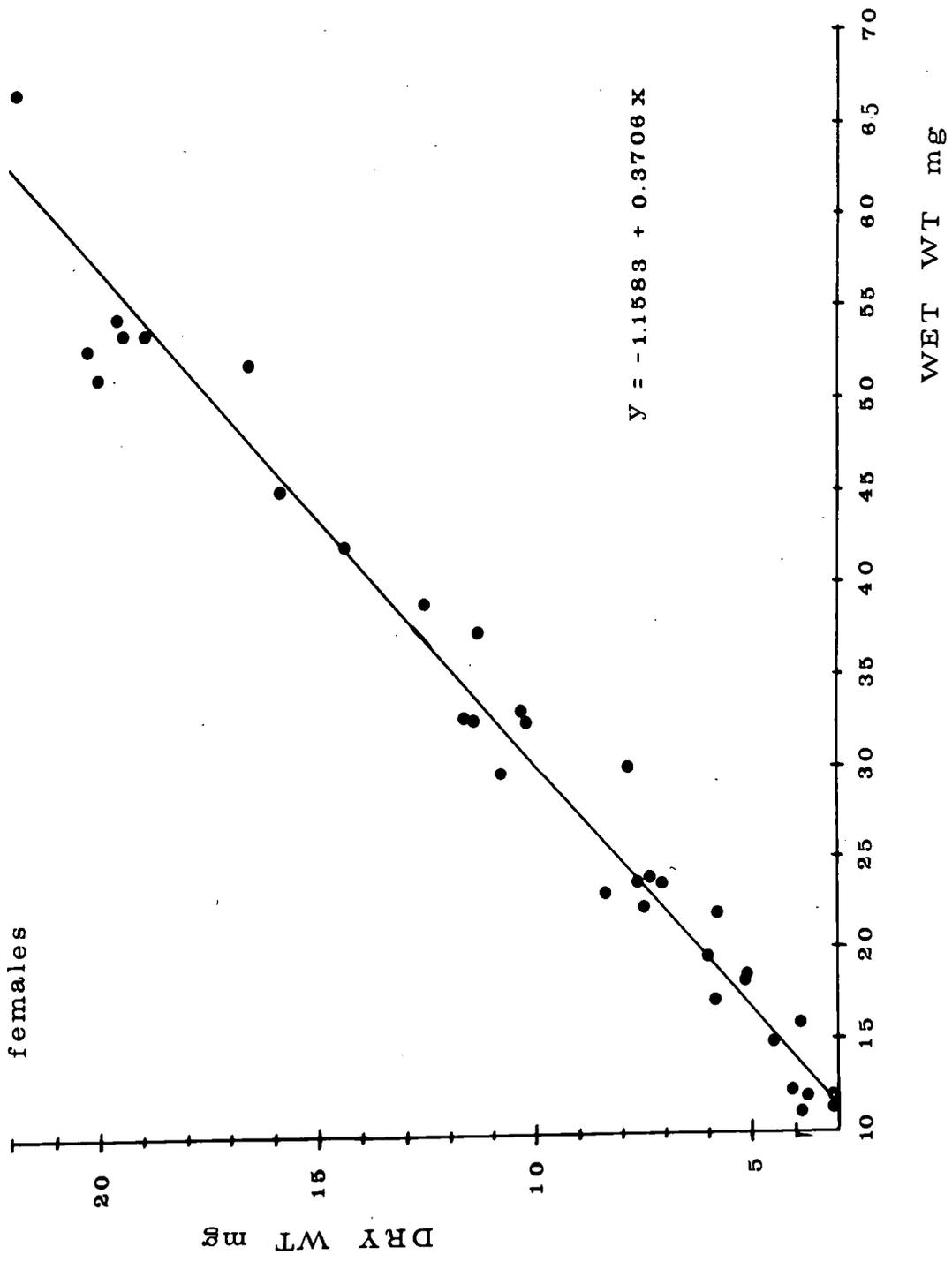
Fig.45. M.segmentata, regression of dry weights(y)

on wet weights (x) in adult males.

males

y = 0.9474 + 0.2531x

DRY WEIGHT mg

WET WEIGHT mg
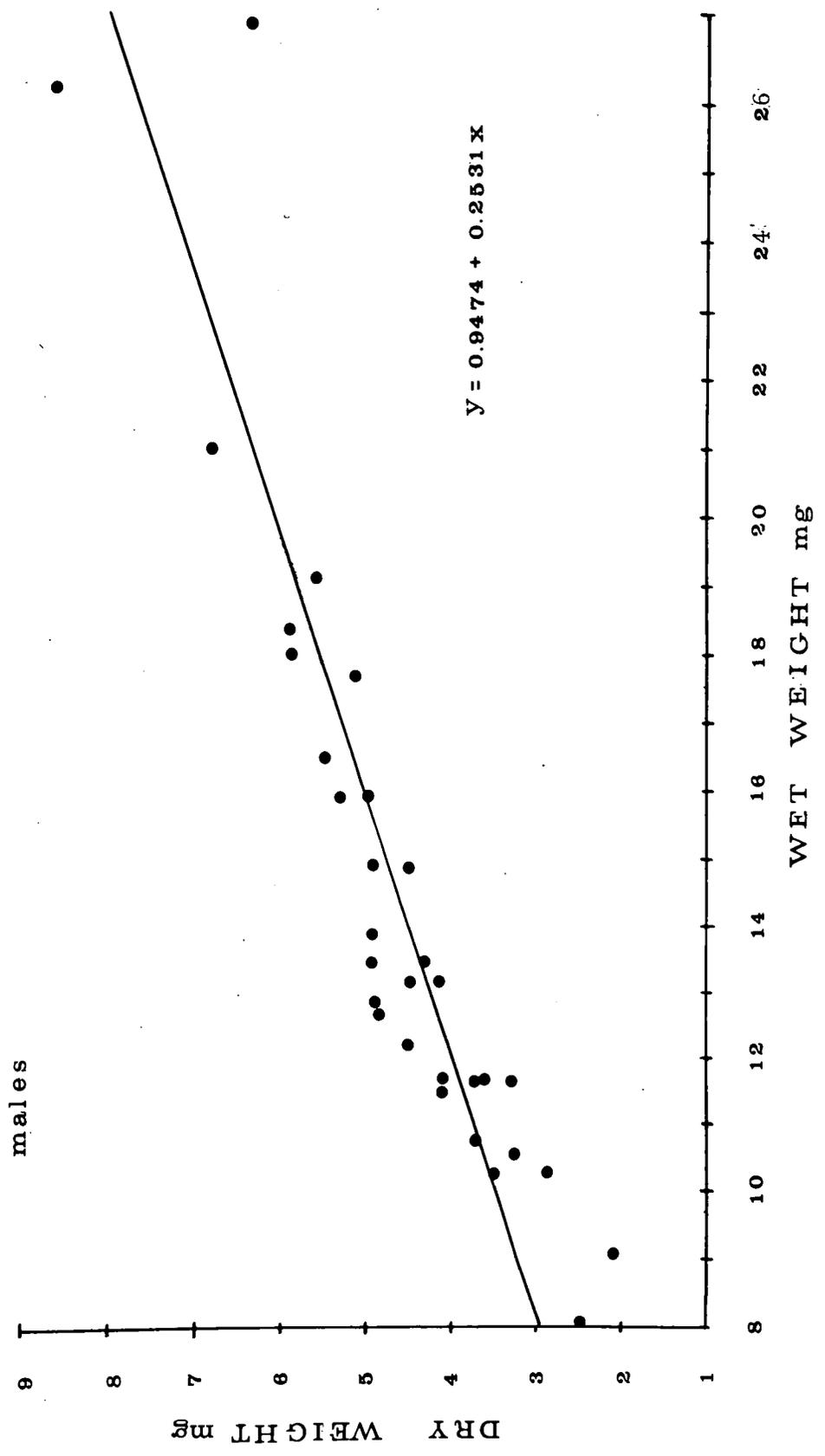
Table 62.   Meta segmentata, relation between wet and dry

bodily weights (Y = dry weight)

season	N	regression equation	stand.dev.	r
May–June	21	$Y = 0.0188 + 0.2293X$	0.0356	.91
July–Aug	28	$Y = 0.3499 + 0.2670X$	0.3823	.97
Aug–Sept	18	$Y = 0.5566 + 0.2725$	0.4187	.95
Sub–adults				
Sept–Oct				
females	33	$Y = 1.1583 + 0.3706X$	1.0472	.98
males	31	$Y = 0.9474 + 0.2531X$	0.5012	.92

(b) Estimating standing crop

The mean live weight of spiders at each census was
multiplied by the mean density per metre^2.   The corresponding
dry weight per metre^2 could then be obtained by applying the
appropriate regression equation.

Weight units were converted to their calorific
equivalents by first interpolating the mean dry weights of
instars on growth curves (e.g. Fig.   ) and marking off
their approximate duration.   The calorific content of a
particular instar (Chapter 4) was multiplied by the dry weight
of spider material prevailing at the time of the census within
the duration of the instar.

The standing crop at each census is given in Tables 63
and 64.   From 2.7mg dry wt/metre^2 in May 1968, the population
biomass for female spiders showed a 30-fold increase four
months later when the value was 93mg/metre^2.   In the males,

the maximum was 28mg/metre^2 which amounted to a 9-fold increase. The standing crop of male spiders then declines while that of females continues to increase.

Development of instars 1, 2, and 3, during 1969 was more rapid than in 1968 so that larger increases in biomass were recorded for the first part of the life cycle. Biomass (dry weight) at the final census for female spiders was 11 times that at the first census. The corresponding difference in male spiders was about 3 times. Hence, the times at which collections are made may affect to a large extent the magnitude of changes in standing crop.

The maximum value for the entire population was 104mg/metre^2 in October 1968, which was equivalent to an energy content of 645 calories/metre^2 (Table 65). These values are very close to those for September 1969, which came to 102mg and 633 calories/metre^2 (Table 66). The difference between the two years may not be significant since times of census influence estimates of biomass.

Table 63.   Meta segmentata, standing crop per metre^2 during 1968

Census date	mean density/m^2	mean wet wt mg	standing crop live wt	dry wt	cals/m^2
Juveniles					
13 May	13.5	0.9673	13.04	2.74	14.24
4 June	29.3	2.2460	65.85	14.55	75.72
10 June	22.2	1.5443	34.25	7.44	38.71
18 July	17.2	4.2476	73.06	13.98	76.51
Females					
12 Aug	12.6	5.5176	69.74	23.04	126.12
18 Aug	10.9	8.0528	88.02	27.32	149.55
1 Sept	11.5	16.6793	192.14	58.77	326.77
7 Sept	7.0	19.9560	139.69	43.66	242.76
19 Sept	8.0	26.4822	211.86	69.25	380.52
3 Oct	7.7	35.9101	275.79	93.31	587.30
Males					
12 Aug	5.2	8.2562	43.01	14.38	78.73
18 Aug	3.0	15.3082	45.92	13.31	72.85
1 Sept	4.8	15.5027	74.41	22.95	129.20
7 Sept	3.5	22.7460	79.84	23.71	133.48
19 Sept	5.0	18.7598	93.80	28.48	152.61
3 Oct	2.1	16.8178	35.15	10.88	58.29

Table 64. Meta segmentata, standing crop per metre^2 during 1969

census date	mean density/m^2	mean wet wt mg	standing crop/m^2 live wt mg	dry wt mg	cals/m^2
Juveniles					
29 May	15.4	2.4278	37.41	8.29	43.14
4 June	24.8	4.1382	102.75	23.09	125.52
18 June	19.0	5.6450	107.25	24.24	131.72
Females					
6 July	19.0	6.6825	126.97	28.61	155.52
15 July	13.6	9.3320	126.91	30.74	169.45
4 Aug	8.3	10.2595	85.36	25.70	141.67
27 Aug	9.5	15.5541	147.76	45.55	253.28
13 Sept	6.3	23.6762	149.63	48.13	264.49
25 Sept	6.0	42.7291	256.37	88.06	554.27
Males					
6 July	7.8	9.0797	70.82	17.07	92.78
15 July	8.1	9.5460	77.23	18.78	103.51
4 Aug	6.3	10.6951	67.59	20.26	111.67
27 Aug	4.1	18.0675	74.26	22.52	126.80
13 Sept	5.5	16.2101	89.48	27.88	149.39
25 Sept	3.6	12.5468	44.67	14.68	78.66

Table 65.   _Meta segmentata_, total population standing crop

per metre^2 for 1968

Census date	mean density/m^2	standing crop /m^2 live wt mg	standing crop /m^2 dry wt mg	biocontent cals
13 May	13.5	13.04	2.74	14.2
4 June	29.3	65.85	14.55	75.7
10 June	22.2	34.25	7.44	38.7
18 July	17.2	73.06	13.98	76.5
12 Aug	17.8	112.76	37.43	204.8
18 Aug	13.9	133.94	40.64	202.4
1 Sept	16.3	266.56	81.72	456.0
7 Sept	10.5	219.53	67.37	376.2
19 Sept	13.0	305.66	97.73	533.1
3 Oct	9.8	310.94	104.19	645.6

Table 66.   _Meta segmentata_, total population standing crop

per metre^2 for 1969

29 May	15.4	37.41	8.29	43.1
4 June	24.8	102.75	23.09	125.5
18 June	19.0	107.26	24.24	131.7
6 July	26.8	197.79	45.68	248.3
15 July	21.7	204.14	49.52	272.9
4 Aug	14.6	152.95	45.96	253.3
27 Aug	13.6	222.02	68.08	380.1
13 Sept	11.8	461.13	76.01	413.9
25 Sept	9.6	301.04	102.74	632.9

(c)   Average population biomass ($\bar{B}$)

The average biomass ($\bar{B}$) _ex definitione_ (Petrusewicz and

Macfadyen 1970) :

$$\bar{B} = \frac{1}{K} \sum_{i=1}^{i=K} B_i$$

As the sampling times were irregularly spaced, weighted averages were calculated by the non-graphical method of Petrusewicz and Macfadyen (p.43. loc.cit). Hence, from the data in Tables 65 and 66 ,

$$\bar{B} = \frac{\overline{BT}}{T} = \frac{29069.4}{143} = 203.3 \text{ cals/m}^2, 1968$$

and,

$$\bar{B} = \frac{\overline{BT}}{T} = \frac{33731.8}{120} = 281.1 \text{ cals/m}^2, 1969,$$

where $\overline{BT}$ represents biomass (calorie) days and T is the time in days of the entire sampling period.

Despite the slightly higher density in 1968, the average population biomass for the year is about 72% of that for 1969.

2. Egg biomass

Kajak (1967) estimated fecundity of web spiders by first counting cocoons which had been constructed in the ground zone, and then estimating the mean number of eggs per cocoon. This approach would appear to be adequate when cocoons can readily be identified to species, are relatively large or conspicuous, occur in accessible sites, and are generally distributed within the litter layer. In the case of Meta segmentata , cocoons were highly aggregated, occurring for the most part between the bark and wood of fallen and decaying logs. Furthermore, it appeared that some spiders may

wander some distance in order to reach suitable sites. For
instance, egg masses were to be found in places where previously
no adult spiders had been seen.

With these observations in mind it was considered
appropriate to estimate the numbers of eggs laid from the density
of full term females in the population on the last date of
sampling. Fecundity in some insects has been shown to be
proportional to body weight (e.g. Richards and Waloff, cited in
Southwood 1966). According to Turnbull (1962), the weight
of eggs in the spider, Linyphia triangularis, was related to
body weight. Numbers of eggs per cocoon, however, were highly
variable and apparently not related to body weight.

(a) Method

So that the risk of excessive sampling was reduced
within the study area, female specimens of Meta segmentata
were caught elsewhere (Satley, Co. Durham during September 1967)
as they were about to descend to the litter layer to lay their
eggs. They were kept in 2lb jam jars, the base of which
contained a layer of moist plaster of paris, while a few twigs
enabled the captive spiders to build webs. Drosophila were
provided as food. Specimens were weighed as soon as they
had laid their eggs, and the combined body and cocoon weights
were taken to represent the weight of the full term females.

Cocoons were weighed after debris had been picked off the webs and excess moisture allowed to evaporate in a warm room for 3 hours. A regression was calculated for wet cocoon weight on body weight. A number of cocoons were then divested of their contents and dry weights and numbers of eggs obtained. A further regression was calculated for dry weight of eggs on wet weight of cocoons. Eggs were dried in a vacuum oven at 60'C for 48 hours.

Although numbers of eggs differed quite considerably from one cocoon to another, dry weights of individual eggs showed little variation. The mean number of eggs per cocoon was estimated by dividing the mean dry weight of eggs per cocoon by the mean weight of individual eggs.

The contribution of webs to weight and biocontent of cocoons was found by drying the webs over anhydrous $CaCl_2$ before weighing and burning them in the miniature bomb calorimeter. Drying webs in the vacuum oven led to inconsistent dry weight, presumably because of electrostatic charges which attracted dust particles.

