ASPECTS OF THE ECOLOGY OF FOUR WEB SPINNING SPIDERS IN WEST CENTRAL SCOTLAND

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Summary

The characteristics used to distinguish the four species are described.

A comparison was made between sweep netting, vacuum sampling and hand sampling as methods for estimating spider density. Vacuum sampling and hand sampling were of comparable efficiency and were more efficient than sweep netting. Hand sampling was selected as the main sampling method and it was found that 40 minutes was the optimum time for sampling the 2x1 m sample units.

Methods for assigning spiders to instar were assessed and it was concluded that the length of tibia 1 was the best feature to use. The use of this feature on field samples gave good agreement with the results obtained from laboratory feeding experiments - where instars can be determined with certainty. The growth rates of the spiders were fairly variable and did not approximate closely to the "growth laws" of either Dyar or Przibram .

The energy content of the four species ranged from 20.08-27.39 J/mg. ash free dry weight. Egg sac silk has the lowest energy content and the early instars have lower values than the later instars. Eggs and gravid females had the highest values.

Laboratory feeding experiments were carried out on three of the species. In these the spiders developed at similar rates to those in the field. The results allowed energy budgets to be constructed and these indicated that the spiders had high ingestion and growth efficiencies.

The life cycles and population age structures of the four species were investigated. M. segmentata and L. triangularis have one year life cycles with five instars. The spiders overwinter in the egg eac and the new generation emerges in the late spring and early summer. The spiders grow very quickly and reach the adult stage in late summer. Egg sacs are produced in the autumn and the females have died by early winter. Spiders in open areas grow faster than those in woodland. L. peltata and some specimens of M. mengei also have a one year life cycle with five instars. The new generation emerges from the egg sacs in mid-summer and grows very quickly. The spiders overwinter mainly as sub-adults and moult to adult the following spring. Egg sacs are produced in the summer and the females die soon afterwards. Some specimens of M. mengei have a two year life cycle with six instars. The new generation emerges in late summer and grows slowly. They overwinter mainly as second instars and grow slowly the following year and reach the adult stage in early autumn. They overwinter for a second time as adults and the females produce egg sacs in early summer and have died by mid-summer.

As might be expected, density values are highest as the spiderlings emerge from the egg sacs and decline sharply thereafter. This reflects the high mortality rates. Peak densities for *M. segmentata* and *L. triangularis* were in early summer and for the other two species in the autumn. The average annual densities of the spiders ranged from $1.1/m^2$ in *M. segmentata* to $6.3/m^2$ in *M. mengei* .

Egg sac production of the four species was investigated. The number of eggs produced ranged from 42 in *L. peltata* to 96 in *M. Mengei* . The number and weight of eggs produced was positively correlated with the size of the female. Egg mortality was estimated in the four species.

Standing crop values were estimated throughout the year. Peak values occurred in the autumn in all four species and these ranged from $96.6\ J/m^2$ in *L. peltata* to $260.3\ J/m^2$ in *M. mengei* . The average annual biomass ranged from $35.2\ J/m^2$ in *L. peltata* to $107.8\ J/m^2$ in *M. mengei* .

The sex ratio of the four species was investigated in different years using various sampling methods in different vegetation types. The results were fairly variable but, in general, females predominated.

The distribution and abundance of the four species was investigated. *M. mengei* and *L. peltata* were more abundant in, and more restricted to, woodlands while *M. segmentata* and *L. triangularis* were found in woodlands and in open areas. The vegetation structure seemed to be an important factor in the distribution of the spiders and the four species showed some degree of vertical stratification with regard to web height. This may allow the species to coexist in one habitat. The spiders show varying degrees of horizontal and vertical seasonal movement. This may allow them to exploit the resources of the environment more efficiently. The results from thermal death point and light preference experiments were in accord with the distribution of the four species.

An ichneumon parasite, *Acrodactyla degener* , attacks *L. triangularis* and *L. peltata* . The parasite is bivoltine with the first generation parasitising *L. triangularis* in the summer and the second generation *L. peltata* in the autumn. The larva overwinters attached to the spider. The growth efficiency for the pupal stage was 36% for the first generation and 40% for the second.

Predators of the four species were considered. Some interspecific and intraspecific predation occurs. A red mite of the genus Anystis kills spiderlings of M Mengei and L. peltata during the summer.

The mating behaviour of the four species was investigated and was found to be, in general, similar to that of most web building spiders. There are, however, some differences between the genera. The males of the Linyphia species display web reduction behaviour but this is absent in the Metellina species. Food sharing occurs in the Metellina species but not in Linyphia . The significance of these differences is discussed.

CHAPTER 1

Introduction

Spiders make up a conspicuous part of the terrestrial invertebrate fauna. In suitable habitats they can occur in high densities and this can be strikingly evident in web building spiders when the webs are covered with dew (Fig.1. 1). The aim of this study is to investigate the ecology and population biology of four web spinning spiders in west central Scotland. The original aim of the project was to compare the ecology of the orb web building spider _Metellina segmentata_ (Clerk) with that of the hammock web spider _Linyphia triangularis_ (Clerk) in the Ross Wood near the Glasgow University Field Station. However, early in the study it became evident that the closely related _M. mengei_ (Blackwall) was more abundant than _M. segmentata_ in most parts of the Ross Wood and also that _L. peltata_ (Wider) was more abundant than _L. triangularis_ in many parts of the wood. Thus the study was expanded to deal with the four species.

The four species occur over the whole of Europe, from Sweden in the north to Spain and France in the south and from European Russia in the east to Ireland in the west (Bristowe 1939; Toft 1983). The two _Linyphia_ species are also found in North Africa and in China (Bristowe 1939). _L. peltata_ is found in Japan (Yaginuma 1977). _M. segmentata_ has also been found in Japan (Yaginuma 1977)

Fig.1.1: Several orb and sheet webs covered with dew.

Fig.1.2: Orb web of *Metellina segmentata* .

Fig.1.3: Orb web of *Metellina mengei* .

Fig.1.4: Sheet web of *Linyphia triangularis* .

Fig.1.5: Sheet web of *Linyphia peltata* .

Fig.1.6: Orb webs of *Metellina segmentata* on a gorse bush.

Fig.1.7: Sheet Webs of *Linyphia triangularis* on a conifer tree.

abies), Sitka spruce (*Picea sitchensis*) and Douglas fir (*Pseudotsuga taxifolia*). The dominant field layer vegetation (Elton & Miller 1954) is blaeberry (*Vaccinium myrtillus*) while bracken (*Pteridium aquilinum*) is dominant in other areas. Scattered clumps of heather (*Calluna vulgaris*) are found in places. Heather, gorse (*Ulex earopaelus*) and bog myrtle (*Myrica gale*) are found on the edge of the woodland, while broom (*Sorothamnus scoparius*) is found scattered, both within, and on the edge of, the woodland.

The study investigates aspects of the ecology and population biology of the four species. This involved studies of the density, age structure, seasonal weight changes, natality and mortality of the spiders. Laboratory feeding experiments were also carried out and these, combined with the population data, allowed the life cycles of the four species to be described in detail. The distribution of the four species was investigated in different vegetation types within the Ross Wood and also in other localities in west central Scotland. Some observations were also made on the natural enemies of the spiders and on the mating behaviour.

CHAPTER 2

Distinguishing the Four Species

The aim of this section is to give an account of the taxonomy of the four species and to describe differences between them - particularly the congeneric species. This was based on the examination of the spiders under a binocular microscope.

Metellina segmentata and *M. mengei* were for many years included in the genus *Meta* and were placed in the family Argiopidae (Locket & Millidge 1953). Locket et al (1974) transferred the genus to the family Tetragnathidae and more recently Merrett et al (1985) placed the genus in the family Metidae. Levi (1980) distinguished *M. segmentata* and *M. mengei* from some of the other members of the genus *Meta* , and placed them in the genus *Metellina* . *M. segmentata* and *M. mengei* are closely related species. *M. mengei* was first described by Menge (1866), who regarded it as a smaller variety of *M. segmentata* . Blackwall (1870) considered it to be a separate species - on the basis of the differences noted by Menge and the fact that *M. mengei* breeds in the spring and *M. segmentata* in the autumn. Locket & Millidge (1953) considered *M. mengei* to be a sub-species of *M. segmentata* but Chrysanthus (1953) carried out a detailed comparison and suggested that they were separate species. This was accepted by Locket & Millidge (1974).

Linyphia triangularis and *L. peltata* are placed in the family Linyphiidae (Locket & Millidge 1953). *L. peltata* was considered by Van Helsdingen (1969) to be in genus *Neriene* but this was not accepted by Locket et al (1974) who regarded it as a sub-genus.

M. segmentata and *M. mengei* are variable in colour - especially the former (Fig.2.1), which displays great colour variation. Casual observation suggests that these variations tend to match the colour of the surrounding vegetation. This variation makes it difficult to distinguish individuals of the two species at certain times of the year (Fig.2.2) and it also creates problems in distinguishing these two species from specimens of *Metellina merianae* which is found in some of the sampling areas. Specimens of the two species, of similar size, occur during the period May to November and adults of both species can be found in early September.

The following characters can be used to distinguish the various stages of the two species with a reasonable degree of certainty. (1) In most cases, instars 1 and 2 of *M. segmentata* are whitish brown in colour while those of *M. mengei* are reddish brown (Fig.2.3). (2) Instars 1-3 of *M. mengei* have distinct patterns on the anterior part of the abdomen (Toft, personal communication) which is absent in *M. segmentata* (Fig.2.3). (3) The

Fig.2.1: Colour variants of *Metellina segmentata* .

Fig.2.2: Similarity in appearance of the species (left to right) *Metellina segmentata* , *M. mengei* and *M. merianae* .

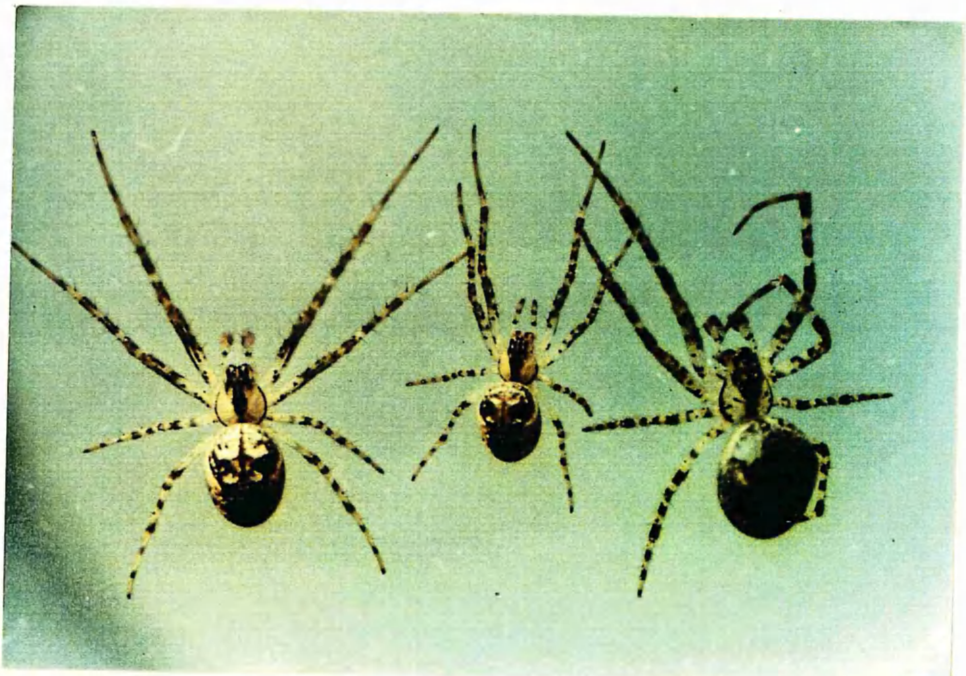


Fig.2.3: Early instars of *Metellina segmentata* (right) and *M. mengei* .

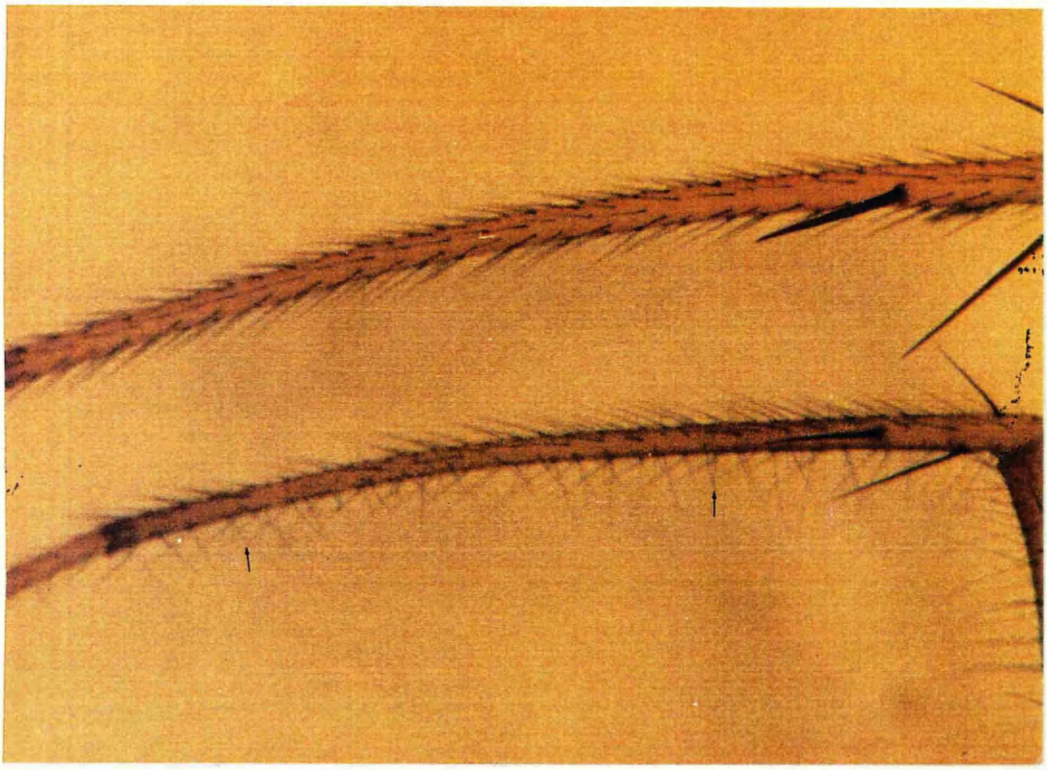
Fig.2.4: *Metellina segmentata* (left) and *M. mengei* showing the black band on the cephalothorax.

cephalothorax of instars 2 - 5 of *M. mengei* has a black V-shaped band which extends to the eyes (Fig.2.4). In *M. segmentata* the band is narrower and is parallel sided rather than V-shaped (Fig.2.4). (4) The metatarsus 1 of adult males of *M. mengei* has a number of long, fine, hairs (trichobothria) which are absent in *M. segmentata* (Fig.2.5). (5) The pedipalps of adult males of the two species are different with respect to the The non-hairy part of the paracymbium and the chitinous band on the bulb of the palp (Fig.2.6) (Locket et al 1974). (6) The sternum of adult males *M. segmentata* is blackish brown in colour whereas the central part of the sternum of *M. mengei* is pale brown (Fig.2.7). (7) Adult females of *M. mengei* may have two white spots on the ventral surface of the abdomen (Fig.2.8). This is never found in *M. segmentata* .

Superficially the two *Linyphia* species look quite similar - especially in early July when individuals of the two species are similar in size. However close examination reveals a number of differences. In *L. triangularis* the cephalothorax is yellow brown with dark margins. There is a median dark line which extends forwards and bifurcates behind the posterior median eyes (Fig.2.9). In *L. peltata* the cephalothorox is blackish brown with no dark margins or median line (Fig.2.9). In *L. triangularis* the dorsal side of the abdomen has a broad, dentated,

Fig.2.5: Metatarsus 1 of adult males of *Metellina segmentata* (above) and *M. mengei* showing the long fine hairs (trichobothria) in the latter species.

Fig.2.6: Pedipalps of adult males of *Metellina segmentata* (right) and *M. mengei* showing differences in the chitinous band of the bulb of the palp (a) and paracymbium (b).



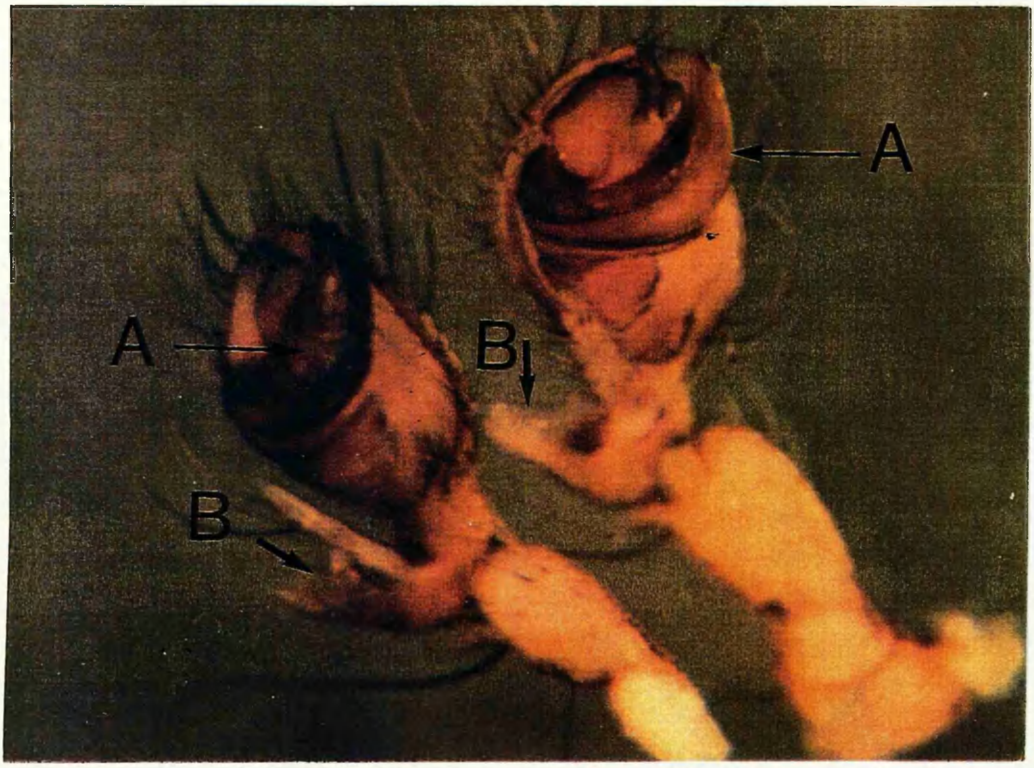
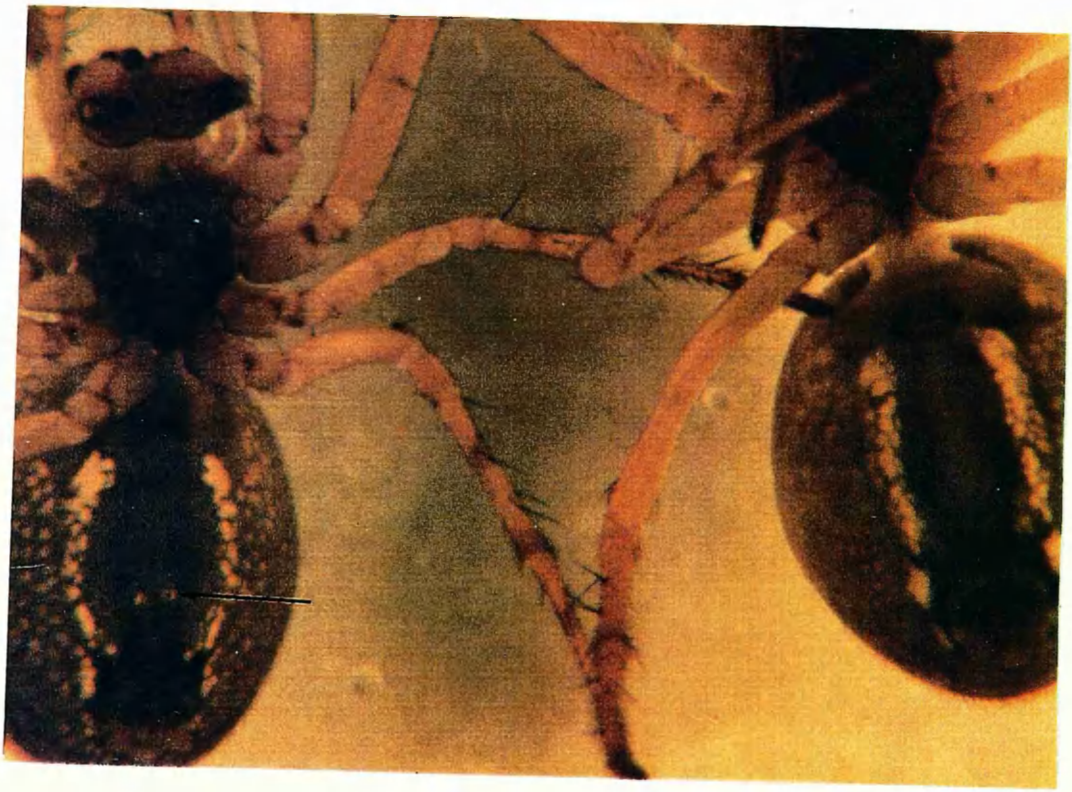

A
A
B
B

Fig.2.7: Sternum of adult males of *Metellina segmentata* (left) and *M. mengei* .

Fig.2.8: Ventral surface of the abdomen of adult females *Metellina segmentata* (right) and *M. mengei* showing two white spots on the latter.



blackish brown band extending back almost to the spinnerets. On either side there is an irregular white band (Fig.2.9) and these unite immediately above the spinnerets. L. peltata has a similar dorsal band but it is brown in colour and the dentation is less sharp (Fig.2.9). In L. triangularis the legs are yellow brown with a tint of green whereas those of L. peltata are pale brown to brown. Spiderlings of L. triangularis show the same colour pattern as the older spiders (Fig.2.10) but those of L. peltata are much paler than the older instars and the colour pattern becomes more distinct with each instar.

CHAPTER 3

Comparisons of Sampling methods

The method used to sample animals in the field depends on the objective of the sampling. For example, the purpose may be to determine the distribution of an animal, or to determine its relative abundance in two different areas, or it may be to determine the absolute numbers of an animal in a given area.

The aim of this section is to evaluate the suitability of various sampling methods for obtaining density estimates of the four spider species. That is, to obtain estimates of the absolute numbers of spiders in a given area. The spiders occur mainly in vegetation between 15 and 150 cm in height, i.e. in the "field layer" vegetation, as defined by Elton & Miller (1954). The methods compared are sweep netting, vacuum sampling and hand collection. In addition, the absolute efficiency of hand collecting was tested by means of laboratory experiments and the optimum duration of hand sampling, for sampling a standard 2x1m sampling unit, was determined in the field.

Southwood (1978) reviewed the methods used for sampling arthropods. He considered vegetation to be the most difficult medium to sample because it is heterogenous and continually changing. He considered that vacuum sampling was a good method for obtaining absolute estimates from vegetation. Duffey (1972,1974) compared hand collecting and vacuum sampling as methods for obtaining estimates of grassland spiders, and concluded that on short vegetation vacuum sampling gave better results but its efficiency was reduced in taller and denser vegetation. He considered hand collecting was an accurate method for obtaining density estimates from fairly open field layer vegetation. Southwood (1978) detailed the advantages and disadvantages of sweep netting. Macfadyen (1963) regarded sweep netting as a very selective method, which can give only estimates of relative numbers, and Lowrie (1971) indicated that the efficiency of sweep netting differed at different times of the day and was affected by the weather.

Comparison of sampling methods for estimating spider density

The sampling areas were located in sections of the Ross Wood where blaeberry (Vaccinium myrtillus) was the dominant field layer vegetation. In July 1980 two sampling areas were laid out. The larger one (Area 6) had an area of 690m^2. It was divided into 280 units each 2x1m with transverse paths 0.5m wide. A second area (Area 2) comprised of 80 units and had an area of 192m^2. Preliminary sampling had indicated that a 2x1m unit was the optimum size, in that it could be sampled from a path without undue trampling on the vegetation of the area.

Smaller units sometimes yielded very small numbers of spiders while larger units were difficult to sample without trampling on the areas.

Sweep netting was carried out using a 50cm diameter net. The area to be swept was sampled in a systematic fashion, each piece of vegetation being swept several times. Spiders were transferred from the net to collecting tubes and the catch was sorted in the laboratory. Vacuum sampling was carried out using a D-vac sampler (Dietrick et al 1959). The samples were transferred to polythene bags and were hand sorted in the laboratory. Hand collecting consisted of searching the vegetation in a systematic fashion, including the ground layer for spiders which may have dropped from the field layer vegetation, and collecting all visible spiders. Small spiders were captured by means of pooter (Southwood 1978). Prior to searching each unit the vegetation was sprayed with a fine jet of water from a garden spray. This made the webs more conspicuous but did not disturb the spiders (Tolbert 1977b). The spiders were transferred to collecting tubes and brought back to the laboratory to be sorted and identified.

On 30/7/1980, eight randomly selected units were sampled from Area 2 by sweep netting and eight units by D-vac sampler. The results are shown in Tables 3.1 and 3.2. The spiders were categorised into the four species under study

Table 3.1: The number of spiders collected by sweep-netting from Area 2 in late July 1980.

Site No.	*M. segm.*	*M. meng.*	*L. tria.*	*L. pelt.*	Total 4 species	Other species	Total spiders
61	0	1	0	0	1	0	1
8	1	1	0	0	2	4	6
18	0	1	0	0	1	0	1
36	0	2	0	0	2	1	3
71	0	8	0	0	8	4	12
64	0	2	0	0	2	4	6
1	0	1	0	0	1	0	1
41	1	0	3	2	6	5	11
Total	2	16	3	2	23	18	41

Table 3.2: The number of spiders collected by D-vac from Area 2 in late July 1980.

Site No.	*M. segm.*	*M. meng.*	*L. tria.*	*L. pelt.*	Total 4 species	Other species	Total spiders
25	0	3	0	2	5	59	64
17	0	8	0	1	9	40	49
13	0	2	0	0	2	19	21
37	2	12	0	3	17	72	89
2	0	8	0	1	9	34	43
7	2	6	1	2	11	26	37
9	0	6	2	1	9	48	57
20	2	20	1	3	26	51	77
Total	6	65	4	13	88	349	437

and "other spiders". These were mainly spiders from vegetation of less than 15cm i.e. "the ground zone" vegetation (Elton & Miller 1954). Sweep netting was less efficient than vacuum sampling for collecting all categories of spider. Thus the efficiency of sweep netting, expressed as a percentage of the catch taken by vacuum sampling, was 24.6% for M. mengei , the dominant field layer spider, 26.1% for the four spiders under study and 5.2% for the "other spiders". This latter value indicates that sweep netting is very inefficient at sampling spiders from low vegetation. Results of comparisons of numbers of spiders collected, by the two sampling methods, are given in Table 3.3. These indicate that vacuum sampling collects significantly more spiders than sweep netting.

In early September 1980 a further comparison of sampling methods was made using vacuum sampling and hand collecting. This involved taking eight samples by each method from Area 6. Hand collecting lasted for 40 minutes in each of the 2x1m units sampled. Justification for this will be given later. The numbers of M. mengei and L. peltata , the two most abundant field layer spiders at this time, were recorded (Table 3.4). The two methods collected similar numbers of spiders (Table 3.5) and differences were not significant ($P>0.05$ in both cases). The D-vac sampler was heavy and noisy and thus physically very tiring to use over extended periods. As hand collecting had a comparable

Table 3.3: Numbers of spiders (mean ± standard deviation), of eight samples in each case, captured by sweep netting and D-vac sampling and the values for t-tests (unequal variance) on comparisons of these samples. ** highly significant (P<0.001), * significant (P<0.05).

Category	Sweep netting	D-vac	t-values
M. mengei	2.00 ± 2.51	8.13 ± 5.72	2.77 *
Four species	2.88 ± 2.64	11.00 ± 7.46	2.90 *
Other species	2.25 ± 2.19	43.63 ±17.48	6.64 **
All species	5.13 ± 4.45	54.63 ±21.99	6.24 **

Table 3.4: The numbers of spiders *Metellina mengei* and *Linyphia peltata* collected by D-vac and hand-collecting methods from the Area 6 in early September 1980.

D-vac 3/9/1980			Hand-collecting 5/9/1980		
Site No.	*M. mengei*	*L. peltata*	Site No.	*M. mengei*	*L. peltata*
18	16	3	66	29	9
196	27	4	22	40	2
57	62	3	58	28	3
43	24	4	117	13	7
220	28	8	190	26	0
48	33	6	197	6	1
148	12	3	120	28	2
67	23	2	47	34	6
Total	225	33	Total	204	30

Table 3.5: The values for t-tests with 14 degrees of freedom for the difference between hand collecting and D-vac. P>0.05.

Species	D-vac	Hand searching	t-values
M. mengei	28.13±15.23	25.50±10.98	0.40
L. peltata	4.13±1.96	3.75±3.20	0.28

efficiency, this method was used in the remainder of the study for estimating spider density.

The efficiency of hand sampling as determined by a laboratory experiment

Hand sampling has been shown to give comparable results to vacuum sampling. However the question remains as to its efficiency with regard to obtaining estimates of absolute numbers of spiders. This was investigated by means of a laboratory experiment. A box 1x0.5m was constructed with a tight-fitting polystyrene sheet placed in the bottom. Branches of blaeberry (_Vaccinium myrtillus_) were inserted into the polystyrene sheet, to simulate a stand of blaeberry. Leaf litter, from which all spiders had been removed, was added to create a habitat similar to that found in the field. The experiment consisted of adding differing numbers of various size categrories of _M. mengei_ , namely adults, sub-adults and spiderlings, to the box which was then closed with a fine mesh cover. After allowing 30 minutes for the spiders to settle down, the vegetation was hand sampled for a total period of 30 minutes. The number of spiders collected was recorded after 15 and 30 minutes. Four replicates were carried out and the results are given in Tables 3.6 a-d.

Table 3.6a: The numbers of spiders introduced and recollected after time intervals in a box of 1x0.5m. Experiment 1.

Category	Number of spiders introduced	Number of spiders collected			Number of spiders missing
		0-15 minutes	15-30 minutes	Total	
Spiderlings	10	6	3	9	1
Sub-adults	5	4	1	5	0
Adults	2	2	0	2	0

Table 3.6b: The numbers of spiders introduced and recollected after time intervals in a box of 1x0.5m. Experiment 2.

Category	Number of spiders introduced	Number of spiders collected			Number of spiders missing
		0-15 minutes	15-30 minutes	Total	
Spiderlings	20	12	6	18	2
Sub-adults	10	4	5	9	1
Adults	18	8	0	8	0

Table 3.6c: The numbers of spiders introduced and recollected after time intervals in a box of 1x0.5m. Experiment 3.

Category	Number of spiders introduced	Number of spiders collected			Number of spiders missing
		0-15 minutes	15-30 minutes	Total	
Spiderlings	20	7	9	16	4
Sub-adults	10	7	3	10	0
Adults	5	4	1	5	0

Table 3.6d: The numbers of spiders introduced and recollected after time intervals in a box of 1x0.5m. Experiment 4.

Category	Number of spiders intruduced	Number of spiders collected			Number of spiders missing
		0-15 minutes	15-30 minutes	Total	
Spiderlings	10	4	5	9	1
Sub-adults	5	4	0	4	1
Adults	4	4	0	4	0

The results for the three categries of spiders, from the four experiments, were analysed separately. Contingency tests, on the results for spiderlings, sub-adults and adults from the four experiments, indicated that the data were homogeneous in each case and they were therefore combined (Table 3.7). As might be expected, larger spiders were collected more quickly than smaller ones. Thus 95% of adults were collected after 15 minutes, 63% of sub-adults and 48% of spiderlings. Significance tests, on the data Table 3.7, confirmed that more adults were caught after 15 minutes than sub-adults ($\chi^2=6.20$, d.f.1, $p<0.05$) or spiderlings ($\chi^2=12.89$, d.f.1, $p<0.05$). After 30 minutes, between 87 and 100% of spiders are recaptured (Table 3.7) and there are no significant differences for the capture rates of the three categories of spiders at the end of 30 minutes. Hence after 30 minutes over 90% of all spiders were captured. The laboratory set-up was rather artificial in that the density of the spiders in the box was considerably higher than that normally found in the field but it does indicate that hand sampling is capable of collecting most spiders from vegetation similar to that found in the field.

Optimum duration of hand sampling in the field

The laboratory experiment indicated that, given a suitable collecting period, hand sampling can collect most spiders

Table 3.7: The numbers of spiders introduced and recollected, with the percentage recollected after time intervals, in a box of 1x0.5m. Combined of the four experiments.

Category	Number of spiders introduced	Number of spiders collected					
		Between 0-15 minutes	%	Between 15-30 minutes	%	Total 0-30 minutes	%
Spiderlings	60	29	48.3	23	38.3	52	86.7
Sub-adults	30	19	63.3	9	30.0	28	93.3
Adults	19	18	94.7	1	5.3	19	100
Total	109	66	60.6	33	30.3	99	90.8

from blaeberry dominated vegetation. The purpose of this section is to determine the optimum duration for sampling in the field. The density of blaeberry can vary considerably from place to place. Casual observation suggested, as might be expected, that spiders were observed and collected more quickly in less dense vegetation. Blaeberry stands were subject to defoliation, probably by phytophagous insects. Spiders, and their webs, were much more visible in such defoliated patches. In order to test the effect of vegetation structure, on the optimum duration of sampling, a field experiment was carried out. This involved hand sampling in two areas of blaeberry close to Area 6 on 15/9/1980. One of these areas (Area 3) had a dense stand of blaeberry while the other (Area 4) was an area where the blaeberry had been extensively defoliated. Four 1x1m quadrats were selected at random in each area and were hand sampled. The cumulative number of spiders in each quadrat was recorded at five minutes intervals. Each quadrat was sampled for a total of 35 minutes. The results are given in Tables 3.8 and 3.9. Contingency tests indicated that the data for the four quadrats in each area were homogeneous and the results were therefore combined. These totals were plotted against time (Fig.3.1). The results indicated that hand collecting was significantly more efficient in the defoliated blaeberry than in the dense blaeberry. Thus after 5, 10 and 15 minutes significantly more of the total numbers of spiders

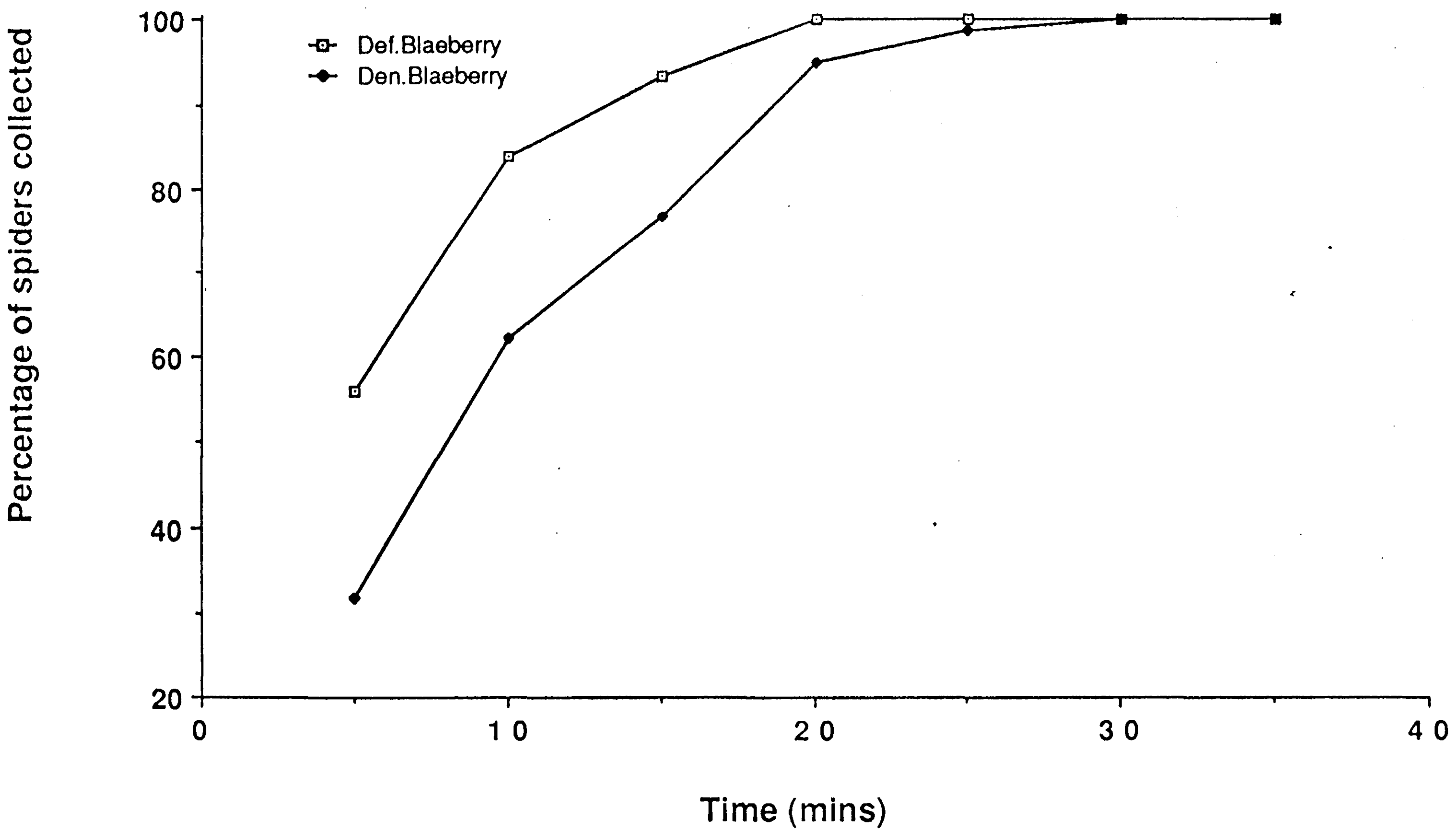
Table 3.8: The number of spiders recorded during time sampling from four quadrats (1x1 m) in dense vegetation (Area 3) and percentage of final total collected after 35 minutes.

	Cummulative number of spiders collected									
Quadrate	1		2		3		4		Total	
Time	No	%	No	%	No	%	No	%	No	%
5	4	23.5	5	31.3	11	36.7	6	31.6	26	31.7
10	9	52.9	9	56.3	21	70.0	12	63.2	51	62.2
15	13	76.5	12	75.0	23	76.7	15	78.9	63	76.8
20	17	100	15	93.8	28	93.3	18	94.7	78	95.1
25	17	100	16	100	29	96.7	19	100	81	98.8
30	17	100	16	100	30	100	19	100	82	100
35	17	100	16	100	30	100	19	100	82	100

Table 3.9: The number of spiders recorded during time sampling from four quadrats (1x1m) from defoliated vegetation (Area 4) and percentage of final total collected after 35 minutes.

	Cumulative number of spiders collected									
Quadrate	1		2		3		4		Total	
Time	No	%	No	%	No	%	No	%	No	%
5	10	55.6	8	66.7	17	56.7	7	46.7	42	56.0
10	15	83.3	11	91.7	25	83.3	12	80.0	63	84.0
15	17	94.4	12	100	28	93.3	13	86.7	70	93.3
20	18	100	12	100	30	100	15	100	75	100
25	18	100	12	100	30	100	15	100	75	100
30	18	100	12	100	30	100	15	100	75	100
35	18	100	12	100	30	100	15	100	75	100

Fig.3.1: Spiders collected during 5 minute time intervals in defoliated and dense blaeberry (expressed as a percentage of the total collected after 35 minutes).


Def.Blaeberry
Den.Blaeberry
Percentage of spiders collected
100
80
60
40
20
0
1 0
2 0
3 0
4 0
Time (mins)

collected during the total duration of the sampling period, were collected in the defoliated blaeberry (Table 3.10).