Population fecundity and standing crop per $metre^2$ in terms of cocoon material could be calculated from information on density of female spiders, i.e. density multiplied by mean weights of cocoons, eggs and webs. Calculations with entire

cocoons and their components provided a useful check on the reliability of data.

Dry egg weight per metre^2, divided by mean dry weight of individual eggs, provided an estimate of numbers of eggs per metre^2.

All captive individuals constructed one cocoon and after a few days invariably died. Although this appeared to be the case in the field, the few spent females which were found being too weak to move from their eggs, it was not known with absolute certainty whether they could return to the field layer if favourable conditions still prevailed.

Results

Weight of cocoon was related to body weight (Fig.46) and dry egg weight was related to weight of cocoon (Fig.47). The regression equations are as follows :

wet weight of cocoon on wet body weight

$Y = 0.5980X - 2.3461$

dry weight of eggs on wet cocoon weight

$Y = 0.2571X - 1.0056$

The mean dry weight of eggs was estimated to be 0.1257 $\pm$ S.D. 0.0018mg, from which it was possible to calculate the number of eggs. Webs used in the construction of cocoons showed little variation despite the wide differences in numbers of eggs, having a mean value of 1.521 $\pm$ S.D. 0.1004mg per cocoon.

Fig.46. <u>M.segmentata</u>, regression of wet cocoon

weight on wet body weight (Y = 0.5980X --2.3461,

where Y represents wet cocoon weight).

Fig.47. <u>M.segmentata</u>, regression of dry egg weight

on wet cocoon weight (Y = 0.2571X - 1.0056,

where Y represents wet cocoon weight).
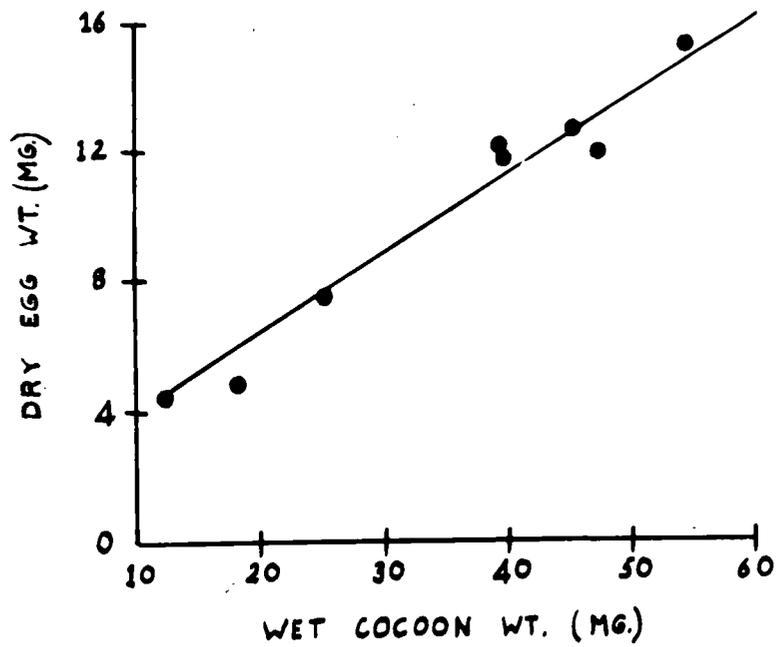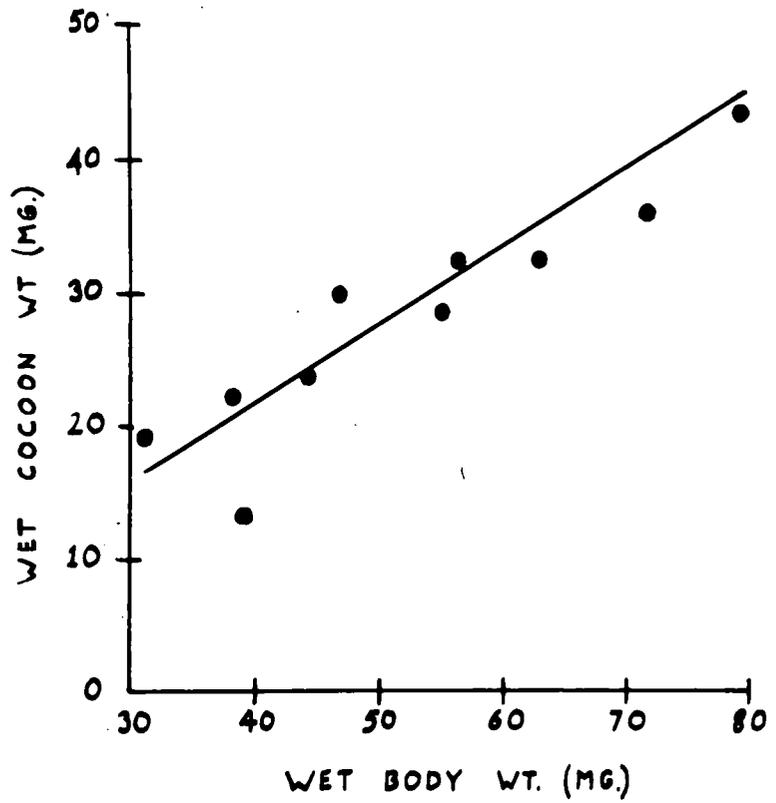
The mean dry weight of gravid spiders was highest in
1967, and, as expected, mean cocoon dry weight and numbers of
eggs exceeded those in the following years (Table 67).
The difference in mean fecundity was small in 1967 and 1969,
with 60 and 55 eggs per cocoon, respectively, while the
mean for 1968 was about 47.

Over the three years, 1967-69, dry weights of eggs
varied between 42 and 47mg per metre^2, while total numbers
ranged from 333 to 378 per metre^2. A slightly higher density
of female spiders in 1968 offset the low mean weight of cocoons,
so that dry weights and numbers of eggs were slightly higher
than in 1969 (Table.68).

Calorific equivalents of cocoons, webs, and eggs
had been determined (Chapter 4(b)) for M.segmentata. The
validity of these values was enhanced by being able to compare
energy content of eggs and webs burnt separately, with values
obtained from the combustion of whole cocoons (Table 69).

Total biocontent of cocoons which constituted the
standing crop from October when they were constructed, to
the April following when the young spiders emerged, amounted
to 357cals per metre^2 in 1967, 342cals in 1968, and about
310cals in 1969 (Table 69).

Table 67. <u>Meta segmentata</u>, data on mean weights (mg) of

gravid females, cocoons, and eggs.

body wt		cocoon wt		eggs/cocoon
dry	wet	wet	dry wt	numbers
1967				
16.02	46.35	25.37	7.528	59.9
1968				
12.15	35.90	19.12	5.922	47.1
1969				
14.68	42.72	23.20	6.970	55.4

Table 68. <u>Meta segmentata</u>, total weights (mg) of cocoon

material and numbers of eggs, per metre^2

density	body dry wt	cocoon wet wt	webs dry wt	dry wt	eggs numbers
1967					
6.32	101.3	160.3	9.68	47.58	378
1968					
7.68	93.3	146.9	11.76	45.48	362
1969					
6.00	88.1	139.2	9.19	41.82	333

Table 69. <u>Meta segmentata</u>, biocontent of cocoon material in calories per metre^2

	Eggs	webs	Total	whole cocoons	mean
1967	303.4	47.3	350.7	354	357.2
1968	290.0	57.5	347.5	325	342.1
1969	266.7	44.9	311.6	308	309.8

Note: calculated from data in Table 14. where

biocontent of eggs = 6.377Kcals/g dry weight

,,   ,, webs = 4.892   ,,   ,,   ,,

,,   ,, whole
          cocoons= 5.981   ,,   ,,   ,,

CHAPTER ELEVEN

ENERGY FLOW IN META SEGMENTATA

(1) Production through growth

An appropriate definition of growth is the formation of body tissue which may be represented by increase in dry bodily weight.   The growth rate is this increase per unit of time, or symbolically,

$$\frac{\Delta W}{\Delta t}$$

The population growth rate is obtained by multiplying the number of individuals or standing crop at successive points in time by the mean or individual growth rate.   Engelmann (1966) and Petrusewicz & Macfadyen (1970) refer to this quantity as net production.

However, it is clear that the food which is absorbed through the gut wall and built into body tissue can be subdivided in terms of its ultimate fate.   In fact, production has more than one component :   growth of body tissue (Pg), growth of reproductive tissue (Pr), and discarded material such as moulted exoskeletons (ML), excreta (U), and webs in the case of spiders.

With reference to Meta segmentata, production (Pg) includes growth of reproductive tissue.

(a) Measurement of growth

Bodily growth or increase in weight per unit time of the population has been calculated from the mean increase in dry weight of size classes of field populations (e.g. Saito 1965; Smalley 1960; and for spiders, Kajak 1967, and Breymeyer 1967). Successive measurements have also been made on individuals enclosed under near natural conditions (Watson 1966) or actually in the study area (Whignarajah 1968).

At Wynyard, it was considered most convenient to sample the field population as frequently as possible in the time that was available. The date of hatching was estimated from field and laboratory observations. The wet weights of at least 15 specimens were recorded on each occasion and the appropriate regression equation was used to obtain corresponding dry weights. Most specimens were then returned to the sample areas.

Although the eggs of M.segmentata hatched over quite a long period, from the end of April to the end of June, the main cohort was readily recognised by its even age and weight distribution, and included over 80% of the population. The sexes of M.segmentata could be distinguished from instar 3 onwards. The mean weights of this instar had been found by weighing specimens which were allocated to this stage on the basis of a 'multivariate'

analysis (Chapter 9 , sec.(b)).   Those individuals which
were caught during the population study and which could
also be distinguished by sex, had in the first instance
mean dry weights very close to those of spiders originally
assigned to instar 3.   Apart from enhancing the credibility
of the method used to denote instars, a useful point of
reference was provided.   Hence, for the production study,
M.segmentata was conveniently divided into three main size
groups : juveniles, which included the first and second
instars, females, and males.

(b)   Individual growth rates and population production (Pg)

On theoretical grounds (Simpson, Roe and
Lewontin, 1960), the relationship between growth and time
can, in some cases, be expressed by the function for
additive growth :

$$Y_t = Y_0 + Kt$$

where Y_0 = initial dry weight, t = the time interval,
Y_t = weight at end of time interval, and K = additive
growth rate.

Alternately, the geometric or instantaneous
growth rate may be described by

$$\log_e Y_t = \log_e Y_0 + K_g t$$

If growth is rectilinear, the values of K or K_g
will be constant with time, accepting random fluctuations

about the mean through sampling errors.

The values of K and K_g in Tables 70 and 71 are seen to vary substantially so that neither the additive nor the instantaneous growth rate equations adequately describe the observations.

In practice, it has been considered appropriate (Petruwicz and Macfadyen 1979) to express the increase in biomass between two sampling occasions by v, the average daily weight gain :

$$v = \frac{w_2 - w_1}{t_2 - t_1} = \frac{\Delta w}{\Delta t}$$

Clearly, the closer together the observations the more accurate will be the average daily weight gain (ADWG).

The daily production of the population is found by multiplying the ADWG by the mean density of the size class. When this in turn is multiplied by the number of days (T), the production (Pg) of the size class is obtained :

$$Pg = v.\bar{N}. \ T$$

Production for the entire life-history is then given by

$$Pg = \sum_{s=1}^{s=m} v_s. \ \bar{N}_s. \ T$$

where s represents the age class or stage. As calorific equivalents for M.segmentata were known (Chapter 4(b)) increase in dry weight could be converted to calories.

Table 70. <u>Meta segmentata</u>, mean or individual growth rates
for 1969 (Y = mean dry body weight; t = time of
census; k = additive growth rate)

		Females			Males		
			increment			increment	
date	$t_2 - t_1$	Y	mg	K	Y	mg	K
8/5	0	0.1143			0.1143		
28/5	20	0.5379	0.4236	0.0211	0.5379	0.4236	0.0211
4/6	7	0.9301	0.3922	0.0560	0.9301	0.3922	0.0560
18/6	14	1.2756	0.3455	0.0246	1.2756	0.3455	0.0247
6/7	18	1.5060	0.2304	0.0128	2.1885	0.9029	0.0502
15/7	9	2.2604	0.7544	0.0838	2.3212	0.1327	0.0147
4/8	20	3.0892	0.8288	0.0414	3.2055	0.8843	0.0441
27/8	23	4.7951	1.7059	0.0742	5.4840	2.2795	0.0991
13/9	17	7.6161	2.8210	0.1660	5.0502	-0.4348	-0.0256
24/9	12	14.6771	7.0610	0.6419	4.1230	-0.9272	-0.0843

Table 71. <u>Meta segmentata</u>, instantaneous growth rates for
1969 (Symbols as in Table 70. Kg = instantaneous
growth rate)

		Females		Males	
date	$t_1 - t_0$	$\log_e Y$	Kg	$\log_e Y$	Kg
8/5	0	$\overline{3}.8310$			
28/5	20	$\overline{1}.3799$	0.0764	$\overline{1}.3799$	0.0764
4/6	7	$\overline{1}.9275$	0.0796	$\overline{1}.9275$	0.0796
18/6	14	0.2438	0.0226	0.2438	0.0226
6/7	18	0.4113	0.0931	0.7830	0.0299
15/7	9	0.8154	0.0449	0.8420	0.0066
4/8	20	1.1270	0.0156	1.1647	0.0661
27/8	23	1.5676	0.0191	1.7020	0.0234
13/9	17	2.0303	0.0272	1.6194	-0.0048
24/9	12	2.6865	0.0597	1.4166	-0.0184

(c) Results and discussion

Production arising through growth and formation
of reproductive tissue is given in Tables 72 and 73.
After emergence from the egg the growth rate was slow
to begin with until about the 3rd instar. During 1968
the mean daily production of juveniles (Table 74) was
only 0.0345mg dry wt, compared with 0.7283mg dry wt in
1969. The low growth rates for juveniles in 1968 may
be related to the high rainfall and low temperatures in
May. Kajak (1967) described the drastic effects of a
cold and wet season on Araneus quadratus when production
was reduced to a tenth of that in a previous year.
However, the influence of weather was less clear at Wynyard.
Although temperatures were higher in 1969, mean daily
production for female and male spiders was somewhat higher
in 1968. The persistence of the main cohort in October
might be explained by the cool and wet conditions which
prevailed in September.

Meta segmentata appeared to moult 4 times
after emergence from the egg during 1968 and 1969.
This observation supports the findings of Turnbull (1962)
with Linyphia triangularis that restricted food supply or
unfavourable conditions, as in 1968, prolong rather than
increase the number of instars.

The mean daily production of female spiders amounted to 1.4 and 1.2mg per metre^2. In 1968 production was 3 times that of male spiders, while production in 1969 was nearly 6 times. Male spiders lost weight towards the end of the season and the mean daily estimates for this sex are based on the time when body weight was increasing. Breymeyer (1967) did not distinguish between the sexes in Trochosa ruricola, while Kajak (1967) quotes a mean value for adults.

Total production in mg dry weight were virtually identical for the 2 years. Clearly, the method of sampling was not refined enough to detect a difference which, possibly, was small. The conversion of the data to calorific values was made possible by determining the likely biocontent of spider material (Tables 75 and 76). As might be expected from a comparison of the dry weights for the two years, production in calories was similar. The most noticeable difference was the larger contribution in 1969 of the juvenile stages. The more numerous males in 1969 were balanced to some extent by the rather larger males in 1968. In like manner, the more numerous female spiders in 1968 were balanced by the larger specimens in 1969. Unfortunately, it cannot be known to what extent these differences represent sampling errors or are determined by a somewhat variable sampling programme, or whether they reflect the true situation in the field.

The mean daily production of M.segmentata, sexes combined, came to about 0.33mg dry weight. This compares with 2.74mg for Araneus quadratus, 0.09 for A.cornutus, and 0.06 for Singa hamata (Kajak 1967). It is interesting to note that the three species cited by Kajak are quoted in order of size and production. M.segmentata would qualify for second place.

Annual production (Pg) in M.segmentata was about 136mg during 1968 and 1969, and compares with 140mg in Trochosa ruricola (Breymeyer 1967), and with 360mg in Araneus quadratus(Kajak 1967). Calorific equivalents have so far not been stated for any species of spiders. Kajak assumed a value of 5.82Kcal/g of body tissue. In M.segmentata, biocontent increases with stage of development, rising from 5.205Kcal/g ash-free at instar 1 to 6.294Kcal/g in the adult female. However, the assumed mean calorific equivalent would have been a reasonable estimate since biocontent calculated on this basis comes to within a few calories of that obtained from calorific yield for each stage.

When female spiders have laid their cocoons, they show a marked diminution in weight. The mean dry weight of these spent females was 5.0mg. Thus the increase in weight during so-called growth is due largely to the formation of reproductive tissue which constitutes as much as 60% by weight of 'full term' females.

Females make the largest contribution to total production in terms of dry weight and calories. Gravid female spiders exceed the weight of adult males and, with their eggs, have a higher calorific value, and are also more numerous in the field.