The results also indicated that in the dense blaeberry, for a 1x1m quadrat, 95% of the total number of spiders collected during the 35 minutes period were taken within 20 minutes (Table 3.8). The standard sampling units in the sampling grids were 2 m^2 and hence it was decided that the optimum sampling period for such units would be 40 minutes. Consequently, all density estimates of spiders involved hand sampling units of 2x1m for periods of 40 minutes.

Discussion

Sweep netting was found to be less efficient than D-vac sampling. This agrees with Macfadyen (1963) who indicated that sweep netting was a very selective method of sampling. Casual observation also indicated that sweep netting is less efficient in wet than in dry vegetation and this agrees with the findings of Lowrie (1971). In both the field and the laboratory experiments hand collecting was found to be an efficient method of capturing spiders. The D-vac sampler had a comparable efficiency to hand collecting and this confirms Southwood's (1978) view that vacuum sampling is a good method for obtaining absolute estimates of arthropods from vegetation. The results of

Table 3.10: Numbers of spiders collected at various time intervals, in defoliated and dense blaeberry, expressed as a proportion of the total numbers of spiders collected during the 35 minutes sampling period.

Time	Type of vegetation	Caught	Not caught	x^2
After 5 minutes	Defoliated	42	33	8.45
	Dense	26	56	
After 10 minutes	Defoliated	63	12	8.30
	Dense	51	31	
After 15 minutes	Defoliated	70	5	7.01
	Dense	63	19	

sampling of dense and defoliated blaeberry agreed with Duffey's (1972, 1974) findings that hand collecting was most effective in fairly open field layer vegetation. Hand collecting was preferred to vacuum sampling because it was a less tiring method and was less damaging to the vegetation. It did have the disadvantage, however, of being more time-consuming than vacuum sampling.

CHAPTER 4

The Determination of Spider Instars

The aim of this section is to assess methods which can be used to separate spiders into instars and to justify the methods used in the present study to determine the number of instars.

An ability to assign spiders to instar was necessary in order to construct age histograms for the population samples. This information was required for three purposes: (1) To assist in the working out of the life-cycle. (2) To allow estimates to be made of mortality at different stages of the life-cycle. (3) To allow the calculation of the amount of energy flowing through the spider population.

Arthropods moult regularly as immature animals and sometimes as adults. The number of instars can be determined directly by observing the number of times the animal moults during its lifetime. This is usually determined in laboratory experiments. Alternatively, the number of instars can be determined by some indirect method. It is often possible to separate arthropods into instars on the basis of measuring characteristics which display discontinuities, which correspond to the number of moults. This method has been widely used to age immature stages of insects (Southwood 1978) and has led to the formulation of various Growth Laws or Rules e.g. Dyar's Law

(Dyar 1890) and Przibram's Rule (Przibram & Megusar 1912) which suggest that certain parts of an arthropod's body increase by a fixed amount from instar to instar. Thus Dyar's Law suggests that sclerotised structures increase by a factor of 1.4 from one instar to the next, while according to Przibram's Rule the factor is 1.26. If such laws hold, then knowing the size of a particular structure in two known instars (e.g. first instar and adult instar) should allow the number of instars between the two stages to be calculated.

There are problems associated with these methods: The direct method usually involves laboratory rearing and it has been shown that the rearing conditions can affect the growth rate and the number of instars (Bonnet 1930; Browning 1941; Deevey 1949; Edgar 1968; Miyashita 1968a; Robinson & Robinson 1978; Edmunds 1982; Franke & Sissom 1984). In general, high temperatures and good feeding result in more rapid growth and fewer instars. Hence growth rate and number of moults may differ from that found in the field because the rearing conditions differ. The indirect method may not work because the plotting of measurements may not reveal clusters of measurements which correspond to the number of instars. This may be because there is considerable individual variability in the growth rate (Miyashita 1968a) or because the sexes have different numbers of instars and/or grow at different rates. Thus the

"Growth Laws" may not hold for the above reasons or, additionally, because some structures may show allometric growth (Juberthie 1954).

Features used to assign spiders to instar.

A variety of features have been used to assign spiders to instar when using the indirect method. These include; the weight of the spider, the overall body length, cephalothorax dimensions, lengths of leg segments (Juberthie 1954; Edgar 1971a; Geyer 1971; Pennington 1977; Toft 1976, 1978, 1983; Akita 1979; Austin 1984). It is now generally accepted that the weight and overall body length are poor indicators of instar.

Methods

In the present study four features were used. These were cephalothorax length and cephalothorax breadth and the length of the tibia of legs 1 and 4. These features were measured for all spiders in a large sample (n=132) of Metellina mengei taken on 24/9/80. The spiders were measured under X30 magnification using an eyepiece graticule. One graticule unit was equivalent to 0.033mm and the features were measured to the nearest 0.033mm. The measurements of leg length could be performed more quickly and reliably than those of the cephalothorax as the spiders needed to be manipulated less.

Results

The results are shown in Fig.4.1 & 4.2. In Fig.4.1 each column in the histogram represents 1 graticule unit i.e. 0.033mm. In Fig.4.2 each column represents 3 graticule units i.e. 0.099mm (0.1mm).

In Fig.4.1 all four characters indicate three distinct size groups are present and tibia 1 and cephalothorax length suggest an additional group of smaller spiders may be present. The three groups correspond to second, third and fourth instars (see next section). In Fig.4.2 three distinct groups are still obvious with respect to tibia 1 and cephalothorax length and to a lesser extent with cephalothorax breadth. Three size groups are not apparent with respect to tibia 4. It was more time-consuming to construct histograms where each column represented 0.033mm than it was when each column represented 0.1mm and hence these results suggest that tibia 1 and cephalothorax length were, on this basis, better features than the other two. As indicated above, leg segments could be measured more quickly and more consistently than cephalothorax dimensions. Hence all field samples which were analysed, to sort the spiders into instar, were done so on the basis of the length of tibia 1 and histograms from such samples were constructed using columns which represented 0.1mm.

Fig.4.1: Separation of instars of Metellina mengei based on the sizes of different features in a sample on 24/9/80. Each column in the histogram represnts 1 graticule unit i.e. 0.033mm.

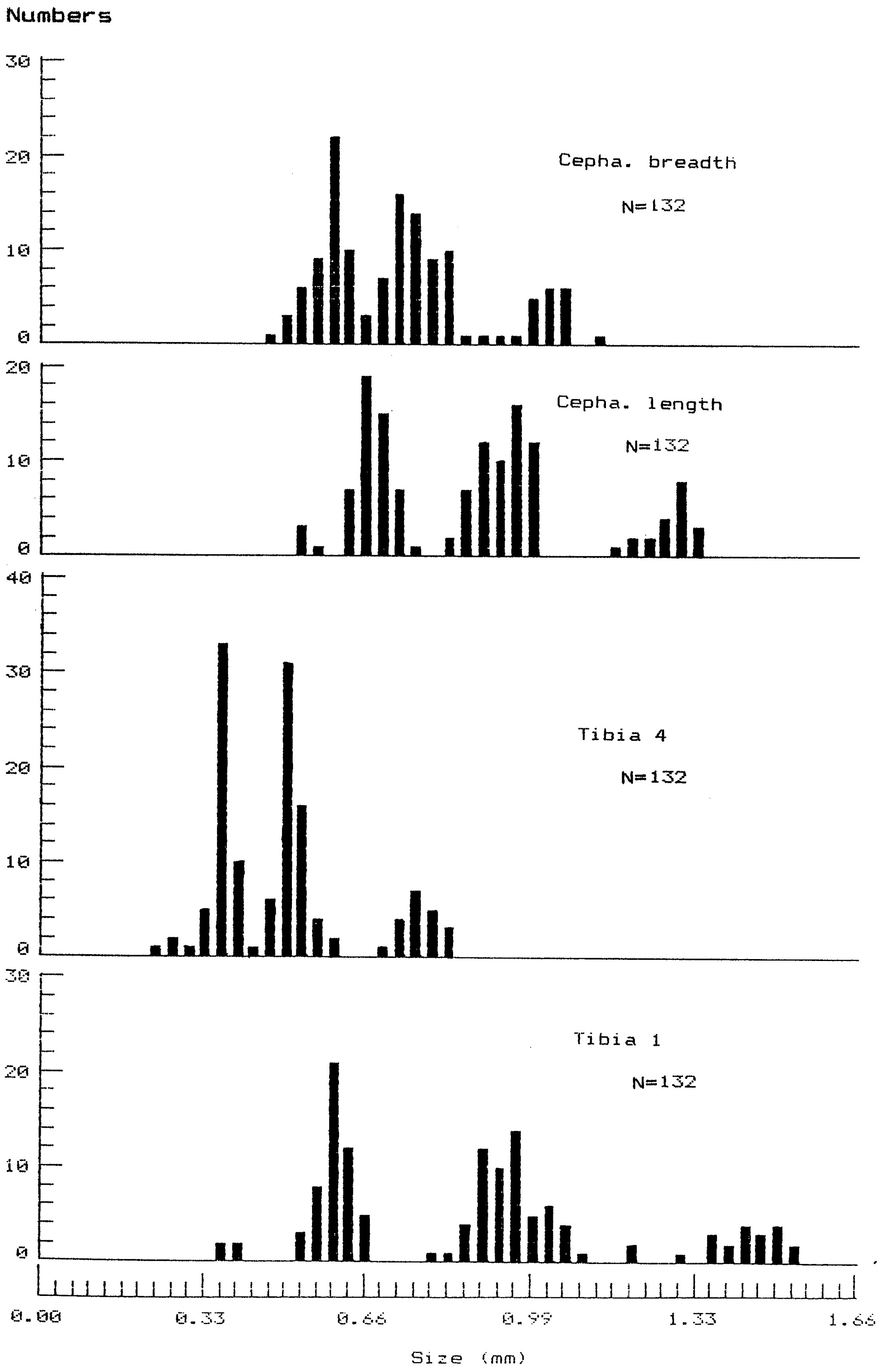
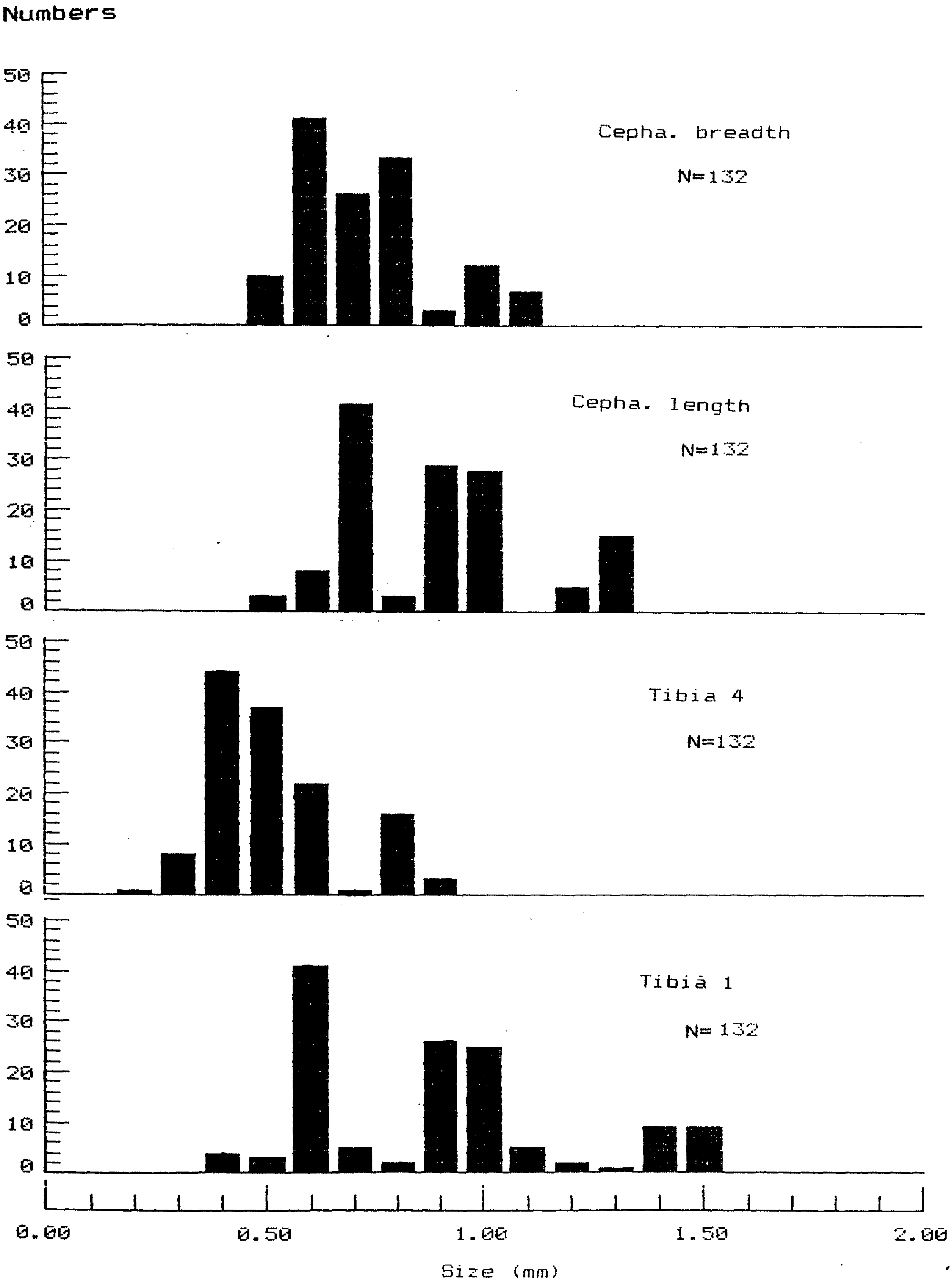

Numbers
30
20
10
0
Cepha. breadth
N=132
20
10
0
Cepha. length
N=132
40
30
20
10
0
Tibia 4
N=132
30
20
10
0
Tibia 1
N=132
0.00
0.33
0.66
0.99
1.33
1.66
Size (mm)

Fig.4.2: Separation of instars of Metellina mengei based on the sizes of different features in a sample on 24/9/80. Each column in the histogram represnts three graticule units i.e. 0.099mm (0.1mm).


Numbers
50
40
30
20
10
0
Cepha. breadth
N=132
Cepha. length
N=132
Tibia 4
N=132
Tibia 1
N=132
0.00
0.50
1.00
1.50
2.00
Size (mm)

Comparison of methods for assigning spiders to instar.

M. mengei was used as the test animal for this assessment. The number of instars which this species has was determined by three methods: (1) Rearing experiments (2) Analysis of field samples (3) Application of "Growth Laws".

Methods

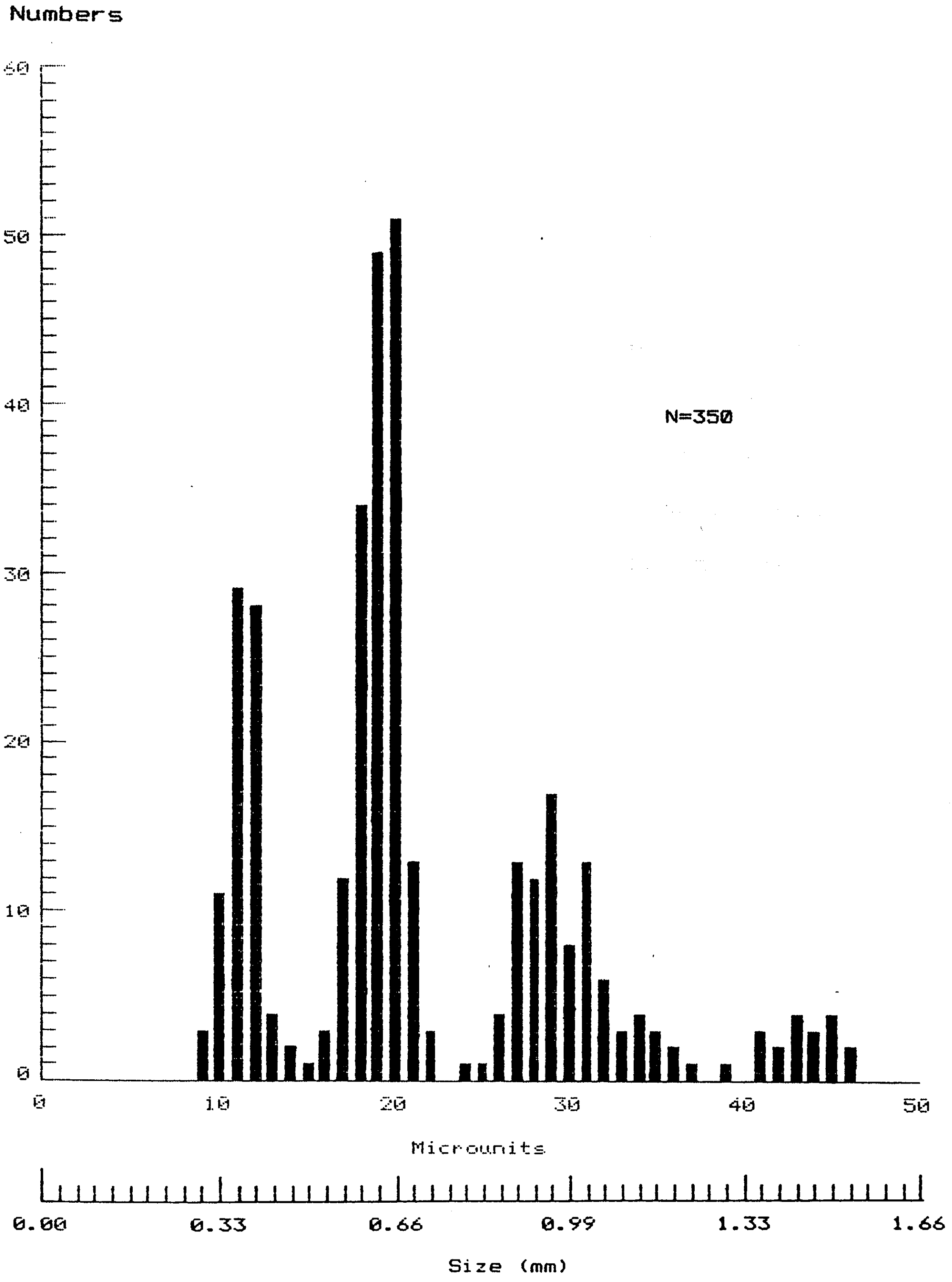
(1) Rearing experiments. Spiderlings were collected from the field in late July 1981 and reared in the laboratory until they moulted. The rearing conditions will be described in another chapter (Laboratory Feeding Experiments). Some spider mortality occurred in these experiments and consequently spiders were brought in from the field at regular intervals to supplement the animals used in the rearing experiments. The cephalothorax breadth and the length of tibia 1 were measured for each spider at the start of the experiment and also after each moult. Cephalothorax breadth was measured rather than cephalothorax length because the latter is difficult to measure in living spiders without damaging the animals.

(2) Field samples. In order to determine field growth rates, and the mean size for several instars, samples were

taken from the field on three occasions during the summer and autumn of 1980. The samples were taken on 6/8/80 (n=51) 5/9/80 (n=167) and 24/9/80 (n=132). The length of tibia 1 was measured for each spider. The three samples were amalgamated and a histogram was constructed for the combined sample of 350 spiders (Fig.4.3). This histogram was used to attempt to determine the number of instars.

Application of "Growth Laws". The rearing experiments allowed spiders to be assigned to instar with absolute certainty. The efficacy of Dyar's Law and Przibram's Rule, in determining the number of instars, was tested by utilizing the sizes of the spiderlings and adult instars from the rearing experiments. Values were inserted into the formula $\log A=\log(Y)+n\log(P)$ (Franke & Sissom 1984) where A is the size of the adult, Y is the size of the known instar (in this case the first instar spiderling), n is the number of moults and P is the progression factor (1.4 for Dyar and 1.26 for Przibram).

Fig.4.3: Separation of instars of Metellina mengei based on tibia 1 in a combined sample in summer and autumn 1980. Each column in the histogram represnts one graticule unit i.e. 0.033mm.


Numbers
60
50
40
30
20
10
0
N=350
0
10
20
30
40
50
Microunits
0.00
0.33
0.66
0.99
1.33
1.66
Size (mm)

Results

The results of the laboratory rearing experiments are summarized in Tables 4.1 & 4.2. These indicate that M. mengei has five instars and that the sub-adult and adult males are larger than the females. Growth progression factors have been calculated for each moult for both tibia and cephalothorax (Table 4.3). It can be seen that the progression factors are greater for tibia than for cephalothorax. The growth factor also varies considerably from instar to instar with respect to tibia. This character appears to display sexual dimorphism - with the sub-adult and adult males having larger tibiae than the females. With respect to cephalothorax; the growth progression factors are less variable than for the tibia and there is no evidence of sexual dimorphism. The growth progression factors for tibia 1 are, in general, greater than the 1.4 postulated by Dyar and the 1.26 by Przibram. With respect to cephalothorax; the values tend to fall between the two factors. These results suggest that the growth progression factors are fairly variable and do not correspond particularly closely to either Dyar's or Przibram's values.

An inspection of Fig.4.3 suggests that the spiders from the field samples fall into four distinct size groups with peaks at 0.36, 0.67, 0.97 and 1.43mm. These peaks correspond well to the values for first, second and third

Table 4.1: Mean size of tibia 1 of specimens of *M. mengei* from laboratory rearing eperiments.

Reared instar	Mean size of tibia 1 (mm) ± S.D. (number of spiders reared)	Subsequent instar	Mean size of tibia 1 (mm) ± S.D. (number of spiders which survived to subsequent instar)
1st	0.35 ± 0.02 (7)	2	0.63 ± 0.04 (3)
2nd	0.64 ± 0.03 (7)	3	0.99 ± 0.02 (4)
3rd	0.98 ± 0.03 (7)	4 female	1.43 ± 0.06 (3)
		4 male	1.70 ± 0.14 (2)
4th female	1.45 ± 0.06 (4)	5 female	2.00 ± 0.20 (3)
4th male	1.73 ± 0.12 (3)	5 male	2.97 ± 0.21 (3)

Table 4.2: Mean breadth of cephalothorax of specimens of *M. mengei* from laboratory rearing experiments.

Reared instar	Mean size of tibia 1 (mm) ± S.D. (number of spiders reared)	Subsequent instar	Mean size of tibia 1 (mm) ± S.D. (number of spiders which survived to subsequent instar)
1st	0.50 ± 0.03 (7)	2	0.62 ± 0.02 (3)
2nd	0.61 ± 0.04 (7)	3	0.78 ± 0.05 (4)
3rd	0.77 ± 0.08 (7)	4 female	1.07 ± 0.06 (3)
		4 male	1.10 ± 0.00 (2)
4th female	1.05 ± 0.06 (4)	5 female	1.37 ± 0.06 (3)
4th male	1.13 ±20.06 (3)	5 male	1.43 ± 0.61 (3)

Table 4.3: Growth progression factors for instars of *M. mengei* for tibia 1 and cephalothorax breadth from laboratory rearing experiments.

Instar	Tibia 1	Cephalothorax
1st - 2nd	1.80	1.24
2nd - 3rd	1.55	1.28
3rd - 4th female	1.46	1.39
3rd - 4th male	1.73	1.43
4th - 5th female	1.38	1.30
4th - 5th male	1.71	1.27

Table 4.4: Mean size of tibia 1 of specimens of *M. mengei* from field samples.

Instar	Mean size of tibia 1 (mm) ± S.D. (number of spiders in sample)
1st	0.38 ± 0.03 (77)
2nd	0.64 ± 0.04 (165)
3rd	0.99 ± 0.09 (88)
4th female	1.45 ± 0.05 (18)

instars and fourth instar females from the laboratory rearing experiment (Table 4.1). The mean tibia lengths for each of the size groups have been calculated (Table 4.4). The single spiders at 0.5mm and 1.30mm (Fig.4.3) have been omitted from the calculations as they cannot be assigned to an age group with certainty and the calculations are therefore based on a total of 348 spiders. A comparison of Table 4.4 with Table 4.1 indicates a very good agreement between the mean values for tibia 1 from the field samples and from the laboratory rearing experiments. Hence it would appear that M. mengei can be assigned to instar in field samples, with a high degree of certainty, on the basis of the length of tibia 1.

The predicted number of instars, using Dyar's and Przibram's progression factors, is given in Table 4.5 for both tibia 1 and cephalothorax breadth. The known number of instars from the rearing experiments is included for comparison. It can be seen that the agreement, between the predicted number of instars and the observed number, was poor - especially for Przibram's factor. The predictions, on the basis of tibia 1, are particularly poor and this reflects the allometric growth shown by this structure.

Table 4.5: Number of instars of *M. mengei* as predicted from Dyar's and Przibram's progression factors and as determined by laboratory rearing experiments.

Structure	Sex	Progression factor		Laboratory rearing experiments
		Dyar's (1.4)	Przibram's (1.26)	
Tibia 1	male	7	10	5
	female	6	9	5
Cephalothorrax breadth	male	4	6	5
	female	4	4	5

Discussion

The results indicate that the length of tibia 1 is a convenient and reliable feature for assigning specimens of M. mengei to instar and this is in agreement with Toft (1976, 1983). Also there is good agreement between the growth rate and the number of instars in the field and in the laboratory rearing experiments. The growth progression factors of Dyar and Przibram do not give good predictions of the number of instars. This is in agreement with the findings of Juberthie (1954) and Miyashita (1968a) who found that the growth factors did not remain constant from instar to instar and also that some spider structures, particularly leg segments, showed marked allometric growth.

CHAPTER 5

The Energy Content of the Four Spider Species

The aim of this section is to present information on the energy content of various stages in the life cycles of *Metellina mengei*, *M. segmentata*, *Linyphia triangularis* and *L. peltata*. This information was required for a population energetics study of the spiders.

Methods

Spiders and their egg sacs were collected from the field and within one day they were killed and dried in a vacuum oven at 60 C for three days. The dried material was made into pellets ranging in weight from 5-25mg. The energy content of these pellets was determined in a Phillipson Microbomb Calorimeter (Phillipson 1964). The calorimeter was calibrated using benzoic acid pellets (Phillipson 1964). Relatively few determinations were made for *L. peltata* but a fairly complete set of results was obtained for the other three species.

Results

The patterns for the energy contents were similar for the four species (Tables 5.1 & 5.2). Thus for the two *Metellina* species and for *L. triangularis* , egg sac silk has the lowest energy content and the values for eggs, gravid females, adult females and adult males are higher than those for sub-adult animals and early instars. Ranking the three species, which have six common categories represented (Table 5.2), confirms this general pattern. Although there are no significant correlations those for *M. segmentata* versus *M. mengei* and *M. mengei* versus *L. triangularis* are close to being significant. For the three species where most of the categories are represented, the ranges in the energy contents are similar. For *M. segmentata* 20.24 - 27.39 Joules/mg, for *M. mengei* 20.08 - 26.64 and for *L. triangularis* 19.78 - 27.36.

The values obtained agree well with published values for energy equivalents for spiders (Tables 5.3, 5.4, 5.5 & 5.6). Table 5.3 gives the published values for spiders, Table 5.4 for spider eggs or egg sacs, Table 5.5 for web silk or egg sac silk and Table 5.6 compares the ranges of published values for these three categories with the ranges found in the present study.

Table 5.1: Energy equivalents (Joules/mg ash free dry weight ± standard deviations; (n) number of samples) of various categories of *M. segmentata*, *M. mengei*, *L. triangularis* and *L. peltata*.

	Species			
Category	*M. segmentata*	*M. mengei*	*L. triangularis*	*L. peltata*
Eggs	25.09 ± 0.72 (5)	24.75 ± 0.50 (2)	27.36 ± 1.77 (5)	
Gravid females	27.39 ± 0.82 (5)	26.64 ± 0.60 (4)	26.70 ± 0.72 (5)	26.58 ± 0.42 (4)
Adult females	26.09 ± 0.42 (4)	25.01 ± 0.40 (4)	25.59 ± 0.98 (5)	
Adult males	26.57 ± 0.43 (4)	24.10 ± 0.31 (4)	24.85 ± 0.57 (4)	25.56 ± 0.12 (3)
Sub-adults	23.61 ± 0.35 (4)	23.48 ± 0.62 (3)	23.42 ± 0.47 (4)	24.89 ± 0.58 (4)
Early Instars	23.96 ± 0.18 (3)		22.72 ± 0.42 (4)	
Egg sac silk	20.24 ± 1.71 (4)	20.08 (1)	19.78 ± 1.21 (4)	

Table 5.2: Ranking of *M. segmentata*, *M. mengei* and *L. triangularis* according to energy equivalents (Joules/mg ash free dry weight) of various categories and Spearman Rank Correlation values for the comparisons of the 3 rankings (categories joined by lines within species indicate no significant difference)

M. segmentata			*M. mengei*			*L. triangularis*		
Gravid females	27.39	¦	Gravid females	26.64		Eggs	27.36	¦
Adult males	26.57	¦¦	Adult females	25.01	¦	Gravid females	26.70	¦
Adult females	26.09	¦	Eggs	24.75	¦¦	Adult females	25.59	¦¦
Eggs	25.09		Adult males	24.10	¦	Adult males	24.85	¦
Sub-adults	23.61		Sub-adults	23.48	¦	Sub-adults	23.42	
Egg sac silk	20.24		Egg sac silk	20.08		Egg sac silk	22.72	

Spearman Rank correlation Values		
M. segmentata & *M. mengei*	*M. mengei* & *L. triangularis*	*L. triangularis* & *M. segmentata*
r = 0.83 N.S.	r = 0.88 N.S.	r = 0.60 N.S.

Table 5.3: Energy equivalents (Joules/mg ash free dry weight) of spiders.

Species or group of spiders	Energy equivalent	Author
Pardosa lugubris (wolf spider)	20.57	Edgar 1971
Lycosa species (wolf spider)	22.51 - 24.52	Van Hook 1971
Metellina segmentata (orb web spider)	22.42 - 26.32	Geyer 1971
Various spider families and genera	23.85 - 25.67	Moulder & Reichle 1972
Pardosa palustris (wolf spider)	24.89 - 26.02	Steigen 1975
Geolycosa godeffroyi (wolf spider)	24.31	Humphreys 1977
Variety of spider species	22.59 - 24.02	Norberg 1978
Zygiella atrica (orb web spider)	22.05	Britten 1979
Linyphia triangularis (sheet web spider)	23.30	
Theridion sisyphuim (comb footed spider)	21.76	
Trochosa terricola (wolf spider)	26.32	Workman 1978
Cyrtophora cicotrosa (orb web spider)	27.30	Palanichamy & Pandian 1983

Table 5.4: Energy equivalents (Joules/mg ash free dry weight) of spider eggs and egg sacs.

Species or group of spiders	Energy equivalent	Author
Pardosa lugubris (wolf spider)	22.64	Edgar 1971
Metellina segmentata (orb web spider)	26.69	Geyer 1971
Pardosa palustris (wolf spider)	25.98	Steigen 1975
Argiope pulchella (orb web spider)	25.73	Prakash & Pandian 1978
Spider species (variety of species)	27.32	Anderson 1978
Cytrophora cicotrosa (orb web spider)	26.94	Palanichamy & Pandian 1983
Geolycosa godeffroyi (wolf spider)	24.70	Humphreys 1977

Table 5.5: Energy equivalents (Joules/mg ash free dry weight) of web silk or egg sac silk.

Species or group of spiders	Energy equivalent	Author
Metellina segmentata (Orb web spider)	20.46	Geyer 1971
Pardosa palustris (wolf spider)	23.01	Steigen 1975
Sosippus janus (sheet web spider)	19.37	Prestwich 1977
Lepthyphantes zimmermanni (sheet web spider)	17.45	Ford 1977
Geolycosa godeffroyi (wolf spider)	18.40	Humphreys 1977

Table 5.6: Range of energy equivalents (Joules/mg ash free dry weight), for spiders, spider eggs and spider silk, from published studies (Tables 5.3, 5.4 & 5.5) and the present work (Table 1).

Category	Published values	Present study
Spiders	20.57 - 27.30	22.72 - 27.39
Eggs	22.64 - 27.32	24.75 - 27.36
Silk	17.45 - 23.01	19.78 - 20.24

Discussion

The energy equivalents are in good agreement with published values. There appears to be a constant pattern within the four species in that the energy content is lower in the early stages of the life cycle than in the later stages with eggs and gravid females tending to have the highest values.

Anderson (1978) found that in spiders which overwintered in the egg sac the energy values of the eggs were higher than in spiders where egg sacs were produced in the summer. The energy values for the eggs of *M. segmentata* and *L. triangularis* , which overwinter in the egg sac, were higher than that of *M. mengei* which has a summer egg sac. However the values for *M. segmentata* was closer to that of *M. mengei* than it was to *L. triangularis* . Hence generic differences may be a more important than the time of the year the egg sacs are produced.

CHAPTER 6

Laboratory Feeding Experiments on the Spiders *Metellina segmentata* , *Metellina mengei* and *Linyphia triangularis* .

The aim of this section is to construct an energy budget for each species. The intention was to combine these results with field data on density, natality and mortality to estimate the flow of energy through the spider populations.

Introduction

There have been few studies, involving laboratory feeding experiments, to construct individual energy budgets for spiders. Most of these studies involved wolf spiders (F.Lycosidae). Edgar (1971) gave an account of the ecological energetics of the wolf spider *Pardosa lugubris* and Steigen (1975) studied the energetics of the spider *Pardosa palustris* . Humphreys (1977) investigated the factors influencing the energy budgets of *Geolycosa godeffroyi* and Workman (1978) studied the effect of temperature on the energy budget of *Trochosa terricola* . Studies by Hagstrum (1970), Van Hook (1971) and Moulder and Reichle (1972) have investigated various aspects of the energetics of spider populations but were not based on feeding experiments. With regard to web-building spiders, Turnbull (1962) carried out laboratory feeding experiments on the spider Linyphia triangularis , but the results of these were not expressed in calorific terms, while Kajak (1967) estimated food consumption and production in a field study of three web spinning spiders.

Life cycle

The life cycles of the three species have been described in detail elsewere but a brief account is given here to facilitate the understanding of this section.

Metellina segmentata and Linyphia triangularis have similar one year life cycles. The adult females produce egg sacs in the autumn. The egg sacs overwinter and the spiderlings emerge from these egg sacs in late spring. They grow very quickly and reach the adult stage in early August, in case of L. triangularis , and in early September in case of M. segmentata . Adult females die in the autumn after producing egg sacs.

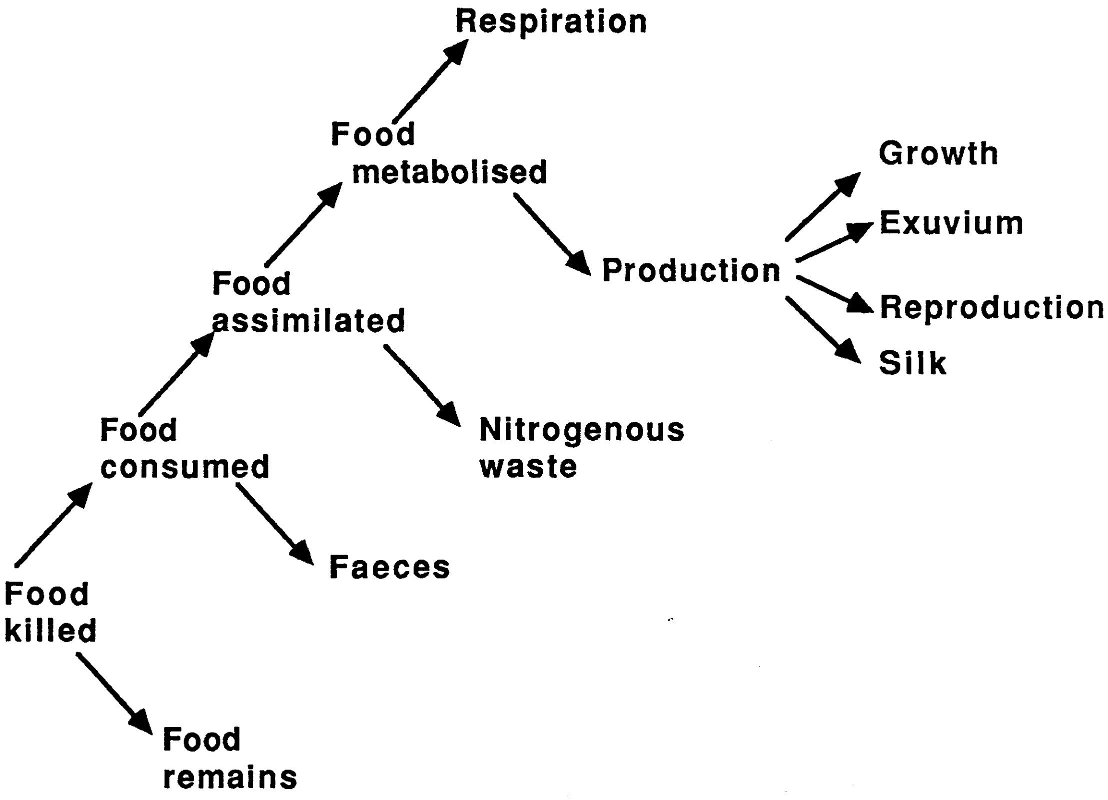
Metellina mengei has two types of life cycle. Some spiders can complete their life cycle in one year while others take two years. The spiderlings from the former emerge from the egg sacs in mid-summer. They grow very quickly and reach the sub-adult stage in late September. They overwinter and moult to adult in the following spring and the adult females die in mid-summer after producing egg sacs. The spiderlings with the two year life cycle emerge in late summer. They grow slowly and overwinter mainly as second instars. During the following spring and summer these animals continue their development and reach the adult stage in early September. The adult females overwinter and die in the early summer after producing egg sacs.

The males of these species cease to build webs soon after reaching the adult stage and seek females for mating. They feed little during the mating season - occasionally feeding on prey items caught in the web of a female.

Materials and methods

The various pathways in an animal's energy budget are indicated in Fig.6.1. In this study the quantity of food killed was known. The food remains were collected and the difference between the two gave an estimate of the quantity of food consumed. As will be discussed later, the amount of energy lost as faeces and nitrogenous waste is considered to be negligible. Consequently, the food assimilated is taken to be equivalent to food consumed. Growth was determined by weighing the spiders after each moult or at the termination of the experiment. This represented the increase in body weight associated with both growth and

Fig.6.1: The various pathways in an animal's energy budget.


Respiration
Food metabolised
Growth
Exuvium
Production
Reproduction
Silk
Food assimilated
Food consumed
Nitrogenous waste
Faeces
Food killed
Food remains

reproduction. Exuvia were collected after moulting. Silk production, as will be discussed later, was considered negligible for the Metellina species but was estimated for Linyphia triangularis . The energy involved in respiration was estimated by subtracting the sum of the energy of production from the energy content of the food consumed.

The small spiders, first and second instars, were reared in tubes 2.5x5 cm with a pad of filter paper in the bottom. These were kept moist and provided the spiders with a source of drinking water (Parry 1954). Large spiders, third instar to adults, were reared in plastic containers 15x15x17 cm. (Fig.6.2). The lid of the container was removed and the container inverted. A circular hole was cut in the bottom of the container and this was covered with fine mesh. This provided ventilation and access for spraying water into the container. A smaller hole was also cut in the bottom and this was plugged with cotton wall. This allowed food to be introduced to the container without disturbing the spider or its web. Twigs were introduced into the tubes and containers to provide attachment sites for web building and moulting.