Table 72. <u>Meta segmentata</u>, growth and rate of production (Pg) per m^2 during 1968

days $t_1 - t_p$	mean dry wt mg	$\frac{\Delta w}{\Delta t}$	mean density	production mg dry wt daily	$t_1 - t_o$
Juveniles					
0	0.1051				
14	0.2030	0.0069	13.48	0.0930	1.3020
22	0.4962	0.0133	29.32	0.3899	8.5778
6	0.3353	−0.0268	22.18	−0.5944	−3.5664
38	0.8128	0.0125	17.20	0.2150	8.1700
Females					
25	1.8231	0.0404	12.64	0.5106	12.7650
6	2.5000	0.1128	10.93	1.2329	7.3974
14	5.1017	0.1858	11.52	2.1404	29.9656
6	6.2374	0.1892	7.00	1.3244	7.9464
12	8.6560	0.2015	8.00	1.6120	19.3440
14	12.1500	0.2495	7.68	1.9161	26.8254
Males					
25	2.7610	0.0779	5.21	0.4058	10.1450
6	4.4372	0.2793	3.00	0.8379	5.0274
14	4.7811	0.2245	4.80	0.1176	1.6464
6	6.7549	0.3289	3.51	1.1544	6.9264
12	5.6955	−0.0882	5.00	−0.4410	−5.2920
14	5.2040	−0.0351	2.09	−0.0733	−1.0262
				Total	136.1542

Table 73. Meta segmentata, growth and rate of production (Pg)

per m^2 during 1969

days $t_1 - t_0$	mean dry wt mg	$\frac{\Delta w}{\Delta t}$	mean density	production mg dry wt daily	$t_1 - t_0$
Juveniles					
0	0.1143				
20	0.5379	0.0211	15.41	0.3251	6.5020
7	0.9301	0.0560	24.83	1.3904	9.7328
14	1.2756	0.0247	19.00	0.4693	6.5702
Females					
18	1.5060	0.0128	19.00	0.2432	4.3776
9	2.2604	0.0838	13.60	1.1397	10.2573
20	3.0892	0.0414	8.32	0.3444	6.8880
23	4.7951	0.0742	9.50	0.7079	16.2127
17	7.6161	0.1660	6.32	1.0491	17.8347
12	14.6771	0.5884	6.00	3.5304	42.3648
Males					
18	2.1885	0.0502	7.80	0.3916	7.0488
9	2.3212	0.0147	8.09	0.1189	1.0701
20	3.2055	0.0441	6.32	0.2787	5.5740
23	5.4800	0.0991	4.11	0.4073	9.3679
17	5.0502	−0.0256	5.52	−0.1413	−2.4021
12	4.1230	−0.0843	3.56	−0.2967	−3.5604

Total   137.8344

Table 74.   <u>Meta segmentata</u>, contribution of developmental

stages of survivors to production during

1968 and 1969

PRODUCTION (Pg) mg dry wt per m^2

	1968		1969	
	mean daily	Total	mean daily	total
Juveniles	0.0345	14.4834	0.7283	22.8050
females	1.4561	104.2438	1.1686	97.9311
males	0.5003	17.4270	0.1895	17.0983
	Total	136.1542	Total	137.8344

PRODUCTION (Pg) in calories per m^2

	1968		1969	
	mean daily	Total	mean daily	total
Juveniles	0.1960	77.2630	3.9309	122.4480
females	8.4990	608.6806	8.3276	587.4381
males	3.5041	98.0374	1.6607	96.2575
	Total	783.9810	Total	806.1436

Table 75. <u>Meta segmentata</u>, production (Pg) in calories/m^2

1968

$t_1 - t_0$	Kcals/g dry wt ash free	production (cals) daily	$t_1 - t_0$
Juveniles			
0			
14	5.205	0.4840	6.7760
22	5.205	2.0294	44.6468
6	5.205	-3.0938	-18.5628
38	5.435	1.1685	44.4030
Females			
25	5.512	2.8144	70.3600
6	5.512	6.7957	37.4578
14	5.560	11.9006	166.6084
6	5.495	7.2775	43.6650
12	6.294	10.1459	121.7508
14	6.294	12.0599	168.8386
Males			
25	5.512	2.2368	55.9200
6	5.512	4.6185	27.7110
14	5.630	0.6621	9.2694
6	5.630	6.4993	38.9958
12	5.359	-2.3633	-28.3596
14	5.359	-0.3928	-5.4992
		Total	783.9810

Table 76. <u>Meta segmentata</u>, production (Pg) in calories/m^2,

1969

$t_2 - t_0$	Kcal/g dry wt ash free	production (cals)	
		daily	$t_2 - t_0$
Juveniles			
0			
20	5.205	1.6921	33.8420
7	5.435	7.5500	52.8976
14	5.435	2.5506	35.7084
Females			
18	5.512	1.3405	24.1290
9	5.560	6.3367	57.0303
20	5.560	1.9148	38.2960
23	5.495	3.8734	89.0882
17	6.294	6.6030	112.2510
12	6.294	22.2203	266.6436
Males			
18	5.512	2.1584	38.8512
9	5.512	0.6553	5.8977
20	5.512	1.5361	30.7220
23	5.630	2.2930	52.7390
17	5.359	-0.7572	-12.8724
12	5.359	-1.5900	-19.0800
		Total	806.1436

(2) <u>Mortality fraction</u> (E)

   (a) <u>Egg mortality</u>

          The number of eggs laid by each female spider was
estimated from the relation between body weight and dry weight
of eggs (Chapter 10(ⅰ)).   Since the individual dry weight
was known, mean numbers per female could be calculated.
The number of females per metre^2 on the last sampling date,
multiplied by the mean number of eggs per female, provided
the estimated number of eggs laid per metre^2.

          It was necessary to assess the proportion of cocoons
which actually produced young.   Since they are left unguarded
by the parent female, they may be eaten by other animals.
Even under field condition eggs did not always hatch, while a
fungus (Moniliales) sometimes attacked them.

          During 1967 and 1968, 20 cocoons were found in, or
adjacent to, the study area and the places marked for future
reference.   In the spring of 1968 spiders emerged from 13
of the cocoons and in the same period in 1968, 15 produced
spiders.   The actual number of emergent spiders in the study
area could then be calculated from the number of eggs laid,
multiplied by the proportion which was likely to hatch.

          Since the number of spiders at instar 1 in the area
was known from the sampling data, the number of individuals
dying or emigrating could be estimated (Table 77).   However,

as it was not known how long the eliminated individuals remained in the study area before they died, their contribution to production could not be calculated precisely. It is likely that a number of cocoons were constructed outside the study area, and of those spiders which emerged from the site, the majority must have moved away almost immediately. At no time were numbers of instar 1 seen or caught which were comparable with the large estimates of numbers hatching.

An appreciable fraction of eggs or emergent spiders failed to colonise the study site because eggs aborted or the young dispersed elsewhere. An approximate estimate of biomass 'lost' was obtained by assuming that the individual weight of the fraction was the same as that of a freshly laid egg, i.e. 0.1257mg dry wt.

The dry weights and calorific equivalents (from Chapter 4) of this fraction which was not realised, is given in Table 78. In 1968, 303 calories/metre^2 were produced in the form of eggs by the previous generation. Since there was a maximum of 29 spiders (from 29 eggs and equivalent to 23 cals/metre^2) at instar 1, 280 calories or about 92% were 'lost'. During the spring of 1969, of the egg material left by the generation in the previous year, only 19 calories survived (equivalent to 24 spiders per metre^2 from census) to start off the population in the study area.

Table 77. Meta segmentata, mortality of eggs and emergent spiders

(numbers per metre^2)

Number of eggs laid	aborted eggs	spiders emerging	number of instar 1 in census	Total lost
1967-68				
378	132	246	29	349
1968-69				
362	91	271	24	338

Table 78. Meta segmentata, mortality of eggs and emergent spiders

(cals per metre^2)

Standing crop eggs realized	No.instar 1 in census	cals equivalent in eggs	cals of eggs lost	% cals realized
1967-68				
303	29	23	280	7.6
1968-69				
290	24	19	271	6.5

(b) <u>Production (Pg) of mortality fraction (E)</u>

The individuals eliminated (V_e) during each time period ($t_2 - t_1$) were calculated from the difference in numbers between two consecutive censuses :

$$V_e = N_{ti} - N_{t2} = \Delta N_{Ti}$$

It was assumed that these individuals had the same growth rate $(\frac{\Delta W}{\Delta t})$ as the survivors in a given time period. It was also assumed that the average mortality fraction survived to the middle of the time period, i.e. survival time was $t_2 - t_i/2$ (in days).

Hence, the production of the mortality fraction for each time period was estimated from :

$$\frac{\Delta W}{\Delta t} . \Delta N_t \cdot \frac{t_2 - t_1}{2}$$

Although the number of spiders on the first sampling occasion was lower than on the second during the two years (recruitment through hatching was still in progress), it was assumed that half the spiders present initially were eliminated before the second census.

Production in mg dry wt/metre^2 was converted to calorific equivalents using the data in Chapter *4* .

Results

Tables 78 and 79 give the contribution of the
mortality fraction to population production.   In 1968 and 1969,
only 5% and 10%, respectively, of total production could be
attributed to mortality.   These low values result from a
mortality which is highest at the egg and juvenile stages
when dry weights are low.   Table 80 is a summary of the data.

Table 78. <u>Meta segmentata</u>, contribution of mortality fraction (Pm)
to population production (Pg) per metre^2, 1968

$\frac{\Delta W}{\Delta t}$	ΔN T	$\frac{t_1 - t_0}{2}$	production mg	cals
Juveniles				
0.0069	–	7	–	–
0.0133	6.74	11	0.9861	5.1326
–0.0268	7.14	3	–0.5740	–2.9877
0.0125	4.98	19	1.1828	6.4285
Females				
0.0404	–	12	–	–
0.1128	1.71	3	0.5787	3.1898
0.1858	–	7	–	–
0.1892	4.52	3	2.5655	14.0974
0.2015	–	6	–	–
0.2495	0.32	7	0.5589	3.5178
Males				
0.0779	1	12	–	–
0.2793	2.21	3	1.8517	10.2066
0.2245	–	7	–	–
0.3289	1.31	3	1.2926	7.2773
–0.0882	–	6	–	–
–0.0351	2.91	7	–0.7150	–3.8317
		Total	7.7273	43.0306

Table 79. <u>Meta segmentata</u>, contribution of mortality fraction (E) to population production (Pg) per metre^2, 1969

$\dfrac{\Delta W}{\Delta t}$	ΔN_T	$\dfrac{t_1 - t_0}{2}$	production mg	cals
Juveniles				
0.0211	7.70	10	1.6247	8.4566
0.0560	7.70	3	1.2936	7.0307
0.0247	5.83	7	1.0080	5.4785
Females				
0.0128	–	9	–	–
0.0838	5.40	4	1.8101	10.0641
0.0414	5.28	10	2.1859	12.1536
0.0742	–	11	–	–
0.1660	3.18	8	4.3230	26.5796
0.5884	0.32	6	1.1297	7.1103
Males				
0.0502	–	9	–	–
0.0147	–	4	–	–
0.0441	1.77	10	0.7806	4.3027
0.0991	2.21	11	2.4091	17.8659
−0.0256	–	8	–	–
−0.0843	1.96	6	−0.9914	−5.3129
		Total	15.4733	93.7291

Table 80. <u>Meta segmentata</u>, total contribution of mortality

fraction (E) to production (Pg) 1968 and 1969

production (Pm) mg dry wt per metre^2

	1968		1969	
	daily mean	Total	daily mean	Total
Juveniles	0.0345	1.5949	0.7283	3.9263
Females	1.4561	3.7031	1.1686	9.3487
Males	0.5003	2.4293	0.1895	2.1983
	Total	<u>7.7273</u>	Total	<u>15.4733</u>

production (Pm) in cals per metre^2

	1968		1969	
	daily mean	Total	daily mean	Total
Juveniles	0.1960	8.5734	3.9309	20.9658
Females	8.4990	20.8050	8.3276	55.9076
Males	3.5041	13.6522	1.6607	16.8557
	Total	<u>43.0306</u>	Total	<u>93.7291</u>

(3) Exuvia (ML)

The approximate duration of instars was obtained graphically by plotting mean dry weight of each instar against the time at which the collections and weighings were made.

The discrete number of individuals (V_s) passing from one stage to another in the population were those found at the end of the duration of one instar and at the beginning of the next instar.

It was assumed that mean numbers per metre^2 on dates of sampling nearest to, or within, the duration of two consecutive instars underwent ecdysis. Hence, the number moulting was found from

$$\frac{N_1 + N_2}{2} = \bar{N}_t$$

As with R.lividus, a number of spiders which were caught in the field had been allowed to develop in the laboratory. Food in the form of a Drosophila sp. was available. Cast skins were weighed and related to the weights of spiders and hence to the number of instar.

The mean dry weights of exuvia for each instar was multiplied by the estimated number of spiders per metre^2 which had moulted. Total production is the sum of exuvial production of all instars. The likely calorific value is 4.071Kcal/g ash free and production in mg per metre^2 is expressed in calorific equivalents (Table 13).

Results and discussion

Estimates for the two years amounted to 12 and 13mg dry wt of exuviae which were equivalent to 50 and 55 calories per metre^2 (Table 81). They represent 6% of total production.

These figures are conservative since it was not assumed that all spiders at the beginning of the next instar had, in fact, moulted. The duration of instars was an approximation, while the dates of sampling from which discrete individuals (V_s) were derived were selected as those being the nearest to the end, or beginning, of each instar.

An alternative method for estimating numbers moulting would have been to plot density of spiders against time of each census, and hence read off the numbers of spiders which correspond to the completion date of an instar. In a situation where density is declining rapidly, such a procedure is essential. When there is a very gradual decline in density, as in M.segmentata, the number found at a particular census agrees very closely with those obtained graphically.

Table 81.　Meta segmentata, numbers moulting and production (ML) from exuviae

Date	instar	V_s/m^2	$\bar{N}_t$	exuviae mg mean ± S.E.	production of exuviae mg/m^2	cal/m^2
1968						
13 May	1	13.5	18.4	0.0246 ± 0.006	0.4526	1.84
10 June	2	22.2	20.0	0.1950 ± 0.050	3.5880	14.61
12 Aug	3	17.8	17.0	0.2053 ± 0.008	3.7775	15.38
1 Sept	4	16.3	13.4	0.2439 ± 0.024	4.4878	18.27
7 Sept	5	10.5		Total	12.3059	50.10
1969						
29 May	1	15.4	20.1	0.0246 ± 0.006	0.4945	22.01
4 June	2	24.8	23.2	0.1950 ± 0.050	3.9195	15.96
15 July	3	21.7	18.1	0.2053 ± 0.008	4.1265	16.80
4 Aug	4	14.6	14.1	0.2439 ± 0.024	4.9024	19.96
27 Aug	5	13.6		Total	13.4429	54.73

(4) <u>Summary</u>

Production through growth (Pg) of survivors and
the mortality fraction (Em), and including exuviae, has
been described.   As with <u>R.lividus</u>, excretion was not
investigated.

Table 82 summarises the data for production.
The figures for 1968 and 1969 came to 0.877 and 0.955Kcals
per metre^2, respectively.   The contribution from exuviae
(moulted skins) amounted to only 6% of total production
and that through mortality did not exceed 10%.

The low mortality figure may have been the result
of several factors.   Egg mortality was high and the majority
of emergent spiders either hatched outside the study area or
moved away very shortly afterwards.   The method of sampling
may have played a part.   That is, as the spiders increased
in size they were more conspicuous and so were sampled with
greater precision.   The possibility, too, exists that
there may have been some movement into the area.   However,
from general observations over the three years of study,
any immigration, if it occurred, was slight.

Table 82.   Meta segmentata, components of production (P)

in calories per m^2.   (Pg = growth of survivors;

E = growth of mortality fraction; ML = production

from moulted skins)

1968	Pg	E	ML	Total
Juveniles	77.26	8.57	16.45	102.28
Females	608.68	20.80	16.82	646.30
Males	98.04	13.65	16.82	128.51
Total	783.98	43.02	50.09	877.09
1969				
Juveniles	122.44	20.96	17.97	161.37
Females	587.44	55.90	18.38	661.72
Males	96.26	16.85	18.38	131.49
Total	806.14	93.71	54.73	954.58

(5)   Population maintenance metabolism

(a)   Method and Results

The method of calculating field metabolism in

M.segmentata was basically the same as that for R.lividus.

Rates of respiration (μl O$_2$/mg live wt/hr) under

laboratory conditions were adjusted to field temperatures

by applying the appropriate regression equations (Table 83).

Although it was convenient to record metabolic rate

for each instar in R.lividus, there was no obvious relation

between instar and rate in M.segmentata. If there are, in

fact, 5 developmental stages in the latter species, excluding

the egg stage, metabolic rates were not consistent for each

instar (Chapter 5(ω)).   Oxygen consumption could be related
to a given range of live body weight: spiders which had a
mean weight of less than 2mg;   individuals of between 2 and
12mg;   sub-adult females and males between 13 and 18mg and
between 11 and 15mg, respectively;   and adult spiders.

Since spiders were collected at known times,
and respirometry was undertaken within a few hours of capture,
it was also possible to relate metabolic rate to the period
between each census.   When the appropriate daily rates
(per mg live weight) were multiplied by the equivalent number
of calories expended per litre of oxygen, the maintenance
metabolism for each time period could be estimated (Table 84
and 85). · Data on total metabolism per metre^2 for the whole
population was then compiled from the mean standing crop for
each time period (Table 86 and 87).

(b) Discussion

Juvenile stages and sub-adults expended, per unit
weight and time, the most calories, losing over 2 or 3 times
the amount expended by other individuals.   However, in terms
of maintenance metabolism per m^2, the large increase in
weight through growth and egg production ensures that the
largest contribution comes from female spiders.   Decline
in numbers through mortality is offset by very large
increases in biomass.

The mean calorific loss per day for juveniles, female and male spiders was slightly higher in 1969 than 1968 (Tables 34-39). When the mean numbers of calories lost per day per metre^2 by each component of the population are compared, the rates for juveniles during 1969 was about twice that for 1968. The differences between means for females, males and the population as a whole, were small but were consistently higher in 1969.

It is not possible to say whether such small differences are significant. The time the spiders are in the field and the precision of estimates of standing crop will influence estimates of metabolic rate of populations. However, the slightly higher field temperatures in 1969 could account for the higher rates recorded for that year.

The total estimates for 1968 and 1969 were 1.01 and 1.42Kcal/metre^2. On the assumption that the ratio of sexes was unity at the juvenile stage, and that there was no difference in metabolic rate during that period, the contribution of female spiders for the two years amounted to 47% and 52% of the total population metabolism, respectively.

Table 83. <u>Meta segmentata</u>, regression equations for mean

rate of respiration (μl O$_2$/mg live wt/hr) on

temperature (X)

mg live body wt	regressions
2	$-0.1562 + 0.079X$
2 - 12	$0.0325 + 0.026X$
sub-adult	
13 - 18♀	$-0.0308 + 0.050X$
11 - 15♂	
adult	
18♀	$-0.0096 + 0.018X$
11 - 16♂	$-0.0041 + 0.020X$

Table 84.   **Meta segmentata**, estimates of mean respiratory
rates adjusted to field temperatures, 1968

date	t_2-t_1	Field temp.	µl O_2/mg live/hr	µl O_2/mg live/day	equivalent cals/mg/day
Juveniles					
13 May	14	7.8	0.4600	11.0400	0.053
4 June	22	12.0	0.7918	19.0032	0.091
10 June	6	12.3	0.8155	19.5720	0.094
18 July	38	13.0	0.8708	20.8992	0.100
Females					
12 Aug	25	13.0	0.3705	8.8920	0.043
18 Aug	6	13.5	0.3835	9.2040	0.044
1 Sept	14	13.2	0.7480	17.9520	0.086
7 Sept	6	13.2	0.7480	17.9520	0.086
19 Sept	12	13.4	0.2316	5.5584	0.027
3 Oct	14	12.8	0.2208	5.2993	0.025
Males					
12 Aug	25	13.0	0.3705	8.8920	0.043
18 Aug	6	13.5	0.3835	9.2040	0.044
1 Sept	14	13.2	0.7480	17.9520	0.086
7 Sept	6	13.2	0.7480	17.9520	0.086
19 Sept	12	13.4	0.2639	6.3336	0.030
3 Oct	14	12.4	0.2519	6.0456	0.029

Table 85.   Meta segmentata, estimates of mean respiratory rates

adjusted to field temperatures, 1969

date	$t_2 - t_1$	Mean temp. $^\circ C$	$\mu l\ O_2/mg$ live/hr	$\mu l\ O_2/mg$ live/day	equivalent cals/mg/day
Juveniles					
29 May	20	10.2	0.6496	15.5904	0.075
4 June	7	10.1	0.6417	15.4008	0.074
18 June	14	13.4	0.9024	21.6576	0.104
Females					
16 July	18	13.9	0.9419	22.6056	0.108
15 July	9	15.0	0.4225	10.1400	0.049
4 Aug	20	14.9	0.4199	10.0776	0.048
27 Aug	23	15.5	0.8837	21.2088	0.102
13 Sept	17	14.0	0.2424	5.8176	0.028
25 Sept	12	13.8	0.2388	5.7312	0.027
Males					
6 July	18	13.9	0.9419	22.6056	0.108
15 July	9	15.0	0.4225	10.1400	0.049
4 Aug	20	14.9	0.4199	10.0776	0.048
27 Aug	23	15.5	0.8837	21.2088	0.102
13 Sept	17	14.0	0.2759	6.6216	0.032
25 Sept	12	13.8	0.2719	6.5256	0.031

Table 86. <u>Meta segmentata</u>, estimates of population

maintenance metabolism, 1968

$t_2 - t_1$	mean live biomass mg	maintenance metabolism	
		cals/m^2/day	cals/m^2/period
Juveniles			
0	-- -	-	-
14	6.25	0.35	4.83
22	39.45	3.60	79.14
6	50.01	4.70	28.20
38	53.66	5.38	204.50
Females			
25	53.14	2.27	56.72
6	78.89	3.49	20.92
14	140.08	12.07	169.05
6	165.91	14.30	85.81
12	176.77	4.69	56.32
14	243.82	6.19	86.70
Males			
25	39.77	1.70	42.57
6	44.47	1.96	11.79
14	60.17	5.19	72.61
6	77.13	6.65	39.89
12	86.82	2.64	31.67
14	64.47	1.87	26.18
		Total	1016.90

Table 87. <u>Meta segmentata</u>, estimates of population

maintenance metabolism, 1969

$t_2 - t_1$	mean live biomass mg	maintenance metabolism	
		cals/m^2/day	cals/m^2/period
Juveniles			
0	-	-	-
20	18.70	1.40	27.96
7	70.08	5.18	36.25
14	105.00	10.91	152.74
Females			
18	90.30	9.80	176.35
9	126.94	6.18	55.64
20	106.14	5.14	102.74
23	116.56	11.87	273.92
17	148.70	4.15	70.53
12	203.00	5.58	66.99
Males			
18	62.22	6.75	121.52
9	74.02	3.60	32.44
20	72.41	3.50	70.09
23	70.93	7.22	166.06
17	81.87	2.60	44.26
12	67.07	2.10	25.19
		Total	1421.70

(6) Energy flow in <u>M.segmentata</u>

Population assimilation (A), or energy flow,
is that part of energy from food which is utilized by
the population to maintain itself (R) and to increase
its biomass (P). Hence,

$$A = R + P$$

Production (Pg) was estimated from mean growth
increments of individuals caught on successive sampling
occasions. Information on biocontent allowed dry weight
values to be converted to calorific equivalents.

Maintenance metabolism (R) was represented by
respiratory energy loss of the mean standing crop between
consecutive sampling dates. Assimilation cannot be
measured directly, hence its expression as the sum of
R + P.

Since energy loss through exertion was not
measured, P is incomplete.

From information on duration of instars, it was
possible to allocate contributions of juveniles, females
and males to specific instars.

Mean net production efficiencies for each stage
was calculated from the ratio of production to assimilation.
This indicates the proportion of total energy which is
directed to tissue formation.

As 'an index of efficiency of biomass production',
P divided by mean biomass ($\bar{B}$) gives production turnover (H),
(Petrusewicz and Macfadyen 1970), i.e.

$$H_p = \frac{P}{\bar{B}}$$

Results

Tables 88 and 89 present the data on energy flow
during 1968 and 1969. Total population assimilation (A)
came to 1.89 and 2.38Kcal/metre^2/year, respectively.

An interesting feature, which may be coincidental,
concerns the relatively constant proportion of energy lost
through respiration by both sexes. In both years, at
instar 3, females lost between 58 and 60% of the total
for this stage. At instar 4, the values are between 61%
and 69%, and for adults, between 67% and 71%. The
explanation is not known.

The first 2 instars which had hatched at an earlier
date in 1968, and so were active in the study area for a
longer time, had a higher maintenance (R) cost than in 1969.
However, production by the same stages during 1969 was
greater and would account for the shorter developmental
time.
In both years, assimilation was at its maximum
during the sub-adult stage when loss of energy through
respiration, prior to the final moult, was high. The
contribution by this stage amounted to over a third of

total energy flow.

Mean net production efficiencies for instars fluctuated between 24% and 64%. However, P/A ratios for the entire populations in both years were about the same. They are very close to the value of 43% obtained by Manga (1970) for a carabid beetle and to the 40% figure for Robertus lividus. The ratio for instar 3 in 1968 was high, at about 62%, as if making up for the low efficiencies in the preceding instars.

Mean standing crop for the two years came to 203 and 281Kcals/metre^2/year. The turnover of biomass for 1968 and 1969 was 4.3 and 3.4, respectively. These values compare with 2.45 obtained by Breymeyer (1967) for Trochosa ruricola.

Table 88. Meta segmentata, energy flow for the population, 1968

Stage		mean standing crop cals/m²/year	Respiration of standing crop cals/m²/year	Production of standing crop cals/m²/year	Assimilation $A = R + P$ cals/m²/annum	$\dfrac{P \times 100}{A}$
instar 1		45	112	37	149	25
2		58	205	66	270	24
3	♀	204	78 } 132	126 } 220	204 } 352	62
	♂		54	94	148	
4	♀	416	255 } 367	243 } 298	498 } 666	45
	♂		113	55	168	
5	♀	589	143 } 201	294 } 256	437 } 457	56
	♂		58	-38	20	
Kcals		0.203	1.017	0.877	1.894	46%

Table 89. <u>Meta segmentata</u>, energy flow for the population, 1969

Stage	mean standing crop cals/m²/year	Respiration of standing crop cals/m²/year		Production of standing crop cals/m²/year		Assimilation A = R + P cals/m2/annum		$\dfrac{P \times 100}{A}$
instar 1	43	28		44		72		61
2	129	189		·117		306		38
3 ♀	261	232 ⎫ 386		108 ⎫ 153		340 ⎫ 539		28
♂		154 ⎭		45 ⎭		199 ⎭		
4 ♀	317	377 ⎫ 613		159 ⎫ 265		536 ⎫ 878		30
♂		236 ⎭		106 ⎭		342 ⎭		
5 ♀	523	138 ⎫ 207		412 ⎫ 375		550 ⎫ 582		64
♂		69 ⎭		-37 ⎭		32 ⎭		
Kcals	281	1.423		0.954		2.377		40

CHAPTER TWELVE

ENERGY FLOW IN TWO SPECIES OF SPIDERS

Robertus lividus (Theridiidae) and Meta segmentata (Argiopidae) are polyphagous carnivores which rely on the chance capture of prey by webs. The former species spins its hammock web on the surface litter while the latter constructs orbwebs in the foliage above.

All stages of R.lividus are found in the litter throughout the year and all pass through at least part of the winter. On the other hand, M.segmentata overwinter as eggs which hatch in April or May, while oviposition takes place in the following autumn.

R.lividus reproduces throughout the year with a considerable overlap of generations. The argiopod species has a well defined cohort with a precise developmental period.

Despite points of difference between the two species in size, distribution and ecology, a direct comparison is made possible by using the calorie. Details of their respective energy budgets and their contributions to total energy flow within the ecosystem, are given in Table 90.

(a) Comparison of population energy budgets

The mean standing crops of both species were similar. However, total energy flow for the theridiid species amounted to 4.59Kcals/m^2/annum which was about twice that for

M.segmentata.   Turnover of biomass was 8.3 in R.lividus
compared with about 4 in M.segmentata.

The estimated growth component of production, P,
was 70% in R.lividus and between 85% and 90% in the argiopid
species.   In the former species about a third of production (P)
came from the mortality fraction, compared with a tenth or
less in M.segmentata.

Moult loss (ML) in both species came to 6% of
total production.

Calories lost through respiration, expressed as
a ratio of production (R/P) was 1.5 in R.lividus and 1.2
and 1.5 in M.segmentata.   The P/R ratios ranged between
67% and 85%.

(b) Reproductive potential

A substantial amount of web is used in the
construction of cocoons.   With a relatively small number
of eggs (mean 20) per cocoon as in R.lividus, just over $^3/_5$
of biocontent is in the silk, compared with out $^1/_5$ in
M.segmentata.

Egg production per metre^2 was very much higher in
the argiopid species, amounting to 27% and 33% of total
production (P).   In R.lividus, the corresponding figure
was only 6%.   The difference may be an adaptation to a
particular mode of life.   In M.segmentata, eggs are left

Table 90. Population energy budgets for 2 species of
spiders (Kcals/m^2/annum)

		R.lividus	M.segmentata	
		1967 - 68	1968	1969
Pr	Eggs	0.113	0.290	0.267
	Cocoons	0.309	0.057	0.045
Pg	G	0.605	0.437	0.494
	E	0.711	0.043	0.093
ML		0.115	0.050	0.055
P		1.853	0.877	0.954
R		2.742	1.017	1.423
A		4.595	1.894	2.377
B̄		0.224	0.203	0.281

unguarded for a considerable period of time, during which
they have to pass the winter and conditions within the habitat
may vary from year to year when hatching occurs. In
R.lividus, the female frequently survives to guard the eggs
which, in addition, have a fairly short incubation period.

In M.segmentata, the calorific values of newly
moulted females and spent females are about the same.
Hence, production of adult females is directly the result
of egg formation. The percentage of this 'reproductive
effort' which survives is a measure of the breeding success

of the population. McNeill (1971), for example, found in
the mirid bug that the higher the level of production, the
lower the reproductive success.

Table 91 records the reproductive efficiency and
success of M.segmentata during 1968 and 1969. Although
production (P) was higher in the latter year, reproductive
efficiency was less. Data should have to be compiled over
several years before drawing firm conclusions. However,
an inverse relationship between reproductive success and
production would reduce the fluctuation in production from
year to year.

The reproductive material that is actually realized
must also be considered, i.e. those eggs which actually hatch
to produce individuals which remain in the area to maintain
continuity of the species. In R.lividus, a total of 627
eggs were laid, equivalent to 113 cals per metre^2 per annum.
Out of that number, 349 spiders were caught at instar 1, i.e.
about 63 calories or 56% of the total, were used to initiate
new generations. In M.segmentata, 303 and 290 calories were
laid per metre^2 in 1967 and 1968, respectively. The
maximum numbers of instar 1 in subsequent populations were
29 and 24 per metre^2, equivalent to 23 and 19 egg calories
and constituting only about 7% of the total laid.

The significance of this information on fate of
reproductive material is apparent when cognizance is taken

Table 91. Meta segmentata, reproductive efficiencies

	cals. of reproductive effort	cals. of eggs laid	cals of pre-ovipositional mortality	Eggs laid reproductive efficiency (%)	production (%)
1967	-	303	-	-	-
1968	294	290	4	98.7	33.1
1969	386	267	19	69.2	26.6

not only of the ecology of the 2 species, but also the
behaviour of emergent spiders. In M.segmentata, the
newly hatched stage may pause only briefly near the
hatching site before dispersing over considerable distances.

(c) **Annual net production and respiration**

The evidence from several studies on the bio-
energetics of species populations suggest that in poikilotherms
and homiotherms the relation between R and P are different
(Engelmann 1966). Furthermore, in the former group the
relation is influenced greatly by the duration of life-
cycles (McNeill and Lawton 1970). The regression equations
given are :

$$\log R = 1.1740 \log P + 0.1352$$

and,

$$\log P = 0.8262 \log R - 0.0948$$

The regression line from the first equation is drawn
in Fig.48, and a plot of the observed values of R and P for
the two species of spiders (Table 92) show close agreement
with those expected (Table 93).

It is debatable whether R and P are statistically
independent variables since estimates of R and P are
calculated from the same biomass data. However, the
regression equations are a useful description of the
relationships. In the case of R.lividus, it was necessary

Fig.48. Regression line (from McNeill and Lawton

1970) of log. respirations on log.

production with corresponding data

for R.lividus and M.segmentata.

(△ R.lividus, ● M.segmentata, 1968,

o M.segmentata, 1969).