The feeding experiments were carried out from May until October 1981 and were supplemented by some additional experiments in the spring of 1982. The experiments were

Fig.6.2: Rearing cages of large spiders in laboratory feeding experiments.

carried out in a hut at the Glasgow University Field Station in Ross Wood at Rowardennan by Loch Lomond. The hut had no facilities for light or temperature control. The spiders were exposed to the external photoperiod and to temperatures which fluctuated with those outside. The temperature was normally within the range 15-22 C. The experiments in 1982 were carried out in the laboratory at the Developmental Biology Building in Glasgow. The temperature in the laboratory fluctuated around 18 C and the spiders were subjected to the external photoperiod from a window. The spiders undertake their first moult within the egg sac and hence it could be argued that the spiderlings should be designated second instar. However it is proposed to follow the terminology of Downes (1987) and refer to the spiderlings which emerge from the egg sac as first instars as they are the first free living instars. The first and second instar spiders were fed on small, winged specimens of the fruit fly Drosophila melanogaster while all other instars were fed on normal sized fruit flies. The feeding method was as follows: Flies were weighed individually and offered to the spiders. If the fly was not captured within three hours it was removed. The remains of the flies which had been eaten were removed and stored. In experiments dealing with adult females, where large quantities of food were consumed, flies were not weighed individually. Group of flies of similar size were weighed collectively and the average weight was calculated by dividing the total weight by the number of flies. The number of flies added was noted, as was the number of flies not eaten. The food consumed by adult females was calculated by subtracting the food remains from the total weight of flies killed. The feeding procedures were continued until the spider moulted or until the experiment was terminated.

The spider was weighed and the food remains and exuvium dried in a vacuum oven at 60 C. All weighings were carried out on an Electromicrobalance sensitive to 0.001 mg. Thus for each instar the initial and final weights were known in terms of live weights, as was the quantity of Drosophila killed. The dry weight of the food remains and of the exuvium was also known. The dry weight/live weight relationships for spiders are shown in Tables 6.1-6.3. These were used to convert live weights of spiders to dry weights. The values for early instars of M. segmentata were used for early instars of M. mengei . The dry weight/live weight relationship for Drosophila is $Y=0.31X-0.03$ ($n=28$) $r=0.99$ and this was used to convert the live weight of Drosophila killed to dry weight. With a view to constructing an energy budget for the spider, the results of feeding experiments were expressed as energy values. Energy values of spiders, their egg sacs, exuvia, Drosophila and the food remains were made using a Phillipson Microbomb Calorimeter and employing standard

Table 6.1: Regressions of dry weight against live weight of the spider Metellina segmentata .

Category	Number	Y = b X + a	r
Early instars	23	Y = 0.31 X + 0.01	0.99
Early instars	41	Y = 0.26 X + 0.02	0.99
Sub-adult females	21	Y = 0.26 X - 0.34	0.98
Sub-adult males	36	Y = 0.27 X - 0.30	0.97
Adult females	35	Y = 0.36 X - 1.91	0.99

Table 6.2: Regressions of dry weight against live weight of the spider Metellina mengei .

Category	Number	Y = b X + a	r
Sub-adult males	19	Y = 0.34 X - 0.55	0.94
Sub-adult females	11	Y = 0.34 X - 0.66	0.98
Adult females	33	Y = 0.36 X - 0.91	0.93

Table 6.3: Regressions of dry weight against live weight of the spider Linyphia triangularis .

Category	Number	Y = b X + a	r
Early instars	18	Y = 0.29 X - 0.03	0.99
Early instars	28	Y = 0.27 X + 0.06	0.99
Sub-adult females	14	Y = 0.26 X + 0.12	0.99
Sub-adult males	16	Y = 0.28 X + 0.05	0.99
Adult females	25	Y = 0.36 X - 2.07	0.98

techniques (Phillipson 1964). The mean energy equivalents, expressed as joules, are shown for spiders and their egg sacs in Table 6.4, and for the food remains in Table 6.5. The mean energy equivalents of exuvia and Drosophila are 20.56 (n=3) and 24.37 (n=5) respectively.

Results

1- Energy Budget of M. segmentata

a- Early Instars: From egg sac emergence until moulting to sub-adult stage.

Egg sacs were collected from the field in the Ross Wood in late May 1981. The spiderlings started to emerge from the egg sacs in mid-June. 32 spiderlings, which emerged from an egg sac on 16 June 1981, were reared and of these 16 survived until they had moulted to the fourth (sub-adult) instar. On moulting to sub-adult eight of the 16 spiders were found to be females. The summary of the results of these is given in Table 6.6. The more detailed results on individual spiders are shown in Appendix 1 (Tables 1-3). The average time from egg sac emergence, on 16 June 1981, until moulting to fourth instar was 45 days. This will take the spiders up to early August. This is the time that moulting to the sub-adult stage occurs in the field - so the rate of development in the laboratory is similar to

Table 6.4: Energy equivalents (Joules/mg ash free dry weight ± standard deviations; (n) number of samples) of various categories of *Metellina segmentata*, *Metellina mengei* and *Linyphia triangularis*.

	Species		
Category	*M. segmentata*	*M. mengei*	*L. triangularis*
Eggs	25.09 ± 0.72 (5)	24.75 ± 0.50 (2)	27.36 ± 1.77 (5)
Gravid females	27.39 ± 0.82 (5)	26.64 ± 0.60 (4)	26.70 ± 0.72 (5)
Adult females	26.09 ± 0.42 (4)	25.01 ± 0.40 (4)	25.59 ± 0.98 (5)
Adult males	26.57 ± 0.43 (4)	24.10 ± 0.31 (4)	24.85 ± 0.57 (4)
Sub-adults	23.61 ± 0.35 (4)	23.48 ± 0.62 (3)	23.42 ± 0.47 (4)
Early Instars	23.96 ± 0.18 (3)		22.72 ± 0.42 (4)
Egg sac silk	20.24 ± 1.71 (4)	20.08 (1)	19.78 ± 1.21 (4)

Table 6.5: Energy equivalents (Joules/mg ash free dry weight ± standard deviations; (n) number of samples) of food remains for various categories of *Metellina* species and *Linyphia* species.

Category	*Metellina*	*Linyphia*
Adult females	22.97 ± 0.57 (6)	23.78 ± 1.12 (5)
Sub-adults	23.64 ± 0.37 (4)	23.18 ± 1.12 (4)
Early Instars	23.02 ± 0.48 (3)	23.90 ± 1.07 (3)

Table 6.6: Summary of feeding experiments on early instars of the spider *Metellina segmentata* (expressed as joules unless otherwise indicated±S.D.). The number of spiders examined are given in parenthesis.

Instar (n)	Initial Weight (mg)	Final Weight (mg)	Weight Increase (mg)	Weight Increase	Exuvia	Food Killed	Food Remains	Food Consumed	Growth Efficiency (%)	Ingestion Efficiency (%)	Duration (days)
1st	0.33	0.87	0.53	4.86	0.20	22.94	13.10	9.85	43.24	42.75	8.25
(16)	± 0.03	± 0.16	± 0.16	± 1.19	± 0.04	± 4.21	± 2.47	± 2.39	± 4.20	± 6.33	±1.29
2nd	0.87	2.14	1.28	9.49	0.40	44.32	18.80	25.52	39.03	58.24	13.08
(16)	± 0.16	± 0.40	± 0.38	± 2.78	± 0.05	±14.09	± 7.09	± 7.56	± 3.32	± 5.82	±1.26
3rd	2.14	4.75	2.61	16.84	0.95	81.22	25.25	55.98	30.47	68.08	22.88
(16)	± 0.40	± 1.39	± 1.27	± 7.90	± 0.31	±22.49	± 8.68	± 17.04	± 8.47	± 9.11	±2.13

Table 6.7: Summary of feeding experiments on fourth instar (sub-adults) of the spider *Metellina segmentata* (expressed as joules unless otherwise indicated±S.D.). The number of spiders examined are given in parenthesis.

4th Instar (n)	Initial Weight (mg)	Final Weight (mg)	Weight Increase (mg)	Weight Increase	Exuvia	Food Killed	Food Remains	Food Consumed	Growth Efficiency (%)	Ingestion Efficiency (%)	Duration (days)
Female	5.43	12.97	7.54	38.64	3.12	136.58	32.70	103.88	40.73	76.38	29.50
(12)	± 0.96	± 1.92	± 1.54	± 9.51	± 0.44	±28.33	±11.57	± 19.97	± 3.46	± 5.59	±2.54
Male	5.90	13.32	7.42	40.90	3.08	147.40	35.07	112.39	39.30	76.55	30.00
(8)	± 1.28	± 2.21	± 1.18	± 7.65	± 0.21	±33.48	±12.29	± 23.76	± 1.96	± 4.46	±1.51

Table 6.8: Results of laboratory feeding experiments on fifth instar (adult females which produced egg sacs) of the spider *Metellina segmentata* (expressed as joules unless otherwise indicated). The number of spiders examined are 4.

Initial Weight (mg)	Final Weight (mg)	Weight Increase (mg)	Weight Increase	Food Killed	Food Remains	Food Consumed	Growth Efficiency (%)	Ingestion Efficiency (%)	Duration (days)
13.84	60.36	46.52	408.52	947.31	138.52	808.79	50.53	85.25	38.00
± 1.06	± 6.65	± 6.88	± 68.18	±133.38	±12.82	±122.93	± 3.41	± 1.21	±4.76

that in the field.

b- Fourth Instar (Sub-adult stage)

Four of the eight males which reached the sub-adult stage in the experiment mentioned above, died before moulting again. Consequently, an additional four males and four females were added to the experiment. These were of a similar size and weight to the animals which had just moulted to sub-adult and they were reared along with the survivors of the experiment. Thus 12 females and eight males were successfully reared to the adult stage. A summary of the results is given in Table 6.7 and more detailed results on individual spiders are shown in Appendix 1 (Tables D&E) for females and males respectively. The mean duration of the sub-adult stage was 30 days and this would take the spiders up to late August. In the field the spiders started to moult to adult in late August. As the rate of development of the spiders in these laboratory experiments was similar to that of spiders in the field, it was assumed that the energy budgets obtained for the spiders in the laboratory would give a good indication of energy requirements of spiders in the field.

c- Fifth Instar (Adult stage)

All of the 12 females were reared until the time of egg production in the field - which is normally in mid-October. However, only four of them produced egg sacs. The reason for the death of the remaining eight spiders was not obvious. During the experiment adult males were added to females's cages to allow mating to take place. Mating was observed during the experiment on a few occasions. A summary of the results for the four females which produced egg sacs is given in Table 6.8. The more detailed results on individual spiders are shown in Appendix 1 (Table 6). From moulting to adult up until the egg sac was produced took, on average, 38 days (Table 6.8). If moulting to adult occurs in late August then this would result in egg sac production in early to mid-October. Field observations indicated that females started to produce egg sacs in mid-October. Hence, the rate of development in the laboratory was similar to that in the field.

On moulting to adult, males ceased to build webs and fed little. Occasionally they were observed to feed on prey caught by females. Attempts to carry out feeding experiments on adult males provided no satisfactory results.

2- Energy Budget of *L. triangularis*

a- Early Instars: From egg sac emergence until moulting to sub-adult stage

Egg sacs were collected, as they were about to hatch, from the field in Ross Wood in mid-May 1981. Of the 25 spiderlings which emerged from the egg sac on 17 May 1981, 15 were reared successfully until they moulted to second instar and 13 of these survived to moult to third instar. Eight of the spiders moulted to fourth instar (sub-adult). On moulting to third instar, seven of the 13 spiders were found to be females and on moulting to fourth instar, six of the eight spiders were found to be females. Because of the level of mortality in this experiment, another experiment was started by collecting spiders from the field in mid-June. They moulted to third instar animals which were similar in size and weight to the 13 spiders which had moulted to third instars in the laboratory experiment. 20 spiders, 10 females and 10 males, were reared and 15 of these, eight females and seven males, reached the sub-adult stage. A summary of results of the first and second instar of the first experiment and the third instar of second experiment is given in Table 6.9. More detailed results on individual spiders are shown in Appendix 2 (Tables 1-3). The average time from egg sac emergence on 17 May 1981 to

Table 6.9: Summary of laboratory feeding experiments on early instars of the spider Linyphia triangularis (expressed as joules unless otherwise indicated). The number of spiders examined are given in parenthesis.

Spider Instar (n)	Initial Weight (mg)	Final Weight (mg)	Weight Increase (mg)	Weight Increase	Exuvia	Food Killed	Food Remains	Food Consumed	Growth Efficiency (%)	Ingestion Efficiency (%)	Duration (days)
1st	0.23	0.76	0.53	2.94	0.20	24.44	17.69	6.75	47.3	27.9	8.40
(15)	± 0.02	± 0.11	± 0.18	± 0.66	± 0.05	± 6.13	± 4.17	± 1.76	± 7.4	± 4.1	± 2.13
2nd	0.77	2.35	1.59	10.00	0.53	66.71	38.33	28.38	37.3	43.4	15.54
(13)	± 0.11	± 0.34	± 0.33	± 2.22	± 0.10	±15.94	±11.38	± 5.12	± 5.8	± 5.2	± 3.38
3rd	2.54	4.84	2.30	14.80	1.10	92.71	34.86	57.85	28.1	63.6	18.93
(15)	± 0.45	± 1.02	± 0.90	± 6.01	± 0.22	± 39.82	±19.79	±22.02	± 6.1	± 7.7	± 3.17

Table 6.10: Summary of laboratory feeding experiments on sub-adults of the spider Linyphia triangularis (expressed as joules unless otherwise indicated). The number of spiders examined are given in parenthesis.

4th Instar (n)	Initial Weight (mg)	Final Weight (mg)	Weight Increase (mg)	Weight Increase	Exuvia	Food Killed	Food Remains	Food Consumed	Growth Efficiency (%)	Ingestion Efficiency (%)	Duration (days)
Female	4.83	11.25	6.43	42.49	2.20	185.55	49.84	135.71	32.6	73.3	32.88
(8)	± 1.23	± 2.67	± 2.47	± 15.24	± 0.28	± 42.62	±19.19	± 34.56	± 6.0	± 8.1	± 2.75
Male)	4.86	12.73	7.87	52.91	2.28	209.11	51.92	157.19	35.0	75.6	29.29
(7)	± 0.82	± 2.91	± 2.73	±18.00	± 0.30	± 44.91	± 17.95	± 33.43	± 8.2	± 5.9	± 2.98

Table 6.11: Results of laboratory feeding experiments on fifth instar (adult females which produced egg sacs) of the spider Linyphia triangularis (expressed as joules unless otherwise indicated). The numbers of spiders examined are 4.

Initial Weight (mg)	Final Weight (mg)	Weight Increase (mg)	Weight Increase	Food Killed	Food Remains	Food Consumed	Growth Efficiency (%)	Ingestion Efficiency (%)	Duration (days)
11.68	33.07	21.39	147.94	493.38	90.33	403.05	36.95	81.62	60.33
± 2.74	± 4.38	± 3.92	± 37.24	±111.63	±21.02	± 92.99	± 6.52	± 1.90	± 5.13

fourth instar was 43 days. This will take them up to early July. In the field the spiders started to moult to sub-adult (fourth instar) in early July so that the rate of development in the laboratory is similar to that in the field.

b- Fourth Instar (Sub-adult stage)

15 spiders, eight females and seven males were subsequently reared and all of them reached the adult stage. A summary of results is given in Table 6.10. More detailed results on individual spiders are shown in Appendix 2 (Tables 4&5) for females and males respectively. The mean duration of the sub-adult stage was 33 days for females and 29 days for males and this would take them to early August. In the field the spiders started to moult to adult stage in early August.

c- Fifth Instar (Adult stage)

All of the eight females were reared until the time of egg sac production in the field, which is in early October. However only six of them produced egg sacs. During the experiment adult males were introduced to females's cages to allow mating to take place. Mating was observed during the experiment on a few occasions. The summary of the results for the six females which produced egg sacs is given in Table 6.11. The more detailed results on individual spiders are shown in Appendix 2 (Table 6). The mean duration of the experiment, until spiders produced egg sacs, was 60 days. This will take them to early October, which is the time when females in the field produce egg sacs. Hence the rate of development in the laboratory is similar to that in the field. Males feed little during the adult stage and attempts to carry out feeding experiments provided no satisfactory results.

3- Energy Budget of *M. mengei*

3.1- Spiders with one year life cycle

a- Early Instars: From egg sac emergence until moulting to sub-adult stage.

Egg sacs were collected, as they were about to hatch, from the field in Ross Wood in mid-July 1981. Of the 15 spiderlings, which were reared after emerging from the egg sac on 16 July 1981, only four were reared successfully until moulting to second instar. Another experiment was started by collecting spiderlings in late July 1981. When they moulted to second instar they were similar in size and weight to the four spiders which had been reared to second instar stage. 15 out of 25 spiders were reared successfully until moulting to fourth (sub-adult) instar. On moulting to sub-adult six of the 15 spiders were found to be females. A summary of the results is given in Table 6.12. More detailed results on individual spiders are shown in Appendix 3 (Tables 1-3). The average time from egg sac emergence on 16 July 1981 to fourth instar was 55 days. This will take them up to early September. In the field the spiders, which have a one year life cycle, started to moult to fourth instar (sub-adults) by mid-September, so that the rate of development in the laboratory is similar to that in

Table 6.12: Summary of feeding experiments on early instars of the spider *Metellina mengei* (expressed as joules unless otherwise indicated±S.D.). The number of spiders examined are given in parenthesis.

Instar (n)	Initial Weight (mg)	Final Weight (mg)	Weight Increase (mg)	Weight Increase	Exuvia	Food Killed	Food Remains	Food Consumed	Growth Efficiency (%)	Ingestion Efficiency (%)	Duration (days)
1st (4)	0.17 ± 0.02	0.51 ± 0.09	0.34 ± 0.07	2.58 ± 0.51	0.13 ± 0.03	12.43 ± 2.42	6.63 ± 1.95	5.72 ± 0.72	47.13 ± 5.33	46.73 ± 6.08	7.50 ± 1.29
2nd (15)	0.55 ± 0.06	1.26 ± 0.23	0.71 ± 0.21	5.24 ± 1.51	0.28 ± 0.06	30.15 ± 4.38	14.20 ± 2.79	15.93 ± 3.26	34.55 ± 6.39	52.73 ± 6.42	19.20 ± 2.18
3rd (15)	1.26 ± 0.23	2.65 ± 0.59	1.39 ± 0.59	9.14 ± 3.59	0.44 ± 0.07	52.23 ±18.32	19.80 ± 6.68	32.43 ± 12.34	29.59 ± 4.31	61.74 ± 4.63	28.47 ± 3.56

Table 6.13: Results of laboratory feeding experiments on fourth instar (sub-adults) of the spider *Metellina mengei* (expressed as joules unless otherwise indicated±S.D.). The number of spiders examined are given in parenthesis.

4th Instar (n)	Initial Weight (mg)	Final Weight (mg)	Weight Increase (mg)	Weight Increase	Exuvia	Food Killed	Food Remains	Food Consumed	Growth Efficiency (%)	Ingestion Efficiency (%)	Duration (days)
Female (4)	2.73 ± 0.64	6.86 ± 0.69	4.13 ± 0.72	17.90 ± 5.84	1.97 ± 0.24	81.83 ±31.73	20.97 ± 8.66	60.94 ±24.86	33.85 ± 4.77	73.98 ± 4.57	48.50 ± 4.04
Male (3)	3.07 ± 0.68	7.01 ± 0.77	± 3.94 1.22	18.86 ± 9.73	1.93 ± 0.37	83.96 ±28.71	19.99 ± 2.88	63.97 ±26.29	31.60 ± 6.81	74.87 ± 5.90	47.33 ± 8.50

the field.

b- Fourth Instar (Sub-adult stage)

Of the 15 spiders which reached the sub-adult stage seven spiders, four females and three males, were successfully reared to the adult stage. A summary of the results is given in Table 6.13. The more detailed results on individual spiders are shown in Appendix 3 (Tables 4&5) for females and males respectively. The mean duration of the sub-adult stage was 48 days and this would take them to late October. In the field some spiders started to moult to adult in early November.

c- Fifth Instar (Adult stage)

Shortly after moulting to adult, all the males died. Females were retained in an incubator at 4 C to keep them over the winter but they were dead by spring 1982.

3.2- Spiders with two year life cycle

a- Fourth Instar

25 spiders which were thought to be third instars were collected in late June 1981. When only two of them moulted to fourth instar it was realized that that the remainder of

the spiders must have moulted to fourth instar before they were collected. All the spiders were reared until they moulted to fifth instar (sub-adult) in early August. However, because most of the spiders were already fourth instar at the beginning of the experiment, no results of the experiment are included in this account.

b- Fifth Instar (Sub-adult stage)

25 spiders, 10 females and 15 males which had just moulted to fifth instar (sub-adults) in early August were reared until they moulted to adult in early September. A summary of the results is given in Table 6.14. The more detailed results on individual spiders are shown in Appendix 3 (Tables 6&7) for females and males respectively. The mean duration of the sub-adult stage was 31 days and this would take them to early September. In the field some spiders started to moult to adult in late August.

c- Sixth Instar (Adult stage) in autumn

All of the 10 females, which moulted to adult in early September, were reared until they became inactive and fed little at the middle of October. During the experiment adult males were added to females's cages to allow mating to take place, but neither courtship or mating was observed. Five of the females were fed <u>ad lib</u> until

Table 6.14: Summary of feeding experiments on fifth instar (sub-adults) of the spider Metellina mengei (expressed as joules unless otherwise indicated±S.D.)

5th Instar (n)	Initial Weight (mg)	Final Weight (mg)	Weight Increase (mg)	Weight Increase	Exuvia	Food Killed	Food Remains	Food Consumed	Growth Efficiency (%)	Ingestion Efficiency (%)	Duration (days)
Female (10)	5.38 ± 1.10	11.65 ± 1.87	2.27 ± 1.22	36.77 ± 9.86	3.02 ± 0.40	141.69 ±28.30	33.69 ± 9.06	108.03 ± 21.10	36.46 ± 4.06	76.30 ± 3.04	30.40 ± 5.70
Male (15)	5.51 ± 0.63	12.46 ± 1.13	6.95 ± 0.80	42.24 ± 7.09	3.63 ± 0.51	165.39 ± 25.38	38.81 ± 8.85	126.75 ± 18.45	36.22 ± 2.65	76.73 ± 2.92	31.47 ± 4.00

Table 6.15: Summary of feeding experiments on adult females (sixth instar) of the spider Metellina mengei in the autumn (expressed as joules unless otherwise indicated±S.D.). The number of spiders examined are 10.

Initial Weight (mg)	Final Weight (mg)	Weight Increase (mg)	Weight Increase	Food Killed	Food Remains	Food Consumed	Growth Efficiency (%)	Ingestion Efficiency (%)	Duration (days)
11.65 ± 1.87	19.74 ± 4.13	8.09 ± 3.11	49.55 ± 27.79	167.13 ± 91.72	27.98 ± 13.64	139.15 ± 78.24	35.71 ± 4.14	82.81 ± 1.68	37.80 ± 3.55

Table 6.16: Summary of laboratory feeding experiments on adult females, which produced egg sacs, of the spider Metellina mengei in spring 1982 (expressed as joules unless otherwise indicated). The number of spiders examined are 2.

Initial Weight (mg)	Final Weight (mg)	Weight Increase (mg)	Weight Increase	Food Killed	Food Remains	Food Consumed	Growth Efficiency (%)	Ingestion Efficiency (%)	Duration (days)
9.52 ±0.84	26.69 ±2.74	17.18 ±1.90	139.33 ±18.00	386.76 ±24.81	68.34 ±00.49	318.42 ±24.32	43.65 ±2.33	82.30 ±0.99	33.50 ±3.54

late November 1981 but they did not produce egg sacs. They were retained until the spring 1982. The other five females were placed in a refrigerator at 4 C from mid-October 1981 to spring 1982. A summary of the results on 10 females until they became inactive, is given in Table 6.15. The more datailed results on individual spiders are shown in Appendix 3 (Table 8). The mean duration of the experiment was 38 days. This will correspond to a period of active feeding until mid-October.

d- Sixth Instar (Adult stage) in spring

Three females out of five which were kept in the incubator at 4 C over the winter survived until early May 1982. They were supplemented with seven females collected from the field. All of these 10 females were reared until the time of egg sac production in the field which is in early June. During the experiment adult males were introduced to females' cages to allow mating to take place. Mating was observed during the experiment on a few occasions. Egg sacs were produced by only two females and the remaining eight females died before producing egg sacs. No reason can be given for the mortality. A summary of the results of the two spiders which produced egg sacs, is given in in Table 6.16. The more detailed results on individual spiders are shown in Appendix 3 (Table 9). The mean time taken until egg sacs were produced was 35.5 days which would result in egg sac production in early June. This corresponds well with the time when egg sacs are produced in the field. Males feed little during the adult stage and attempts to carry out feeding experiments provided no satisfactory results.

Growth and ingestion efficiencies

The growth efficiency is defined as the ratio of the energetic equivalent of the weight increase, including exuvia, during the instar to that of the food consumed, expressed as percentage. The ingestion efficiency is the ratio of the food consumed to the food killed. These efficiencies of the various instars for the three species are shown in Tables 6.17-6.18 and presented in Fig.6.3 & 6.4.

Statistical tests (t-tests) indicated that, in general, the growth efficiency decreases from first instar to the second and from the second to the third. It then increases towards the adult stage - with the exception of L. triangularis . The growth efficiencies of sub-adult females and males are similar.

T-tests on the results indicated that, in general, the ingestion efficiency increases from first instar to second instar, with the exception of M. mengei . It then increases through to the adult stage. The ingestion efficiencies of sub-adult females and males are similar.

Table 6.17: Growth efficiencies (mean ± S.D.) of various instars of the spiders *Metellina segmentata*, *Metellina mengei* and *Linyphia triangularis*. The numbers in parenthesis are the numbers of samples. * values for spiders with two year life cycle. # adult females *M. mengei* which produced egg sacs.

Instar	*Metellina segmentata*	*Metellina mengei*	*Linyphia triangularis*
1st	43.24 ± 4.28 (16)	47.13 ± 5.33 (4)	47.3 ± 7.4 (15)
2nd	39.03 ± 3.32 (16)	34.55 ± 6.39 (15)	37.3 ± 5.8 (13)
3rd	30.47 ± 8.47 (16)	29.59 ± 4.31 (15)	28.1 ± 6.1 (15)
Subadult female	40.73 ± 3.46 (12)	33.85 ± 4.77 (4) * 36.46 ± 4.06 (10)	32.6 ± 6.0 (8)
Subadult male	39.30 ± 1.96 (8)	31.60 ± 6.81 (3) * 36.22 ± 2.65 (15)	35.0 ± 8.2 (7)
Adult female	50.53 ± 3.41 (4)	* 35.71 ± 4.13 (10) # 43.65 ± 2.33 (2)	36.95± 6.52 (6)

Table 6.18: Ingestion efficiencies (mean ± S.D.) of various instars of the spiders *Metellina segmentata*, *Metellina mengei* and *Linyphia triangularis*. The numbers in parenthesis are the numbers of samples. * values for spiders with two year life-cycle. # adult females *M. mengei* which produced egg sacs.

Instar	*Metellina segmentata*	*Metellina mengei*	*Linyphia triangularis*
1st	42.75 ± 6.33 (16)	46.73 ± 6.08 (4)	27.9 ± 4.1 (15)
2nd	58.24 ± 5.82 (16)	52.73 ± 6.42 (15)	43.4 ± 5.2 (13)
3rd	68.08 ± 9.11 (16)	61.74 ± 4.63 (15)	63.6 ± 7.7 (15)
Subadult female	76.39 ± 5.59 (12)	73.98 ± 4.57 (4) * 76.30 ± 3.04 (10)	73.3 ± 8.1 (8)
Subadult male	76.55 ± 4.46 (8)	74.87 ± 5.90 (3) * 76.73 ± 2.92 (15)	75.6 ± 5.9 (7)
Adult female	85.25 ± 1.21 (4)	* 82.81 ± 1.68 (10) # 82.30 ± 0.99 (2)	81.62 ± 1.90 (6)

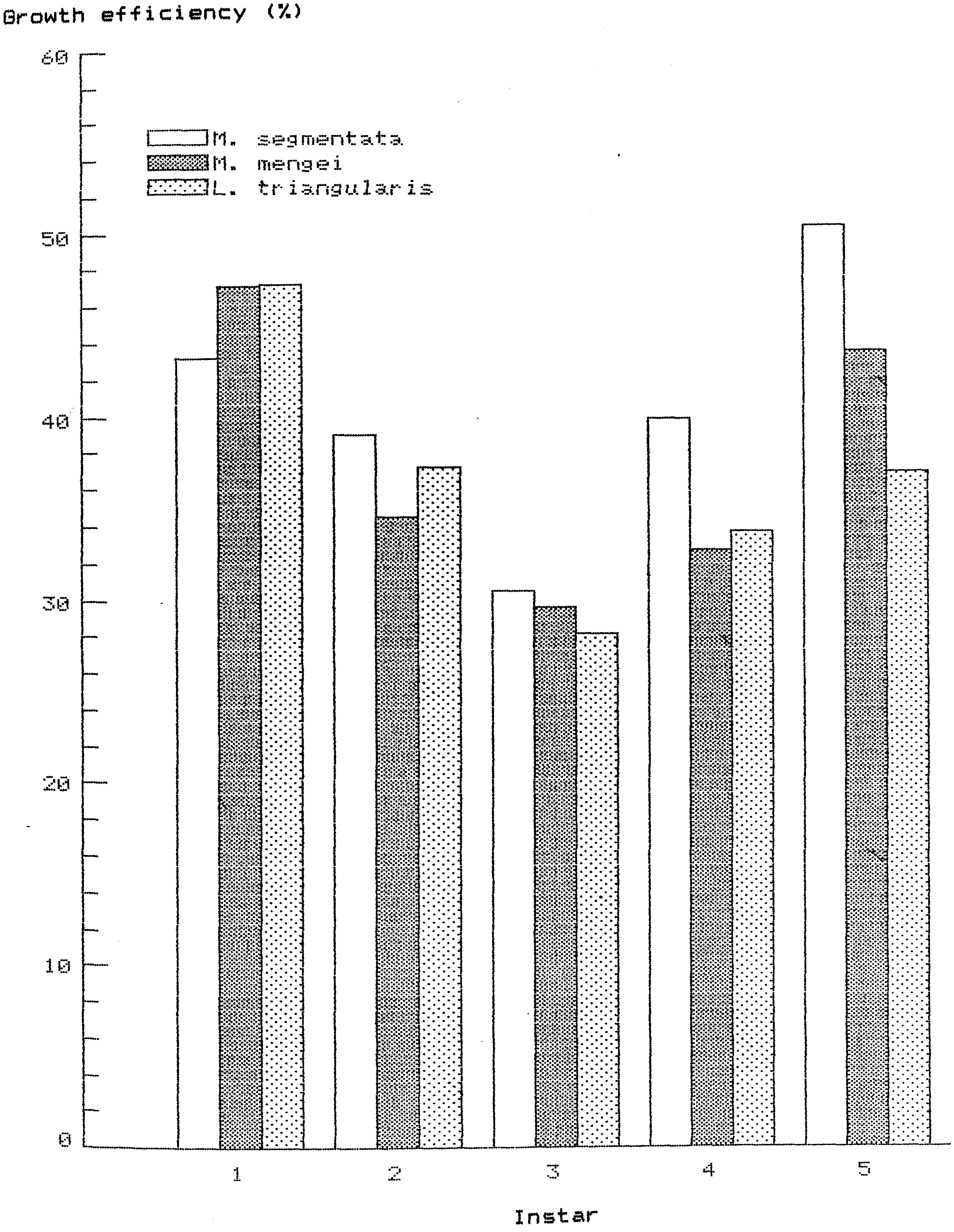
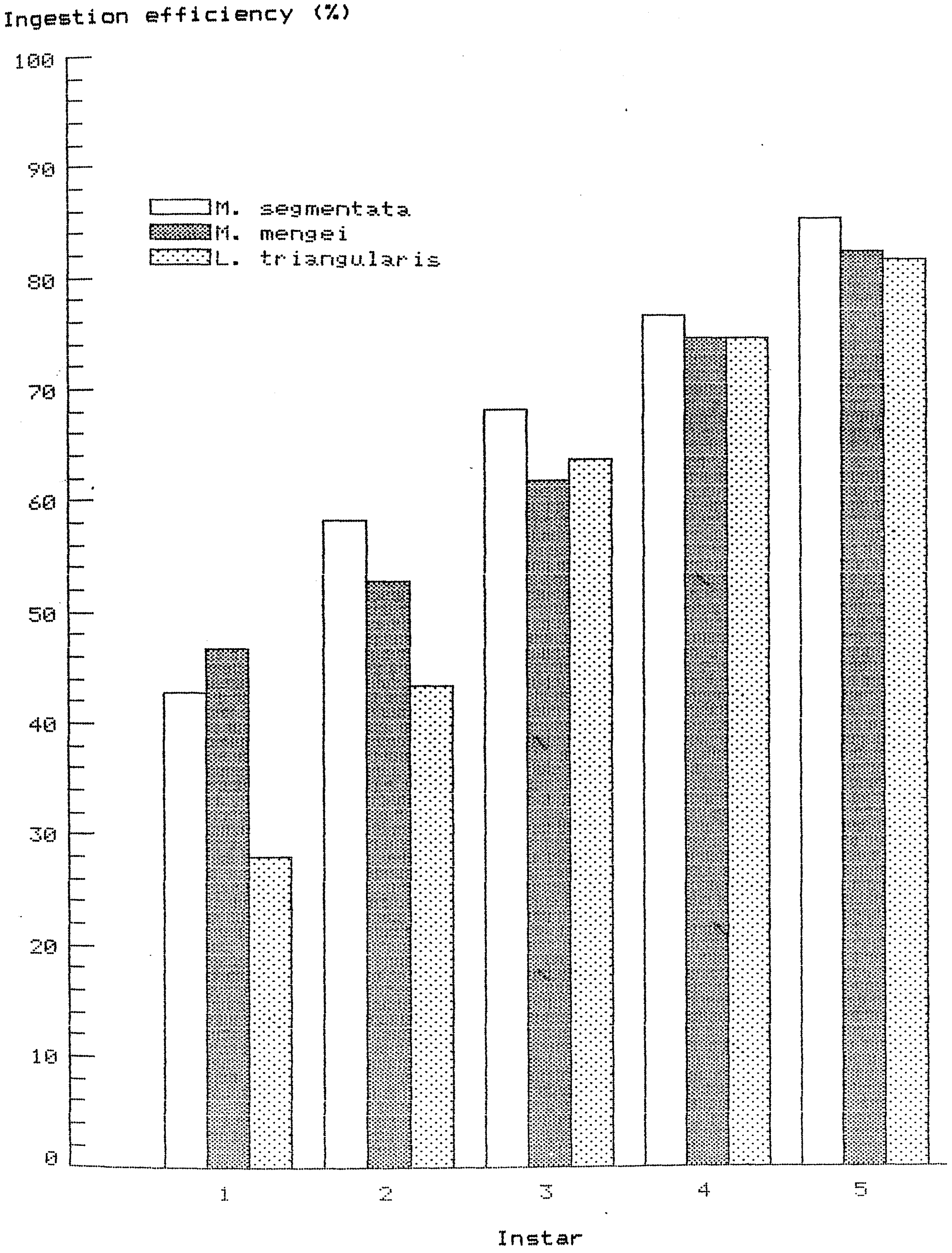

Growth efficiency (%)
60
50
40
30
20
10
0
M. segmentata
M. mengei
L. triangularis
1
2
3
4
5
Instar

Fig.6.4: Changes of ingestion efficiencies with age in the three species.


Ingestion efficiency (%)
100
90
80
70
60
50
40
30
20
10
0
M. segmentata
M. mengei
L. triangularis
1
2
3
4
5
Instar

Duration of instar

The durations of instars are shown in Table 6.19. The length of instar increased with age - with the first instar being the shortest and the sub-adult the longest.

Total Energy Budget

On the basis of these results the amount of food required by the spider species from emergence from egg sacs to death can be calculated. The energy budgets for the various stages of the life cycle of males and females of the three species are given in Tables 6.20-6.30. The growth efficiency for adult females is mainly production efficiency as most of the increase in body weight is related to gamete production - which is the energy going into the egg sac. Exuvia production is considered as part of body growth and the growth efficiency was calculted on this basis.

Table 6.19: Duration (mean ± S.D.) in days of various instars of the spiders *Metellina segmentata*, *Metellina mengei* and *Linyphia triangularis*. The numbers in parenthesis are the numbers of samples. * values for spiders with two year life-cycle.

Instar	*Metellina segmentata*	*Metellina mengei*	*Linyphia triangularis*
1st	8.3 ± 1.3 (16)	7.5 ± 1.3 (4)	8.4 ± 2.1 (15)
2nd	13.9 ± 1.3 (16)	19.2 ± 2.2 (15)	15.5 ± 3.4 (13)
3rd	22.9 ± 2.1 (16)	28.5 ± 3.6 (15)	18.9 ± 3.2 (15)
Subadult female	29.5 ± 2.5 (12)	48.5 ± 4.0 (4) * 30.4 ± 5.7 (10)	32.9 ± 2.8 (8)
Sub-adult male	30.0 ± 1.5 (8)	47.3 ± 8.5 (3) * 31.5 ± 4.0) (15)	29.3 ± 3.0 (7)
Adult female	38.0 ± 4.8 (4)		60.3 ± 5.1 (6)

Table 6.20: Energy budget of *M. segmentata* male until adult stage (expressed as joules unless otherwise indicated).

Instar	Food killed	Food remains	Food consumed	Weight increase	Exuvia	Growth efficiency
1st - 3rd	148.48	57.15	91.33	30.39	1.55	34.97
4th	147.40	35.07	112.32	40.90	3.08	39.13
Total	295.88	92.22	203.65	71.29	4.63	37.28

Table 6.21: Energy budget of *M. segmentata* female until adult stage (expressed as joules unless otherwise indicated).

Instar	Food killed	Food remains	Food consumed	Weight increase	Exuvia	Growth efficiency
1st - 3rd	148.48	57.15	91.33	30.39	1.55	34.97
4th	136.58	32.70	103.88	38.64	3.12	40.20
Total	285.06	89.85	195.21	69.03	4.67	37.75

Table 6.22: Total energy budget of *M. segmentata* female, which produced egg sacs (expressed as joules unless otherwise indicated)

Instar	Food killed	Food remains	Food consumed	Weight increase	Exuvia	Growth efficiency
1st - 3rd	148.48	57.15	91.33	30.39	1.55	34.97
4th	136.58	32.70	103.88	38.64	3.12	40.20
Adult	947.31	138.52	808.79	408.52		50.53
Total	1232.37	228.37	1004.00	477.55	4.67	48.03

Table 6.23: Energy budget of L. triangularis male until adult stage (expressed as joules unless otherwise indicated)

Instar	Food killed	Food remains	Food consumed	Weight increase	Exuvia	Growth efficiency
1st - 3rd	183.86	90.88	92.98	27.74	1.83	31.80
4th	209.11	51.92	157.19	52.91	2.28	35.08
Total	392.97	142.80	250.17	80.65	4.11	33.88

Table 6.24: Energy budget of L. triangularis female until the adult stage (expressed as joules unless otherwise indicated)

Instar	Food killed	Food remains	Food consumed	Weight increase	Exuvia	Growth efficiency
1st - 3rd	183.86	90.88	92.98	27.74	1.83	31.80
4th	185.55	49.84	135.71	42.49	2.20	32.93
Total	369.41	140.72	228.69	70.23	4.03	32.47

Table 6.25: Total energy budget of L. triangularis female, which produced egg sacs (expressed as joules unless otherwise indicated.

Instar	Food killed	Food remains	Food consumed	Weight increase	Exuvia	Growth efficiency
1st - 3rd	183.86	90.88	92.98	27.74	1.83	31.80
4th	185.55	49.84	135.71	42.49	2.20	32.93
Adult	493.38	90.33	403.05	147.94		36.95
Total	862.79	231.05	631.74	218.17	4.03	35.17

Table 6.26: Energy budget of M. mengei male until adult stage (expressed as joules unless otherwise indicated)

Instar	Food killed	Food remains	Food consumed	Weight increase	Exuvia	Growth efficiency
1st - 3rd	94.81	40.68	54.13	16.96	0.85	32.90
4th	83.96	19.99	63.97	18.86	1.93	32.50
Total	178.77	60.67	118.10	35.82	2.78	32.68

Table 6.27: Energy budget of M. mengei female until adult stage (expressed as joules unless otherwise indicated)

Instar	Food killed	Food remains	Food consumed	Weight increase	Exuvia	Growth efficiency
1st - 3rd	94.81	40.68	54.13	16.96	0.85	32.90
4th	81.83	20.97	60.86	17.90	1.97	32.61
Total	176.64	61.65	114.99	34.86	2.82	32.77

Table 6.28: Energy budget of fifth instar (sub-adult) M. mengei (expressed as joules unless otherwise indicated).