The plot shows $\log_{10} R$ versus $\log_{10} P$ with the fitted line:

$$\log R = 1.1740 \ \log P + 0.1352$$
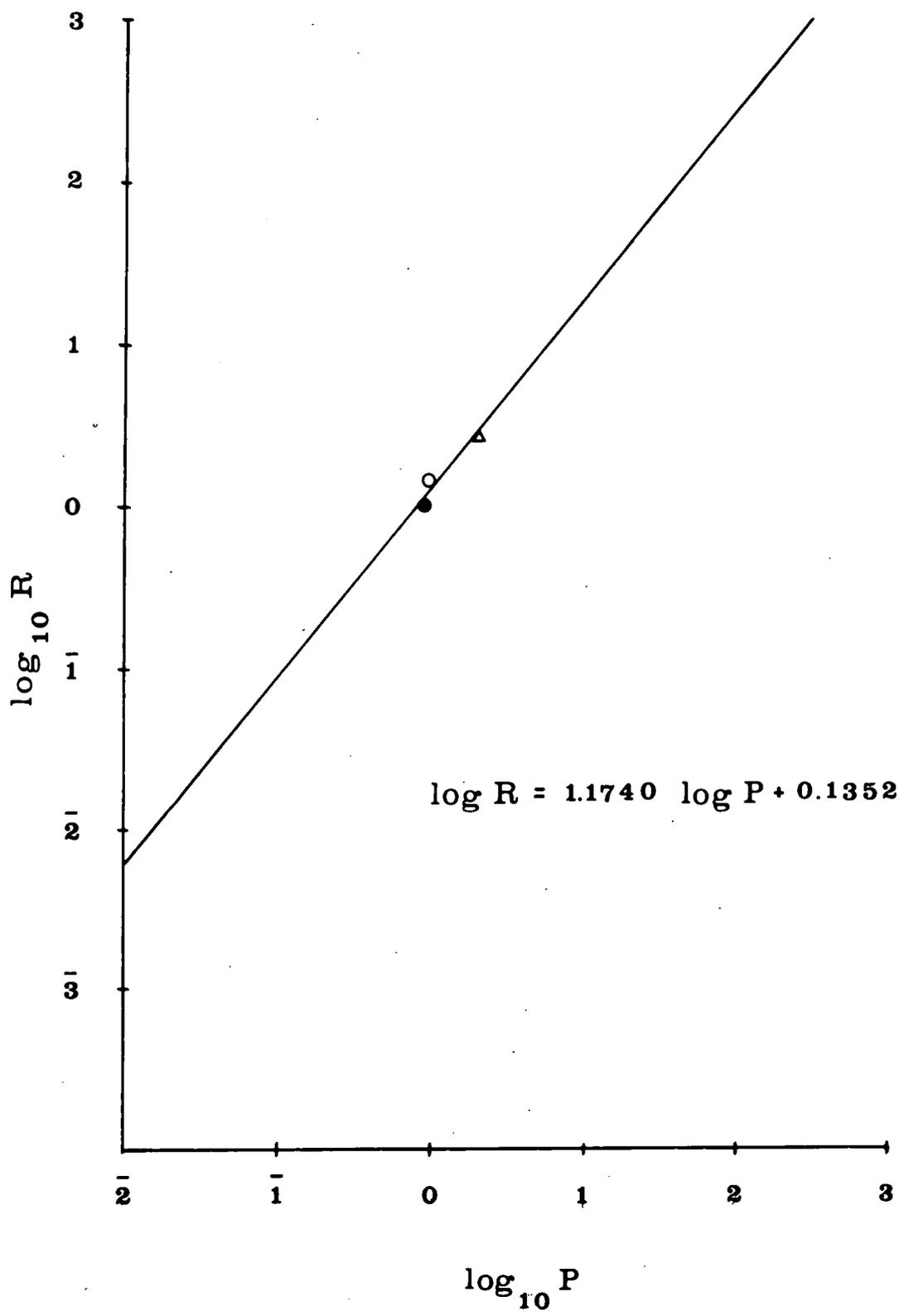
to distinguish between numbers (N) and discrete individuals (Vs) passing through the population. Respiration (R) was calculated on the basis of N while production (Pg) was derived from Vs. It would appear that this procedure was appropriate since there is close agreement between the observed data and that expected from the regression equations (Table 93).

Mean net production efficiency

The ratio of P to A, where A = R + P, is a measure of the efficiency with which body material in spiders is laid down. Table 93 records the observed ratios for R.lividus and M.segmentata with those expected from the regression equations. The values of both species are similar, ranging between 40% and 46%.

Table 92. The parameters R and P for 2 species of spiders

		R	$\log_{10}R$	P	$\log_{10}P$
R.lividus	1967-68	2.742	0.4381	1.853	0.2679
M.segmentata	1968	1.017	0.0072	0.877	T.9430
,,	1969	1.423	0.1532	0.954	T.9795

Table 93.   R.lividus and M.segmentata, a comparison between observed (o) data and those expected (E) from regressions for short-lived poikilotherms (McNeill and Lawton, loc.cit.).   Except where stated, figures are in K.cals/m^2/annum

	A		P		R		$\frac{R \times 100}{A}$	
	O	E	O	E	O	E	O	E
R. lividus	4.59	4.66	1.85	1.85	2.74	2.81	40%	39%
M. segmentata	1.89	1.91	0.88	0.79	1.01	1.12	46%	43%
-,,-	2.38	2.31	0.96	1.05	1.42	1.26	40%	42%

CHAPTER THIRTEEN

ANALYSIS OF THE SPIDER COMMUNITY II

Species composition, the sampling methods, seasonal distribution, and the order of dominance in terms of numbers and biomass, have been considered. These aspects provide a backcloth against which the species chosen for an energetics study are examined.

The second part of the analysis of the spider community is concerned with its structure. The total density of spiders reveals the 'receptivity' of the habitat towards this trophic group. Community biomass or standing crop indicates the amount of spider material which can be supported at any given time. When units of weight are replaced by their equivalents in calories, the data are available for comparisons of 'standing states' between trophic groups within the same, or different, ecosystems.

(1) Density

By far the greatest contribution to the spider fauna as a whole comes from the ground zone or, more specifically, from litter and soil (Table 94). Above this layer, numbers fall sharply with increasing height (Fig.49) and density for the field layer and canopy combined never exceeds 20% of the total in any given month.

Turnbull (1960) had found greatest numbers in the field layer of an oak wood, probably because the ground zone was inadequately sampled.

In January and February no spiders were found in the canopy layer and numbers in the field layer had declined to a few overwintering individuals. At this time, however, there was a definite suggestion of an increase in the ground zone, from 493 spiders in January, to 587 spiders in February. This was sustained in March, to be followed by a fall in April, coinciding with an increase in the field layer and lower canopy. A further increase in the ground zone occurred in May with 597 spiders, which apparently generated a second wave in the field layer in June.

It was not until June that spiders were conspicuous in the upper canopy, after the full development of foliage. At Wytham Great Woods, Oxford, activity was apparent in mid-April in 1955 (Turnbull 1960), and greatest numbers were reached in June.

The decline in density above the ground zone was first apparent in the upper canopy, with a drop from 17 to 5 spiders per metre^2, in October 1968. This coincuded with leaf fall and declining temperatures and was followed by a diminition in the field layer and lower canopy in November. It was also accompanied by an increase in the ground zone. Gravid female spiders were descending to

lay their eggs, while immature stages and some adults were retiring to winter quarters, and in the ground zone the autumnal hatch was taking place.

The separation of two maxima in September and November by a low estimate in October 1968 is difficult to explain. The mean temperature of 9.4'C for November was well above the average, and compares with 4.7'C for the same month in 1967. This may have prolonged activity in the ground zone. On the other hand, 1967 was generally warmer and sunnier than 1968, and so possibly brought forward the autumnal hatch in the former year to October.

Spiders appear to overwinter mainly in the ground zone and to a lesser extent in the field layer. Few, if any, spiders remained in the canopy. <u>Theridion pallens</u> exhibited a marked migration from the ground zone to the canopy in May, and in the reverse direction in September. Duffey (1969) recorded a massive movement of spiders down oak trees at Monkswood, Huntingdon, commencing in September.

Total density was quite high at Wynyard, with a low species diversity. A maximum value of 965 spiders was obtained in October 1967, and a minimum of 502 spiders in the following January. Reasonably efficient sampling of the ground zone and field layer possibly accounted for the generally high numbers. However, it is difficult to compare the data with that gained elsewhere. There have

been few investigations in woodlands and such as there
are have been concerned with relative estimates (e.g.
Turnbull 1960; Luczak 1966) or have been restricted to
the study of a few species (e.g. Luczak 1963), or the
forest floor only has been considered (Van der Drift 1951;
Luczak 1959; Gabutt 1956) when the efficiency of
extraction was possibly low.

Numbers fluctuate little in the ground zone
when compared with those in higher strata which have a
marked seasonal pattern. With the exception of the lower
canopy which is really an extension of the field layer,
each stratum has its characteristic fauna. Although
many species may be found at some time in any layer,
there is a marked preference for a particular stratum.

(2) Monthly Standing crop of the spider community

(a) Procedure

Biomass was calculated from the dry weights
obtained after specimens were dehydrated in a vacuum oven
for 48 hours at 60'C. However, specimens had been stored
in alcohol for some time. Marples, cited in Breymeyer (1967),
had found a percentage loss in arthropods of 17% and
Breymeyer applied an appropriate correction factor when
determining the biomass of wandering spiders.

Table 94. Total monthly density of spiders per metre^2 in the study area at Wynyard

Month	ground zone	field layer	lower canopy	upper canopy	Total (all strata)
1967					
October	874	63	21	7	965
November	690	44	18	7	759
December	485	12	8	4	509
1968					
January	493	9	0	0	502
February	587	9	0	0	596
March	576	23	7	5	611
April	445	40	12	7	504
May	597	38	15	6	656
June	541	57	23	12	633
July	586	80	21	15	702
August	528	66	20	14	628
September	691	85	21	17	814
October	523	53	17	5	598
November	814	38	13	2	867

The likely error in the case of spiders was investigated by weighing a number of freshly killed and dried spiders.   After storage in alcohol for over a year, the same specimens were re-weighed after the usual process of drying.   The results which were obtained with species of Linyphiids are given in Table 95.

The loss in weight could be both substantial and highly variable.   The tendency was for the larger forms to lose more weight than the smaller, although there was no statistically significant difference between them.

Table 95.   Loss in dry weight as a result of storage

size group dry wt	no. of specimens	% loss mean	range
4mg	15	30.6	18.7-40.7
2mg (mature)	10	26.2	16.3-43.3
1mg (mature)	12	24.3	12.1-31.0

It was considered sufficient to multiply the dry weights by 1.25.   However, it was clear that precise estimates for a single species study would have to be based on recently killed specimens.

Cherrett (1961) had used the wet alcohol weights to provide estimates of biomass.   By adopting a similar procedure to the one used with dry weight estimates, the error in weight loss was investigated.

Table 96.   Loss in wet weight as a result of storage

size group wet weight	no. of specimens	% loss mean	range
14mg	10	10.2	2.1-15.6
8mg	7	7.5	2.0-11.0
4mg	10	3.8	3.0- 5.0

The loss in weight, with excess alcohol removed from the specimens prior to weighing, amounted to as much as 15% (Table 96).   Dry weight estimates can be obtained from these, but unless the dry/wet weight relationship is known for a species or stadia, an equally large error may occur.

Spiders removed from soil samples by the extractor, or those caught in the sweep net or beating tray, were oven dried. The factor of 1.25 was used to compensate dry weights for any loss due to storage. Further appropriate factors, described in the sampling programme, were used to adjust weights to a metre^2.

(b) Results

Monthly estimates of total biomass for the study area (Table 97) are lowest from December to April with values ranging from 122 to 139mg dry weight per metre^2. It was during this period that all strata yield relatively low values (Fig.49).

From May to September, monthly standing crop increases from 174 to nearly 400mg per metre^2. Although the main contribution usually comes from the ground zone, during August, September and October, the combined values of higher strata exceed those at the base.

As with density, biomass declines from the ground zone towards the upper canopy. This spatial diminution, however, is less pronounced than density.

The factors which influence biomass are, firstly, abundance. This is always high in the ground zone compared with other strata, and biomass is correspondingly high even though the spider community consists of spiders

which are generally small and have a large proportion of immature stages. The ground zone has the most consistent values because density fluctuates less than in the upper regions of the study area. Spiders which disperse or die are constantly being replaced by hatching of eggs.

Secondly, change in species composition may lead to a change in the quantity of spider material. This was evident, particularly in the field layer and lower canopy. The increase in ratios of biomass to density rose sharply from about July (Table 98) when the young of large species formed a major part of the population in the field layer. In contrast to the ground zone with its high proportion of immatures, and to the upper canopy with its peculiar spider community, where low ratios of biomass to density prevailed.

Clearly biomass has to be expressed per unit area and not as a ratio of dry weights to density, as was done, for example, by Cherrett (1961). Ratios reflect a change in mean size of individual spiders which may not occur to any appreciable extent in some areas as the ground zone and upper canopy. On the other hand, as larger species take longer to mature than small spiders, larger ratios are seen towards the end of the season. Although these ratios may coincide with periods of greater biomass, they are in

the first instance the result of a change in species composition. High ratios of biomass to density do not necessarily mean that an overall increase in biomass is taking place. In the field layer, for example, the highest ratio is 2.75 in October 1968 with a biomass of 141mg per metre^2. The largest biomass was in September with a ratio of 1.8 and a biomass of 150mg. Again, the highest ratio in the ground zone was 0.35 in December 1967 with a biomass of 117mg per metre^2. The greatest biomass recorded, however, in that layer was 178mg. In September, with a ratio of 0.26.

Biomass in the study area was based on catches which were stored in alcohol for several months before being weighed. Although a correction of 1.25 was applied to the dry weights, these may still have been under-estimates. Furthermore, parts of the habitat were not adequately sampled. However, it is felt that the overall estimates of biomass are a reasonable approximation to the real situation.

Table 97.   Total monthly standing crop (based on dry

weights (mg) per metre^2) in the study area at

Wynyard

Month	ground zone	field layer	lower canopy	upper canopy	Total (all strata)
1967					
Oct	135.3	120.7	31.1	4.7	291.8
Nov	118.3	33.4	14.8	5.2	171.7
Dec	117.4	15.1	0.4	1.6	134.5
1968					
Jan	113.3	12.3	0	0	125.6
Feb	104.9	12.3	0	0	117.2
Mar	117.1	15.5	4.5	2.2	139.3
Apr	94.3	16.5	8.5	3.2	122.5
May	139.3	21.7	8.6	4.4	174.0
June	104.5	30.9	15.9	5.8	157.1
July	126.7	65.0	29.5	6.1	227.3
Aug	91.5	106.8	55.4	6.1	259.8
Sept	178.5	150.0	56.3	10.2	395.0
Oct	138.2	141.0	15.7	2.8	297.7
Nov	152.6	22.1	7.6	0.6	182.9

Table 98.   Ratios of monthly biomass to monthly density,

to show the influence of size of species on biomass

Month	ground zone	field layer	lower canopy	upper canopy
1967				
Oct	0.1	1.9	1.0	0.7
Nov	0.3	0.7	0.8	0.7
Dec	0.3	1.2	0.4	0.5
1968				
Jan	0.2	1.3	0	0
Feb	0.2	1.3	0	0
Mar	0.2	0.6	0.7	0.4
Apr	0.2	0.4	0.7	0.4
May	0.2	0.6	0.6	0.7
June	0.2	0.5	0.7	0.5
July	0.2	0.8	1.4	0.4
Aug	0.2	1.6	2.8	0.4
Sept	0.3	1.8	2.7	0.5
Oct	0.3	2.7	0.9	0.6
Nov	0.2	0.6	0.6	0.2

Fig.49. Density and biomass of all spiders in each
of four main structural layers of the
study area.
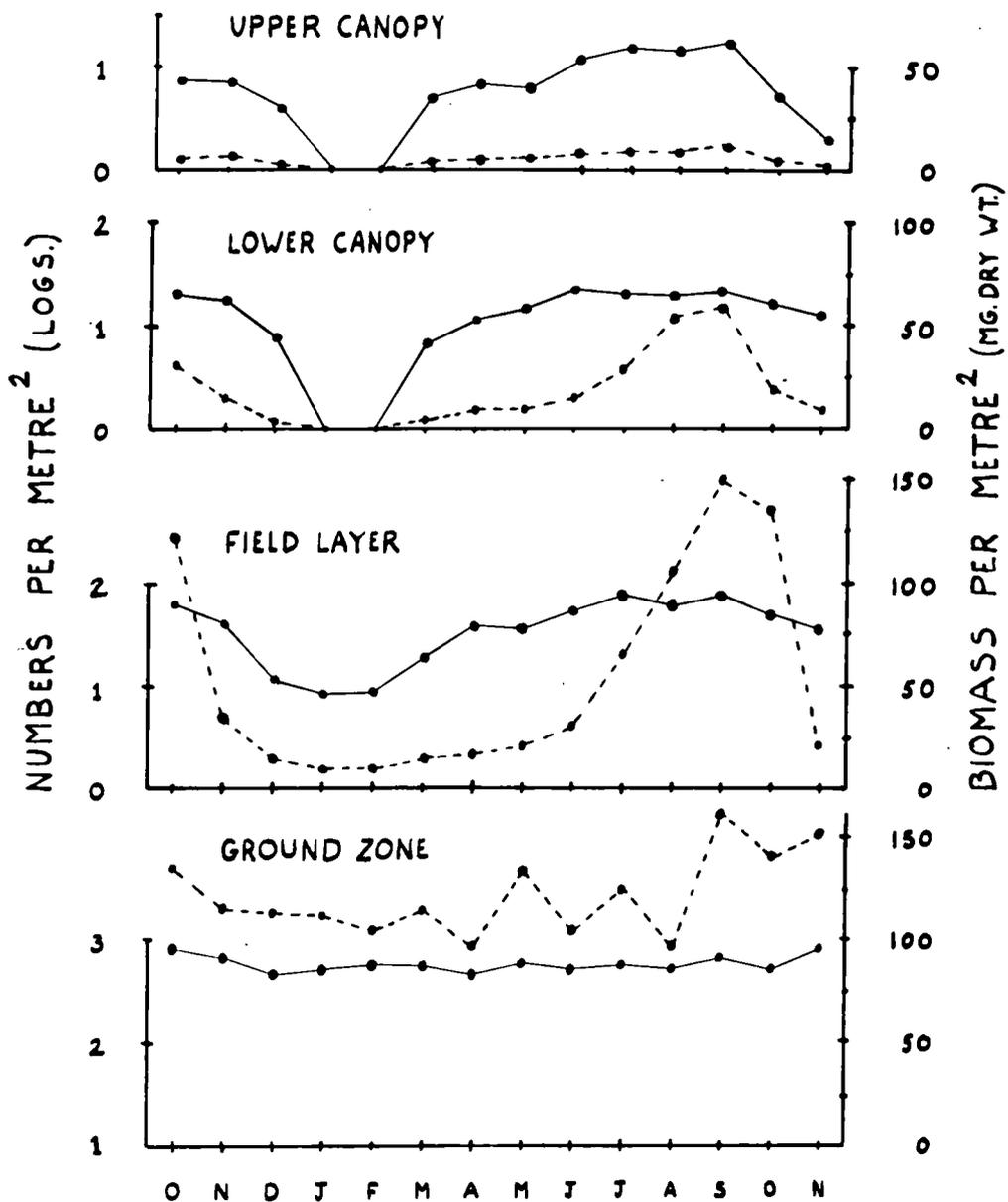
(3) Biocontent of standing crop

The energy retained by spider material and expressed as biocontent depends on stage of development, reproductive condition, and even the species which make up the community (Chapter 4). In collective estimates, as with biomass, the various contributing factors become obscured. Nonetheless, an indication of the magnitude of biocontent in the community at any given time is provided.