	Food killed	Food remains	Food consumed	Weight increase	Exuvia	Growth efficiency
Female	141.69	33.69	108.00	36.77	3.02	36.83
Male	165.39	38.68	126.71	42.24	3.63	36.20

Table 6.29: Energy budget of adult females (sixth instar) M. mengei in the autumn (expressed as joules unless otherwise indicated)

Food killed	Food remains	Food consumed	Weight Increase	Growth efficiency
167.13	27.98	139.15	49.55	35.61

Table 6.30: Energy budget of adult females (sixth instar) M. mengei in spring (expressed as joules unless otherwise indicated)

Food killed	Food remains	Food consumed	Weight increase	Growth efficiency
295.51	52.28	243.23	99.63	40.85

Discussion

The main reason for carrying out feeding experiments is to construct an energy budget for three of the species. An alternative method for constructing energy budgets for animals is to carry out respirometery experiments. Although respiration experiments are much less time consuming than feeding experiments, there are many variables which can affect an animal's respiratory rate and these are often difficult to control (Phillipson 1962, 1963; Ito 1964; Miyashita 1969; Anderson 1970; Humphreys 1975). Hence feeding experiments will normally allow more reliable energy budgets to be constructed.

Another reason for carrying out feeding experiments is that they can give an additional insight into the life cycles of the spiders. As was indicated in the results section, the duration of the various instars in the feeding experiments corresponded well with those found from the population study. Thus they confirm that M. segmentata and L. triangularis have a one year life cycle. They indicate that M. mengei has a one year life cycle but may also have a two year life cycle.

In all the feeding experiments the spiders ceased to feed prior to moulting. The duration of this fasting period was greatest in the largest instars. These findings are in agreement with with those found in other studies (Bristowe 1958; Humphreys 1977).

The results from the field study and the feeding experiments indicated that M. segmentata , L. triangularis and L. peltata all had five instars. When M. mengei had a one year life cycle, like these three species, it also had five instars but had six instars when the life cycle took two years. Some feeding experiments on spiders have indicated that the number of instars varied with the feeding rate (Deevey 1949; Miyashita 1968; Benforado & Kistler 1973) while other studies indicated that the number of instars did not vary with feeding rates (Turnbull 1962, 1965). Some studies have shown that the number of instars can vary when the spiders are reared under similar conditions of food and temperature (Whitcomb et al 1966; Edgar 1968; Levy 1970)

In the present study the length of the instar increased with age and this agrees with the finding of Miyashita (1968). Edgar (1971) found a similar trend except that the first instar was longer than the second. Deevey (1949) found that the duration of the various instar varied with the feeding rate while other studies revealed no trend with regard to duration of the instars (Levy 1970; Geyer 1971; Humphreys 1976; Workman 1978).

With regard to constructing an energy budget, difficulties occurred with respect to estimating the energy equivalent of faeces, nitrogenous waste and silk.

Silk production is considered to be part of the "production" in the energy budget (Fig.6.1). It was not measured during the feeding experiments. In the Metellina species the loss of energy through silk production was considered to be negligible. Metellina , like other orb web spinning spiders, eats the old web - thus recycling the protein. This process has been shown to be 92-96% efficient (Peakall 1971; Peakall & Witt 1976)

Webs of Linyphia species were collected from the field. Webs were collected for small instars, sub-adults and adult animals. These were dry weighed and gave average values, for the three categories, of 0.14, 0.40 and 1.03 mg respectively. Energy determinations of Linyphia silk were obtained using the bomb calorimeter and these gave average values, for the webs of early instars, sub-adults and adults of 2.67, 7.81 and 20.29 Joules, respectively. These are considered underestimates of the total cost of web production as the spiders repair their webs from time to time. Energy is also expended in the spinning of the web. Because of these uncertainties and because the energy going into silk production was small compared with that of other categories, no figures are given in the energy budget for silk production in the Linyphia species.

Faeces and nitrogenous waste materials are produced by spiders in a semi-liquid form. Attempts were made to estimate the amounts produced by collecting the material, on pieces of filter paper which had previously been dried and weighed. These were placed on the bottom of the rearing tubes or containers. Periodically these pieces of paper were removed and dried, to estimate the amount of waste material produced. In most cases no significant difference in weight was recorded - indicating that insignificant amounts of faeces and nitrogenous waste were produced. This is in agreement with the studies of Celerier (1971) and Edgar (1971) who argued that as spiders digest their food externally, and ingest their food in a fluid form, it is to be expected that most of the food consumed will be assimilated and hence little faeces will be produced. Because of this and the fact that the energy content of excretory material is known to be low (Van Hook 1971; Moulder & Reichle 1972), the energy lost as faeces and nitrogenous waste was assumed to be negligible.

Celerier (1986) indicated that loss of energy in the form of exuvia was a not insignificant part of the energy budgets of spiders. In the present study energy loss in the form of exuvia, as a percentage of the total production, varied, in the different instars, from 4.1-7.8 in M.

segmentata , from 4.2-6.9 in L. triangularis and from 4.6-9.9 in M. mengei . Larger specimens of Metellina species lost proportionally more energy in exuvia than smaller ones but there was no such trend in L. triangularis . No explanation can be given for these differences. Geyer (1971) reported that exuvia represent 6% of total production in M. segmentata .

These values are low compared with those reported for other spiders. Edgar (1971) found values ranging from 8.2-23.9% in the wolf spider Pardosa lugubris and Humphreys (1978) from 4.0-28.1% in the wolf spider Geolycosa godeffroyi . Steigen (1975) reported a remarkable value of 42.1% for the 6th instar female of the wolf spider Pardosa palustris - the values for the other instars ranged from 4.0-24.8%. The wider range in values in these studies compared with the values in the present study, may reflect the fact that these spiders have a two year life cycle and consequently have lower growth rates than the spiders with an annual life cycle.

Lindeman (1942) indicated that animals at progressively higher levels in the food webs utilized their food progressively more efficiently. With regard to feeding efficiency, there are three different "efficiencies" which can be considered - namely ingestion efficiency, assimilation efficiency and growth efficiency.

Ingestion efficiency is the ratio of energy of food consumed / food killed, expressed as a percentage. In the current study *M. segmentata* had a higher ingestion efficiency than *M. mengei* which had a higher efficiency than *L. triangularis* . The ingestion efficiency increased from first to second instar, except in *M. mengei* , and thereafter increased with each instar, up to the adult stage. This trend was also found for *L. triangularis* by Turnbull (1962) and in the wolf spiders *Pardosa palustris* (Steigen 1975) and *Trochosa terricola* (Workman 1978). The amount of food which young spiders can ingest may be limited by gut capacity (Nakamura 1968; Hagstrum 1970) and the increase in ingestion efficiency with body size may reflect, at least in part, gut capacity in relation to prey size. Edgar (1971), working on the wolf spider *Pardosa lugubris* , fed the smaller instars on much smaller prey than the larger ones and did not find that ingestion efficiency increased with size. Thus the first instar of *P. lugubris* had an ingestion efficiency of 71.9% and this compares with values in the range 27.9-46.8% for the first instars of the three spiders in the current study.

It is likely that in the field situation prey size will be a better match for spider size and gut capacity and that ingestion efficiencies will consequently be higher. Small specimens of web building spiders might be able to catch relatively larger prey items than small hunting spiders, which might account for the higher ingestion efficiencies on the part of the latter.

The energy content of the food remains, which ranged from 23.0-23.9 J/mg dry weight, was lower than the energy content of Drosophila (24.8 J/mg dry weight). This indicates that the food ingested by the spiders has a higher energy content of that of the prey as a whole, and this is in agreement with the findings of Steigen (1975), Humphreys (1977) and Workman (1978).

Assimilation efficiency is the ratio of the energy of the food assimilated / food ingested, expressed as a percentage.

Invertebrate carnivores, including spiders, have much higher assimilation efficiencies than invertebrate herbivores (Wiegert 1964; Moulder & Reichle 1972). This reflects the nature of the food they ingest. As indicated earlier, spiders predigest their food - which is ingested in a semi-liquid form. Hence it might be expected that most of this food is assimilated and little faeces is produced. The assimilation efficiencies quoted for spiders, which are in the range 89-93% (Van Hook 1971); Moulder & Reichle 1972; Humphreys 1977; Workman 1978), confirm this expectation. For the purposes of this study the energy lost as faeces was assumed to be negligible and consequently food assimilated was taken to be equivalent to food ingested. A similar assumption was made by Celerier (1971) and Edgar (1971).

Growth efficiency can be expressed either as gross growth efficiency or net growth efficiency (Phillipson 1966). Gross growth efficiency is the ratio of the energy of growth / food ingested, expressed as percentage. Net growth efficiency is the ratio of the energy of growth / food assimilated, expressed as a percentage. Phillipson (1966) indicated that the former had a range from 6-37% and the latter from 5-60%. As food assimilated is assumed to be equivalent to food ingested in the present study, gross and net growth efficiencies are the same. When growth efficiencies are quoted in the literature they normally refer to gross growth efficiency.

Long lived poikilotherms (ectotherms) tend to have lower growth efficiencies than short lived ones (Mc Neill & Lawton 1970) as respiratory costs become relatively higher as the lifespan is increased. Phillipson (1966) indicated that growth efficiencies are lower in older animals and this has been confirmed in some spiders (Edgar 1971; Steigen 1975; Humphreys 1976). Workman (1978) found no trend in this respect while Kajak (1967) and Celerier

(1971) found an increase. These differences may be partly explained by whether or not later instars are of a longer duration than earlier instars.

In the present study the growth efficiency decreased from first to third instar and then, with the exception of *L. triangularis*, increased up to the adult stage. The growth efficiencies of sub-adult males and females are similar in the *Metellina* species but in *L. triangularis* it was higher in males. This may account for the fact that males moult to adult earlier than the females in this species. In species of *Pardosa* (F. Lycosidae) the females had higher growth efficiencies than the males (Edgar 1971; Steigen 1975) - which reflects the fact that adult females are much heavier than males. Adult females of *M. mengei* in the spring have a higher growth efficiency than in the autumn. This reflects the fact that the spider is feeding actively in the spring, prior to producing an egg sac.

As indicated earlier, growth efficiencies in carnivores are higher than in herbivores. Thus growth efficiencies for invertebrate herbivores ranged from 6-11% (Van Hook 1971) while those for spiders ranged from 16.1-32.5% (Van Hook & Moulder 1969; Hagstrum 1970; Edgar 1971; Humphreys 1978). The growth efficiencies for the spiders in the current study are higher than those previously quoted. Thus for the three species up to moulting to adult the growth efficiencies ranged from 32.5–37.8% with the values for females of *M. segmentata* and *L. triangularis* , up to the stage when they produced egg sacs, being 48.0% and 35.2% respectively. These higher values may reflect the fact that these spiders are sit-and-wait predators with a one year life cycle while most of the values in the literature are for wolf spiders with two year life cycles. Geyer (1971) gave an average value of 46% for the production efficiency of a population of *M. segmentata* . What is less easy to explain is the differences from the value of 26.9% obtained by Turnbull (1962) for *L. triangularis* . Kajak (1967) quoted values ranging from 33.8–57.4% for two *Araneus* species. Some doubt must be cast on the validity of these results as Kajak assumed that all the food killed was consumed.

CHAPTER 7

The Life Cycles of the Four Species

These accounts are based on information obtained from laboratory rearing experiments and from field samples taken to elucidate the age structure and seasonal weight changes in the population. Thus the accounts are partly based on information which will be presented later.

Metellina mengei

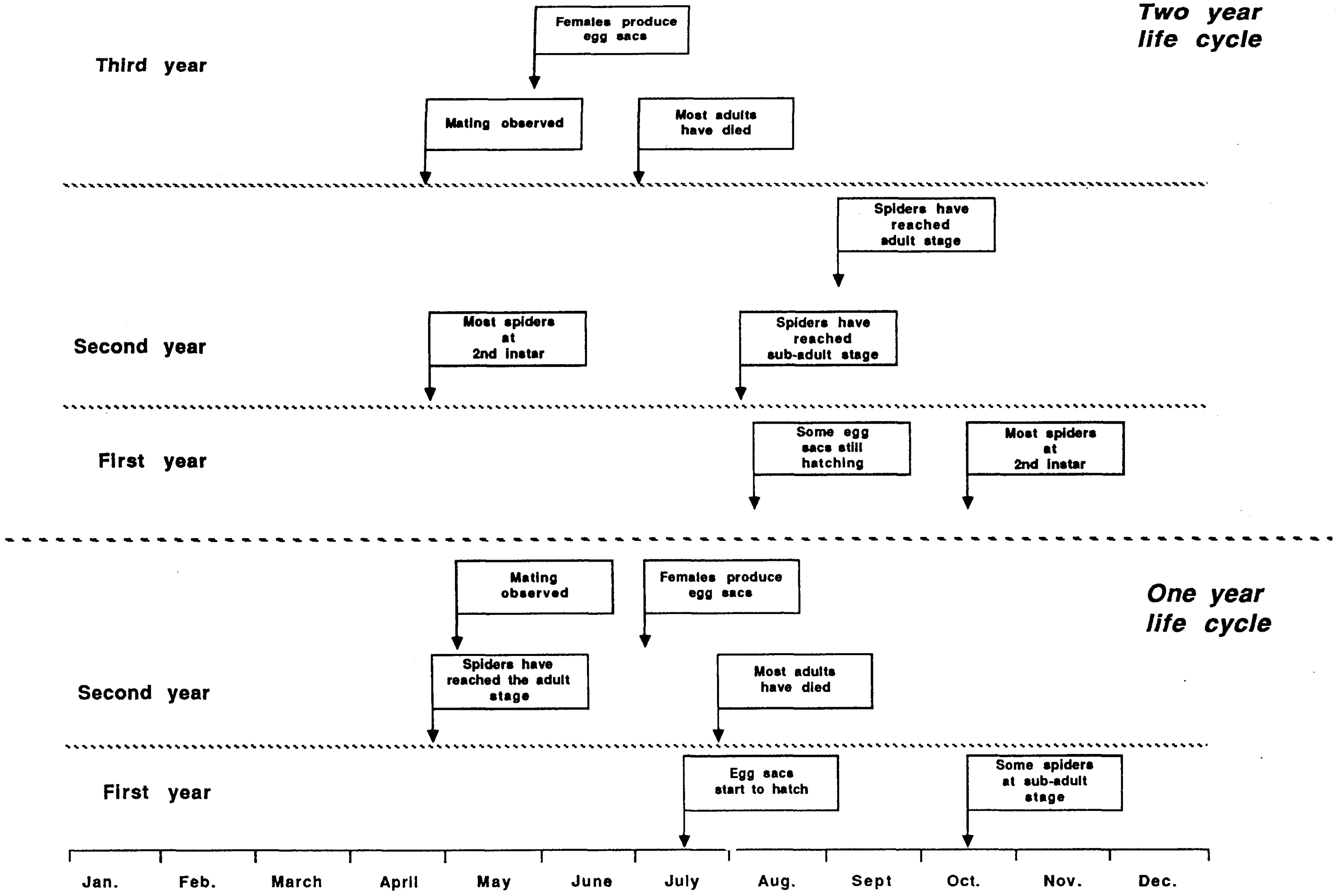
The life cycle of *M. mengei* is complex - with some of the spiders having a one year life cycle and some a two year one.

Females start to produce egg sacs in early June and by mid-July the spiderlings begin to emerge. The fastest growing of these spiders have reached the fourth instar (sub-adult) stage by mid-October while the slowest growing animals are first or second instars by the late autumn. The spiders overwinter among the leaf litter and become active in the spring. The sub-adult animals moult to adult about mid-April. These fifth instar adults mate in early May and the adult males die in early July. At this time the females are producing egg sacs and by the end of July most of the females have died.

The bulk of the spiders which emerged from the egg sacs in mid-late July in the previous year overwinter as second and third instars. These animals have a two year life cycle. They grow fairly slowly during the spring and summer and reach the sub-adult stage, which in this case is the fifth instar, in August. Thus the two year animals have an extra instar. By late September they have moulted to adult and overwinter with the spiders which emerged from the egg sacs during the summer. Mating occurs in late April and in May and egg sacs are produced in early June.

Thus in any year the adult population consists of sixth instar (two year) adults and fifth instar (one year) ones. The former breed earlier in the year and the presence of the two groups results in an extended breeding season with spiderlings emerging from egg sacs over a considerable part of the summer. It is likely that most of the animals with a one year life cycle have offspring which have a two year life cycle, and vice versa. However, there is considerable variability in the life cycle and there is probably no rigidly fixed pattern. A summary of the life cycle is given in Fig.7.1.

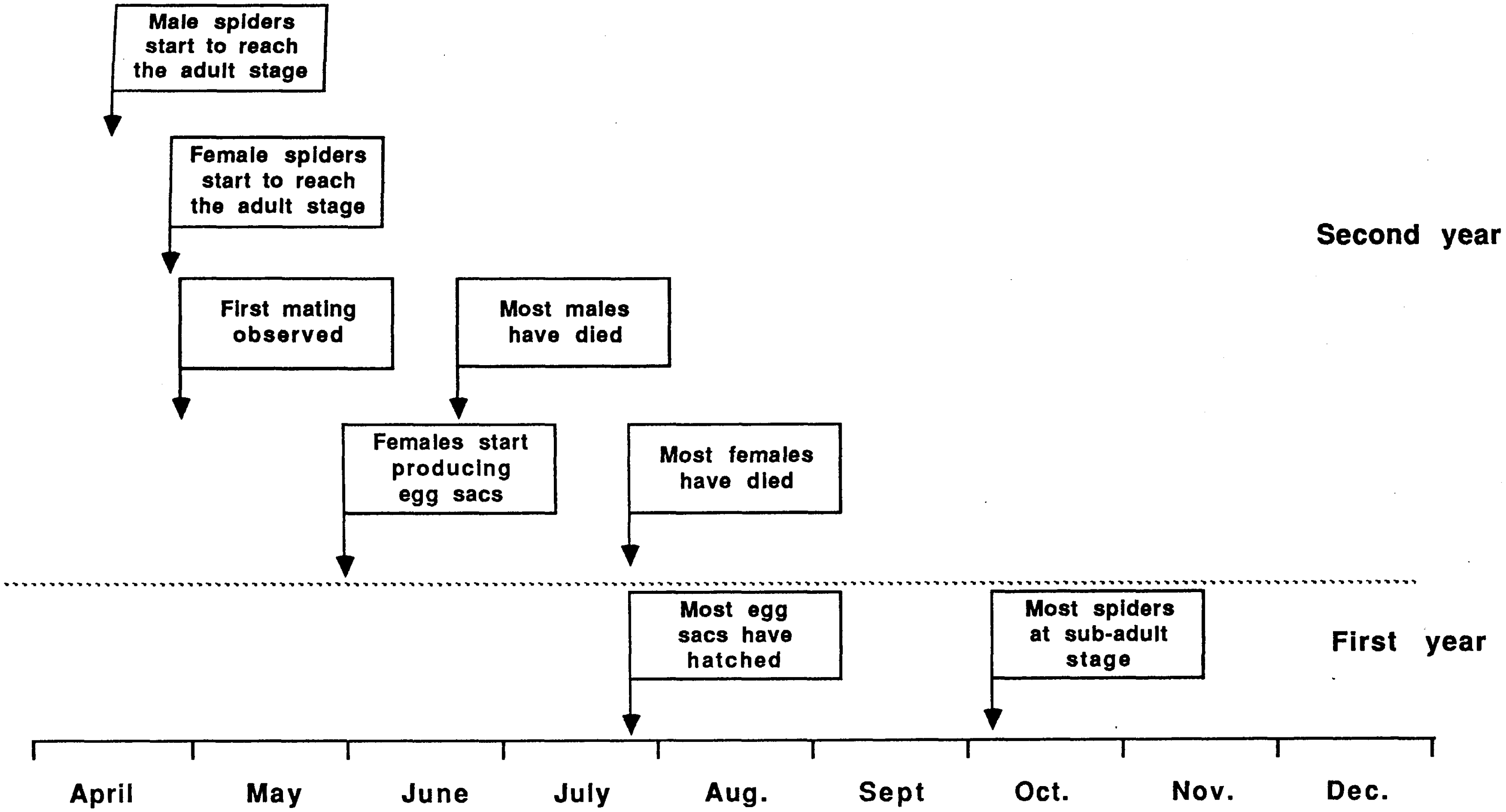
Fig.7.1: Phenology of the major events in the life cycle of *Metellina mengei* .

Two year life cycle
Third year
Females produce egg sacs
Mating observed
Most adults have died
Spiders have reached adult stage
Second year
Most spiders at 2nd instar
Spiders have reached sub-adult stage
First year
Some egg sacs still hatching
Most spiders at 2nd instar
One year life cycle
Mating observed
Females produce egg sacs
Second year
Spiders have reached the adult stage
Most adults have died
First year
Egg sacs start to hatch
Some spiders at sub-adult stage
Jan.
Feb.
March
April
May
June
July
Aug.
Sept
Oct.
Nov.
Dec.

Linyphia peltata

Females of L. peltata start to produce egg sacs in early June. The spiderlings start to emerge in mid-July and most spiderlings have emerged by late July. The spiders grow quickly and start to reach the sub-adult (fourth instar) stage by late August and by late September most of the spiders are sub-adult. Thus the overwintering population consists mainly of fourth instars, with some third instars and a few fifth instar males - which have reached the adult stage by the late autumn. The spiders overwinter among the leaf litter and become active again in the early spring. The bulk of the sub-adult males moult to adult in mid-April, while the females are approximately two weeks later in their development. Mating occurs in early May and the adult males start to die in early June. At this time the females are producing egg sacs and by the end of July most of the spiders have died. A summary of the life cycle is given in Fig.7.2.

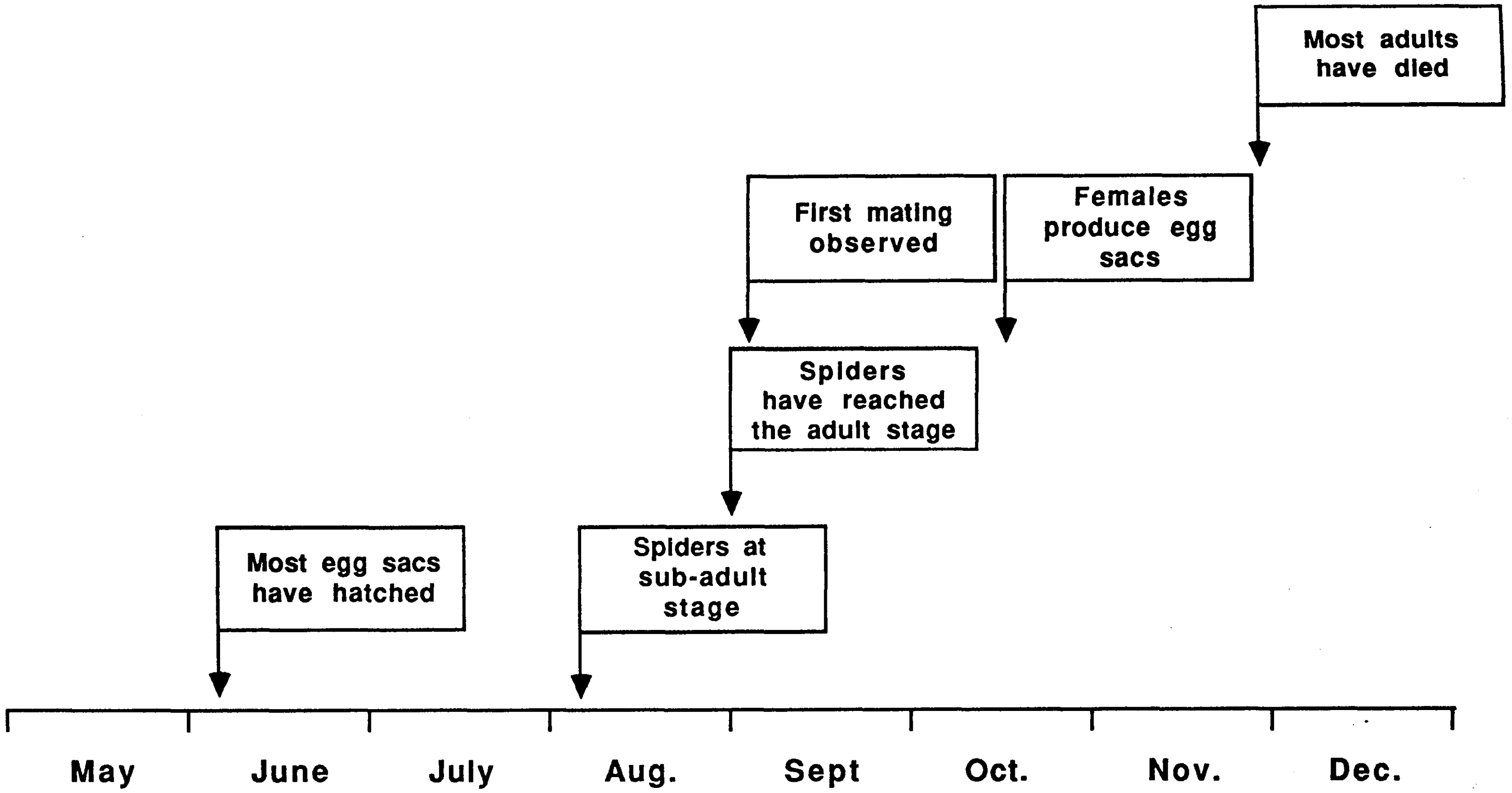
Fig.7.2: Phenology of the significant events, of the major cohort in the life cycle of Linyphia peltata .


Male spiders start to reach the adult stage
Female spiders start to reach the adult stage
First mating observed
Most males have died
Females start producing egg sacs
Most females have died
Second year
Most egg sacs have hatched
Most spiders at sub-adult stage
First year
April
May
June
July
Aug.
Sept
Oct.
Nov.
Dec.

Metellina segmentata

Females of *M. segmentata* start to produce egg sacs in mid-October. The spiderlings from these emerge in early June in woodland areas and slightly earlier in more open areas. The spiders grow quickly and start to reach the sub-adult (fourth instar) stage by early August and by mid-August most of the spiders are sub-adult. The first adults are found in early September - with females moulting to adult slightly earlier than the males. On reaching the adult stage the males cease building webs and start to search for females. Mating occurs in mid-late September and adult males start to die off in early October. By mid-October the females are starting to produce egg sacs and by mid-November most of the spiders have died. A summary of the life cycle is given in Fig.7.3.

Fig.7.3: Phenology of the significant events in the life cycle of *Metellina segmentata* .

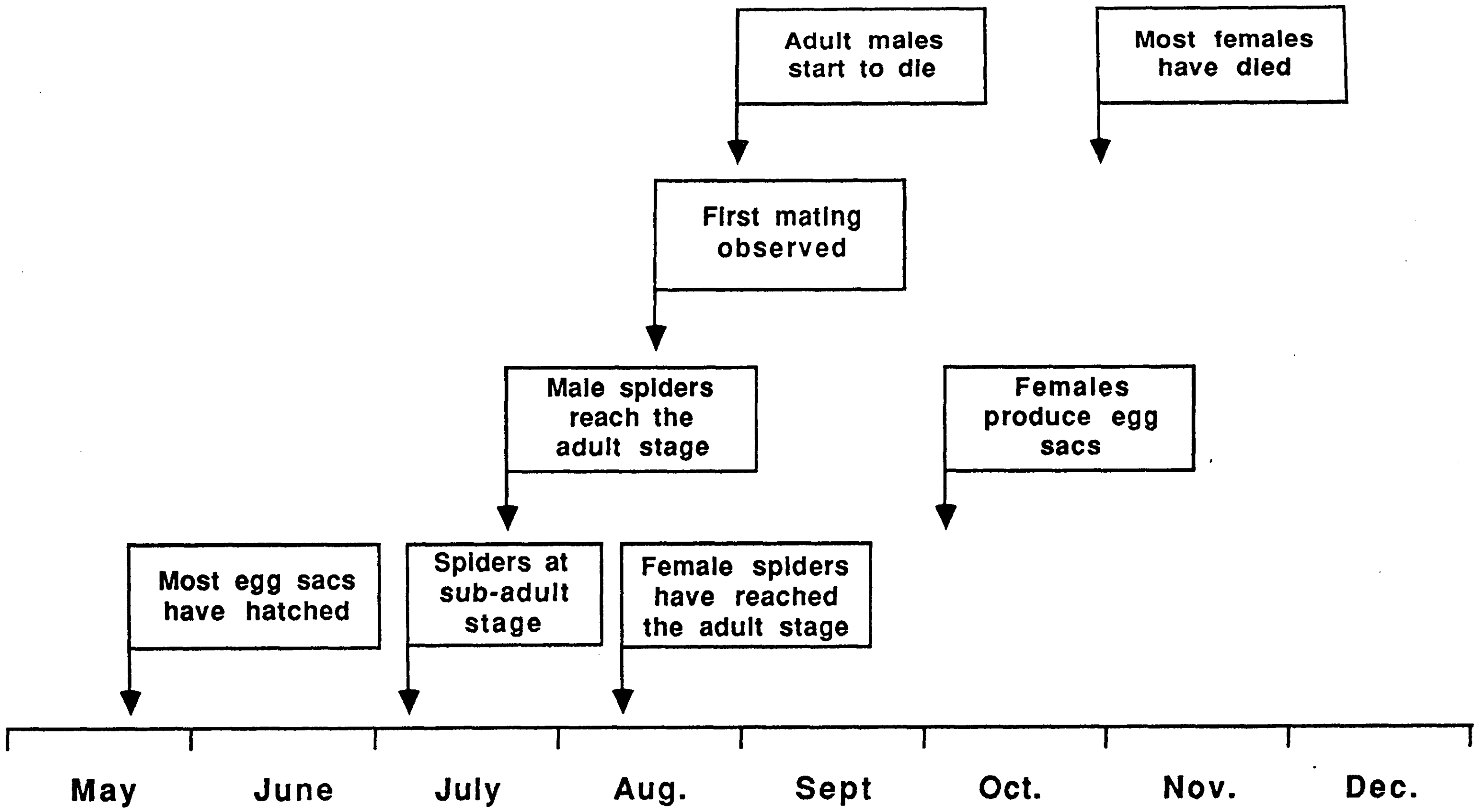

Most adults have died
First mating observed
Females produce egg sacs
Spiders have reached the adult stage
Most egg sacs have hatched
Spiders at sub-adult stage
May
June
July
Aug.
Sept
Oct.
Nov.
Dec.

Linyphia triangularis

Females of *L. triangularis* start to produce egg sacs in early October. The spiderlings start to emerge in late May in woodland areas and a little earlier in more open areas. The spiders grow quickly and start to reach the sub-adult (fourth instar) stage by mid-July and by late July most of the spiders are sub-adult. Males start to moult to adult in early August, while females are approximately two weeks later in their development. On reaching the adult stage the males cease building webs and start to search for females. Mating occurs in mid-late August and males start to die in early September. The females start to produce egg sacs in early October and by early November most of the spiders have died. A summary of the life cycle is given in Fig.7.4.

A discussion on the life cycles of these spiders will be presented at the end of the chapter on Population Age Structure and Life Cycles.

Fig.7.4: Phenology of the significant events in the life cycle of *Linyphia triangularis* .


Adult males start to die
Most females have died
First mating observed
Male spiders reach the adult stage
Females produce egg sacs
Most egg sacs have hatched
Spiders at sub-adult stage
Female spiders have reached the adult stage
May
June
July
Aug.
Sept
Oct.
Nov.
Dec.

CHAPTER 8

Population Age Structure and the Life Cycles of the Four Species

The aim of this section is to examine the size (age) structure of the populations of the four species throughout the year and from this to deduce their life cycles.

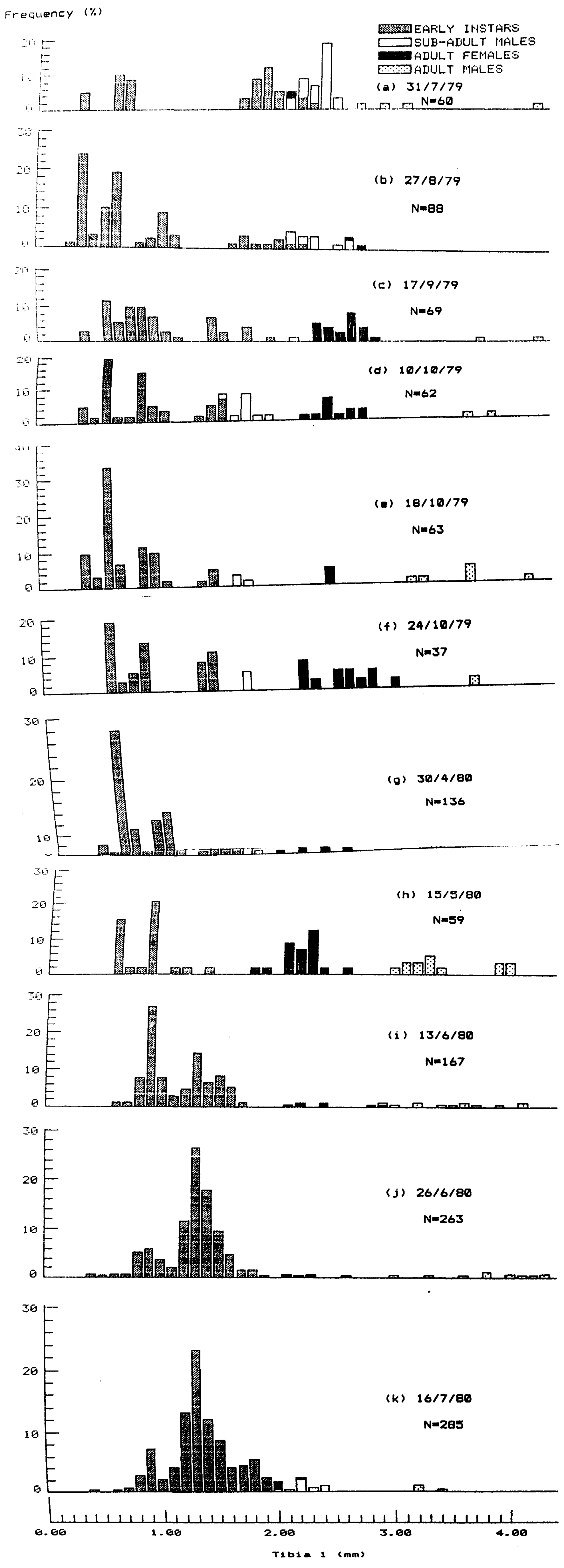
Metellina mengei

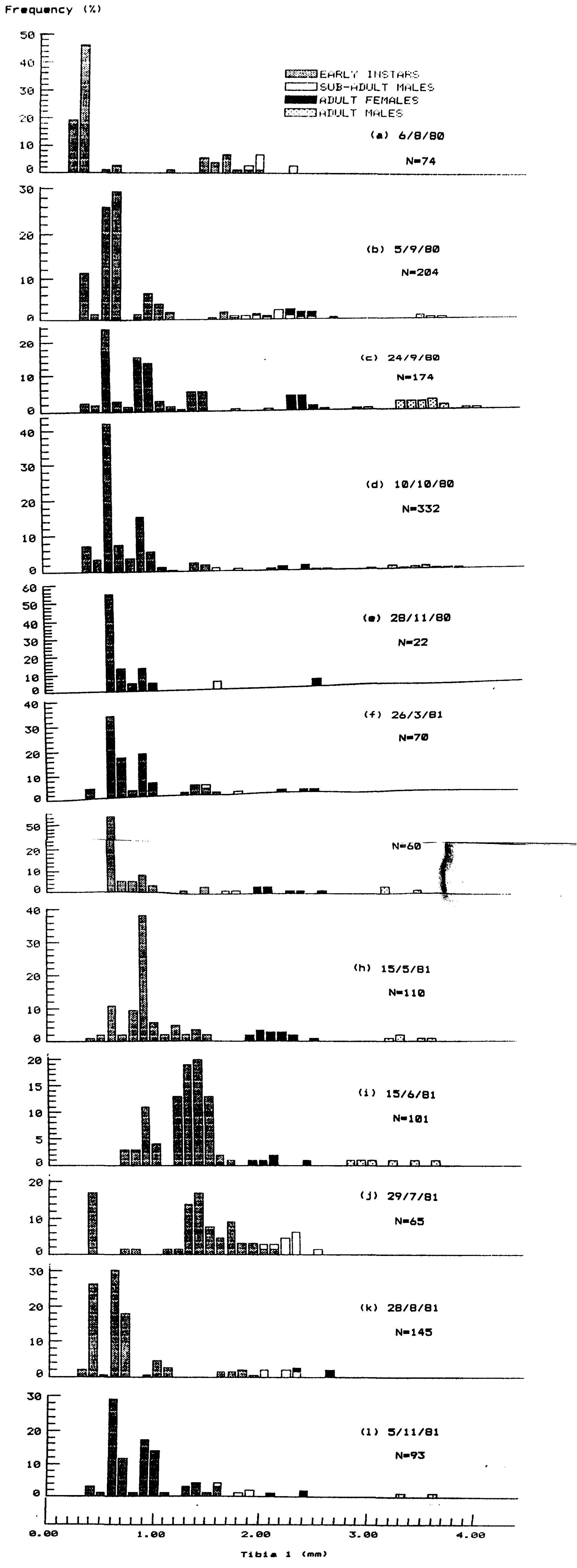
Methods

Regular samples were taken from a large area dominated by blaeberry, Vaccinium myrtillus , from late July 1979 to early November 1981. Up until mid-July 1980 these were taken by sweep netting but thereafter part of the area was designated as the main sampling area (Area 6) and all subsequent sampling was done by hand collecting - as this method provided better representative samples of the spider population (see chapter on Sampling Comparisons). The spiders were assigned to instar on the basis of the length of tibia 1 (see chapter on Determination of Instars) and histograms were plotted of the size (age) distribution of the spiders (Fig.8.1 & 8.2). The separation of the later instars, on the basis of tibia 1, was less clear than that of the earlier instars. Hence for sub-samples from mid and late June and from mid-July 1980, cephalothorax length of the spider was also measured, to provide an addition

Fig.8.1: Size (age) distribution of Metellina mengei throughout the year 1979-1980 in Area 7. Samples were taken by sweep netting.

Fig.8.2: Size (age) distribution of Metellina mengei throughout the year 1980-1981 in Area 6. Samples were taken by hand collecting.


Frequency (%)
EARLY INSTARS
SUB-ADULT MALES
ADULT FEMALES
ADULT MALES
(a) 31/7/79
N=60
(b) 27/8/79
N=88
(c) 17/9/79
N=69
(d) 10/10/79
N=62
(e) 18/10/79
N=63
(f) 24/10/79
N=37
(g) 30/4/80
N=136
(h) 15/5/80
N=59
(i) 13/6/80
N=167
(j) 26/6/80
N=263
(k) 16/7/80
N=285
0.00
1.00
2.00
3.00
4.00
Tibia 1 (mm)


Frequency (%)
EARLY INSTARS
SUB-ADULT MALES
ADULT FEMALES
ADULT MALES
(a) 6/8/80
N=74
(b) 5/9/80
N=204
(c) 24/9/80
N=174
(d) 10/10/80
N=332
(e) 28/11/80
N=22
(f) 26/3/81
N=70
N=60
(h) 15/5/81
N=110
(i) 15/6/81
N=101
(j) 29/7/81
N=65
(k) 28/8/81
N=145
(l) 5/11/81
N=93
0.00
1.00
2.00
3.00
4.00
Tibia 1 (mm)

feature on which to separate instars, and histograms were constructed on this basis (Fig.8.3 & Fig.8.4).