During 1969, a miscellany of Linyphiid spiders was prepared for the miniature bomb calorimeter, together with adult specimens of Meta segmentata, Helophora insignis, and Linyphia triangularis (Chapter 4). The mean adult biocontent was calculated to be 5.826Kcal per g (ash free) dry weight. However, the adults of those species quoted have the highest biocontent but were not typical of the ground zone. For this stratum it was considered appropriate to select a lower mean for adult spiders by omitting the larger species from the calculation. Hence, a mean of 5.615Kcal/g which was based on calorific values for Robertus lividus and various species of adult Linyphiids was used to convert monthly dry weights in the ground zone to their calorific equivalents.

As a difference in biocontent exists between young and adult spiders, combustions were performed

separately.   A mean of 5.440Kcal/g dry weight of spider

tissue was considered to be a reasonable estimate for

immature spiders.

The monthly biomass (mg dry weight) of young and

adult spiders in each stratum was multiplied by the appropriate

calorific equivalents to produce corresponding estimates of

monthly biocontent.

(a)   Ground zone

Biocontent (Table 99) falls just short of 1Kcal

per metre^2 in September 1968 and coincides with the period

of highest biomass.   In fact, biocontent is closely related

to adult biomass, the tissues of mature spiders$_\wedge$having a
                                                   also

higher calorific value.   The peak of biocontent is highest

in the autumn, usually exceeding 700 cals per metre^2 in any

given month.

Biomass was least in April and August, with a

monthly biocontent of only 533 and 506 cals per metre^2.

Adult spiders in particular had either dispersed to other

layers, or having achieved maturity and oviposited, had

died.   A peak of 773 cals per metre^2 occurred in May

when many overwintering immatures became adult.

The highest contribution from young stages came

in June and July, accounting for 60% and 51%, respectively,

of total biomass.   During this period sub-adult spiders

were particularly abundant.   In the remaining months,
contributions varied from 25% to 46% of total biomass.

The fluctuations in biocontent over the 14 month
period were quite small, with the lowest value in August
only half the maximum in September 1968.

(b) Field layer

As expected, total biocontent was closely related
to biomass (Table 100).   January and February yielded
low calorific values of only 71 cals per metre^2.   An
increase which at first was gradual took place until
June when it accelerated to produce a peak of 868 cals
in September.   The peak is maintained at about the same
level in October, after which a decline occurred.

Although numbers of young spiders were in excess
of adults from December 1967 to July 1968, biomass and
biocontent always fell below that of mature spiders.
The contribution of young stages to total biocontent
reached about 40% in June, July and August.   In the
remaining months, contributions were very much smaller,
especially in the autumn when large species had become
mature.   For example, immature spiders only made up
4% of the monthly total in October 1968.

The seasonal pattern seen with density and
biomass, with low values in spring and high values in
autumn, was equally apparent with biocontent.   When

compared with the ground zone, high monthly calorific values were only attained in the field layer from August to October.

(c) Lower canopy

Biocontent data (Table 101) shows a seasonal pattern which has already been described for the field layer. With fewer spiders per metre^2, calorific values are much lower than in the field layer. Few, if any, spiders overwinter so that biocontent was negligible in January and February. Maximum values were found in August and September with 309 and 322 cals per metre^2. A sharp decline to less than 100 cals then occurred in both years during October.

The main contribution of young stages is represented by a sharp peak in August when biocontent reached 188 cals per metre^2. Apart from July and August, adult biomass and hence biocontent exceeded values for immature stages.

(d) Upper canopy

Even allowing for inadequate sampling of spiders at this level, it is probable that far fewer spiders occur here than elsewhere. Individual dry weights were also low ($<$1 mg). In consequence, monthly biocontent was very low (Table 102). While other layers yielded high

values in late° summer and autumn, the upper canopy only achieved a biocontent of 58 cals per metre^2 in September. This amounted to less than a 1/5 of the biocontent in the lower canopy in the same month.

The seasonal pattern was preserved, albeit on a smaller scale and over a shorter period with calorific values rising in the spring to reach the maximum in September. Immature and adult contributions to monthly biomass were about the same.

(e) Total biocontent

Biocontent is related to biomass of adult spiders which not only have a greater weight than their young but yield more calories per g (ash free) dry weight. Total standing crop in terms of biocontent was highest in September with 2.24Kcal per metre^2 (Table 103). Biomass at the time was the maximum recorded during the investigation with 395mg per metre^2, and in all strata adult spiders made the largest contribution. In the field layer, for instance, the females of large species which included Meta segmentata and Linyphia triangularis had become mature and laden with eggs.

The September peak was preceded by values in excess of 1Kcal during July and August when the young of species in the ground zone and field layer had increased in size to become sub-adult. In October 1968 biocontent

had declined from 2.248Kcal to 1.701Kcal per metre^2, and
so marked the end of a seasonal phase. Although a number
of large species had died after oviposition, _Helophora_
insignis and _Lepthyphantes alacris_ were still active
and helped maintain a relatively large standing crop in
November.

An increase in density in the ground zone took
place in February which led to colonisation of the upper
strata in March and April. As spiders were all of small
size, even when mature, calorific values amounted to about
0.6 and 0.7Kcal per metre^2. The young of large species
invaded the foliage from the ground zone in May and June
so increasing biocontent to about 0.8Kcal. As these
individuals underwent a striking increase in size, they
were responsible for the large calorific values recorded
from July to November.

(f) Discussion

Fig.50 depicts the likely changes in density,
biomass and biocontent which took place in the study area
from October 1967 to November 1968. Standing crop in
terms of dry egg weights and corresponding calorific
equivalents were not investigated.

Density is seen to fluctuate between 502 and 965
spiders per metre^2 with quite a considerable change from
one month to the next during some periods. The pattern

for the study area as a whole is based on density
in the ground zone where numbers far exceeded those in the
strata above.

The curves for biomass and biocontent (Fig.50)
are much more even than density. This suggests that
sampling errors alone are not responsible for the oscillations
in density. Rather, that biomass (dry weights) and biocontent
are probably better indications of just how much spider
material can be supported in the habitat.

While abundance and biomass appear to be related
in a general way, increase in biomass tends to lag behind
increase in density. In February an increase in density
is seen to be followed by a small increase in biomass in
March. Again, an increase in density in May is followed
in June and July by a corresponding increase in biomass.
This may be explained by visualising a hatching of eggs
in the ground zone, or the invasion of, say, the field
layer, which is then followed by a period of growth
of individual spiders and hence an increase in population
biomass, despite the mortality which occurs. The extent
of the increase in biomass will depend as much on numbers
as on the size of the species which make up the population
at any given time. Large species will inflate estimates
of biomass and their effect will be seen in large ratios
of biomass to density.

Biocontent is clearly dependent on biomass,
in particular the population dry weights of adult spiders.
This was strikingly seen in November 1968 when, despite
the increase in density due to an appearance of large
numbers of young spiders in the ground zone, biomass and
biocontent both continued to decline.

As far as is known, no thorough investigations
have been undertaken in woodland to estimate standing crop.
To what extent values at Wynyard are typical, either of
woodland in general, or of alder and birch in particular,
or of a northern temperate region, must remain uncertain
for the present. Sampling techniques were considered
adequate for the ground zone, field layer and lower canopy.
The upper canopy requires specialist apparatus and time
for a detailed treatment on its own. In the present
situation, however, it must remain debatable whether the
overall estimates for the study area would have been much
altered by intensive sampling of the upper canopy. The
contribution of the ground zone with all three parameters
is striking, bearing in mind the volume of soil and litter
which was sampled, when compared with the volume of the
strata above.

Table 99. Monthly biocontent (per metre^2) of all spiders

in the ground zone

Month	metre^2 density	biomass (mg)	biocontent cals young	adult	Total
1967					
Oct	873.6	135.3	193.6	559.7	753.3
Nov	689.6	118.3	218.2	438.9	657.1
Dec	484.8	117.4	191.9	461.2	653.1
1968					
Jan	492.8	113.3	265.1	362.2	627.4
Feb	587.2	104.9	186.6	396.2	582.8
Mar	576.0	117.0	268.1	380.5	648.6
Apr	444.8	94.3	233.6	299.3	532.9
May	596.8	139.3	266.8	506.9	773.7
June	540.8	104.5	339.4	236.3	575.7
July	585.6	126.7	360.0	339.8	699.8
Aug	528.0	91.5	231.0	275.4	506.4
Sept	691.2	178.5	271.9	721.4	993.3
Oct	523.2	138.1	204.9	564.2	769.1
Nov	814.4	152.6	261.1	587.1	848.2

Table 100. Monthly biocontent (per metre^2) of all spiders

in the field layer

Month	density	biomass (mg)	young	adult	Total
1967					
Oct	63	120.7	12.5	689.8	702.3
Nov	44	33.4	14.7	178.8	193.5
Dec	12	15.1	20.7	65.8	86.5
1968					
Jan	9	12.3	13.6	57.1	70.7
Feb	9	12.3	13.6	57.1	70.7
Mar	23	15.5	16.3	72.8	89.1
Apr	40	16.5	34.3	59.4	93.7
May	38	21.7	52.2	70.5	122.7
June	57	30.9	65.8	109.5	175.3
July	80	65.0	136.0	233.0	369.0
Aug	66	106.8	197.0	411.3	608.3
Sept	85	150.0	87.0	780.7	867.7
Oct	53	141.0	31.0	794.1	825.1
Nov	38	22.1	16.3	111.3	127.6

Table 101.   Monthly biocontent (per metre^2) of all spiders

in the lower canopy

Month	metre^2		biocontent cals		
	density	biomass	young	adult	Total
1967					
Oct	21.5	31.1	15.2	164.9	180.1
Nov	18.3	14.8	19.6	65.3	84.9
Dec	7.9	3.4	0	19.8	19.8
1968					
Jan	0	0	0	0	0
Feb	0	0	0	0	0
Mar	6.8	4.5	8.7	16.9	25.6
Apr	11.6	8.5	16.9	31.4	48.3
May	14.7	8.6	21.2	27.4	48.6
June	22.9	15.9	36.5	53.6	90.1
July	21.0	29.5	93.6	71.6	165.2
Aug	19.7	55.4	188.2	121.2	309.4
Sept	20.8	56.3	78.3	244.1	322.4
Oct	16.9	15.7	8.2	82.7	90.9
Nov	13.0	7.6	4.3	39.6	43.9

Table 102.   Monthly biocontent (per metre^2) of all spiders

in the upper canopy

Month	density	biomass	young	adult	Total
1967					
Oct	7.2	4.7	12.0	14.6	26.6
Nov	7.1	5.2	16.9	12.2	29.1
Dec	4.4	1.6	0	9.3	9.3
1968					
Jan	0	0	0	0	0
Feb	0	0	0	0	0
Mar	5.1	2.2	8.2	4.1	12.3
Apr	7.0	3.2	9.2	8.7	17.9
May	6.2	4.4	16.9	7.6	24.5
June	12.1	5.8	16.3	16.3	32.6
July	14.8	6.1	20.7	13.4	34.1
Aug	14.3	6.1	13.1	21.5	34.6
Sept	16.7	10.2	22.3	35.5	57.8
Oct	4.7	2.8	5.4	10.5	15.9
Nov	2.4	0.6	3.3	0	3.3

Table 103.   Total monthly biocontent (cals per metre^2)

in the study area at Wynyard

Month	ground zone	field layer	lower canopy	upper canopy	Total (all strata)
1967					
Oct	753.3	702.3	180.1	26.6	1662.3
Nov	657.1	193.5	84.9	29.1	964.6
Dec	653.1	86.5	19.8	9.3	768.7
1968					
Jan	627.4	70.7	0	0	698.1
Feb	582.8	70.7	0	0	653.5
Mar	648.6	89.1	25.6	12.3	775.6
Apr	532.9	93.7	48.3	17.9	692.8
May	773.7	122.7	48.6	24.5	969.5
June	575.7	175.3	90.1	32.6	873.7
July	699.8	369.0	165.2	34.1	1268.1
Aug	506.4	608.3	309.4	34.6	1458.7
Sept	993.3	867.7	322.4	57.8	2241.2
Oct	769.1	825.1	90.9	15.9	1701.0
Nov	848.2	127.6	43.9	3.3	1023.0

Fig.50.   Monthly standing crop per m^2 of the spider community.

MONTHLY STANDING CROP PER METRE^2
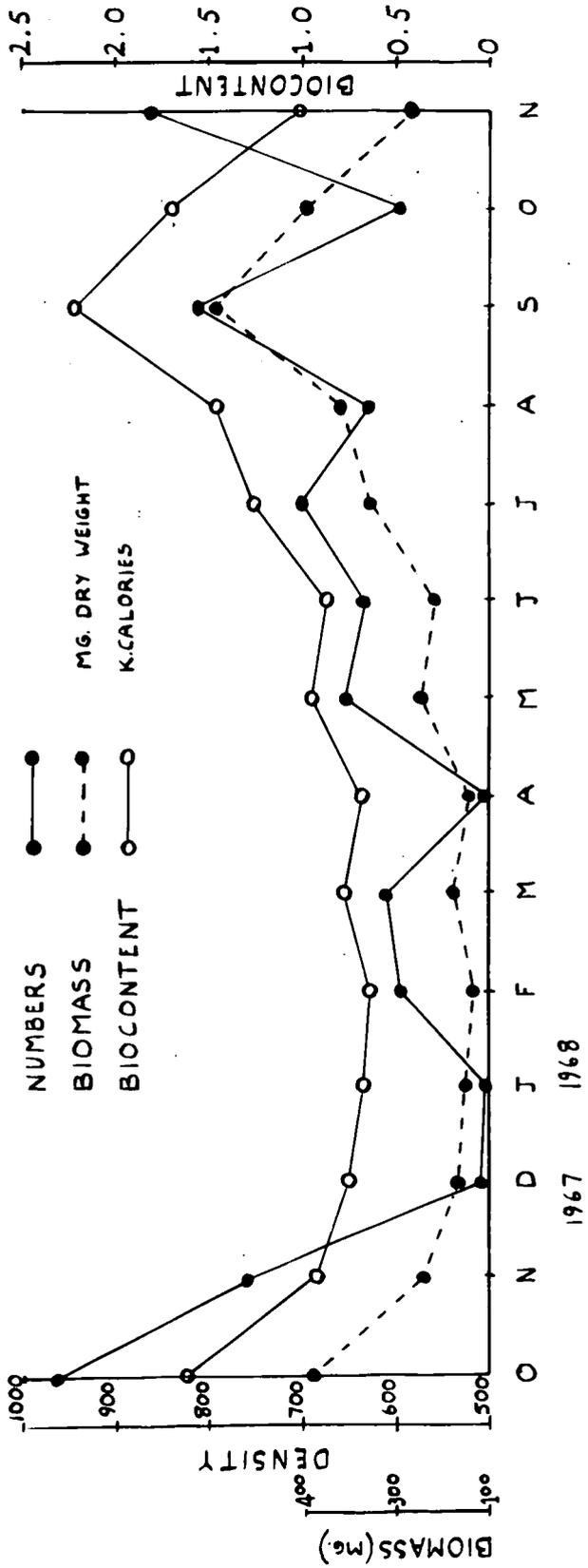
GENERAL DISCUSSION

1. Life cycles

The elucidation of energy flow in species populations
can only spring from a knowledge of life cycles' under field
conditions.