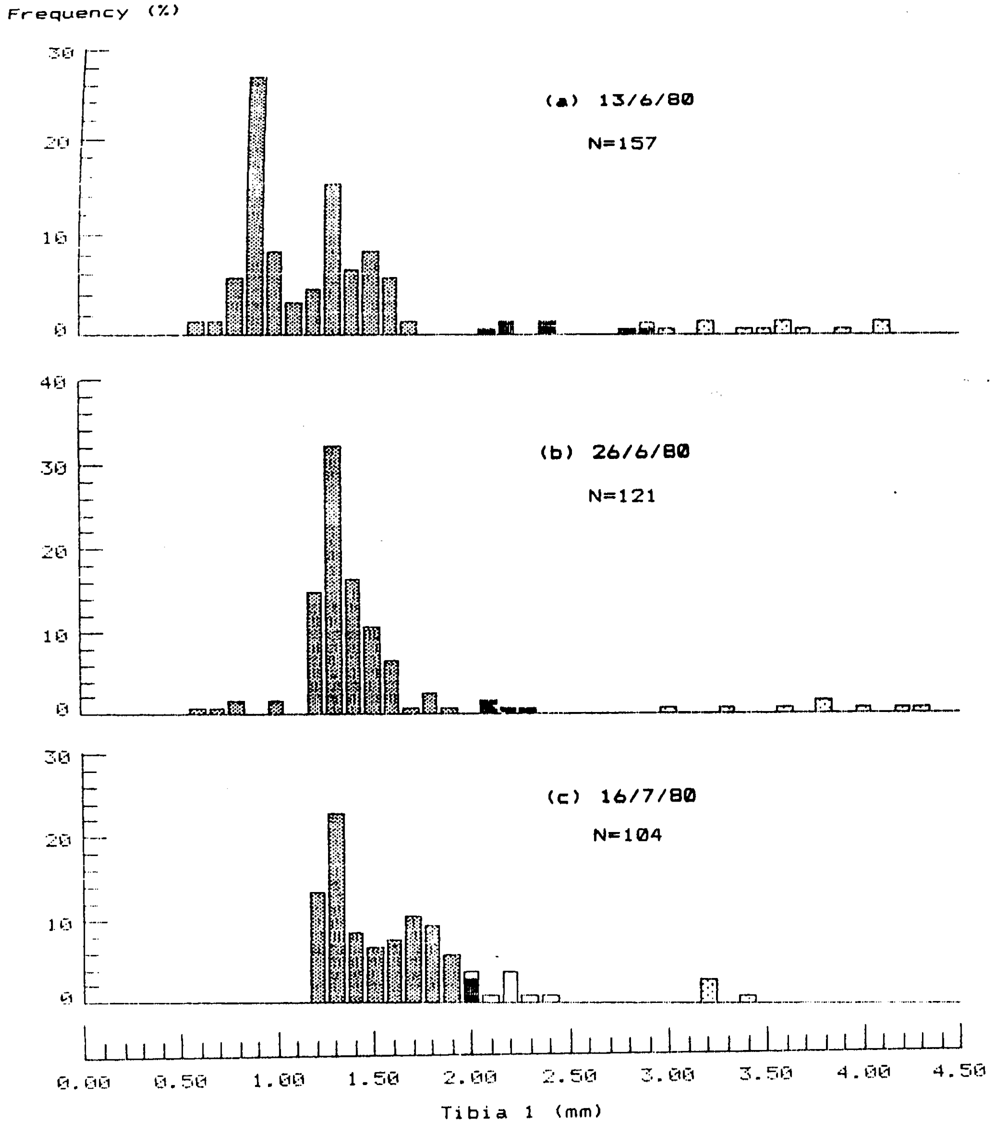
Results

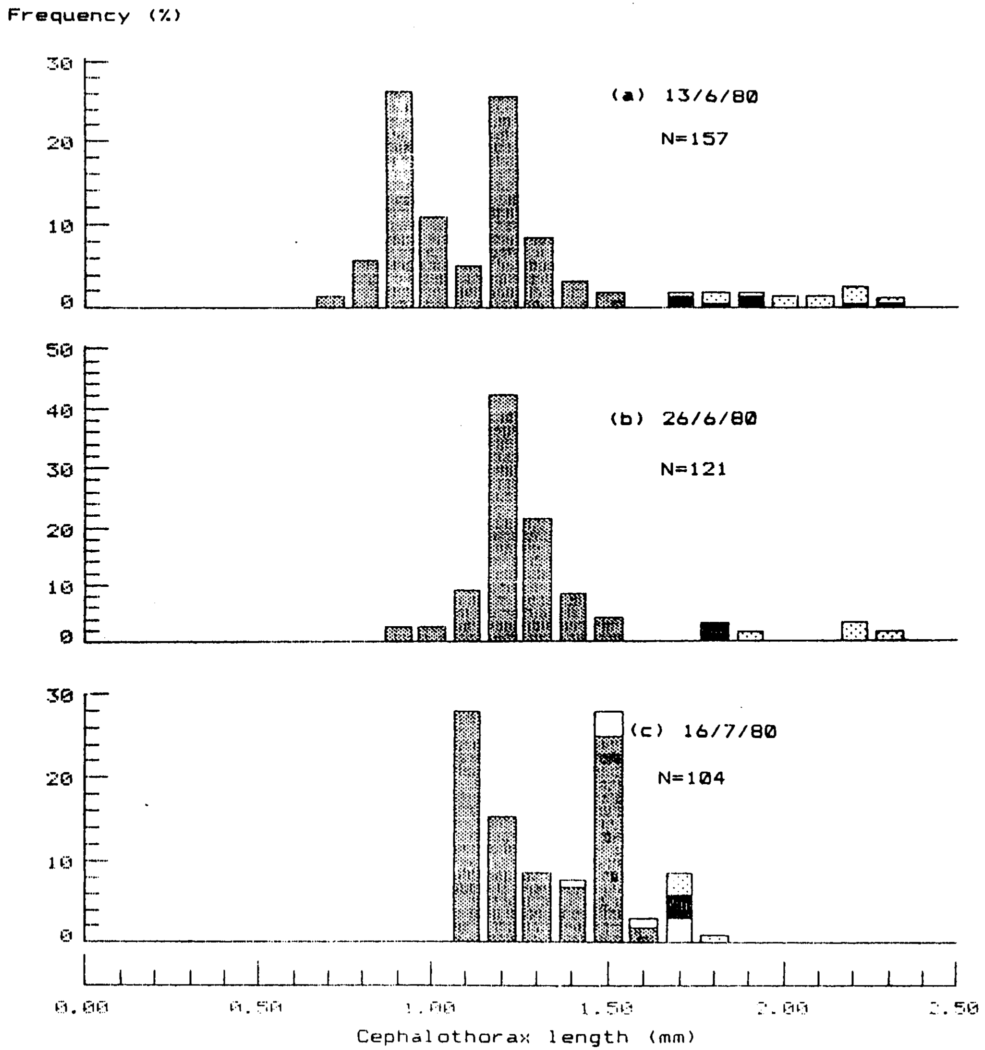
The chapter on the Determination of Instars indicated that M. mengei has five instars. In the field some of the spiders have five instars and complete their life cycle in one year. However, examination of Fig.8.1 & 8.2 indicates that there is a wide size range present in most samples - and this is indicative of the fact that some of the spiders have a two year life cycle. It will be argued that these animals have an extra instar i.e. they are adult in instar six, and they attain a larger adult size than spiders with a one year life cycle.

Despite the two different sampling methods used, the pattern of the age distribution was similar in the two years of the study. The new generation emerges in mid-July and grows rapidly so that second instars are present by late July and third instars by late August (Fig.8.1a,8.1b, 8.2a & 8.2j). By mid-September some of these have reached fourth instar (Fig.8.1c & 8.2c). Males appear to grow more slowly than females, as fourth instars with swollen pedipalps (sub-adult males) are not evident until mid-October (Fig.8.1c, 8.1d, 8.1e, 8.2b, 8.2c, 8.2d) and are larger than females (Fig.8.1d, 8.1e, 8.1f, 8.2c &

Fig.8.3: Size (age) distribution of Metellina mengei in June and July 1980, in sub-samples which were taken from Area 7, based on cephalothorax length.

Fig.8.4: Size (age) distribution of Metellina mengei in June and July 1980, in sub-samples which were taken from Area 7, based on the length of tibia 1.


Frequency (%)
30
20
10
0
(a) 13/6/80
N=157
40
30
20
10
0
(b) 26/6/80
N=121
30
20
10
0
(c) 16/7/80
N=104
0.00
0.50
1.00
1.50
2.00
2.50
3.00
3.50
4.00
4.50
Tibia 1 (mm)


Frequency (%)
30
20
10
0
(a) 13/6/80
N=157
50
40
30
20
10
0
(b) 26/6/80
N=121
30
20
10
0
(c) 16/7/80
N=104
0.00
0.50
1.00
1.50
2.00
2.50
Cephalothorax length (mm)

8.2d). This sexual dimorphism is even more striking in the adult stage where the front legs of the males are much longer than those of the females (see section on Mating Behaviour). This generation overwinters as a few first instars, a peak of second instars, some third instars and some fourth (sub-adult) instars (Fg.8.1f, 8.1g, 8.2d & 8.2f). The fourth instars appear to moult to adult in late April and early May (Fig.8.1g ,8.1h, 8.2g & 8.2h).

The rest of the overwintering population is made up of adult animals. These are spiders with a two year life cycle and it will be argued that they are adult in the sixth instar. This can be seen by following the fate of the spiders which overwinter as second and third instars. By mid-June they are mainly third and fourth instars (Fig.8.1i 8.2i) and by mid/late July they are mainly fourth and fifth instars (Fig.8.1k & 8.2j) and some sub-adult males are present. By August the bulk of these animals are fifth instars (sub-adults) (Fig.8.1a, 8.2a & 8.2k) and by late September most have reached the adult stage (Fig.8.1c & 8.2c). These animals overwinter and are joined as adults, in the following May, by the overwintering sub-adults with the one year life cycle. Mating occurs in late April, May and June (see section on Mating Behaviour). Egg sacs are produced in June, July and early August (see section on Egg Sac Production) and most adults have died off by August (Fig.8.2a).

As indicated earlier, interpretation of the age structure is most difficult in June and July. This is the stage at which sexual dimorphism is becoming evident with respect to tibia 1. The difficulty is compounded by the fact that males appear to reach the sub-adult stage later than females. Support for this interpretation comes from Fig.8.3 where the age structure is represented in terms of cephalothorax length - a feature which does not display the striking sexual dimorphism which is found with respect to tibia 1 (Fig.8.4). The July sample shows clear peaks of fourth and fifth (sub-adult) instars.

An analysis of size changes within instars, at different times of the year, gives support for the interpretation that some specimens can complete the life cycle in one year while others take two years. The second and third instars in late August/early September are larger than those in October in both 1979 and 1980 (Tables 8.1 & 8.2). The interpretation of this is that the August animals are fast-growing one year specimens and the October ones are slow-growing two year animals. The fourth instars in late March are significantly larger than those in mid-May (Table 8.3). The March animals are considered to be sub-adult (one year) animals while those in May are the two year animals with the extra instar. There is an increase in the size of fourth instars between mid-May and mid-June (Table 8.3). This is thought to reflect the fact that males develop more

Table 8.1: Size (mean ± S.D.) of tibia 1 (mm) of second and third instars of *M. mengei* in 1979 (numbers of spiders in parenthesis)

	27/8/1979	10/10/1979
2nd	0.65 ± 0.07 (29)	0.60 ± 0.04 (14)
	t=2.92, d.f.=41, P<0.01	
3rd	1.09 ± 0.08 (14)	0.94 ± 0.08 (15)
	t=4.97, d.f.=27, P<0.001	

Table 8.2: Size (mean ± S.D.) of tibia 1 (mm) of second and third instars of *M. mengei* in 1980 (numbers of spiders in parenthesis)

	5/9/1980	10/10/1980
2nd	0.65 ± 0.04 (116)	0.61 ± 0.04 (176)
	d=6.76, d.f.=290, P<0.001	
3rd	1.05 ± 0.08 (28)	0.92 ± 0.07 (87)
	d=7.28, d.f.=113, P<0.001	

Table 8.3: Size (mean ± S.D.) of tibia 1 (mm) of fourth instars of *M. mengei* in 1981 (numbers of spiders in parenthesis)

26/3/1981		15/5/1981		15/6/1981
1.44 ± 0.01 (7)		1.29 ± 0.13 (15)		1.36 ± 0.13 (68)
	t=2.64, d.f.=20 P<0.05		t=2.04, d.f.=81 P<0.05	

slowly than females and that the June sample has a larger proportion of males. At this stage the sexual dimorphism, with regard to tibia 1, is thought to be having an effect - so that fourth instars which eventually become males are larger than those which develop into females.

The sub-adult males in late July/early August are larger than those in October and November in 1979, 1980 and 1981 (Table 8.4). The July/August animals are considered to be fifth instar (two year) animals and the October/November ones fourth instar (one year) specimens.

The size of adult males and females remains constant throughout the autumn (Tables 8.5 & 8.6) in 1979 and 1980. This indicates that none of the one year (fourth instar) sub-adults moult to adult in the autumn.

The adult females in late spring are smaller than those of the previous autumn (Table 8.7). This is interpreted as being due to the moulting of fourth instar (one year) sub-adults to adult in the spring, which reduces mean adult size. With experience, it is possible to distinguish fifth instar and sixth instar adult females with a reasonable degree of certainty. In May the fifth instar animals are smaller, lighter and have a lighter coloration than the sixth instar ones. In June the colour is similar in the two groups but most of the sixth instars have produced egg sacs

Table 8.4: Size (mean ± S.D.) of tibia 1 (mm) of sub-adult males of *M. mengei* in different years (numbers of spiders in parenthesis)

31/7/1979	10/10/1979
2.44 ± 0.12 (21)	1.80 ± 0.11 (9)
t=13.94, d.f.=28, P<0.001	
6/8/1980	10/10/1980
2.07 ± 0.16 (7)	1.68 ± 0.11 (5)
t= 4.70, d.f.=10, P<0.001	
29/7/1981	5/11/1981
2.24 ± 0.13 (10)	1.80 ± 0.14 (4)
t=5.44, d.f.=12, P<0.001	

Table 8.5: Size (mean ± S.D.) of tibia 1 (mm) in adult females of *M. mengei* , in Area 6, in autumn of 1979 and 1980 (numbers of spiders in parenthesis)

17/9/1979	10/10/1979	24/10/1979
2.62 ± 0.16 (19)	2.57 ± 0.16 (11)	2.63 ± 0.27 (12)
t=0.80, d.f.=28 P>0.05	t=0.65, d.f.=21 P>0.05	
5/9/1980	24/9/1980	10/10/1990
2.37 ± 0.19 (12)	2.41 ± 0.15 (18)	2.32 ± 0.16 (13)
t=0.72, d.f.=28 P>0.05	t=0.65, d.f.=29 P>0.05	

Table 8.6: Size (mean ± S.D.) of tibia 1 (mm) in adult males of _M. mengei_, in Area 6, in autumn of 1980 (numbers of spiders in parenthesis)

24/9/1980	10/10/1980
3.50 ± 0.22 (22)	3.41 ± 0.23 (13)
t=1.26, d.f.=33, P>0.05	

Table 8.7: Size (mean ± S.D.) of tibia 1 (mm) in adult females of _M. mengei_, in Area 6, from autumn to the following spring (numbers of spiders in parenthesis)

24/10/1979	15/5/1980
2.63 ± 0.27 (12)	2.18 ± 0.15 (19)
t=5.31, d.f.=11, P<0.001	
10/10/1980	15/5/1981
2.32 ± 0.16 (13)	2.12 ± 0.17 (15)
t=3.19, d.f.=26, P<0.005	

by this time and the abdomen has a characteristic shrunken appearance. They also look larger than the fifth instars - although they may weigh less. The size of adult males shows no change between mid-October and mid-May (Table 8.8).

Some additional samples in other areas during this period, and some samples from 1983, 1984 and 1985, indicated that details of the life cycle may vary from habitat to habitat and from year to year and that instar size can also differ between habitats and between years.

Whereas the size of adult females in the main sampling area (Area 6) remained constant during the autumn (Table 8.5), samples from an adjacent area (Area 7) indicated that adult females decreased in size from late September to mid-October (Table 8.9). An explanation for this could be that there is some moulting of fourth instar (1 year) animals to adult in the autumn.

In Area 6 the size of adult females decreases from autumn to the following spring (Table 8.7) in both years. In Area 7, however, there was no decrease between mid-October 1980 and late March 1981 (Table 8.10). In 1984/85, sampling was carried out in an area dominated by blaeberry and in an area where heather was the dominant vegetation, in early winter and in the following spring. There was an increase in size in the blaeberry during this period but no change in the

Table 8.8: Size (mean ± S.D.) of tibia 1 (mm) in adult males of *M. mengei* , in Area 6, from autumn to the following spring (numbers of spiders in parenthesis)

10/10/1980	15/5/1980
3.41 ± 0.23 (13)	3.38 ± 0.16 (5)
t=0.25, d.f.=16, P>0.05	

Table 8.9: Size (mean ± S.D.) of tibia 1 (mm) in adult females of *M. mengei* , in Area 7, in autumn 1980 (numbers of spiders in parenthesis)

10/10/1980	14/10/1980
2.47 ± 0.17 (43)	2.37 ± 0.16 (83)
d=2.84, d.f.=124, P<0.005	

Table 8.10: Size (mean ± S.D.) of tibia 1 (mm) in adult females of *M. mengei* , in Area 7, in autumn 1980 and spring 1981(numbers of spiders in parenthesis)

14/10/1980	31/3/1981
2.37 ± 0.16 (83)	2.39 ± 0.19 (23)
d=0.28, d.f.=104, P>0.05	

heather area (Table 8.11).

There was no change in the size of adult males from mid-October to mid-May in Area 6 (Table 8.8) and no change in size was found in Area 7 during the same period (Table 8.12). The size of adult females decreases, from September to the following May, in Area 6 in 1979-80 and 1980-81 and in Area 7 in 1980-81 (Table 8.13). This is interpreted as being due to the one year, fourth instar, moulting to adult - either in the autumn or the early spring. The size of adult males in Areas 6 and 7 does not change between September 1980 and May 1981 (Table 8.14). This is difficult to explain in terms of the description of the life cycle given. One might have expected a decrease during this period as the smaller one year animals were recruited into the adult population.

The picture which emerges from this section is one of considerable variability, with regard to body size, between areas. This makes interpretation of the results more difficult. The biological variability is further displayed if comparisons are made of similar stages of the life cycle in different years.

The sizes of sub-adult (fifth instar) males found in the summer are given for four different years in Table 8.15. The animals in 1979 are significantly larger than those in

Table 8.11: Size (mean ± S.D.) of tibia 1 (mm) of adult females of *M. mengei* in an area of blaeberry and an area of heather in November 1984 and April 1985 (numbers of spiders in parenthesis)

	19/11/1984	3/4/1985
Blaeberry	2.65 ± 0.18 (45)	2.67 ± 0.18 (90)
	d=3.27, d.f.=133, P<0.005	
Heather	2.59 ± 0.20 (10)	2.56 ± 0.18 (45)
	d=0.50, d.f.=56, P>0.05	

Table 8.12: Size (mean ± S.D.) of tibia 1 (mm) in adults males of *M. mengei* , in Area 7, from autumn to following spring (numbers of spiders in parenthesis)

14/10/1980	15/5/1981
3.49 ± 0.25 (50)	3.40 ± 0.25 (18)
d=1.37, d.f.=66, P>0.05	

Table 8.13: Size (mean ± S.D.) of tibia 1 (mm) in adult females of *M. mengei* in Areas 6 and 7 (numbers of spiders in parenthesis)

	17/9/1979	15/5/1980
Area 6	2.62 ± 0.16 (19)	2.18 ± 0.15 (19)
	t=8.73, d.f.=36, P<0.001	
	5/9/1980	15/5/1981
Area 6	2.37 ± 0.19 (12)	2.12 ± 0.17 (15)
	t=3.63, d.f.=25, P<0.005	
	23/9/1980	15/5/1981
Area 7	2.47 ± 0.10 (12)	2.27 ± 0.20 (20)
	t=3.83, d.f.=11, P<0.005	

Table 8.14: Size (mean ± S.D.) of tibia 1 (mm) in adult males in Areas 6 and 7 (numbers of spiders in parenthesis)

	24/9/1980	15/5/1981
Area 6	3.50 ± 0.22 (22)	3.38 ± 0.16 (5)
	t=1.2, d.f.=25, P>0.05	
	23/9/1980	15/5/1981
Area 7	3.62 ± 0.13 (5)	3.40 ± 0.25 (18)
	t=1.89, d.f=21, P>0.05	

Table 8.15: The mean size of summer sub-adult males of *M. mengei* in different years. Values joined by a line are not significantly different at P=0.05 using t-test.

	1979	1984	1980	1981
Mean	2.43	2.38	2.12	2.20
± S.D.	± 0.14	± 0.12	± 0.18	± 0.13
No	32	8	22	18

Table 8.16: The mean size of autumn sub-adult males of *M. mengei* in different years. Values joined by a line are not significantly different at P=0.05 using t-test.

	1979	1984	1980	1981
Mean	1.80	1.77	1.68	1.80
± S.D.	± 0.11	± 0.14	± 0.11	± 0.14
No	9	14	5	4

Table 8.17: Size (mean ± S.D.) of tibia 1 (mm) in adult females of *M. mengei* in May 1980 and 1981 and in "Blaeberry" area in May 1985 (numbers of spiders in parenthesis)

15/5/1980	15/5/1981	6/5/1985
2.18 ± 0.15 (19)	2.12 ± 0.17 (15)	2.63 ± 0.20 (103)
t=1.18, d.f.=32 P>0.05		d=10.78, d.f.=116 P<0.001

1980 (t=6.79, d.f.=52, P<0.001) and those in 1981 significantly smaller than those in 1984 (t=3.44, d.f.=24, P<0.005). The sizes of the sub-adult males (fourth instars) found in the autumn, did not differ significantly between the four years (Table 8.16). The size of adult females in Area 6 in May 1980 did not differ significantly from those in May 1981 but were smaller than those in the blaeberry area sampled in 1985 (Table 8.17).

Spider size also varies in different vegetation types within a year. This is seen from the size of adult females and males in the blaeberry and heather areas sampled in 1984/85 (Tables 8.18 & 8.19). There was no significant difference in the two areas, with regard to female size, in mid-November 1984 and with regard to both male and female size in June 1985. However both males and females, in heather in April and May 1985, are smaller than in blaeberry during the same period (Tables 8.18 & 8.19). These differences may simply reflect differences in the rates of development in the two vegetation types.

Thus the life cycle of M. mengei can be of one or two years duration. It seems likely that most animals which have a one year life cycle will produce offspring which will have a two year life cycle, and vice versa . However, it is clear that there is considerable variability in the life cycle and there is probably no fixed pattern.

Table 8.18: The difference of the mean size (tibia 1 in mm) of adult female of <u>M. mengei</u> between different habitats (Blaeberry and Heather) in late autumn 1984 and spring 1985.

Date	Blaeberry	Heather	t-test
	Mean ± S.D. No	Mean ± S.D. No	d.f. P
19/11/1984	2.56 ± 0.18 45	2.59 ± 0.20 10	d=0.44 53 >0.05
3/4/1985	2.67 ± 0.18 90	2.56 ± 0.18 48	d=3.39 136 <0.001
6/5/1985	2.63 ± 0.20 103	2.51 ± 0.20 38	d=3.21 139 <0.005
6/6/1985	2.55 ± 0.23 79	2.47 ± 0.19 10	d=1.21 87 >0.05

Table 8.19: The difference of the mean size (tibia 1 in mm) of adult males of <u>M. mengei</u> between different habitats (Blaeberry and Heather) in late autumn 1984 and spring 1985.

Date	Blaeberry	Heather	t-test
	Mean ± S.D. No	Mean ± S.D. No	d.f. P
3/4/1985	3.84 ± 0.22 46	3.66 ± 0.33 20	2.25 27 <0.05
6/5/1985	3.90 ± 0.25 53	3.58 ± 0.25 31	5.54 82 <0.001
6/6/1985	3.84 ± 0.29 52	3.79 ± 0.32 10	0.42 60 >0.05

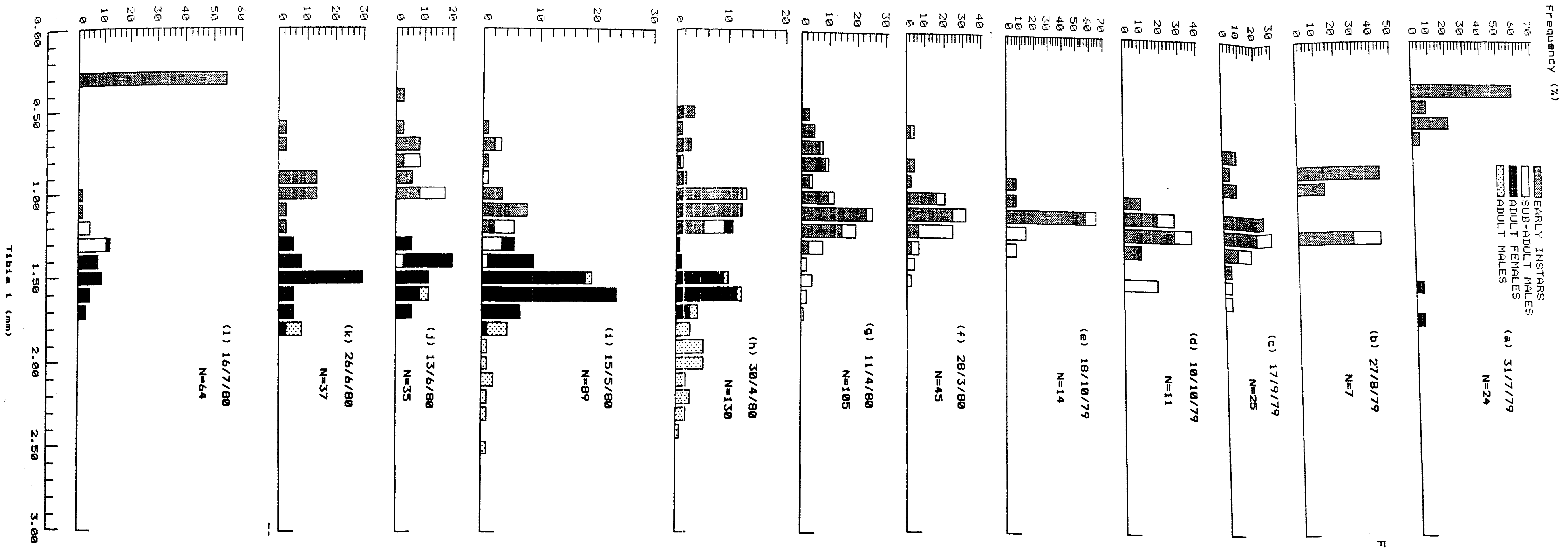
Linyphia peltata

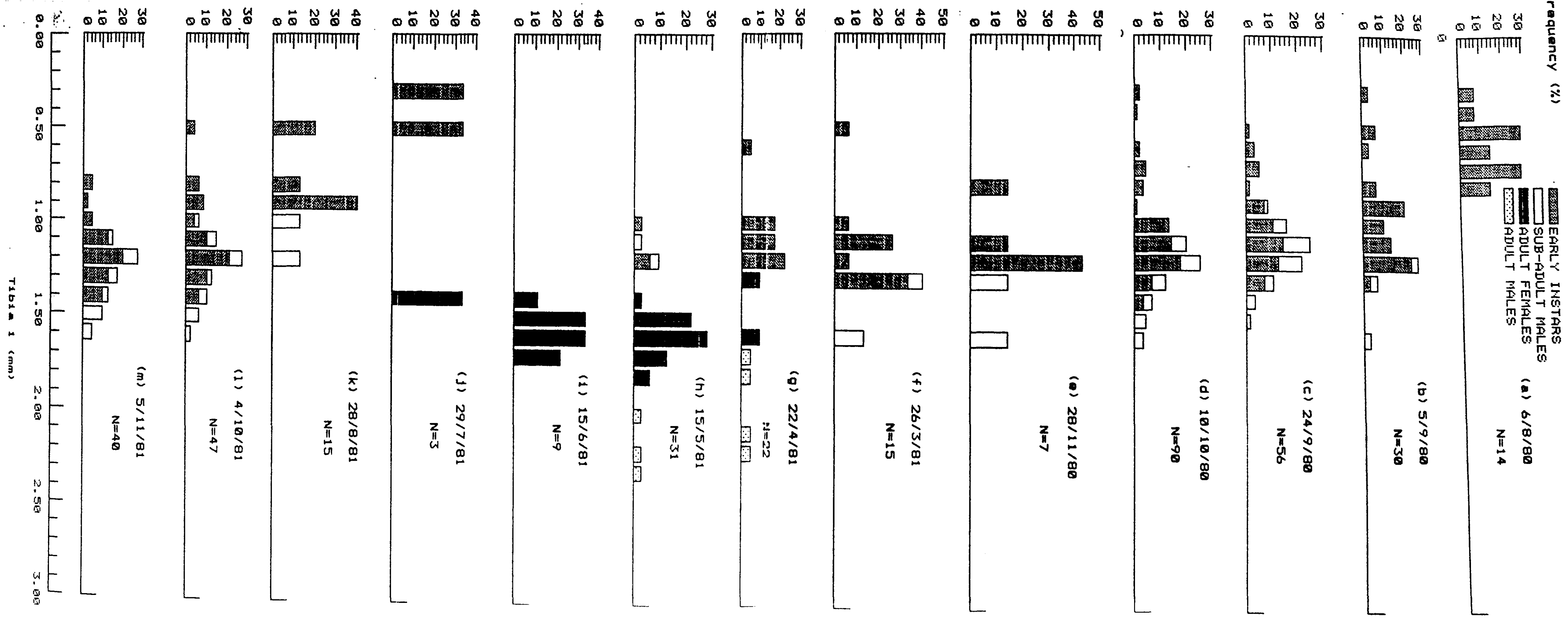
Methods

Regular samples were taken from a large area, where the dominant vegetation was blaeberry (*Vaccinium myrtillus*), from late July 1979 to early November 1981. Up until mid-July 1980 these were taken by sweep netting but thereafter part of this area was designated as the main sampling area (Area 6) and all subsequent sampling was done by hand collecting - as this proved to be the best method for obtaining representative samples (see chapter on Sampling Comparisons). The spiders were assigned to instars on the basis of the length of tibia 1 (see chapter on Determination of Instars) and histograms were plotted of the size (age) distribution of the spiders (Fig.8.5 & 8.6). Additional information was provided by sweep net samples from an area of small coniferous trees in late August and early September 1980 and from an area of heather (*Calluna vulgaris*) in September and late November 1980. Additional sweep net samples were also taken in the spring of 1980 to determine precisely when sub-adult animals moult to adult.

Fig.8.5: Size (age) distribution of *Linyphia peltata* throughout the year 1979-1980 in Area 7. Samples were taken by sweep netting.

Fig.8.6: Size (age) distribution of *Linyphia peltata* throughout the year 1980-1981 in Area 6. Samples were taken by hand collecting.


Frequency (%)
EARLY INSTARS
SUB-ADULT MALES
ADULT FEMALES
ADULT MALES
(a) 31/7/79 N=24
(b) 27/8/79 N=7
(c) 17/9/79 N=25
(d) 10/10/79 N=11
(e) 18/10/79 N=14
(f) 28/3/80 N=45
(g) 11/4/80 N=105
(h) 30/4/80 N=130
(i) 15/5/80 N=89
(j) 13/6/80 N=35
(k) 26/6/80 N=37
(l) 16/7/80 N=64
Tibia 1 (mm)
0.00
0.50
1.00
1.50
2.00
2.50
3.00


Frequency (%)
EARLY INSTARS
SUB-ADULT MALES
ADULT FEMALES
ADULT MALES
(a) 6/8/80 N=14
(b) 5/9/80 N=30
(c) 24/9/80 N=56
(d) 10/10/80 N=90
(e) 28/11/80 N=7
(f) 26/3/81 N=15
(g) 22/4/81 N=22
(h) 15/5/81 N=31
(i) 15/6/81 N=9
(j) 29/7/81 N=3
(k) 28/8/81 N=15
(l) 4/10/81 N=47
(m) 5/11/81 N=40
Tibia 1 (mm)
0.00
0.50
1.00
1.50
2.00
2.50
3.00

Results

Despite the two methods of sampling used, the pattern of the age distribution was fairly similar throughout the two years of the study.

The results indicate that L. peltata has a one year life cycle. There is, however, an indication that there are two distinct cohorts within the population. The larger of these has females which start to produce egg sacs in early June. The spiderlings from these start to emerge in mid-July and grow rapidly so that second and third instars are present in late July and early August (Fig.8.5a, 8.6a & 8.6j). By late August/early September some of these have reached the fourth instar (sub-adult) stage (Fig.8.5b & 8.6b). Most of the spiders are sub-adult by mid/late September (Fig.8.5c & 8.6c). The majority of spiders overwinter as third instars or sub-adults (Fig.8.5e, 8.6e & 8.6m). The spiders overwinter amongst the leaf litter and no change takes place in the age structure of the population during the winter (Fig.8.5f & 8.6f). Males start moulting to adult approximately two weeks earlier than females (Table 8.20). By mid-May most of the spiders are adult (8.5i & 8.6h). Most males have died by early June (Fig.8.5j & 8.6i). At this time the females start to produce egg sacs and by mid/late July most of the females have died (Fig.8.5l & 8.6j).

Table 8.20: Number of males and females spiders of Linyphia peltata recorded in samples in early spring 1980 during moulting to adults. (Numbers in parenthesis are percentage of the spiders in that sex)

Date of sampling	Males		Females	
	Sub-adult	Adult	Sub-adult	Adult
31/3/1980	7 (100)	0 (0)	11 (100)	0 (0)
11/4/1980	23 (100)	0 (0)	52 (100)	0 (0)
14/4/1980	16 (84.2)	3 (15.8)	21 (100)	0 (0)
18/4/1980	12 (36.4)	21 (63.6)	27 (100)	0 (0)
24/4/1980	2 (8.7)	21 (91.3)	13 (76.5)	4 (23.5)
30/4/1980	6 (15.4)	33 (84.6)	42 (53.8)	36 (46.2)

Evidence for the existence of the smaller cohort is less complete. It is suggested that it is represented by the adult females which are present in mid and late July (Fig.8.5a 8.5l & 8.6j). The indication is that these animals have recently moulted to adult (Fig.8.5l) and that they are not the survivors of the adults which produced egg sacs in early summer. Support for interpretation is given by Fig.8.5h - 8.5k, as there is a group of spiders, at the "tail" of the distribution, which does not fit in with the group which reaches adult in early summer. Thus the smallest spiders in the overwintering group seem to give rise to a cohort which reaches adult in mid-summer. The offspring of these spiders seem to be represented by a group of small spiders present in samples in autumn and spring (Fig.8.6b, 8.6d, 8.6f & 8.6g). These give rise to adults in late July (Fig.8.6j)

Metellina segmentata

Methods

M. segmentata is a widely distributed species. It occurs on a variety of vegetation e.g. small trees, bushes, grasses and is found both in woodlands and in more open areas. Samples were taken from June to October 1980, by hand collecting, in two different areas. One area, Area 11, was located in the Ross Wood and was dominated by blaeberry. The other, Area B3, in Dawsholm Park (on the outskirts of Glasgow) and was dominated by grass and different kinds of small shrubs.

Spiders were assigned to instar on the basis of the length of tibia 1 (see chapter on Determination of Instars) and histograms were plotted of the size distribution of the spiders in samples from Dawsholm Park (Fig.8.7) and the Ross Wood (Fig.8.8). In most of the samples the spiders fell into two, or at most three, distinct size categories - which were taken to correspond to the various instars. In order to try to determine the number of instars all the samples taken in each area were amalgamated. The results are shown in Fig.8.9 (Dawsholm Park) and Fig.8.10 (Ross Wood).

Fig.8.7: Size (age) distribution of *Metellina segmentata* throughout the year 1980 in Area B3 in Dawsholm park.

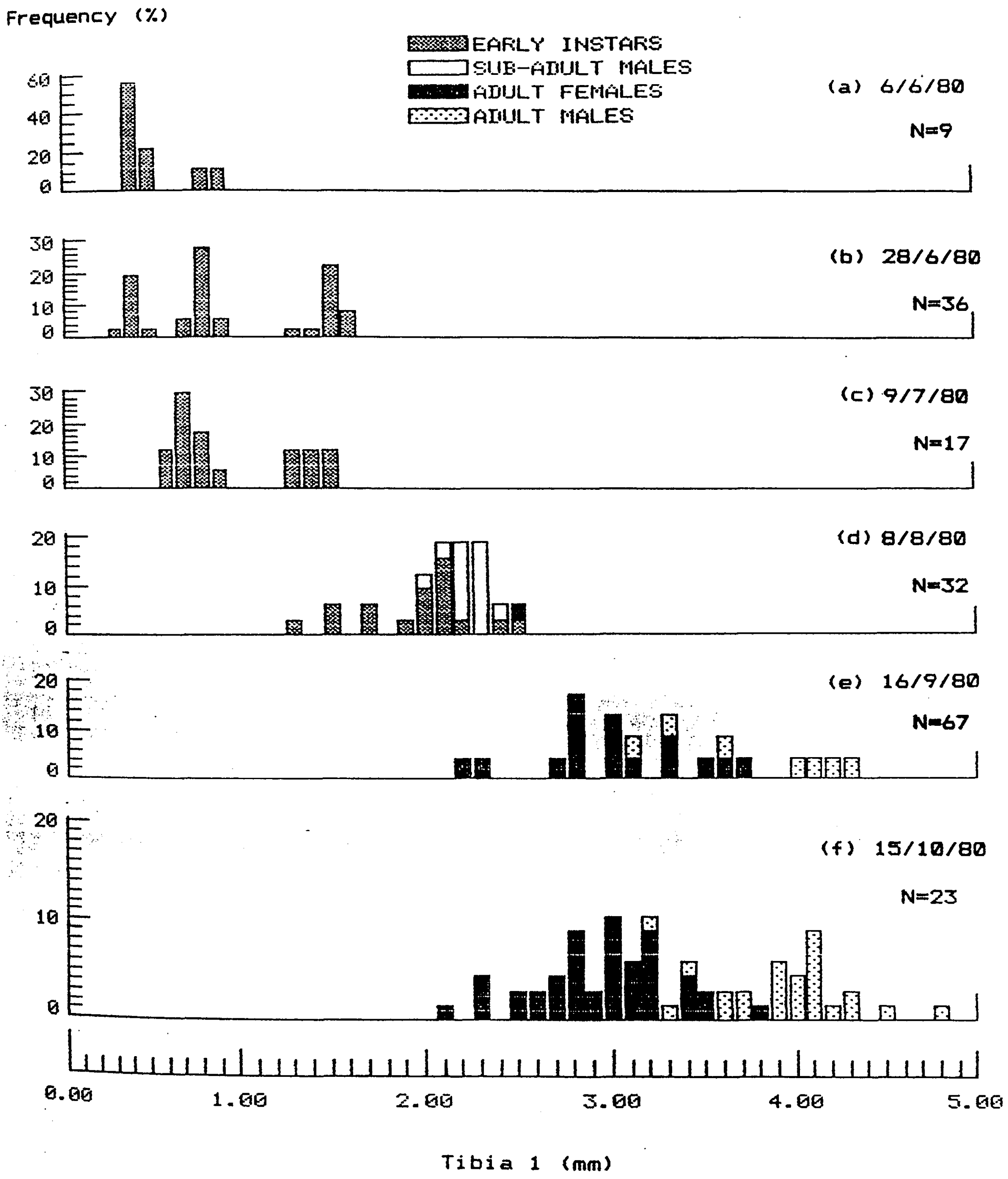

Frequency (%)
EARLY INSTARS
SUB-ADULT MALES
ADULT FEMALES
ADULT MALES
(a) 6/6/80
N=9
60
40
20
0
(b) 28/6/80
N=36
30
20
10
0
(c) 9/7/80
N=17
30
20
10
0
(d) 8/8/80
N=32
20
10
0
(e) 16/9/80
N=67
20
10
0
(f) 15/10/80
N=23
20
10
0
0.00
1.00
2.00
3.00
4.00
5.00
Tibia 1 (mm)

Fig.8.8: Size (age) distribution of Metellina segmentata throughout the year 1980 in Area 11 in Ross Wood.