Ecological studies on spiders generally fall into
one of two groups. First, those which represent surveys
of communities in which adults only are named and described
(e.g. Turnbull 1960; Luczak 1963, 1966; Duffey 1962, 1968).
The second group is concerned with some of the factors which
influence the microdistribution of adults (e.g. Savory 1930;
Nørgaard 1951, 1952; Cherrett 1961). Immature stages are
referred to in a collective sense (Gabbutt 1956; Cherrett 1961).
Single species populations, comprising all developmental stages
have rarely been quantitatively expressed. In preliminary
studies on production of spiders, Breymeyer (1967) has described
the structure of a population of Trochosa ruricola while
Kajak (1967) has done the same for Araneus quadratus,
A.cornutus and Singa hamata.

One of the difficulties is the identification of
immature stages, especially in families other than the
Argiopidae. However, the present study has shown that
in a restricted area it is possible to establish filial
connections between the adults and young of at least a few
species. Breymeyer (1967) was able to distinguish the

·immature stages of <u>Trochosa ruricola</u> from those of other wandering spiders.

The classification of spiders in terms of the duration of life cycles is difficult except in a restricted area. Although interspecific differences occur, for example, <u>Atypus affinis</u> has a longevity of 4 years (Bristowe 1959) while <u>Ciniflo similis</u> lays eggs only after 2 years have elapsed (Cloudsley-Thompson 1955), regional variations also arise as with <u>Meta merianae</u> (Cherrett 1961, Turnbull 1960).

The study of the spider community at Wynyard suggests that species inhabiting the litter layer have an overlap of generations since they are able to reproduce continuously throughout most of the year. In the foliage above, most species have well defined cohorts, e.g. <u>Meta segmentata</u>, <u>Helophora insignis</u>, and <u>Linyphia triangularis</u>, imposed presumably by the restricted growing season.

All species at Wynyard appeared to complete their life cycle within 12 months. Within the ground zone the majority of species passed the winter as adults. In the field layer, some species like <u>M.segmentata</u>, <u>H.insignis</u>, <u>L.triangularis</u>, and <u>Lepthyphantes alacris</u>, laid their eggs in the autumn and hatching took place in the following spring and early summer. Those species which were dominant as adults in the spring and early summer overwintered as adults or sub-adults. These were <u>Theridion pictum</u>, <u>Meta segmentata</u>

mengei, _Cornicularia cuspidata_, _Trachynella nudipalpis_ and _Linyphia peltata_.

The general conclusion is that to ensure survival of the population in the following year, spiders in woodland overwinter either as diapause eggs or as relatively advanced stages with reserves of (food) body fat. Although eggs of litter forms like _R.lividus_ may hatch in January or February, mortality is likely to be heavy if very cold conditions persist. With an overlap of generations, some late instars will survive to mature and lay eggs when favourable conditions return.

The emergent stages of _Meta merianae_ and _Araneus cornutus_ apparently overwinter in pennine moorland (Cherrett 1961). The very low temperatures which prevail during the winter at that elevation would presumably depress metabolic rates considerably, and so reduce drastically energy loss at a time when feeding did not occur. Although Miyashita (1969) has detected diapause in the penultimate stage of _Lycosa T-insignata_, the extent of this phenomenon in spiders is not known (Dondale and Legendre 1971).

In terms of life cycles at Wynyard, spiders could be divided into 3 main groups. First, those that reproduce more or less continuously and rely on advanced developmental stages for survival during the winter. This group includes the majority of ground zone forms such as _R.lividus_. Second, spiders which have well defined cohorts to ensure that most of

the population reaches maturity to lay eggs by the onset of winter.   These include M.segmentata with eggs apparently undergoing diapause.   Third, spiders with less well defined cohorts which nevertheless ensure that some advanced stages overwinter to exploit the environment immediately favourable conditions return in the spring.   This group includes M.segmentata mengei and Trachynella nudipalpis.

2. Energy flow

The total energy assimilated (A) by species populations may be estimated from A = C - FU and/or A = R + P (nomenclature after Petrusewicz and Macfadyen 1970). Both equations have been the subject of investigation (e.g. Wiegert 1964;   Smalley 1960;   McNeill 1971;   Manga 1970). Apart from the preliminary study of Kajak (1967) which involved a number of assumptions, the values in the equation have not been precisely determined for spiders.

Estimates of assimilation from the sum of respiration (R) and production (P) has been made by Saito (1965, 1967) and Whignarajah (1968).   Although this equation was used in the present study, ideally A should be arrived at by two independent pathways (Phillipson 1967).

From the Second Law of Thermodynamics the energy available for carnivores will be less than that for herbivores in most cases.   This is borne out by the data in Table 104. With the exception of the mirid bug Leptoterna dolabrata

the species populations of primary consumers were represented

by numerous individuals, and were either dominant or sole

representatives of their respective orders.

While Nebria brevicollis (Manga 1970) was the

dominant carabid beetle in an area of grassland, the centipedes

studied by Whignarajah (1968) were the sole chilopod's in the

study area at Wynyard.   The spider, R.lividus, ranked fifth

in the order of numerical dominance in the ground zone at

Wynyard.   Besides being a common species in the field layer,

M.segmentata had the largest individual biomass in the study

area as a whole.   While R.lividus was active throughout the

year, the argiopid species was seen only from April to October.

(i)   Maintenance metabolism (R)

The present work has shown the dependence of

respiration on temperature and accords with the results of

Miyashita (1969) and Anderson (1970).   Values of weight

specific metabolism were converted to calorific equivalents

on the basis of 4.8Kcal/litre of oxygen.   The daily loss

of several species of spiders is given in Table 105.

Precise comparisons are difficult to make because

experimental animals, at different stages of development, have

been subjected to different temperatures.   While Q_{10} values

have been used to standardise rates (Engelmann 1966), they

are themselves temperature dependent.

Table 104. Some assimilation values for species populations
of terrestrial invertebrates (Kcals/m^2/annum)

Primary consumers

Ligidium japonicum	19	(Saito 1965)
Japonaria l.armigera	58	(,, ,,)
Orchelimum fidicinium	29	(Smalley 1960)
Philaenus spumarius	39	(Wiegert 1964)
Leptoterna dolabrata	0.126	(McNeill 1971)
Pogonomyrmex badius	31	(Golley & Gentry 1960)

Secondary consumers

Lithobius forficatus		2.080	(Whignarajah 1968)
L.crassipes		1.340	(,, ,,)
Nebria brevicollis		0.803	(Manga 1970)
Robertus lividus		4.595	This thesis
Meta segmentata	1968	1.894	,, ,,
,, ,,	1969	2.377	,, ,,

The range of values given in Table 105 is small despite
differences in experimental details. The higher end of the
range for R.lividus and M.segmentata relate to young stages,
which per unit weight and time have a higher metabolic rate
than adults. The effects of walking and resting states
on loss of energy is strikingly shown by Lycosa T-insignata.
It raises the vexed problem of whether respiratory energy

loss of mobile animals is the better guide to the situation in the field.

The constant pressure respirometers of Kajak (1967) were run at 20'C only, although the mean field temperature was 14.3'C. Over-estimates of energy loss were considered adequate compensation for lack of mobility in experimental animals. Breymeyer (1967) subjected species of wandering spiders to temperatures of between 15'C and 30'C.

In the present study respirometers were run at 5', 10' and 15'C to cover the likely range in the field. Regression equations were used to relate respiratory rates to field temperatures. This approach has been used by Dutton (1968), Manga (1970), and Whignarajah (1968) with species of predatory arthropods.

The maintenance cost (R) of the species populations of spiders, expressed as a ratio of production (P), came to 1.5% in R.lividus and 1.2% and 1.5% in M.segmentata. These values are evidently typical of poikilotherms (Phillipson 1966) since body heat has not to be generated as in homiotherms.

The P/R ratio used by some authors varied between 67% and 85% in the present work. A value of 57% was calculated from the data of Kajak (1967) on Araneus quadratus. Comparable values of about 50% were obtained for certain orthopteran species by Wiegert (1965) and Smalley (1960).

Higher percentages of about 100% were found in a carabid

beetle (Manga 1970) and a mirid bug (McNeill 1970).

The highest value so far recorded is 124% in Chorthippus

parallelus (Qastrawi 1966). The significance of these

differences is not clear. However, in centipedes which have

a life span in excess of two years, a low value of 4% was

obtained (Whignarajah 1968). It appears that ecological

longevity and possibly assimilation efficiency (G/C)

will influence P/R ratios.

(ii) Production (P)

The components of production (P) are Pg + Pr + ML + U,

to which reference has already been made in the appropriate

sections.

Population production arising through growth (Pg)

is calculated from survivorship and individual growth curves,

the methods for which are given by Petrusewicz and Macfadyen

(1970). Table 105 gives the data so far published on spiders.

Since the results of Kajak and Breymeyer were expressed in

millegrammes, the corresponding calorific values were obtained

by multiplying weight units by 5.8Kcal/g dry weight.

Cohorts were recognisable in all species given in

Table 106 with the exception of R.lividus. The pattern of

development was complicated in the latter by an extended

breeding period. However, by considering the discrete number

Table 105. Respiratory energy loss in spiders

Species	cals respired g/wet wt/24hrs	Live wt of individuals(mg)	Temperature 'C'	authority
Lycosa pseudoannulata (Lyco)	36	1 - 150	29	Ito 1964
Achaearanea tepidariorum (Ther.)41		73	20	*Anderson 1970
Theridion rufipes (Ther.)	24	25	20	* ,, ,,
Lycosa lenta (Lyco.)	11	970	20	* ,, ,,
Lycosa T-insignata (Lyco)	110 (walking)	30 - 60	15	Miyashita 1969
,,	18 (resting)	30 - 60	15	,, ,,
Robertus lividus (Ther.)	60 - 152	0.13 - 7.4	15	Thesis
Meta segmentata (Arg.)	30 - 115	1 - 66	15	Thesis

* figures for weight specific metabolism converted to energy equivalents on

  the basis of 4.8Kcal/litre O_2

of individuals (Vs) passing through the population, a
'mean' cohort was envisaged, and from which a survivorship
curve was drawn.

P_r was determined separately in R.lividus since
gravid females were rarely captured. In the argiopid,
Pr was first incorporated in the estimate for Pg. From
the data on weight of eggs produced by the population,
estimated indirectly from the relation between body and
cocoon weights, Pr could be deduced.

Production from cast skins (ML) was about the same
for both species, constituting 6% of total production (P).
There are no published data for spiders but the results
compare with 4.5% in Leptoterna dolabrata (McNeill 1971)
and 2% in a carabid beetle (Manga 1970).

Excretion (U) was not investigated in either species
of spiders. The material is largely fluid and presumably
the amount depends on feeding rates which are best estimated
in the laboratory. It should be possible to relate U to
increase in weight in developing spiders. An estimate
of this parameter might then be related to growth increments
in field populations. The calorific value of spider
excrement is not known. According to Gilmour (1961),
quanine is an important component.

A provisional and, perhaps debatable, estimate of
excretion was made by Kajak (1967) for Araneus quadratus.

If the figure of 26% of production (Pg) is realistic, then estimates of production (P) which lack the element U will be seriously under-estimated.

The value of Kajak's (1967) preliminary studies, despite the limited data, is that production was examined over 2 years. The degree of fluctuation which may be encountered in field populations was shown by <u>A.quadratus</u> in which production (Pg) on one year was one tenth that of the previous year.

No study so far, including the present work, has provided an estimate of production from the webs used to ensnare prey.

(iii) <u>Assimilation</u> (A)

The level of assimilated energy for several species of invertebrates is given in Table 104. In the case of the ant colony, <u>P.badius</u>, the high value results from high respiratory rates. In centipedes, which are long-lived poikilotherms, as much as 95% of the assimilated energy is expended through maintenance (R), compared with just over half in the spiders, <u>R.lividus</u>, and <u>M.segmentata</u>, which are relatively short-lived.

In the grasshopper, <u>Orchelimum fidicinium</u>, (Smalley 1960), fluctuations in energy flow were out of phase with density and biomass. With a stable age distribution in centipedes (Whignarajah 1968), changes

Table 106. Production (Pg) values which have been estimated for spiders

	Mean density ($\bar{N}/m^2$)		Production (Pg) (in $Kcal/m^2$)		site
	year 1	year 2	year I	year 2	
<u>Trochosa ruricola</u>	-	-	*0.863	-	Meadow (Breymeyer 1967)
<u>Araneus quadratus</u>	6.36	5.33	*1.740	0.188	Meadow (Kajak 1967)
<u>A.cornutus</u>	1.90	1.20	*0.058	0.095	Meadow (" , ")
<u>Singa hamata</u>	2.44	-	*0.057	-	Meadow (" , ")
<u>Robertus lividus</u>	105.85	-	1.85	-	Woodland (thesis)
<u>Meta segmentata</u>	10.8	11.0	0.88	0.96	" , "

* dry weight of population production multiplied by 5.8Kcal/g.

in all three parameters coincided. In R.lividus, the
emergence of young spiders occurred when adult females
were also much in evidence. Hence, the high level of
energy flow could be related to density and biomass.
However, in winter a high density of emergent spiders
is out of phase with both biomass and metabolism, since
adult spiders are numerically low and field temperatures
have fallen. The large size of adult females in M.segmentata
led to a correlation between biomass and assimilated energy
despite a decline in numbers.

In the argiopid spider, the high level of
assimilation (A) by the population preceded the mass laying
of eggs. The peak energy for carabid beetles occurred
just before diapause. In some cases it seems that maximum
energy flow is related to major events in life-histories.

The mean net production efficiencies (P/A) of
between 40% and 46% for both species of spiders agree
with those recorded by several authors (e.g. Wiegert 1964;
Saito 1967; Manga 1970) for invertebrates. However, the
ratio may not be consistent throughout the life-cycle.
The early instars of spiders generally have low P/A ratios
because of relatively high respiratory rates. Growth
efficiencies (G/C) may also rise with age as in Araneus
quadratus and A.cornutus (Kajak 1967).

In a review of the literature, McNeill and Lawton (1970) concluded that mean net production efficiencies tend to increase as total annual production (P) falls. This ability to compensate for restricted levels of P can also apply to particular developmental stages as in M.segmentata during 1968. On the other hand, growth efficiency (G/C) in A.quadratus (Kajak 1967) was higher in those stages which experienced food shortages.

The juveniles (mainly instar 3) and adults of R.lividus overwinter and have a production in excess of log. $P = 0$. On the other hand, M.segmentata passes the winter in the egg stage and production is log. $p < 0$. These 'life-history effects' (McNeill and Lawton 1970) in short-lived poikilotherms may be explained by the need to increase annual production to offset the high cost of maintaining individuals during the winter when production is negligible. In terms of the spider community as a whole, it also helps explain why emergent stages and sub-adults, with relatively high respiratory rates, are numerically low during the winter months.

REFERENCES

ANDERSON, J.F. (1970). Metabolic rates of spiders.

Comp.Biochem.Physiol. <u>33</u>, 51-72.

BAILEY, N.T.J. (1959). <u>Statistical methods in Biology</u>.

London, 200 pp.

BERTHET, P.(1960). La mesure ecologique de la temperature par

determination de la vitesse d'inversion du saccharose.

Vegetatio acta geobotanica <u>9</u>, 197-207.

BOLTON, P. (1969). Studies in General Ecology, Physiology and

Bioenergetics of Woodland Lumbricidae.

Ph.D. Thesis, University of Durham.

BORNEBUSCH, C.H. (1930). The fauna of forest soil :

Forstl.Forsg.Danm. <u>11</u>, 1-224.

BREYMEYER, A. (1967). Preliminary data for estimating the

biological production of wandering spiders. In

Secondary Productivity of Terrestrial Ecosystems.

Warszawa-Krakow. 821-834.

BRISTOWE, W.S.(1939-41). The comity of spiders.

Vol. I and II, Ray Soc., London.

BRISTOWE, W.S.(1958). The world of spiders.

Collins' New Naturalist, London.

CHERRETT, J.M. (1961). Ecological research on spiders associated

with moorlands. Ph.D. Thesis, University of Durham.

COMSTOCK, J.H. (1940). The Spider Book (revised by W.J. Gertsch), New York.

CUMMINS, K.W. (1967). Calorific equivalents for studies in ecological energetics. Duplicated sheets; University of Pittsburgh.

DAVEY, K.G. (1965). Reproduction in the insects. Oliver and Boyd, Edinburgh and London.

DEBAUCHE, H.R. (1962). The structural analysis of animal communities of the soil. in Progress in Soil Zoology, ed. Murphy, P.W. London. 10-25.

DEEVY, G.B. (1949). The developmental history of Lactrodectus mactans (Fabr) at different rates of feeding. Amer. Midland Nat. 42(1), 189-219.

DONDALE, C.D. (1961). Life histories of some common spiders from trees and shrubs in Nova Scotia. Can.J.Zool. 39 : 777-87.

DONDALE, C.D. and LEGENDRE, R. (1971). Winter diapause in a Mediterranean population of Pisaura mirabilis (Clerck). Bull.Brit.Arach.Soc. 2, (1) 1-5.

DUFFEY, E. (1956). Aerial dispersal in spiders. J.Anim.Ecol. 25, 85-98.

DUFFEY, E. (1962). A population study of spiders in limestone grassland. Description of study area, sampling methods and population characteristics. J.Anim.Ecol. 31, 571-99.

DUFFEY, E. (1963). Ecological studies on the spider fauna of
the Malham Tarn area. Field Studies,1,5. 1-23.

DUFFEY, E. (1969). The seasonal movements of _Clubiona brevipes_
Blackwall and _C.compta_ C.L. Koch on oak trees in
Monks Wood, Huntingdonshire. Bull.Brit.Arach.Soc. 1(3) 29-32.

DUTTON, R. (1969). Studies into the Ecological Energetics of the
wireworm _Melanotus rufipes_ (Hbst) (Coleoptera Elateridae)
Ph.D. Thesis, University of Durham.

ELTON, C.G. and MILLER, R.S. (1954). The ecological survey of
animal communities with a practical system of classifying
habitats. J.Ecol. **42,** 460-96.

ENGELMANN, M.D. (1966). Energetics, terrestrial field studies, and
animal productivity. Advances in Ecological Research 3
(ed. Cragg, J.B.) pp. 73-115. London and New York.

GABBUTT, P.D. (1956). The spiders of an oak wood in S.E. Devon.
Ent.Mon.Mag. **92,** 351-8.

GILMOUR, D. (1961). Biochemistry of insects. New York and London.

GOLLEY, F.B. and GENTRY, J.D. (1964). Bioenergetics of the
southern harvester ant, _Pogonomyrmex badius_.
Ecology, **45,** 217-25.

GREIG-SMITH,P.(1964). Quantitative plant ecology. London.

HEALEY, J.M. (1967). The energy flow through a population of soil
Collembola. In Secondary Productivity of Terrestrial
Ecosystems (Principles and Methods), ed. K.Petrusewicz.
Warszawa-Krakow, 695-708.

HEALY, M.J.R. (1962).   Some basic statistical techniques in soil

       zoology.   In: Proceedings of the Coloquium on Research

       Methods in Soil Zoology.   Rothamsted (ed. P. Murphy).

HEALEY, V. (1964).   The density and distribution of 2 species

       of Aptinothrips (Thysanoptera) in the grass of woodland.

       Entomologist 97, 258-63.

HUGHES, M.K.H. (1970).   Investigations of the ecosystem energetics

       of an English woodland.   Ph.D. Thesis, University of Durham.

ITÔ, Y. (1964).   Preliminary studies on the respiratory energy loss

       of a spider, Lycosa pseudpannulata.

JOHNSON, C.G., SOUTHWARD, T.R.E. and ENTWISTLE, H.M. (1957).   A new

       method of extracting arthropods and molluscs from

       grassland and herbage with a suction apparatus.

       Bull.ent.Res. 48, 211-218.

KAJAK, A. (1967).   Productivity of some populations of web spiders.

       In Secondary Productivity of Terrestrial Ecosystems.

       ed. K.Petrusewicz. Warsaw. 807-820.

KEMPSON, D., LLOYD, M. and GHELARDI, R. (1963).   A new extractor

       for woodland litter.   Pedobiologia 3, 1-21.

LEWIS, T. and TAYLOR, L.R. (1967).   Introduction to experimental

       ecology.   London.

LOCKET, G.H. and MILLIDGE, A.F. (1951).   British Spiders. Vol.1.

       Ray Soc.London.

LOCKET, G.H. and MILLIDGE, A.F. (1953).   British Spiders. Vol.2.

       Ray Soc.London.

LUCZAK, J. (1959). The community of spiders of the ground flora of pine forest. EKol.Pol.A. 7, 285-315.

LUCZAK, J. (1963). Differences in the structure of communities of web spiders in one type of environment (young pine forest) Ekol.Pol.A. 11, 159-221.

LUCZAK, J. (1966). The distribution of wandering spiders in different layers of the environment as a result of interspecies competition. Ekol.Pol.A. 15, 233-244.

MACFADYEN, A. (1955). A comparison of methods for extracting soil arthropods. In Soil Zoology, ed. D.K. McE. Kevan. London. 315-332.

MACFADYEN, A. (1962a). Soil Arthropod Sampling. In Advances in Ecological Res. ed. J.B. Cragg, 1. 1-34.

MACFADYEN, A. (1962b). Control of humidity in three funnel-type extractors for soil arthropods. In Progress in Soil Zoology, ed. P.W. Murphy, London. 158-168.

MANGA, N. (1970). Bioenergetics of a predatory beetle, Nebria brevicollis (F). Ph.D. Thesis, University of Durham.

McNEILL, S. and LAWTON, H. (1970). Annual production and respiration in animal populations. Nature, London. 225, 472-74.

McNEILL, S. (1971). The energetics of a population of Leptopterna dolabrata (Heteroptera : Miridae). J.Anim.Ecol. 40, 127-140.

MERRETT, P. (1967).   The phenology of spiders on heathland in

      Dorset.   J.Anim.Ecol. <u>36</u>, 363-374.

MIYASHITA, K. (1968a).   Growth and development of <u>Lycosa T-insignata</u>

      (Araneae : Lycosidae) under different feeding conditions.

      Appl.Ent.Zool. 3(2), 81-88.

MIYASHITA, K. (1969b).   Effects of locomotory activity, temperature

      and hunger on the respiratory rate of <u>Lycosa T-insignata</u>

      Boes. et Str. (Araneae : Lycosidae).

      Appl.Ent.Zool. 4(3) : 105-113.

MIYASHITA, K. (1969).   Seasonal changes of population density and

      some characteristics of overwintering Nymph of <u>Lycosa</u>

      <u>T-insignata</u> Boes. et Str. (Araneae : Lycosidae).

      Appl.Ent.Zool. 4 : 1-8.

MURPHY, P.W. (1955).   Ecology of the Fauna of Forest Soils

      in Soil Zoology, ed. D.K. McE. Kevan, London.

NØRGAARD, E. (1951).   The ecology of two Lycosid spiders from

      a sphagnum bog.   Oikos, <u>3</u>, 1-10.

NØRGAARD, E. (1952).   The habits of the Danish species of

      <u>Pirata</u>. Ent.Medd. <u>26</u>, 415-423.

NEWELL, R.C. and NORTHCROFT, H.R. (1967).   A re-interpretation of

      the effect of temperature on the metabolism of certain

      marine invertebrates.   J.Zool.Lond. <u>151</u>, 277-298.

ODUM, E.P. (1959).   Fundamentals of Ecology. 2nd ed.

      Philadelphia and London.

PETRUSEWICZ, K. and MACFADYEN, A. (1970).   Productivity of
        terrestrial animals. I.B.P. Handbook No.13.
        Oxford and Edinburgh.

PHILLIPSON, J. (1960).   A contribution to the feeding biology
        of Mitopus morio (F) (Phalangiida).
        J.Anim.Ecol. 29, 35-43.

PHILLIPSON, J. (1962).   Respirometry and the study of energy
        turnover in natural systems with particular reference
        to harvest spiders (Phalangiida).   Oikos, 13, 311-22.

PHILLIPSON, J. (1963).   The use of respiratory data in estimating
        annual respiratory metabolism, with particular reference
        to Leiobunum rotundum (Latr.) (Phalangiida). Oikos, 14, 212-23.

PHILLIPSON, J. (1964).   A miniature bomb calorimeter for small
        biological samples.   Oikos, 15, 130-139.

PHILLIPSON, J. (1966).Ecological Energetics. London. pp. 1-53.

PHILLIPSON, J. (1967).   Invertebrates reproducing more than once
        in a life-time.   In Secondary productivity of Terrestrial
        Ecosystems. (Principles and Methods). ed. Petrusewicz, K.
        Warsawa-Krakow, 679-683.

PHILLIPSON, J. and WATSON, J. (1965).   Respiratory metabolism of
        the terrestrial isopod. Oniscus asellus L.
        Oikos, 16, 78-87.

PROSSER, C.L. and BROWN, F.A. (1962). Comparative animal

physiology. Philadelphia and London. pp 106-134.

QASTRAWI, H. (1966). A study of the energy flow in a natural

population of the grasshopper, Chorthippus parallelus.

Zett. (Acrididae). Ph.D. Thesis, University of Exeter.

RUSSELL, E.J. (1950). Soil Conditions and plant growth.

Longmans, London.

SAITO, S. (1965). Structure and energetics of the population of

Ligidium japonica (Isopoda) in a warm temperate forest

ecosystem. Jap.J.Ecol. 15, 47-55.

SAITO, S. (1967). Productivity of high and low density populations

of Japonaria laminata armigera (Diplopoda) in a warm

temperate forest ecosystem. Res.Popul.Ecol. 9, 153-66.

SALT, G. and HOLLICK, F.S.J. (1944). Studies of wireworm populations 1.

Ann.Appl.Biol. 31, 52-64.

SAVORY, T.H. (1930). Environmental differences of spiders of

the genus Zilla. J.Ecol. 18, 384-389.

SLOBODKIN, L.B. and RICHMAN, S. (1961). Calories per gram in

species of animals. Nature, London. 191, (4785). 299.

SLOBODKIN, L.B. (1962). Energy in Animal Ecology. in Adv.Ecol.Res.

ed. Cragg, J.B. 69-101. London and New York.

SMALLEY, A.E. (1960). Energy flow of a salt marsh grasshopper

population. Ecology 41, 672-77.

SOLOMON, M.E. (1957).   Estimation of humidity with cobalt

thiocyanate papers and permanent colour standards.

Bull.ent.Res. 48, 489-506.

SOUTHWOOD, T.R.E. (1966).   Ecological methods, with particular

reference to the study of insect populations, London.

TANSLEY, A.G. (1954).   Introduction to Plant Ecology.   London.

TAYLOR, L.R. (1961).   Aggregation, variance, and mean.

Nature, 189, 732-5.

TEAL, J.M. (1957).   Community metabolism in a temperate cold

spring.   Ecol.Monogr. 27, 283-302.

TRIBE, M.A. and BOWLER, K. (1968).   Temperature dependence of

"standard metabolic rate" in a poikilotherm.

Comp.Biochem.Physiol., 25, 427-436.

TURNBULL, A.L. (1960).   The spider population of a stand of oak

(Quercus robur L.) in Wythan Woods, Berks.

Can.Ent. 92, 110-124.

TURNBULL, A.L. (1962).   Quantitative Studies of the food of

Linyphia triangularis Clerck (Araneae : Linyphiidae).

Can.Ent. 1962, 12, 1233-1249.

VAN DER DRIFT, J. (1951).   Analysis of the animal community of

a beech forest floor.   Tijdschr.Ent. 94, 1-168.

VAN DER DRIFT, J. (1953).   Analysis of the animal community

in a beech forest floor.   Meded.Inst.Toeger.Biol.Onderz. 9:1.

WATSON, J. (1966). Studies on the bioenergetics of certain
        terrestrial isopods. Ph.D. Thesis, University of Durham.

WHIGNARAJAH, S. (1968). Energy dynamics of centipede
        populations in woodland ecosystems.
        Ph.D. Thesis, University of Durham.

WHITCOMB, W.H., HITE, M. and EASON, R. (1966). Life history
        of the green lynx spider Peucetia viridans (Hertz)
        (Araneida : Oxyopidae) 39, 259-267. J. Kansas Ent. Soc.

WHITTAKER, J.B. (1965) The biology of Neophilaenus
        lineatus (L) and N. exclamationis (Thunberg)
        (Homoptera : Cercopidae) on Pennine moorland.
        Proc.R.ent.Soc.Lond. (A) 40 (4-6), 51-60.

WIEGERT, R.G. (1964). Population energetics of meadow
        spittlebugs (Philaenus spumarius L.) as affected
        by migration and habitat. Ecol.Monogr. 34, 225-241.

WIEGERT, R.G. (1965). Energy dynamics of the grasshopper
        populations in old field and alfalfa field
        ecosystem. Oikos, 16, 161-176.

WIGGLESWORTH, V.B. (1950). The principles of insect
        physiology. Methuen, London.

APPENDIX 1

R.lividus   Numbers of instar 1 + 2 extracted per sample unit,

1967-68

Sample units

	1	2	3	4	5	6	7	8	9	10
Oct	0	0	7	5	2	3	9	2	4	1
Nov	0	3	10	3	0	3	6	0	9	0
Dec	1	0	0	3	5	8	0	4	0	1
Jan	0	5	17	4	10	2	0	0	9	6
Feb	0	6	13	0	10	0	7	17	5	6
Mar	5	5	0	27	8	8	0	14	3	0
Apr	0	0	0	8	7	2	1	5	3	5
May	0	4	9	11	5	0	0	8	13	11
Jun	0	0	3	0	12	0	5	2	1	0
Jul	0	0	1	0	2	0	0	1	0	1
Aug	0	1	0	0	1	2	0	0	0	0
Sep	1	7	2	3	33	2	0	2	0	1
Oct	3	2	2	5	10	1	1	5	3	13
Nov	0	7	9	6	5	0	4	6	6	0

(Log (N + 1) transformations used)

2.

R.lividus   Numbers of instar 3 extracted per sample unit,

1967-68

Sample units

	1	2	3	4	5	6	7	8	9	10
Oct	0	2	0	3	2	0	1	2	0	1
Nov	0	4	3	1	0	0	2	3	0	0
Dec	0	2	1	1	0	1	2	0	0	0
Jan	0	4	8	2	5	0	0	0	2	2
Feb	0	0	0	0	2	2	0	0	4	2
Mar	0	0	0	0	1	0	2	0	1	0
Apr	3	4	3	1	0	0	5	3	1	0
May	0	2	0	3	0	0	0	2	0	0
Jun	1	0	3	1	2	3	0	0	2	0
Jul	2	4	2	2	4	1	4	2	3	5
Aug	0	3	1	1	3	0	0	0	2	1
Sep	2	2	4	6	3	2	0	5	2	0
Oct	0	0	3	0	4	1	0	1	1	4
Nov	0	1	0	2	1	2	1	0	0	2

(Log (N + 1) transformations used)

3.

<u>R.lividus</u>   Total numbers extracted per sample unit,

1967-68

Sample units

	1	2	3	4	5	6	7	8	9	10
Oct	3	3	7	9	5	5	10	4	4	2
Nov	1	8	16	6	1	3	9	5	10	0
Dec	3	2	3	6	5	10	2	4	0	1
Jan	3	9	25	6	15	3	1	1	1	8
Feb	2	6	15	1	12	3	7	17	10	8
Mar	5	5	1	33	12	9	3	16	4	1
Apr	5	5	4	9	7	6	7	8	6	7
May	3	8	12	15	5	2	4	12	13	12
Jun	3	1	8	5	14	5	8	5	7	2
Jul	4	4	4	3	7	6	4	3	4	7
Aug	0	4	2	2	6	3	0	0	3	2
Sep	4	11	8	11	37	6	1	9	4	3
Oct	4	3	8	6	14	3	3	8	6	17
Nov	4	10	10	9	8	5	7	8	8	5

(Log (N + 1) transformations used)

4.

R.lividus

Test of homogeneity   Seasonal distribution of instar 4, 1967-68

	'Winter'		'Spring'		'Summer'		'Autumn'	
Dec	2	Mar	5	Jun	20	Sep	12	$\Sigma N = 100$
Jan	3	Apr	12	Jul	5	Oct	10	$\bar{N} = 25$
Feb	4	May	4	Aug	8	Nov	15	
ΣX	9		21		33		37	
χ^2	10.02		0.64		2.56		5.76	

$\chi^2_{(3)} = 18.98$ (p < 0.001)

Test of homogeneity   Seasonal distribution of adults, 1967-68

	"Winter'		'Spring'		'Summer'		'Autumn'	
Dec	5	Mar	5	June	3	Sep	8	$\Sigma N = 59$
Jan	3	Apr	2	July	7	Oct	3	$\bar{N} = 14.7$
Feb	3	May	11	Aug	1	Nov	6	
ΣX	13		18		11		17	
χ^2	0.197		0.742		0.932		0.361	

$\chi^2_{(3)} = 2.232$ (p > 0.05)