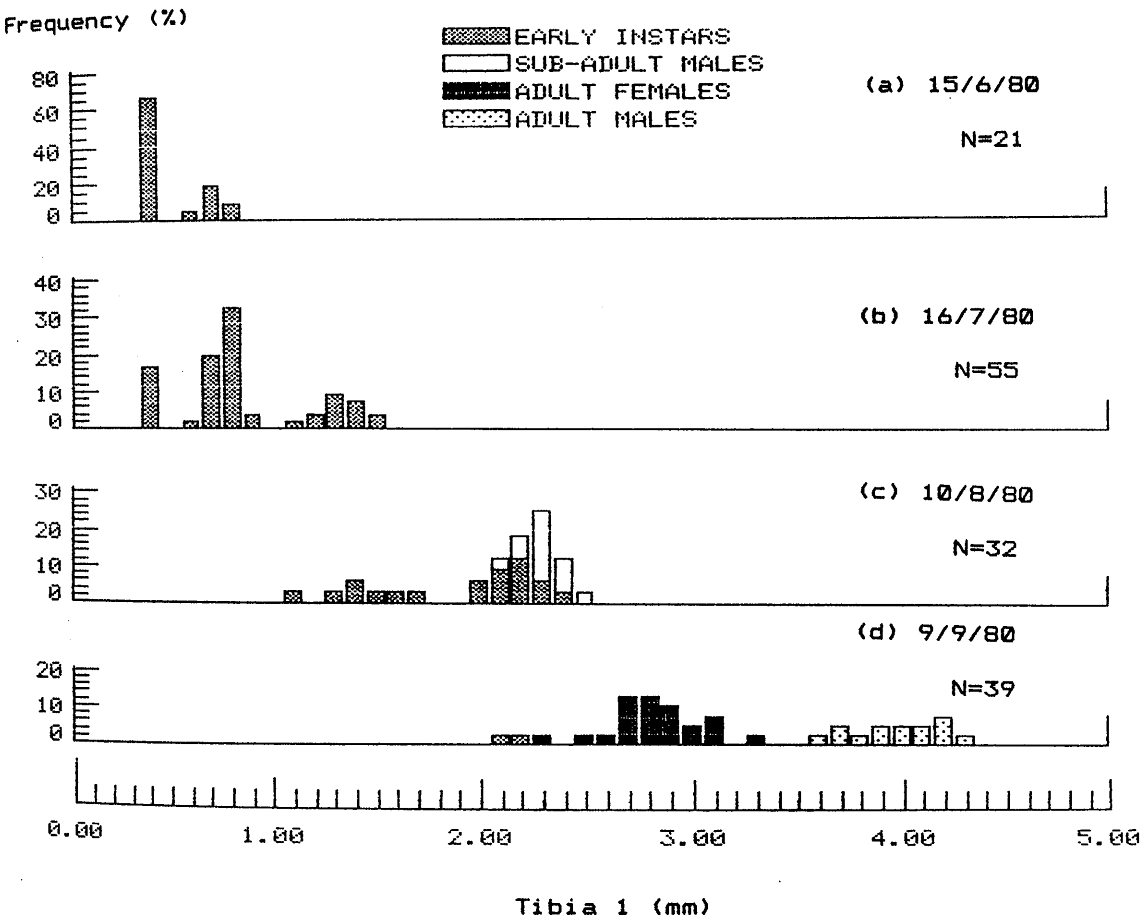
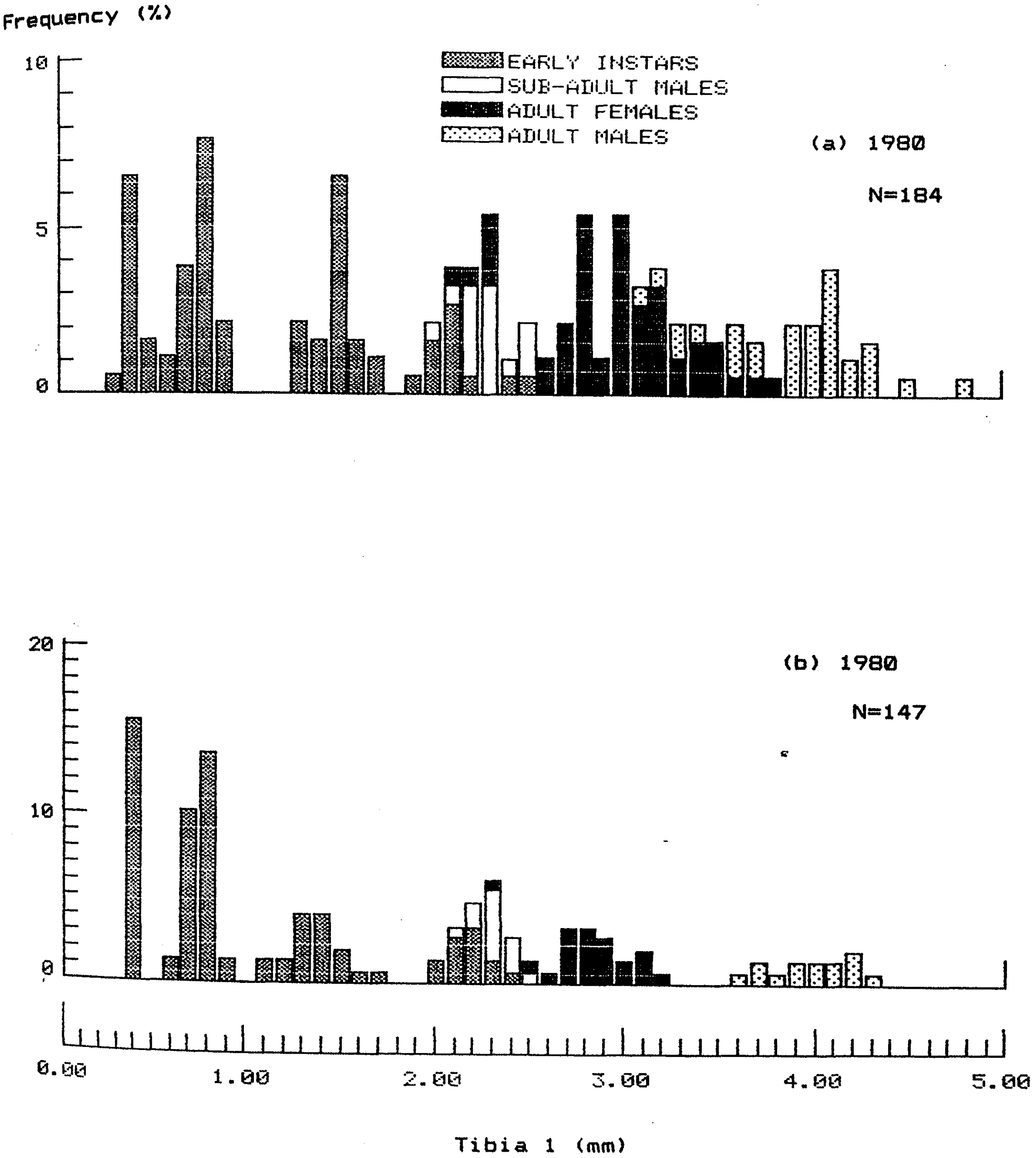

Frequency (%)
EARLY INSTARS
SUB-ADULT MALES
ADULT FEMALES
ADULT MALES
(a) 15/6/80
N=21
80
60
40
20
0
(b) 16/7/80
N=55
40
30
20
10
0
(c) 10/8/80
N=32
30
20
10
0
(d) 9/9/80
N=39
20
10
0
0.00
1.00
2.00
3.00
4.00
5.00
Tibia 1 (mm)

Fig.8.9: The number of instars of *Metellina segmentata* based on samples from Area B3 in Dawsholm park in 1980.

Fig.8.10: The number of instars of *Metellina segmentata* based on samples from Area 11 in Ross Wood in 1980.


Frequency (%)
10
5
0
EARLY INSTARS
SUB-ADULT MALES
ADULT FEMALES
ADULT MALES
(a) 1980
N=184
20
10
0
(b) 1980
N=147
0.00
1.00
2.00
3.00
4.00
5.00
Tibia 1 (mm)

Results

The pattern of the age distribution is similar in the two areas (Fig.8.7 & 8.8). At Dawsholm Park the new generation emerges from the egg sacs in May (see chapter on Egg Sac Production) and by early June some of the spiders have reached the second instar (Fig.8.7a) and by late June some of them are third instars (Fig.8.7b). By early August most of the spiders are at the sub-adult stage and a few adults are present (Fig.8.7d). By mid-September all the spiders are adult (Fig.8.7e).

In the Ross Wood the pattern of the age distribution is similar but spider development is slightly slower. Thus the new generation emerges later than at Dawsholm Park (see chapter on Egg Sac Production). By mid-June some second instars are present (Fig.8.8a) and by mid-July some of the spiders have reached the third instar (Fig.8.8b). By early August most of the spiders are sub-adults (Fig.8.8c) and by early September most of them are adult (Fig.8.8d).

An examination of the amalgamated samples from the two areas (Fig.8.9 & 8.10) suggests that *M. segmentata* has 5 instars. There are three well separated peaks in the size distribution at 0.3-0.5mm, 0.6-0.9mm and 1.1-1.7mm, corresponding to the first three instars. Sub-adults range from 1.9-2.5mm and adults from 2.1-4.8mm.

Linyphia triangularis

Methods

This species, like M. segementata, is widely distributed on a variety of vegetation types and occurs both in woodlands and in more open areas. Samples were taken from May to October 1980, by hand collecting, in two different areas. One area, Area 8, is in the Ross Wood and the dominant vegetation is blaeberry. The other area, Area 82, is in Dawsholm Park and is in an open area of short grass.

Spiders were assigned to instar on the basis of the length of tibia 1 (see chapter on Determination of Instars) and histograms were plotted of the size distribution of spiders in samples from Dawsholm Park (Fig.8.11) and the Ross Wood (Fig.8.12). Additional samples were taken from Area 8 in 1981 (Fig.8.13). In most of the samples the spiders fell into one or two distinct size categories - which were taken to correspond to the various instars. In order to try to determine the number of instars all the samples taken in each area in 1980 were amalgamated. The results are shown in Fig.8.14 (Dawsholm Park) and Fig.8.15 (Ross Wood).

Fig.8.11: Size (age) distribution of *Linyphia triangularis* throughout the year 1980 in Area B2 in Dawsholm park.

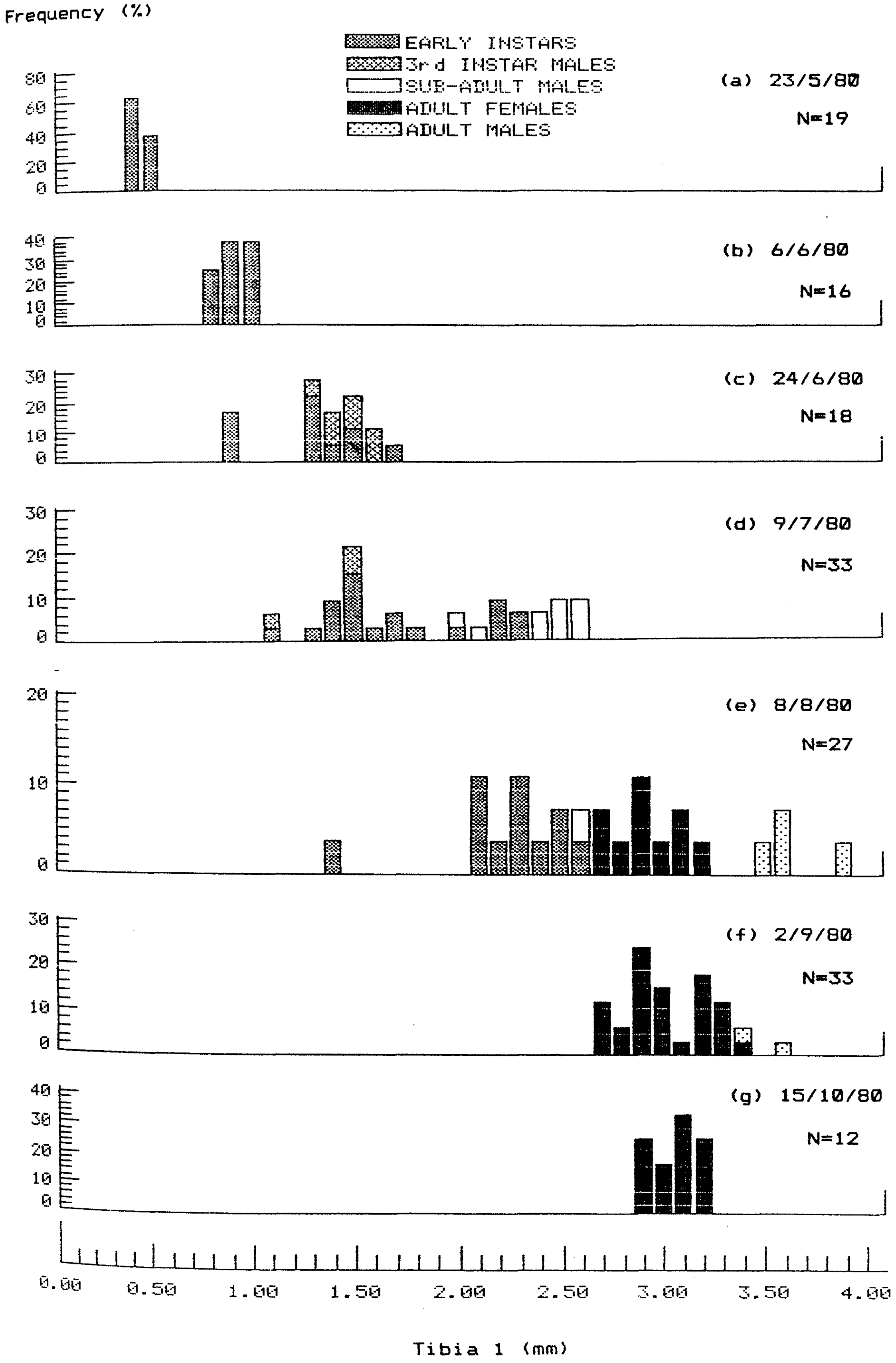

Frequency (%)
EARLY INSTARS
3rd INSTAR MALES
SUB-ADULT MALES
ADULT FEMALES
ADULT MALES
(a) 23/5/80
N=19
0 20 40 60 80
(b) 6/6/80
N=16
0 10 20 30 40
(c) 24/6/80
N=18
0 10 20 30
(d) 9/7/80
N=33
0 10 20 30
(e) 8/8/80
N=27
0 10 20
(f) 2/9/80
N=33
0 10 20 30
(g) 15/10/80
N=12
0 10 20 30 40
0.00 0.50 1.00 1.50 2.00 2.50 3.00 3.50 4.00
Tibia 1 (mm)

Fig.8.12: Size (age) distribution of *Linyphia triangularis* throughout the year 1980 in Area 8 in Ross Wood.

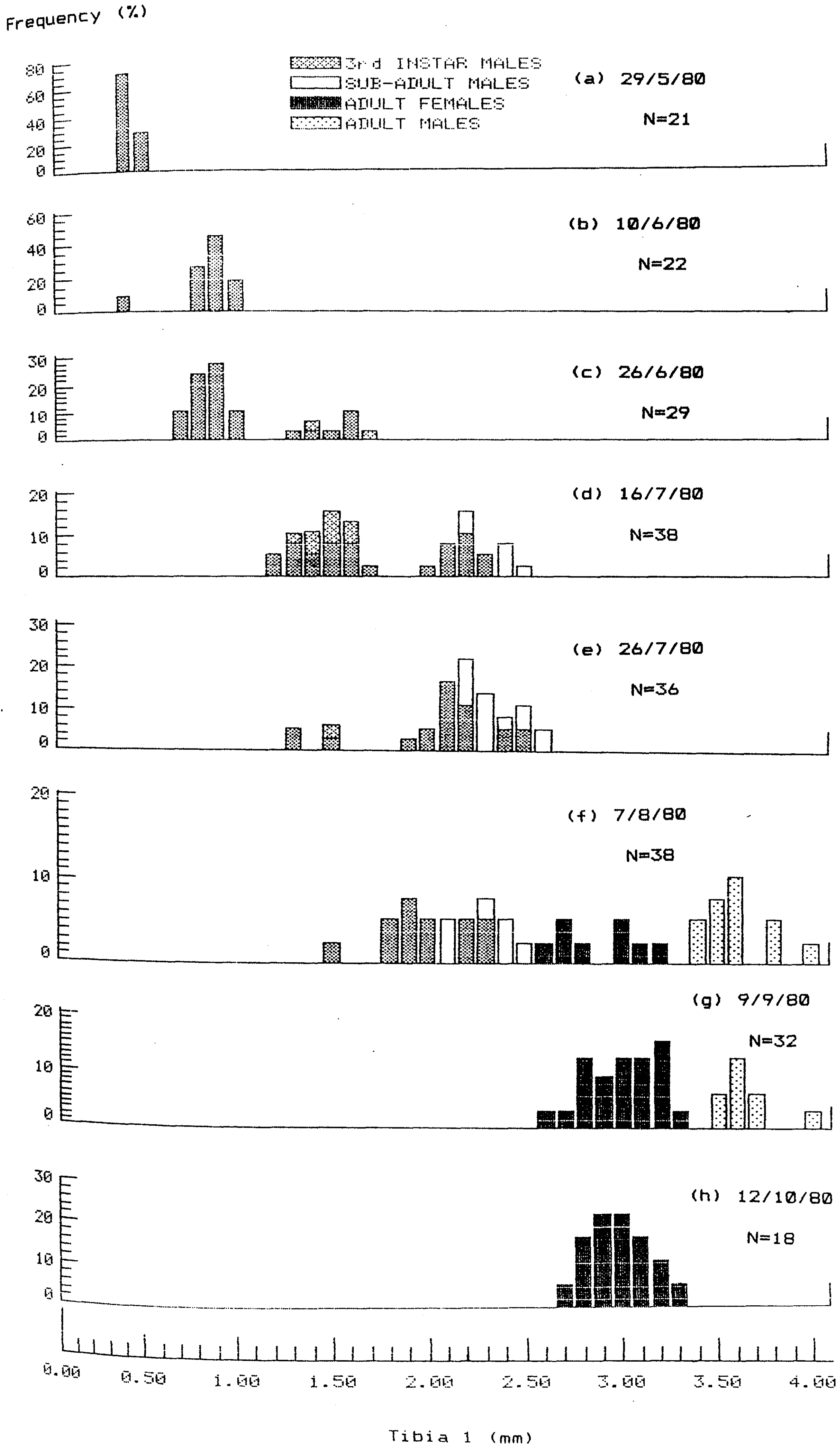

Frequency (%)
3rd INSTAR MALES
SUB-ADULT MALES
ADULT FEMALES
ADULT MALES
(a) 29/5/80
N=21
80
60
40
20
0
(b) 10/6/80
N=22
60
40
20
0
(c) 26/6/80
N=29
30
20
10
0
(d) 16/7/80
N=38
20
10
0
(e) 26/7/80
N=36
30
20
10
0
(f) 7/8/80
N=38
20
10
0
(g) 9/9/80
N=32
20
10
0
(h) 12/10/80
N=18
30
20
10
0
0.00
0.50
1.00
1.50
2.00
2.50
3.00
3.50
4.00
Tibia 1 (mm)

Fig.8.13: Size (age) distribution of Linyphia triangularis throughout the year 1981 in Area 8 in Ross Wood.

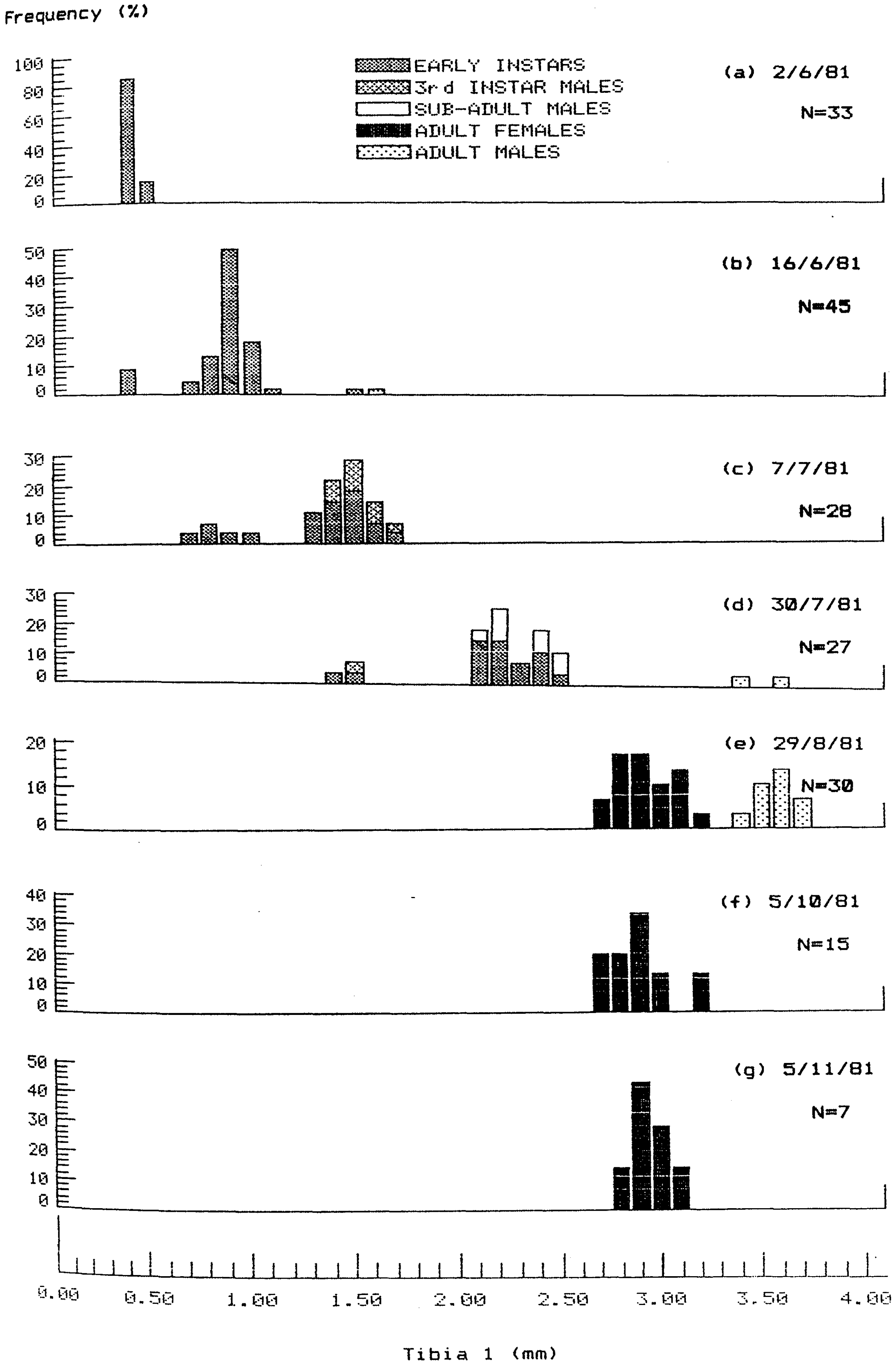
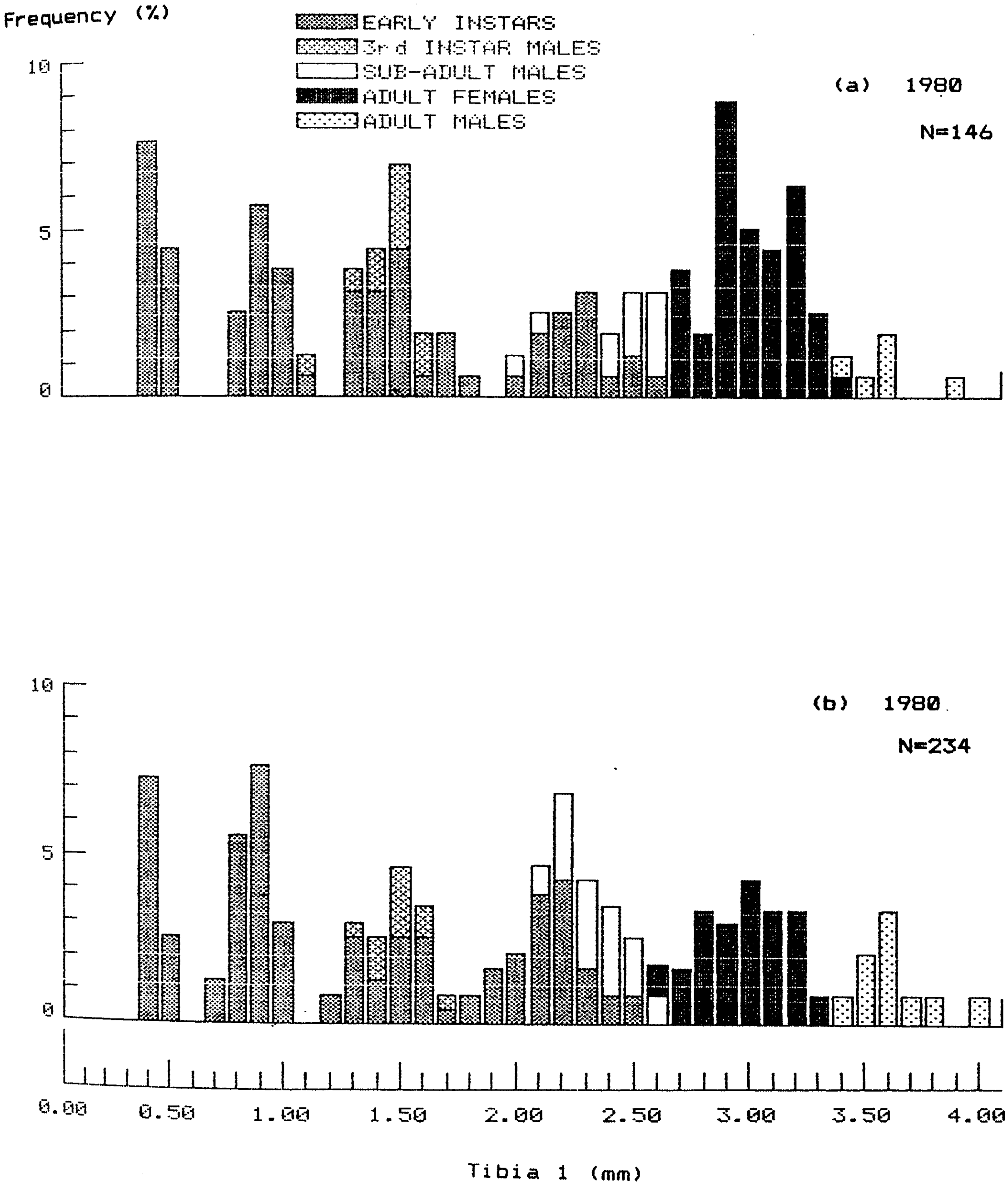

Frequency (%)
EARLY INSTARS
3rd INSTAR MALES
SUB-ADULT MALES
ADULT FEMALES
ADULT MALES
(a) 2/6/81
N=33
100
80
60
40
20
0
(b) 16/6/81
N=45
50
40
30
20
10
0
(c) 7/7/81
N=28
30
20
10
0
(d) 30/7/81
N=27
30
20
10
0
(e) 29/8/81
N=30
20
10
0
(f) 5/10/81
N=15
40
30
20
10
0
(g) 5/11/81
N=7
50
40
30
20
10
0
0.00
0.50
1.00
1.50
2.00
2.50
3.00
3.50
4.00
Tibia 1 (mm)

Fig.8.14: The number of instars of *Linyphia triangularis* based on samples from Area B2 in Dawsholm park in 1980.

Fig.8.15: The number of instars of *Linyphia triangularis* based on samples from Area 8 in Ross Wood in 1980.


Frequency (%)
EARLY INSTARS
3rd INSTAR MALES
SUB-ADULT MALES
ADULT FEMALES
ADULT MALES
(a) 1980
N=146
10
5
0
(b) 1980
N=234
10
5
0
0.00
0.50
1.00
1.50
2.00
2.50
3.00
3.50
4.00
Tibia 1 (mm)

Results

The pattern of the age distribution is similar in the two areas in 1980 and in Area 8 between 1980 and 1981. At Dawsholm Park the new generation emerges from the egg sacs in early/mid-May (see chapter on Egg Sac Production and Birth Rate) and the spider population in late May consists of first instars (Fig.8.11a). By early June the spiders have reached the second instar (Fig.8.11b) and by late June most of the spiders have reached the third instar (Fig.8.11c). By the third instar male spiders can be distinguished by their slightly clubbed pedipalps. By early July some of the spiders have reached the sub-adult stage (Fig.8.11d). The pedipalps of the sub-adult males are more swollen than those of the third instars. By early August about half of the spiders present were adult (Fig.8.11e) and by early September only adult animals were present (Fig.8.11f). By mid-October all the adult males had died and the population comprised of adult females (Fig.8.11g).

In the Ross Wood the pattern of the age distribution is similar but spider development is slightly slower (compare Fig.8.11 & 8.12). Thus in Dawsholm Park on 24/6/80 (Fig.8.11c) most of the spiders were third instars whereas in the Ross Wood on 26/6/80 most of the spiders were second instars (Fig.8.12c). The changes in the age distribution in the Ross Wood are similar in 1980 and 1981 (compare

Fig.8.12 and Fig.13).

An examination of the amalgamated samples from the two areas in 1980 (Fig.8.14 & 8.15) suggests that L. triangularis has five instars. There are three well separated peaks in the size distribution at 0.4-0.5mm, 0.8-1.1mm and 1.3-1.8mm, corresponding to the first three instars. Sub-adults range from 1.9-2.6mm and adults from 2.6-4.0mm.

Discussion

Savory (1964) suggested that the number of instars required by a spider to reach maturity varied. Bonnet (1930) suggested that the life span and number of instars could be increased by food shortages and Bristowe (1958) suggested that these factors could be influenced by both feeding and temperature. Bonnet (1930) suggested that the length of life cycle varied with latitude and Bristowe (1939) suggested that it varied with both latitude and altitude. Thus it is argued that in lower latitudes, where temperatures are higher and food more abundant, spiders will have a shorter life cycle, will have fewer instars and will have a smaller adult body size. Conversely in higher latitudes spiders will have longer life cycles, more instars and a larger adult size.

There is support for this view in the literature. Thus Edgar (1972) found that the wolf spider Pardosa lugubris had a two year life cycle in Central Scotland but a mixture of a one and a two year life cycle in the Netherlands. Toft (1983) found that M. mengei had a two year life cycle in the northern part of its range and a one year life cycle in lower latitudes. Pennington (1977) reported that M. mengei has a two year life cycle in west central Scotland while Geyer (1971) indicated that the species has a one year life cycle in the north of

England. The current study indicates that the species in Central Scotland can have a one or a two year life cycle.

Edgar (1971) found that *P. lugubris* with a two year life cycle had an extra instar and the same was found for *M. mengei* in the current study. This flexability, with respect to the number of instars, may allow the spiders to exploit, in an optimum fashion, the resources and climatic characteristics of a particular habitat or latitude. The size of *M. mengei* varies with latitude. Thus it is smaller in the south of England (Locket & Millidge 1953; Bristowe 1958) and in France (Toft 1983) than it is in Scotland and in Scandinavia (Toft 1983).

With regard to the other three species in the current study, they all have a one year life cycle and five instars. Geyer (1971), Toft (1983) and Pennington (1977) all reported that *M. segmentata* had a one year life cycle but Pennington reported that the species had six instars rather than the five found in the other two studies. The life cycle and the number of instars reported in the present studies for the two *Linyphia* species agree with those of Toft (1976). The current study did reveal, in *L. peltata* , a small cohort of spiders which grow more slowly than the others and this suggests that a minority of the spiders may have a two year life cycle during years with cold summers and autumns.

CHAPTER 9

Egg Sac Production and the Birth Rates of the Four species

The aim of this section is to provide information on egg sac production and birth rates of the four species. This includes the weight of the egg sacs and the weight and number of eggs. It also considers the duration of the egg sac period and the time of hatching of the spiderlings. All this information gives a greater insight into the life cycles of the spiders and their mortality rates.

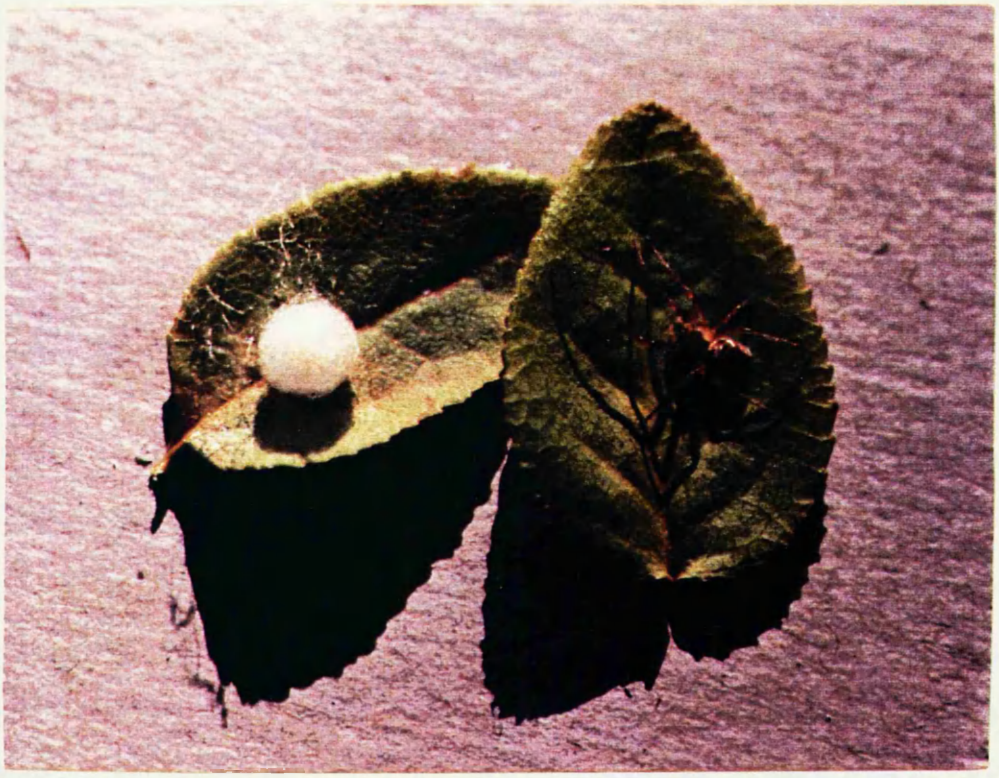
Metellina mengei

Females of *M. mengei* deposit their eggs in a spherical mass of loose silk (Fig.9.1). (The whole structure, eggs plus surrounding silk, will be termed the egg sac while the surrounding silk will be called the cocoon). The egg sacs are deposited among plant stems, close to the ground, or in crevices in logs. After depositing their egg sacs and camouflaging them with debris, females normally stay for a short time beside the egg sacs.

Methods

Two batches of egg sacs were collected in early June 1981. One batch was collected from the field and the other from gravid females, which had been brought into the laboratory a few days earlier. The egg sacs were weighed and then

Fig.9.1: Egg sac of *Metellina mengei* .



opened and the weight of eggs and cocoon determined separately. The weight of the females, which produced the egg sacs in the laboratory, was also determined. To obtain information on spider emergence 20 egg sacs were located in the field in late June 1982 and these were observed from time to time and the number of egg sacs which hatched was recorded. This gave some indication of the minimum duration of the egg sac period but to obtain better information on this, five egg sacs, produced in the laboratory, were retained until the spiderlings emerged.

Results

The results obtained from the analyses of the two egg sac batches are given in Tables 9.1 & 9.2. There is no significant difference between the two batches with respect to total egg weight, number of eggs, weight of individual eggs and weight of the silk cocoons. Of the 20 egg sacs observed in the field 17(85%) emerged. Two egg sacs disappeared, presumably eaten by predators, and a third failed to hatch. Most of the egg sacs had hatched by late July (Fig.9.2). In the laboratory the egg sacs hatched in approximately six weeks ($\bar{X}$=41.4 ± 2.6 days, n=5, range 38-44 days). As might be expected, the larger the amount of egg material produced the greater the amount of silk laid down as a cocoon. Thus there is a significant correlation between the weight of eggs per egg sac and the weight of

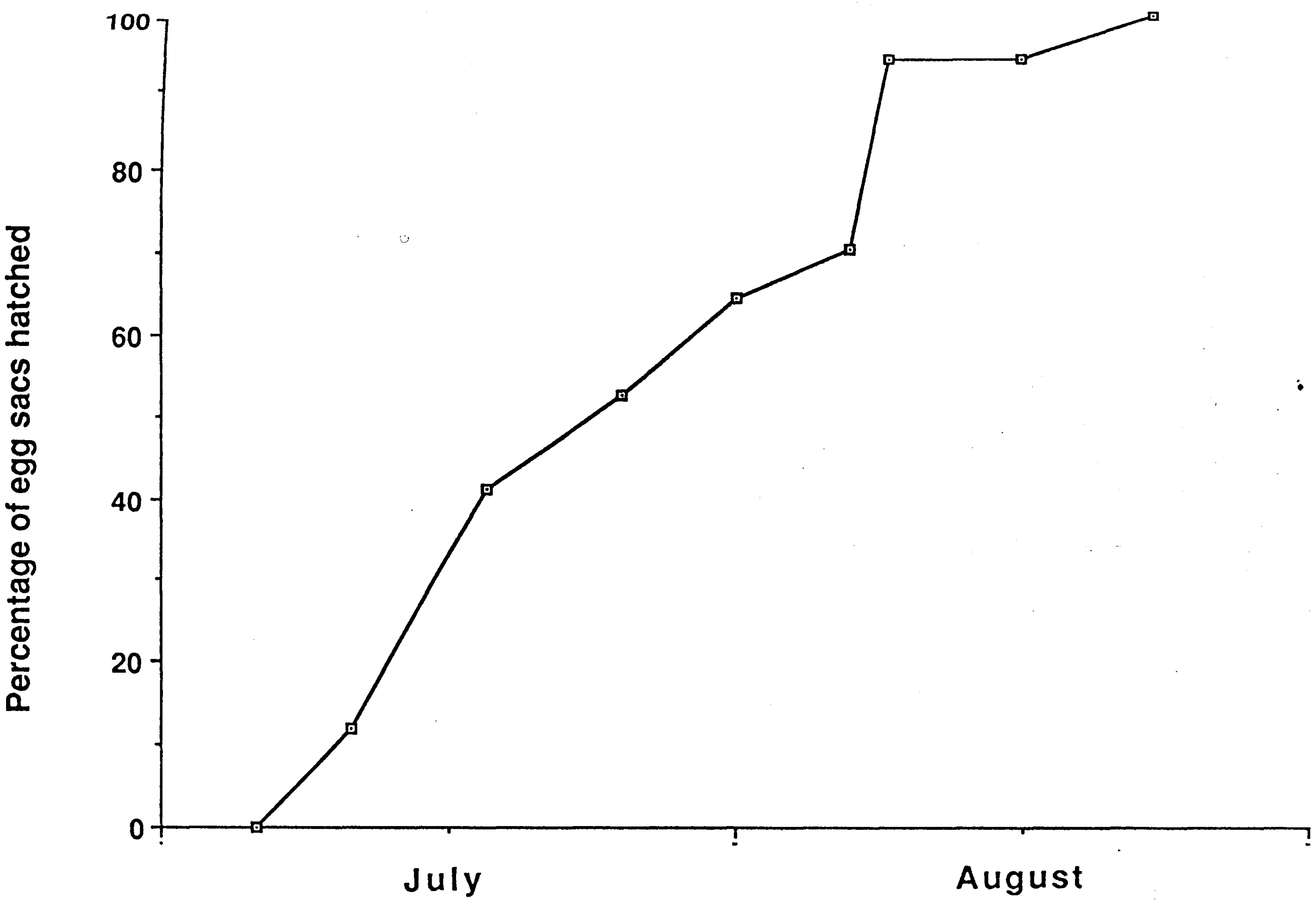
Table 9.1: Weight and number of eggs in the egg sac, the weight of the egg and egg cocoon in *M. mengei* from the field (values are mean ± S.D.). The figures in parenthesis are the numbers which were examined. The weight unit is mg.

Wet weight of eggs	Dry weight of eggs	Number of eggs	Wet weight of egg	Wet weight of cocoon	Dry weight of cocoon
9.68 ±2.91 (16)	3.13 ±0.95 (16)	49.38 ±13.47 (16)	0.19 ±0.02 (16)	0.57 ±0.09 (16)	0.50 ±0.09 (16)

Table 9.2: Weight and number of eggs in the egg sac, the weight of the egg and egg cocoon and weight of spent females of *M. mengei* from the laboratory (values are mean ± S.D.). The figures in parenthesis are the numbers which were examined. The weight unit is mg.

Wet weight of eggs	Dry weight of eggs	Number of eggs	Wet weight of egg	Wet weight of cocoon	Dry weight of cocoon	Wet weight of female
10.28 ±1.94 (14)	3.24 ±0.61 (14)	52.00 ±8.12 (14)	0.20 ±0.01 (14)	0.62 ±0.10 (14)	0.53 ±0.10 (14)	10.39 ±2.01 (14)

Fig.9.2: Hatching of egg sacs of *Metellina mengei* in 1982.

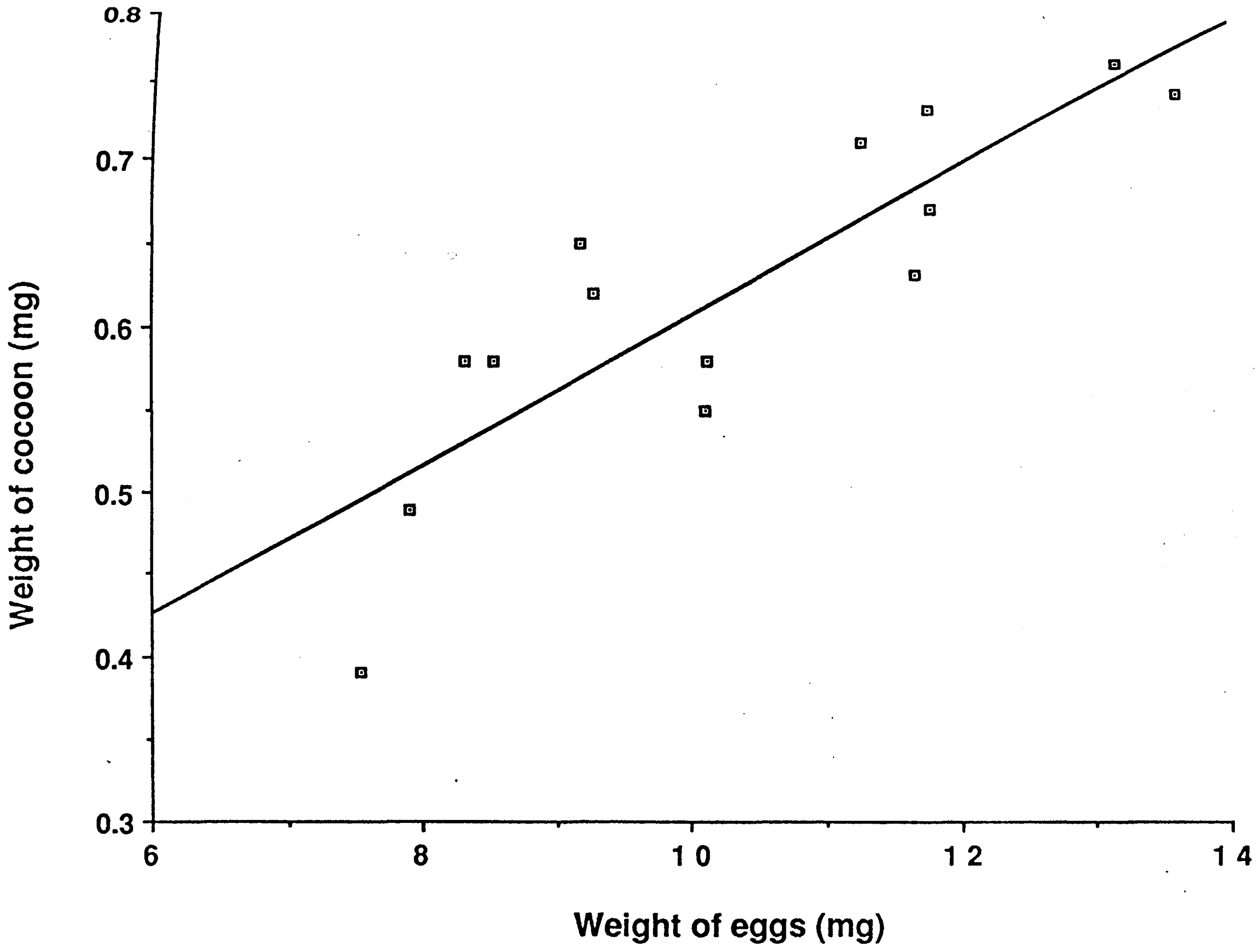

Percentage of egg sacs hatched
100
80
60
40
20
0
July
August

the cocoon (r=0.85, d.f.=14, P<0.001) (Fig.9.3).

To estimate the birth rate it is necessary to know the number of eggs produced per female and the number of these eggs which develop to emerge as spiderlings. From the observation of the egg sacs in the field it is known that spiderlings emerge from 85% of the egg sacs. An examination of the egg sacs, after the spiderlings have emerged, indicated that in M. mengei , unlike M. segmentata and the two Linyphia species, almost all the eggs develop into spiderlings.

Obtaining an estimate of the number of eggs produced per female has proved to be difficult for a number of reasons. There is evidence to suggest that the sixth instar adults may produce two egg sacs within a few days. Thus, for example, on 31/5/81 a gravid female, brought into the laboratory, produced an egg sac which contained 49 eggs (8.53mg) and two days later produced a second egg sac of 47 eggs (10.24mg). A second female produced 48 eggs (8.48mg) on 1/6/81 and 41 eggs (7.16mg) three days later. It is possible that some other females brought into the laboratory had produced egg sacs in the day or two before capture. Hence the information on egg sac production in Table 9.2 may not give a good indication of the total number of eggs produced per female.

Fig.9.3: The relationship between the weight of eggs and the weight of the surrounding silk cocoon in egg sacs of *Metellina mengei* .


0.8
0.7
0.6
0.5
0.4
0.3
Weight of cocoon (mg)
6
8
10
12
14
Weight of eggs (mg)

Another possibility is that females produce an additional egg sac after a further period of feeding. This is thought to be unlikely, as casual observation has shown that females which produce two egg sacs, within a few days, have a characteristic appearance - with a shrunken abdomen and a moribund appearance. Such animals, retained in the laboratory, soon die. The work of Toft (1974) suggests that M. mengei produces two egg sac batches between mid-May and late July. This work involved dissecting animals and counting developing eggs. Thus he calculated that an average of 117.6 ± 18.7 eggs were produced in the first batch and 62.5 ± 23.0 in the second. As these determinations were not based on examining egg sacs, they would not reveal the possibility that M. mengei produces two egg sacs within a few days. Thus the two spiders which produced two egg sacs in the laboratory, within a few days, in late May and early June, produced a total of 96 and 89 eggs. This is in reasonable agreement with the estimate of 117 given by Toft, particularly if one assumes that not all the developing eggs in the abdomen are deposited in the egg sacs.

The second batch of eggs recorded by Toft are interpreted as being those produced by the one year (fifth instar) females. In the current study six females, collected in early July, produced an egg sac. The egg sacs had an average weight of 8.95mg. The eggs in these egg sacs were not counted or weighed but, assuming that egg size was similar to that in the batches produced in late May/early June, an egg sac weight of 8.95mg would be equivalent to 42 eggs. Another female produced two egg sacs within a day (6.49 and 4.75mg) giving a total egg sac production of 11.24 - which is equivalent to 53 eggs. The value given by Toft for the second egg sac was 62.5 ± 23.0 eggs. The large standard deviation indicates much greater variability in egg sac production than for the first egg sac and it could be that some spiders produce two egg sacs and some only one. Again, assuming that not all eggs in the abdomen are deposited in an egg sac, the results of the current study are in reasonable agreement with those of Toft.

On the basis of the above, one might argue that the 6th instar adults produce two egg sacs within a few days and that this represents between 90 - 100 eggs/female. There are greater uncertainties in attempting to estimate the number of spiderlings produced by fifth instar adults, as it is not clear whether these animals produce one or two egg sacs. The limited evidence from Toft (1974), and from the present study, suggests that egg production by the fifth instars shows much more variability than for sixth instars. In the light of this no reliable estimate can be given for egg production per female.

Linyphia peltata

L. peltata produces an oval-shaped egg sac which has an outer layer of fine silk (Fig.9.4). The egg sacs are normally deposited in depressions in dead leaves, among grass roots or in crevices in logs or under stones. This tendency to deposit the egg sacs in crevices is also seen in the laboratory - where they are deposited in the corners of the rearing containers (Fig.9.4). After depositing their egg sacs and camouflaging them with debris, females normally stay for a short time beside the egg sacs.

Methods

Two batches of egg sacs were collected in early June 1981. One was collected from the field and the other from gravid females which had been brought into the laboratory a few days earlier. Egg sacs were weighed and then opened and the eggs and cocoon were weighed separately. The weight of the females, which produced the egg sacs in the laboratory, was also determined.

To obtain information on spider emergence, 18 egg sacs were located in the field, in late June 1982, and were observed from time to time to record the number of egg sacs which hatched and the date of hatching. To obtain more accurate information on the duration of the egg sac period, five egg

Fig.9.4: Egg sac of <u>Linyphia</u> <u>peltata</u>

sacs, produced in the laboratory, were retained until the spiderlings emerged. The number of these spiderlings, along with the number of undeveloped eggs or spiderlings, was recorded. This provided information on mortality within the egg sac.

Results

The results obtained from the analysis of the two egg sacs batches are given in Tables 9.3 & 9.4. There is no significant difference between the two batches with respect to total egg weight, the number of eggs, weight of individual eggs and weight of the silk cocoons. There is no correlation between the number of eggs per egg sac and mean egg weight (Fig.9.5) and (Fig.9.6). As might be expected, the larger the amount of egg material the greater the amount of silk laid down as a cocoon. Thus there is a significant correlation ($r=0.85$, d.f.=16, $P<0.001$) between the weight of eggs per egg sac and the weight of the cocoon (Fig.9.7).

Of the 18 egg sacs observed in the field, 14 (78%) produced spiderlings. Three disappeared - presumably eaten by predators, and a fourth failed to develop and had a fungal growth in it. The majority of egg sacs (87%), which produced spiderlings, had hatched by the end of July (Fig.9.8). In the laboratory the egg sacs hatched in

Table 9.3: Weight and number of eggs in the egg sac, the weight of egg and egg cocoon in L. peltata from the field (values are mean ± S.D.). The figures in parenthesis are the numbers which were examined. The weight unit is mg.

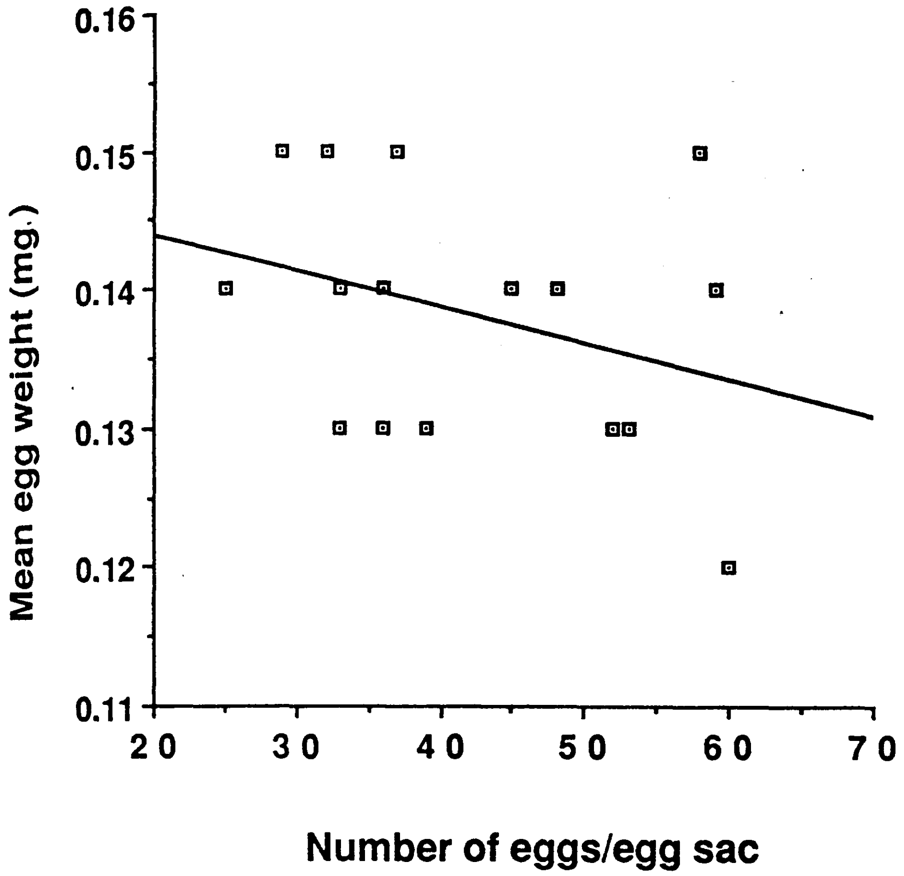
Wet weight of eggs	Dry weight of eggs	Number of eggs	Wet weight of egg	Wet weight of cocoon	Dry weight of cocoon
5.85 ±1.57 (16)	1.90 ±0.55 (16)	42.19 ±11.43 (16)	0.14 ±0.01 (16)	0.29 ±0.04 (16)	0.25 ±0.04 (16)

Table 9.4: Weight and number of eggs in the egg sac, the weight of egg and egg cocoon and weight of spent females of L. peltata from the laboratory (values are mean ± S.D.). The figures in parenthes is are the numbers which were examined. The weight unit is mg.

Wet weight of eggs	Dry weight of eggs	Number of eggs	Wet weight of egg	Wet weight of cocoon	Dry weight of cocoon	Wet weight of female
5.30 ±1.24 (16)	1.69 ±0.45 (16)	36.81 ±8.38 (16)	0.14 ±0.01 (16)	0.28 ±0.05 (16)	---	10.39 ±2.01 (14)

Fig.9.5: The relationship between the number of eggs in an egg sac and the mean egg weight per egg sac in egg sacs of *Linyphia peltata* collected in the field.

Fig.9.6: The relationship between the number of eggs in an egg sac and the mean egg weight per egg sac in egg sacs of *Linyphia peltata* produced in the laboratory.


0.16
0.15
0.14
0.13
0.12
0.11
Mean egg weight (mg.)
20
30
40
50
60
70
Number of eggs/egg sac

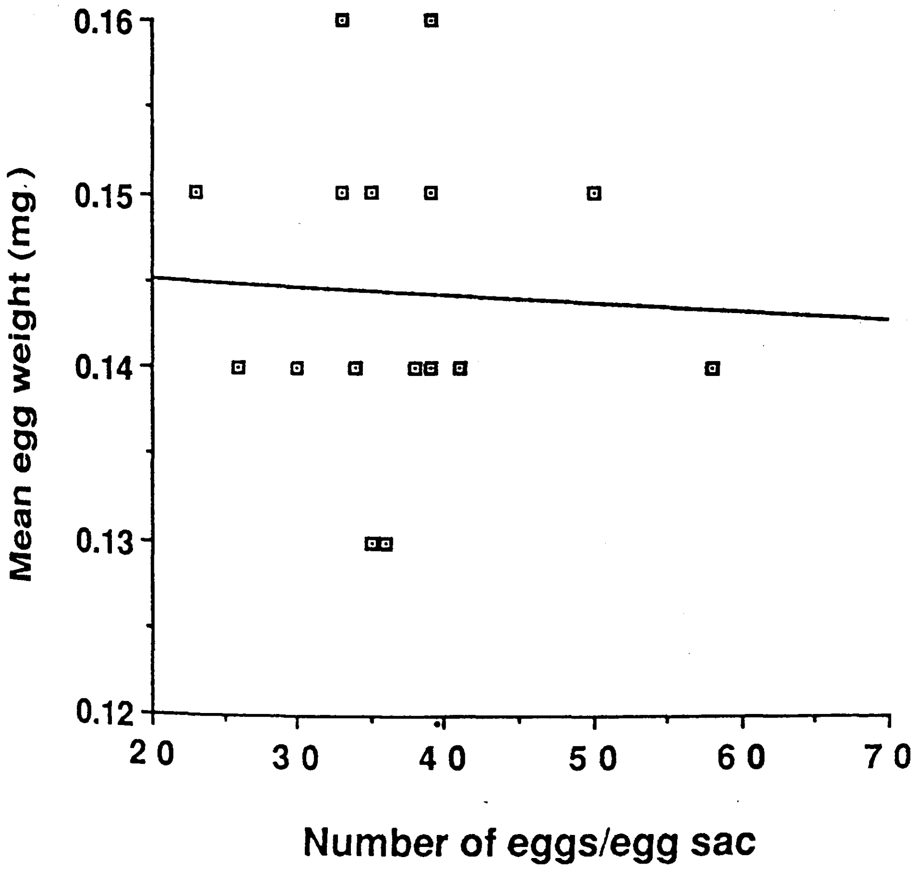

0.16
0.15
0.14
0.13
0.12
Mean egg weight (mg.)
20
30
40
50
60
70
Number of eggs/egg sac

Fig.9.7: The relationship between the weight of eggs and the weight of the surrounding silk cocoon in egg sacs of *Linyphia peltata* in the laboratory.

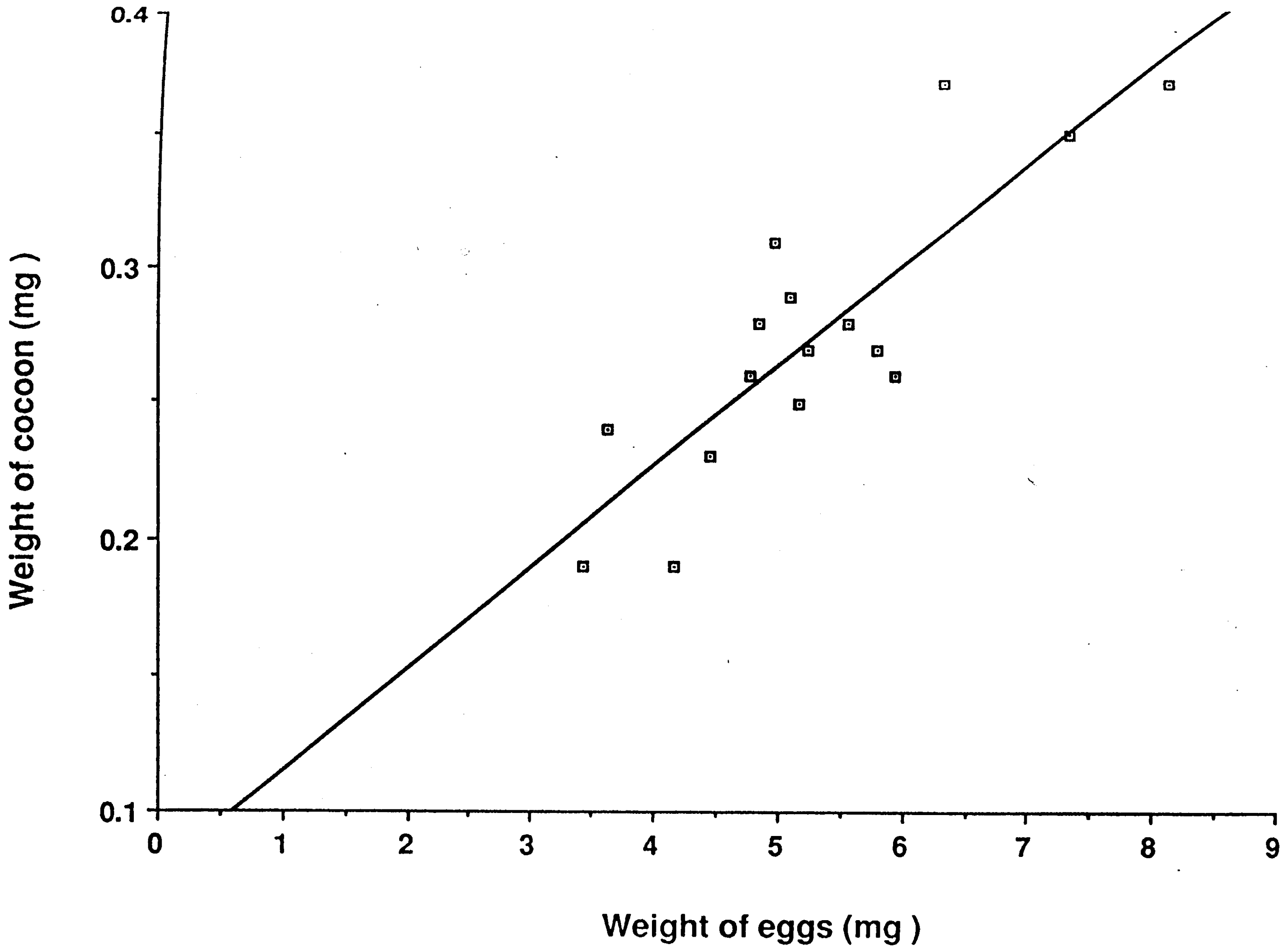
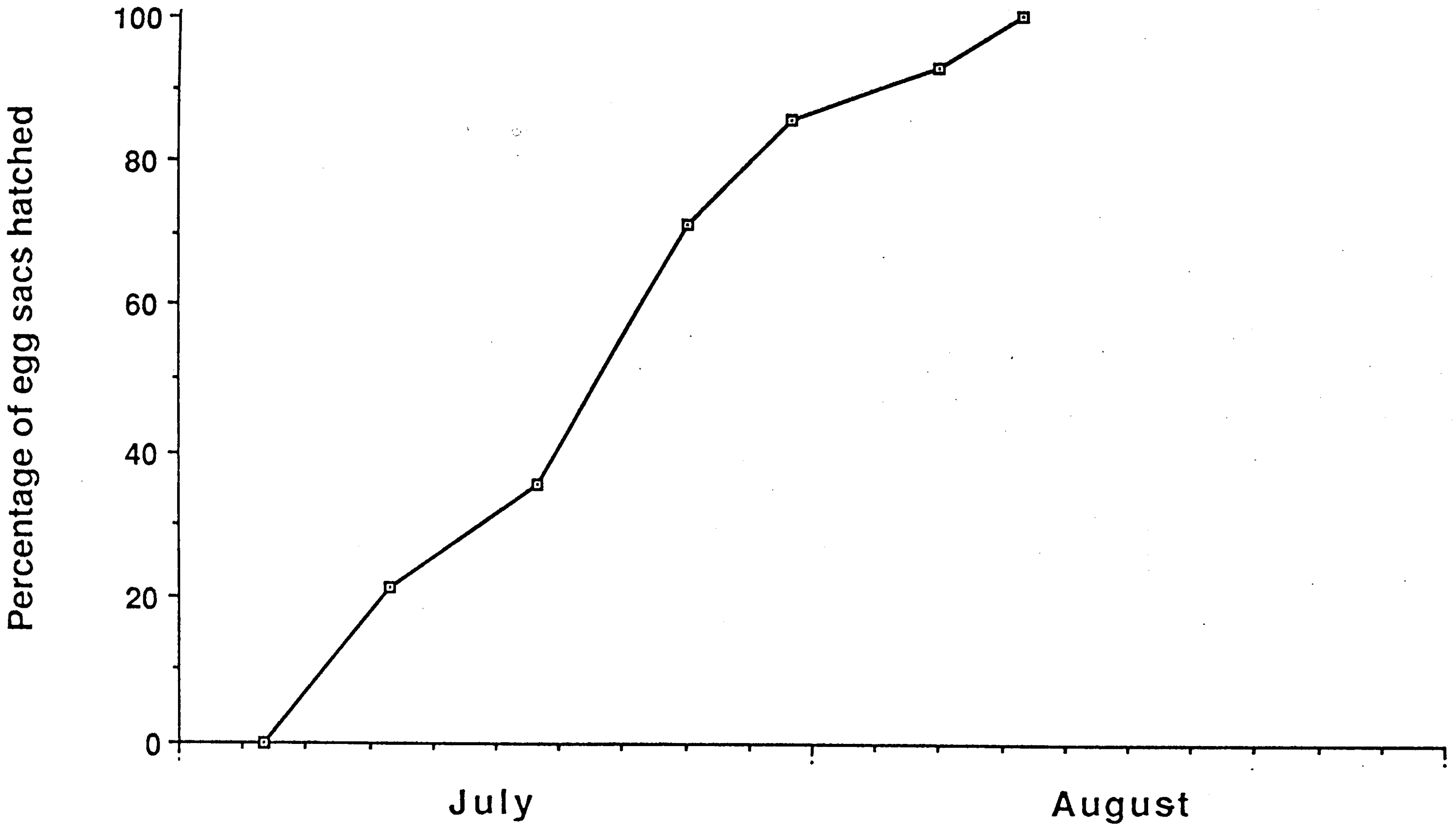

0.4
0.3
0.2
0.1
Weight of cocoon (mg)
0
1
2
3
4
5
6
7
8
9
Weight of eggs (mg)

Fig.9.8: Hatching of egg sacs of _Linyphia peltata_ in 1982.


Percentage of egg sacs hatched
0
20
40
60
80
100
July
August

approximately six weeks (X=42.6 ± 1.1 days, n=5, range 41-44 days). The total number of spiderlings which emerged from the five egg sacs in the laboratory was 170, while 28 eggs failed to develop. Thus the mortality of eggs within the egg sac was 14.1%.

There is no indication that L. peltata produces more than one egg sac. Spent females feed little, have a characteristic shrunken abdomen, and a moribund appearance. Field samples have indicated a high mortality rate (61%) between mid-May and mid-June - the period when egg sacs are produced. Thus the mean number of eggs per egg sac in the field samples, 42.2 (Table 9.3), can be taken as the reproductive potential of L. peltata females. Mortality within the egg sac was estimated at 14.1%, hence the average number of spiderlings emerging from each egg sac is 36.2.

M. segmentata

M. segmentata produces a spherical-shaped egg sac. The cocoon comprises of a loose mesh of silk. The egg sacs are deposited in crevices. These may be amongst plant stems near the ground, near the base of tufts of grass, in the bark of trees or logs, or in a variety of similar situations. Females do not guard their egg sacs but stay for a short time. They may camouflage them with debris.

Methods

Two batches of egg sacs were collected in October 1982 from Ross Wood. One batch was collected from the field and the other from gravid females which had been brought into the laboratory a few days earlier. Egg sacs were weighed and then opened and the weight and number of eggs were determined. The weight of cocoons were determined after the removal of the eggs. The weights and sizes (tibia 1) of adult females which produced the egg sacs in the laboratory were determined. A further batch of egg sacs was obtained in late October 1981 and another in late October 1983 from Dawsholm Park. The number and weight of eggs in these additional egg sacs were calculated.

To obtain information on spider emergence and hatching success, in two different localities, 25 egg sacs were located in early November 1981 in Dawsholm Park and, at the same time, seven egg sacs were located in Ross Wood. They were observed from time to time to record the number of egg sacs which hatched and the date of hatching. To obtain accurate information on the duration of the egg sac period seven egg sacs were retained in the laboratory until the spiderlings emerged. Mortality of eggs within the egg sac was estimated by two methods: (a) By examining 10 randomly selected egg sacs of those which hatched in Dawsholm Park to record the number of undeveloped eggs or spiderlings. The numbers of spiderlings which emerged were estimated by counting, under a binocular microscope, the exuvia which remained inside the egg sacs. These are the casts of the first moulting, which occurs inside the egg sac. (b) By examining the egg sacs which hatched in the laboratory. The number of spiderlings which emerged, and the number of undeveloped eggs or spiderlings, were recorded.

Results

The results obtained from the analysis of the two egg sacs batches are given in Tables 9.5 and 9.6. There is no significant difference between the two batches with regard to total egg weight, number of eggs, weight of individual eggs and weight of silk coccon. There is no significant correlation between the number of eggs and the weight of individual eggs (Fig.9.10) and (Fig.9.11). As might be

Table 9.5: Weight and number of eggs in the egg sac, the weight of the egg and egg cocoon in *M. segmentata* from the field (values are mean ± S.D.). The figures in parenthesis are the numbers which were examined. The weight unit is mg.

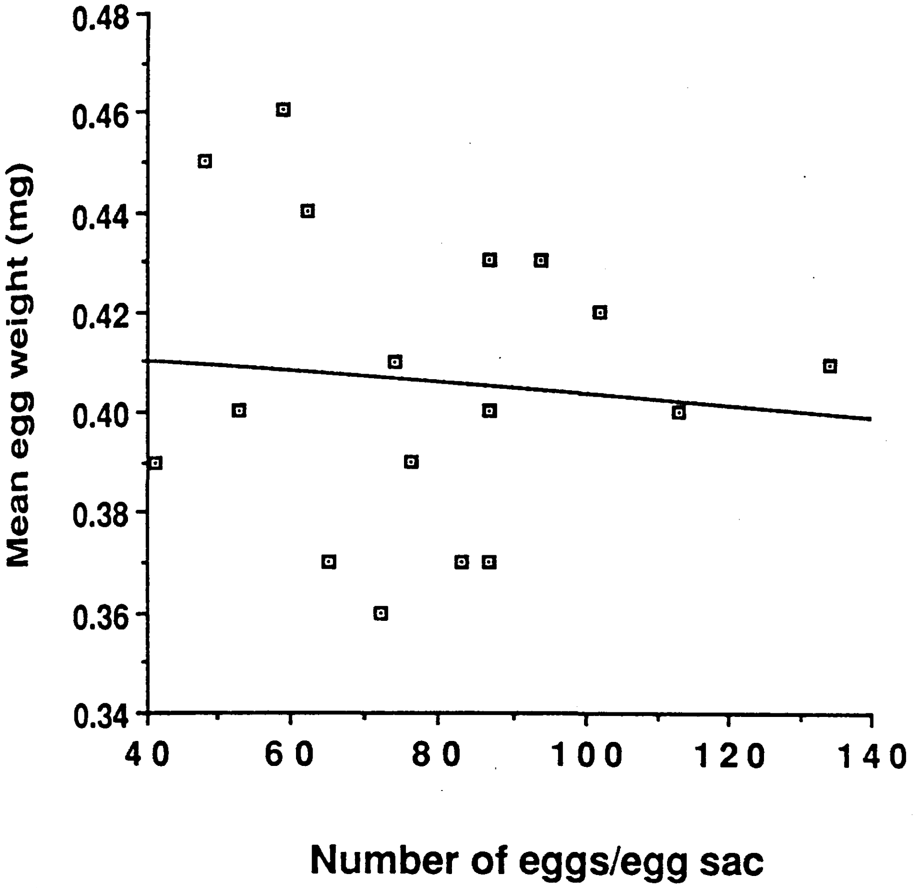
Wet weight of eggs	Dry weight of eggs	Number of eggs	Wet weight of egg	Wet weight of cocoon	Dry weight of cocoon
31.97	9.93	78.65	0.41	1.95	1.69
±9.91	±2.92	±23.97	±0.03	±0.49	±0.47
(17)	(17)	(17)	(17)	(17)	(17)

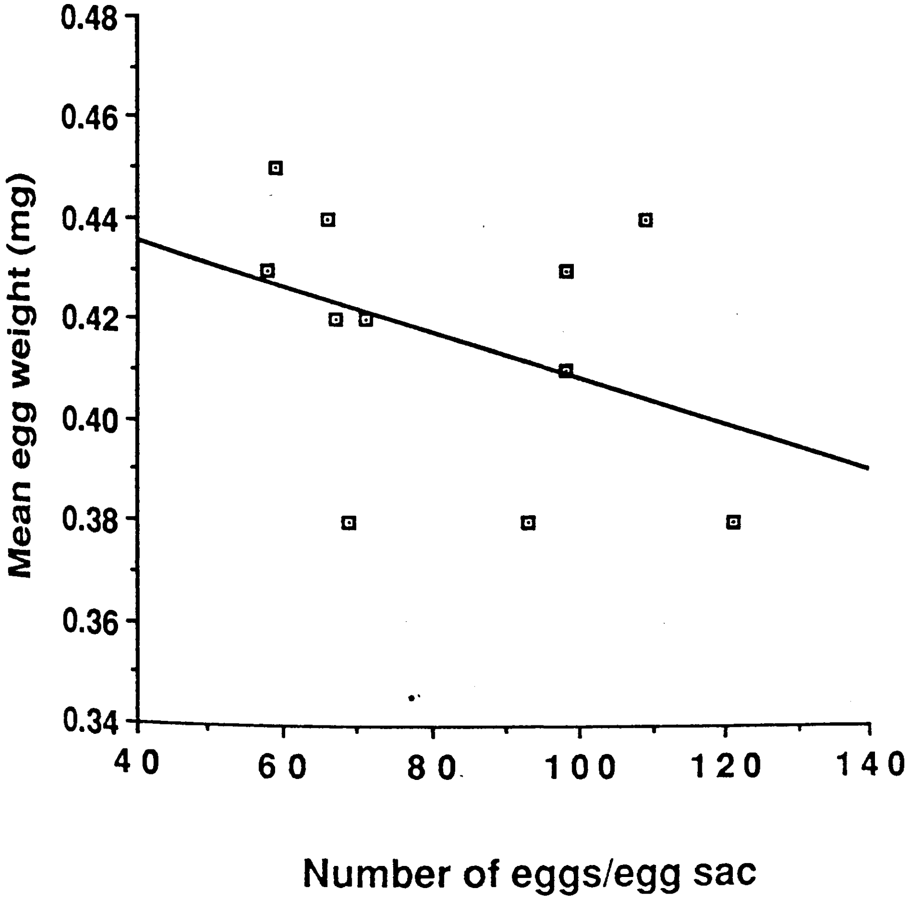
Table 9.6: Weight and number of eggs in the egg sac, the weight of egg and egg cocoon and weight of spent females of *M. segmentata* from the laboratory (values are mean ± S.D.). The figures in parenthesis are the numbers which were examined. The weight unit is mg.

Wet weight of eggs	Dry weight of eggs	Number of eggs	Wet weight of egg	Wet weight of cocoon	Dry weight of cocoon	Wet weight of female
33.91	10.52	82.18	0.41	2.06	1.80	16.30
±8.63	±2.65	±22.17	±0.03	±0.43	±0.42	±2.95
(11)	(11)	(11)	(11)	(11)	(11)	(11)

Fig.9.10: The relationship between the number of eggs in an egg sac and the mean egg weight per egg sac in egg sacs of *Metellina segmentata* collected in the field.

Fig.9.11: The relationship between the number of eggs in an egg sac and the mean egg weight per egg sac in egg sacs of *Metellina segmentata* produced in the laboratory.


Mean egg weight (mg)
0.48
0.46
0.44
0.42
0.40
0.38
0.36
0.34
40
60
80
100
120
140
Number of eggs/egg sac


Mean egg weight (mg)
0.48
0.46
0.44
0.42
0.40
0.38
0.36
0.34
40
60
80
100
120
140
Number of eggs/egg sac

expected, the larger the amount of egg material produced the greater the amount of silk laid down as a cocoon. Thus there is a significant correlation ($r=0.80$, d.f.=9, $P<0.05$) between the weight of eggs per egg sac and the weight of the cocoon (Fig.9.12). There is a significant correlation between the size of the adult female and the weight of eggs produced ($r=0.85$, d.f.=9, $P<0.05$) (Fig.9.13).

Of the 25 egg sacs which were observed in the field, at Dawsholm Park, 24 (96.0%) produced spiderlings. One egg sac disappeared - presumably eaten by a predator. Of the seven egg sacs observed in the field, at Ross Wood, six (85.7%) produced spiderlings. One of them disappeared - presumably eaten by a predator. At Dawsholm Park the majority of egg sacs (75.0%) had hatched by 13/5/1981 while at Ross Wood the majority of egg sacs (60.0%) had hatched by 5/6/1981 (Fig.9.14). In the laboratory the egg sacs hatched in approximately seven months ($X=205.6\pm5.6$ days, n= 7, range 198-213 days). The mortality of eggs within the egg sacs was estimated to be 22.0% in the field (Table 9.7) and 16.2% for those in the laboratory (Table 9.8).

There is no indication that M. segmentata produces more than one egg sac, hence the number of eggs in Table 1 (78.65 eggs) can be regarded as the total output of adult female in the field. Eggs are subjected to a mortality within the egg sacs of 22.0%, so the birth rate in the

Table 9.7: The number (mean ± S.D.) of exuvia (which represents the number of spiderlings which emerged from the egg sacs) the number of eggs and spiderlings which failed to develop and the mortality estimate within the egg sacs, of the spider <u>M.</u> <u>segmentata</u> in the field. The figures in parenthesis are the numbers which were examined.

Number of exuvia	Number of dead eggs	Number of dead spiderlings	Actual number of eggs / egg sac	Mortality %
53.10 ±31.28 (10)	1.40 ±2.50 (10)	13.60 ±19.04 (10)	68.10 ±22.76 (10)	22.0

Table 9.8: The number (mean ± S.D.) of spiderlings which emerged from the egg sacs, the number of failed eggs and spiderlings and the mortality estimate within the egg sacs, of the spider <u>M.</u> <u>segmentata</u> in the laboratory. The figures in parenthesis are the numbers which were examined.

Number of emerged spiderlings	Number of dead eggs	Number of dead spiderlings	Actual number of eggs / egg sac	Mortality %
68.57 ±9.50 (7)	10.00 ±6.71 (7)	3.29 ±4.61 (7)	81.86 ±10.35 (7)	16.2

Table 9.9: Weight (mg.) and number of eggs in the egg sac, of the spider, <u>M.</u> <u>segmentata</u> in different years (values are mean ± S.D.) The figures in parenthesis are the numbers which were examined.

Year	Weight of eggs	Number of eggs
1981	47.27 ±14.10 (12)	106.58 ±32.47 (12)
1983	30.68 ±7.00 (12)	79.33 ±16.09 (12)

Fig.9.12: The relationship between the weight of eggs and the weight of the surrounding silk cocoon in egg sacs of *Metellina segmentata* in the laboratory.

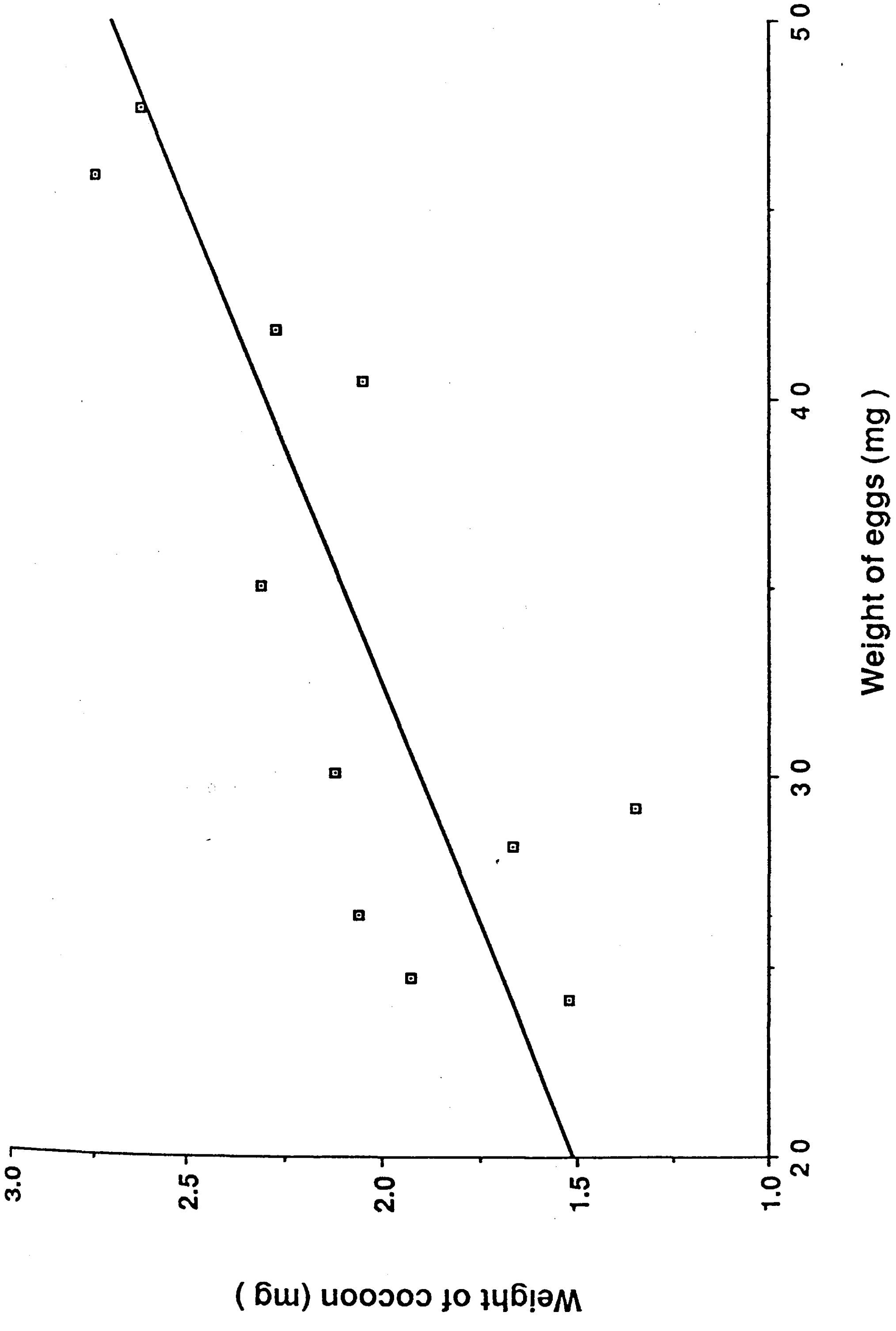

Weight of cocoon (mg)
3.0
2.5
2.0
1.5
1.0
2 0
3 0
4 0
5 0
Weight of eggs (mg)

Fig.9.13: The relationship between the weight of eggs produced and the female size (as indicated by the length of tibia 1) in *Metellina segmentata* .

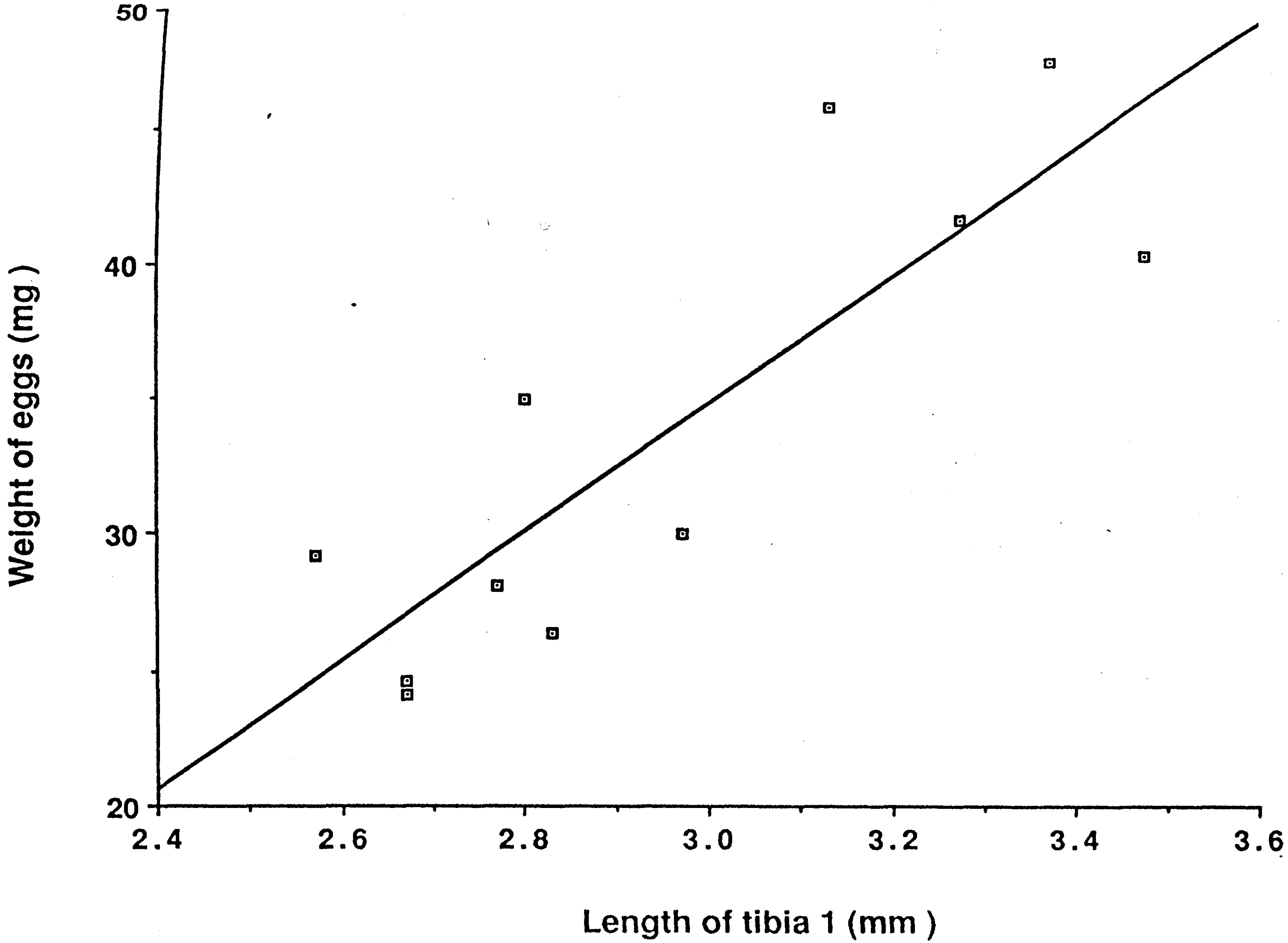
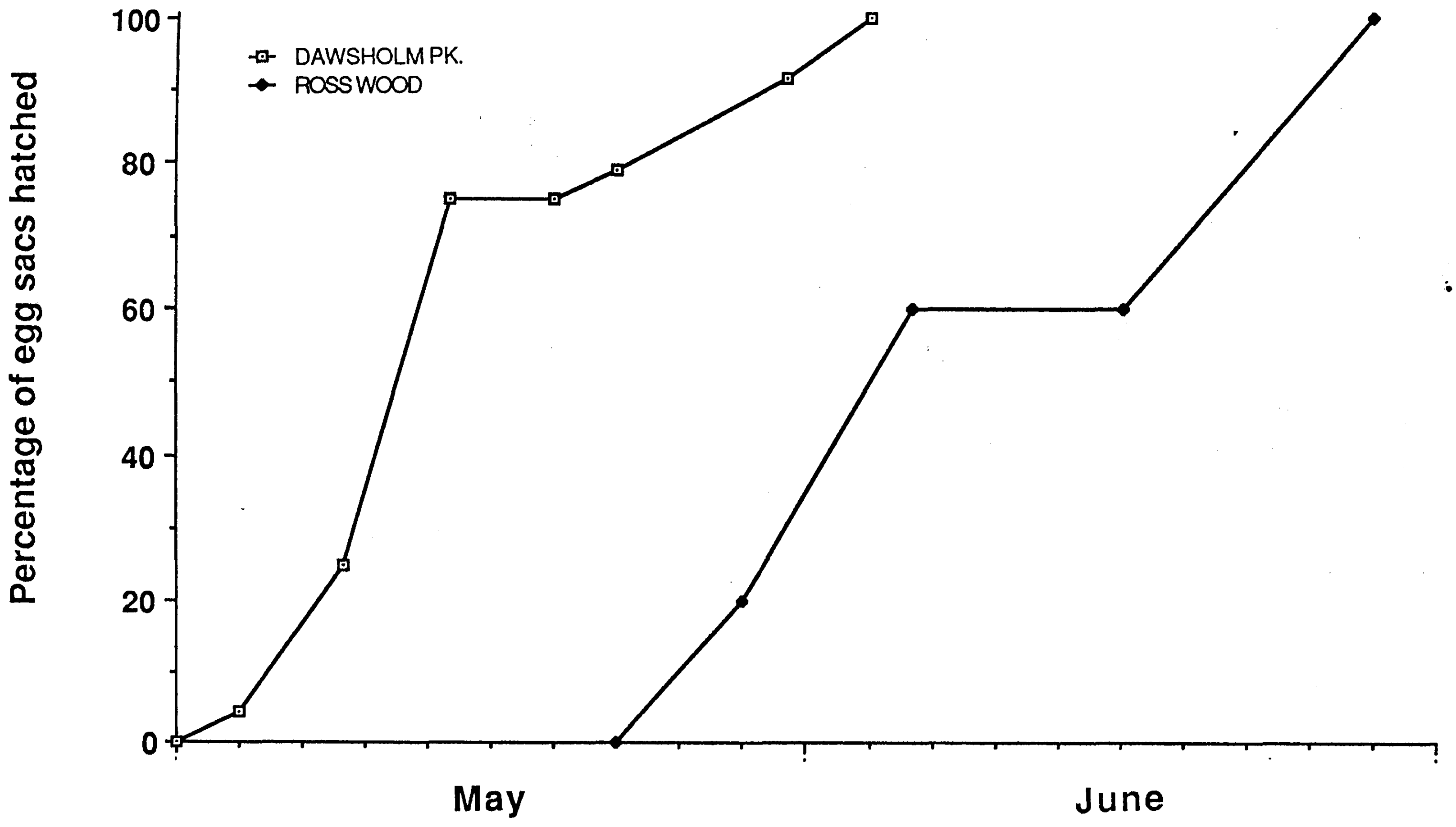

50
40
30
20
Weight of eggs (mg)
2.4
2.6
2.8
3.0
3.2
3.4
3.6
Length of tibia 1 (mm)

Fig.9.14: Hatching of egg sacs of *Metellina segmentata* in 1982.


Percentage of egg sacs hatched
100
80
60
40
20
0
DAWSHOLM PK.
ROSS WOOD
May
June

field is 61.35 spiderlings per female.

Egg production differs from year to year (Table 9.9). Thus significantly more egg material ($t=3.58$, d.f.=11, $P<0.05$) and significantly more eggs ($t=2.61$, d.f.=11, $P<0.05$) are produced in 1981 than in 1983.

L. triangularis

L. triangularis produces a lens-shaped egg sac which has an outer layer of dense silk (Fig.9.15). The egg sacs are deposited in the hollows of dead leaves, among plant stems close to the ground, or deposited near the base of tufts of grass or mosses. Females do not guard their egg sacs but stay for a short time. They may camouflage them with debris.

Methods

Two batches of egg sacs were collected in October 1982 from the Ross Wood. One batch was collected from the field and the other from gravid females which had been brought into the laboratory a few days earlier. Egg sacs were weighed and then opened and the weight and number of eggs were determined. The weight of cocoons was determined after removal of the eggs. The weights and sizes (tibia 1) of adult females which produced the egg sacs in the laboratory were determined. A further batch of egg sacs was obtained in late October 1981 and another in late October 1983 from Dawsholm Park. The number and weight of eggs in these egg sacs were calculated.

To obtain information on spider emergence and hatching success, in two different localities, 25 egg sacs were

Fig.9.15: Egg sac of *Linyphia triangularis* .

located early November 1981 in Dawsholm Park and, at the same time, 11 egg sacs were located in Ross Wood. They were observed from time to time to record the number of egg sacs which hatched and the date of hatching. To obtain accurate information on the duration of the egg sac period seven egg sacs were retained in the laboratory until the spiderlings emerged. Mortality of eggs within the egg sac was estimated by two methods: (a) By examining 10 randomly selected egg sacs of those which hatched in Dawsholm Park to record the numbers of undeveloped eggs or spiderlings. The numbers of spiderlings which emerged were estimated by counting, under a binocular microscope, the exuvia which remained left inside the egg sacs. (b) By examining the egg sacs which hatched in the laboratory. The number of spiderlings which emerged and the number of undeveloped eggs or spiderlings were recorded.

Results

The results obtained from the analysis of the two egg sacs batches are given in Tables 9.10 and 9.11. There is no significant difference between the two batches with regard to total egg weight, number of eggs, weight of individual eggs and weight of the silk cocoon. There is a negative correlation ($r=0.66$, d.f.$=20$, $P<0.05$) between the number of eggs and the weight of individual eggs for the field batch (Fig.9.16). In the case of laboratory batch, there is also

Table 9.10: Weight and number of eggs in the egg sac, the weight of the egg and egg cocoon in *L. triangularis* from the field (values are mean ± S.D.). the figures in parenthesis are the numbers which were examined. The weight unit is mg.

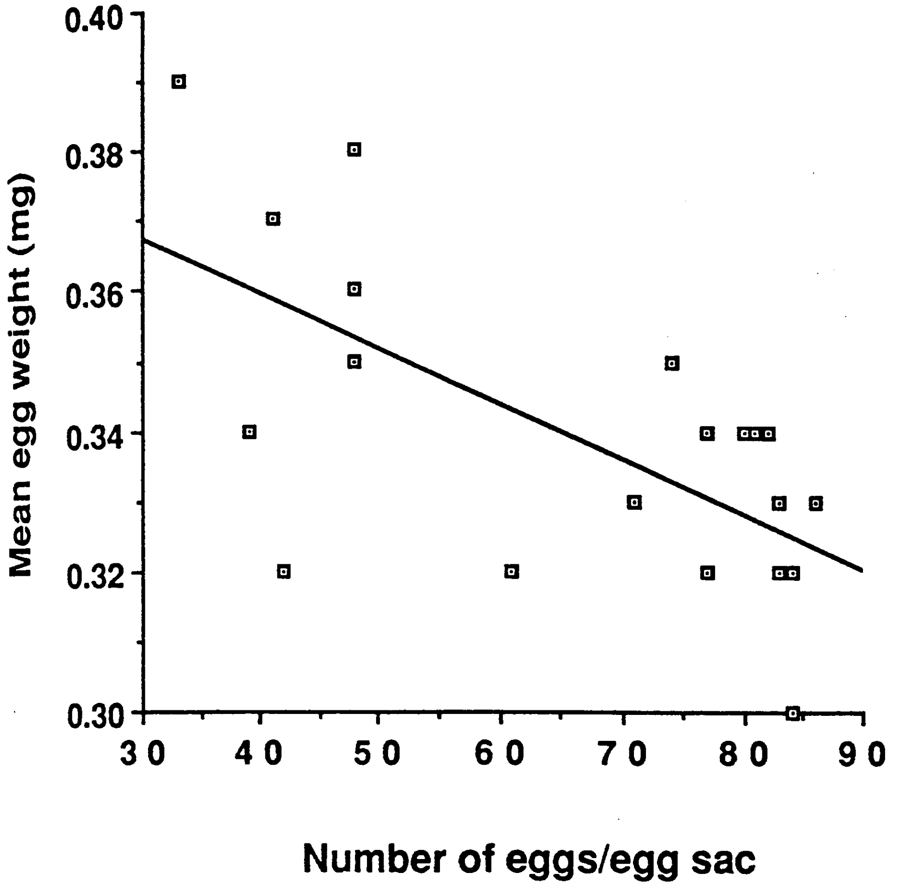
Wet weight of eggs	Dry weight of eggs	Number of eggs	Wet weight of egg	Wet weight of cocoon	Dry weight of cocoon
22.69	7.31	67.68	0.34	1.64	1.40
±5.58	±1.79	±18.52	±0.02	±0.36	±0.33
(22)	(22)	(22)	(22)	(22)	(22)

Table 9.11: Weight and number of eggs in the egg sac, the weight of the egg and egg cocoon and weight of spent females of *L. triangularis* from the laboratory (values are mean ± S.D.). The figures in parenthesis are the numbers which were examined. The weight unit is mg.

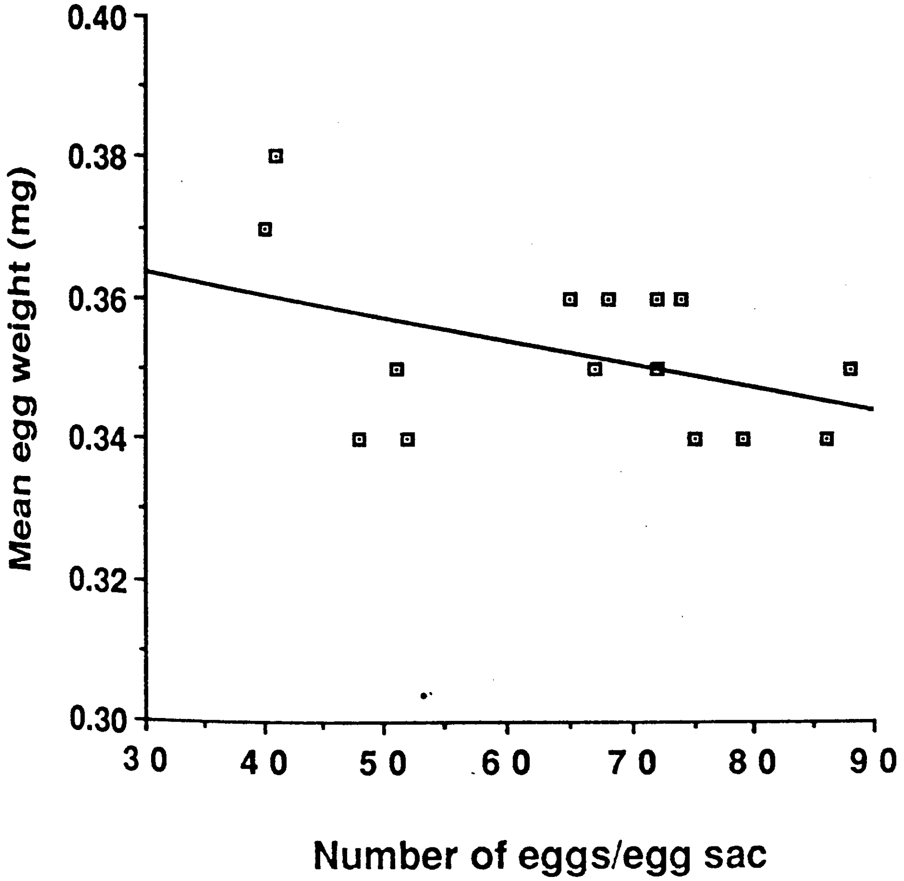
Wet weight of eggs	Dry weight of eggs	Number of eggs	Wet weight of egg	Wet weight of cocoon	Dry weight of cocoon	Wet weight of female
22.70	7.55	59.81	0.35	1.51	1.36	12.81
±5.27	±1.66	±21.99	±0.01	±0.26	±0.24	±1.68
(11)	(11)	(11)	(11)	(11)	(11)	(11)

Fig.9.16: The relationship between the number of eggs in an egg sac and the mean egg weight per egg sac in egg sacs of *Linyphia triangularis* collected in the field.

Fig.9.17: The relationship between the number of eggs in an egg sac and the mean egg weight per egg sac in egg sacs of *Linyphia triangularis* produced in the laboratory.



Mean egg weight (mg)
0.40
0.38
0.36
0.34
0.32
0.30
30
40
50
60
70
80
90
Number of eggs/egg sac



Mean egg weight (mg)
0.40
0.38
0.36
0.34
0.32
0.30
30
40
50
60
70
80
90
Number of eggs/egg sac

an indication of a negative correlation, but this failed to be significant (Fig.9.17). As might be expected, the larger the amount of egg material produced the greater the amount of silk laid down as a cocoon. Thus there is a significant correlation ($r=0.87$, d.f.=14, $P<0.05$) between the weight of eggs per egg sac and the weight of the cocoon (Fig.9.18). There is a significant correlation ($r=0.75$, d.f.=14, $P<0.05$) between the size of the adult female and the weight of eggs produced (Fig.9.19).

Of the 25 egg sacs observed at Dawsholm Park, 15 (60.0%) produced spiderlings, 10 egg sacs disappeared - presumably were eaten by predators. Of the 11 egg sacs observed in Ross Wood, eight (72.7%) produced spiderlings. Three of them disappeared - presumably were eaten by predators. At Dawsholm Park the majority of egg sacs (87.0%) had hatched by 13/5/1981 while at Ross Wood the majority of egg sacs (75.0%) had hatched by 22/5/1981 (Fig.9.20). In the laboratory the egg sacs hatched in approximately seven months ($X=203.6\pm3.8$ days, $n=7$, range 197-207 days). The mortality of eggs within the egg sacs was estimated to be 8.5 % in the field (Table 9.12) and 7.0 % for those in the laboratory (Table 9.13).

There is no indication that *L. triangularis* produces more than one egg sac, hence the number of eggs in Table 9.10 (67.68 eggs) can be regarded as the total output of

Table 9.12: The number (mean ± S.D.) of exuvia, (which represents the number of spiderlings which emerged from the egg sacs), the number of eggs and spiderlings which failed to develop and the mortality estimate within the egg sacs, of the spider L. triangularis in the field. The figures in parenthesis are the numbers which were examined.

Number of exuvia	Number of dead eggs	Number of dead spiderlings	Actual number of eggs / egg sac	Mortality %
57.80 ±17.49 (10)	0.30 ±0.67 (10)	5.10 ±3.54 (10)	63.20 ±15.07 (10)	8.5

Table 9.13: The number (mean ± S.D.) of spiderlings which emerged from the egg sacs, the number of failed eggs and spiderlings and the mortality estimate within the egg sacs of the spider L. triangularis in the laboratory. The figures in parenthesis are the numbers which were examined.

Number of emerged spiderlings	Number of dead eggs	Number of dead spiderlings	Actual number of eggs / egg sac	Mortality %
60.43 ±9.62 (7)	4.14 ±3.53 (7)	0.43 ±0.79 (7)	65.00 ±11.82 (7)	7.0

Table 9.14: Weight (mg.) and number of eggs in the egg sac, of the spider, L. triangularis in different years (values are mean ± S.D.) The figures in parenthesis are the numbers which were examined.

Year	Weight of eggs	Number of eggs
1981	23.47 ±5.52 (13)	68.15 ±15.46 (13)
1983	19.27 ±3.40 (10)	55.90 ±12.56 (10)

Fig.9.18: The relationship between the weight of eggs and the weight of the surrounding silk cocoon in egg sacs of <u>Linyphia triangularis</u> in the laboratory.

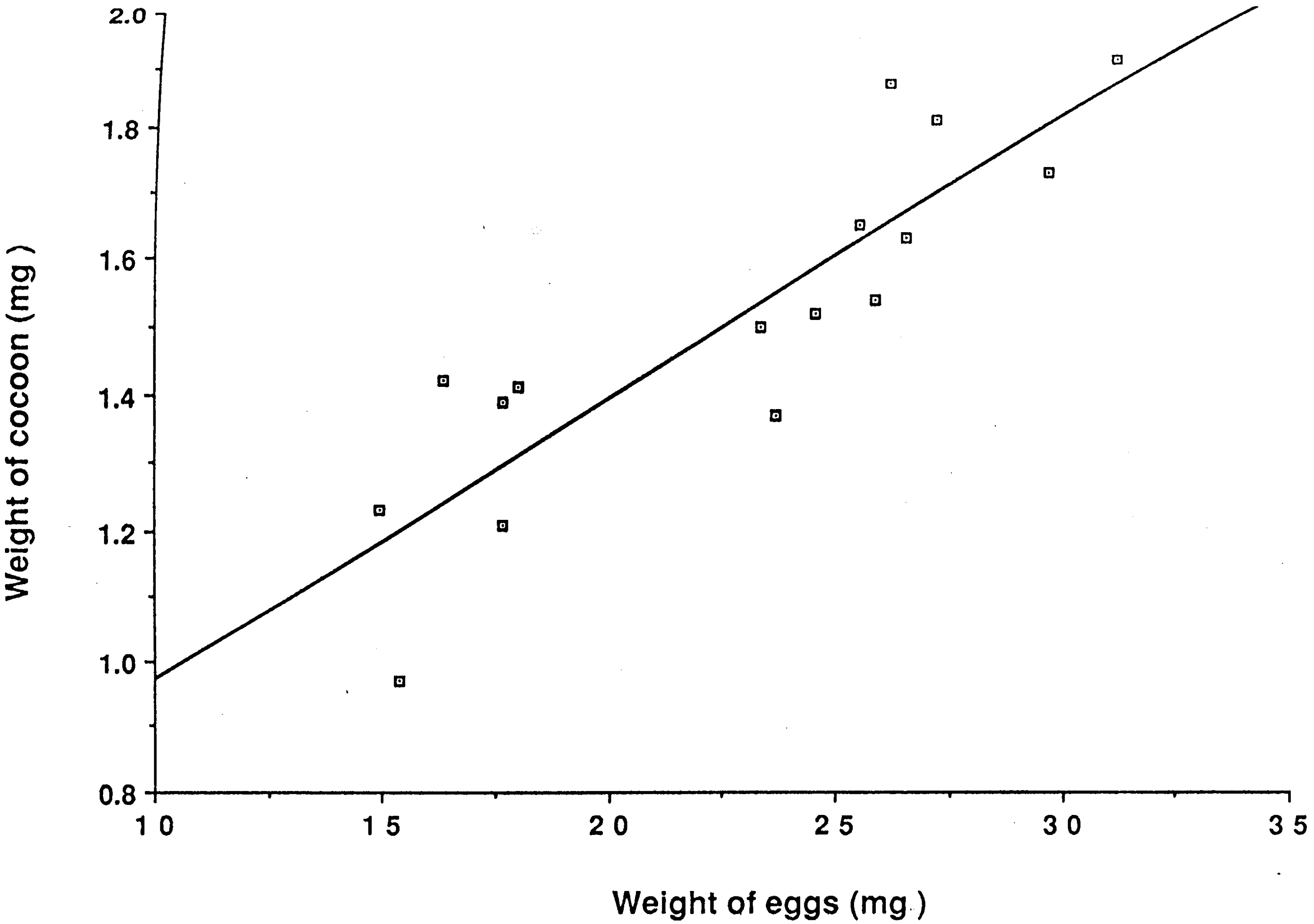

2.0
1.8
1.6
1.4
1.2
1.0
0.8
Weight of cocoon (mg)
1 0
1 5
2 0
2 5
3 0
3 5
Weight of eggs (mg.)

Fig.9.19: The relationship between the weight of eggs produced and the female size (as indicated by the length of tibia 1) in *Linyphia triangularis* .

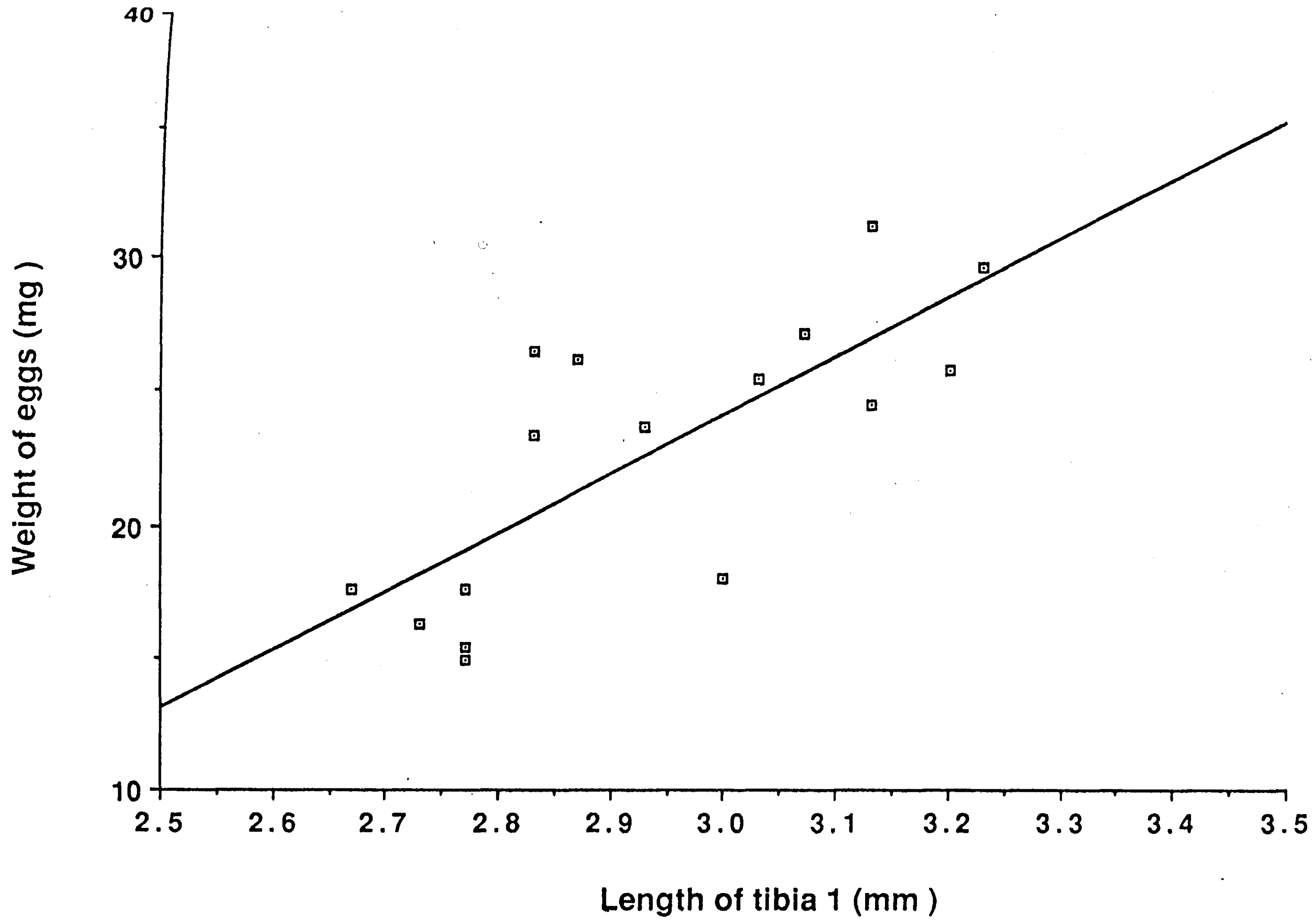
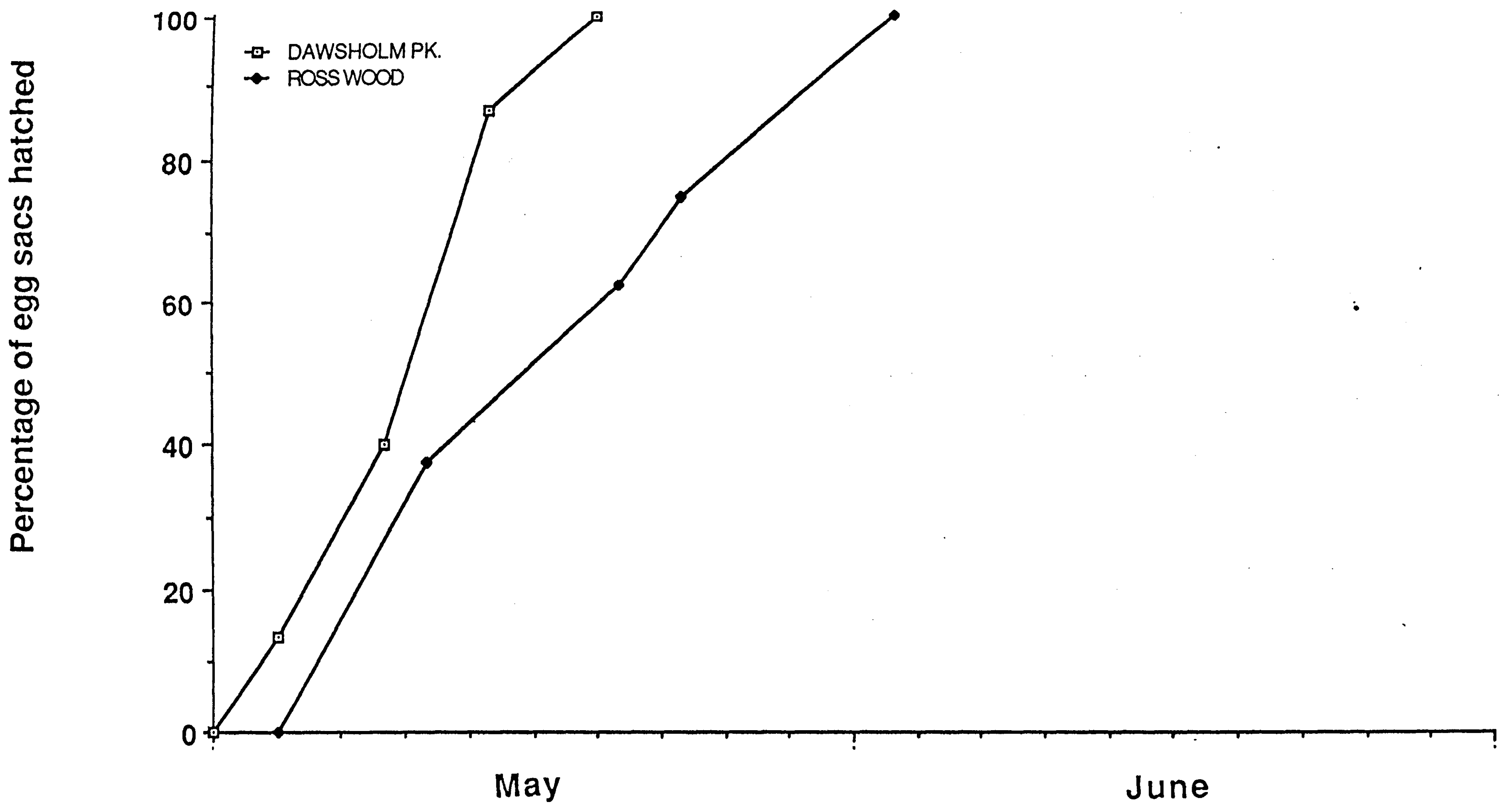

40
30
20
10
Weight of eggs (mg)
2.5
2.6
2.7
2.8
2.9
3.0
3.1
3.2
3.3
3.4
3.5
Length of tibia 1 (mm)

Fig.9.20: Hatching of egg sacs of <u>Linyphia</u> <u>triangularis</u> in 1982.


Percentage of egg sacs hatched
100
80
60
40
20
0
DAWSHOLM PK.
ROSS WOOD
May
June

adult female in the field. As egg sacs were subjected to a mortality within the egg sacs of 8.5 % (Table 9.12), the birth rate can be taken as 61.93 spiderlings per female.

Egg production differs from year to year (Table 9.14). Thus significantly more egg material (t=2.03, d.f.=21, $P<0.05$) and significantly more eggs (t=2.04, d.f.=21, $P<0.05$) are produced in 1981 than in 1983.

Discussion

Spiders show varying degrees of parental care. Crab spiders guard their eggs (Levy 1970) whereas wolf spiders carry their egg sacs and also care for the young for several days after they emerge (Bristowe 1958). Some spiders of the family Therididae feed their young (Norgaard 1956; Bristowe 1958). The four species under study display little care of their offspring. They may camouflage the egg sac with debris and hide it in crevices or other similar situations and the females may stay with the egg sac for a short period of time.

The four species differ in the timing of egg sac production. In *M. segmentata* and *L. triangularis* the egg sacs are produced in the autumn and the spiderlings emerge from these about seven months later. In *M. mengei* and *L. peltata* the egg sacs are produced in early summer and the spiderlings emerge in about six weeks. It was found that spiderlings of *M. segmentata* and *L. triangularis* in open areas emerged from overwintering egg sacs earlier than those in woodland sites. This is presumably due to the higher temperatures in the open areas.

The number of eggs produced by the four species in the current study are broadly in agreement with the figures given by Toft (1976)- although his figures are based on dissections of gravid females rather than examining egg sacs. The most striking differences was that Toft recorded an average egg production, for *L. peltata* , of 25 eggs, compared with a figure of 42 in the present study. The figures were similar for the other species, but Toft considered that the eggs were deposited in two batches, compared with the one batch found in the current study.

In the present study the relationship between spider size and the weight or number of eggs produced was investigated in *M. segmentata* and *L. triangularis* and a significant positive correlation was found. A similar correlation has been found in many spiders (Peterson 1950; Hackman 1956; Kessler 1971, 1973; Koponen 1975; Wise 1976; Harrington 1978 ; Fritz & Morse 1985). This relationship has also been found to exist in interspecific studies (Peterson 1950; Enders 1976; Koponen 1976). Kessler (1973) found that the relationship held, in general, for *Pardosa* species but there were exceptions. He found that some species, of similar size, produced eggs of different sizes. A similar situation was found in the current study for the two *Metellina* species where, although the adult females are similar in size, the weight of an egg of *M. segmentata* is about twice that of *M. mengei* . Bearing this in mind a more meaningful relationship might be between spider weight and egg batch weight.

Turnbull (1962) indicated that L. triangularis , in laboratory feeding experiments, produced a normal number of eggs when reared in conditions of food shortage, but that these eggs were lighter than normal. Riechert & Tracy (1975) also found that the weight of individual eggs was determined by the amount of food. Kessler (1971) found that in some Pardosa species lighter eggs were produced in conditions of food shortage but in other Pardosa species fewer eggs were produced but these were of a normal size. In the current study there were variations in the numbers of eggs produced and also in the weight of individual eggs. This occurred both within years and between years. It was not clear whether these reflected variations in food supplies or differences in adult female body size.

In M. mengei there is little or no egg mortality but in M. segmentata and the two Linyphia species egg mortality ranged from 7-22%. Geyer (1976) and Lindley (1974) both recorded undeveloped eggs in M. segmentata . Geyer (1976) reported a remarkable value of 93.0% - which is far higher than the maximum value of 22% found in the current study. Kessler (1973) also found undeveloped eggs in Pardosa species and egg mortality has been recorded in other wolf spiders. However these tend to be fairly low with a value of 1.7% for the egg sacs of Pardosa palustris (Steigen 1975) and one of 3.4% in egg sacs of

P. agricola (Albert & Albert 1976). Humphreys (1976) reported a value of 5.1% for Geolycosa godeffroyi while Hackman (1957) and Edgar (1971) found that all the eggs developed into spiderlings in the wolf spiders which they studied. Harrington (1978) reported egg mortality up to 19.5% in the funnel web spider Agelenopsis potteri and Fritz & Morse (1985) found a mortality of 5.5% in eggs of the crab spider Misumena vatia . Geyer (1976) reported a high mortality (40%) within the egg sacs of theridiid spider Robertus lividus . Lindley (1974) reported that mortality of the whole egg sac could occur in M. segmentata and in the present study, which monitored egg sacs in the field, egg sacs also disappeared. This was presumably due to predation - possibly by birds or carabid beetles.

CHAPTER 10

Density Estimates of the Four Species

Introduction

Density values were obtained with a view to estimating mortality rates and spider biomass. It was intended to use this information to calculate the rate of energy flow through the spider populations.

To work out generation mortality rates of an animal it is necessary to know the numbers of reproducing adults, the numbers of young recruited into the population and the numbers of animals present at different stages in the life cycle. In the case of _M. mengei_ there are difficulties in obtaining this information. The fact that some animals have a one year life cycle and some a two year one, means that each generation has to be considered separately. No separate density estimates have been obtained for the two life cycles. As indicated in the section on Egg Sacs, no reliable estimate can be given for the number of spiderlings recruited into the population. Because of these difficulties, no estimate can be given of generation mortality. What is given in this section, for _M. mengei_ and the other three species, is estimates of spider density at various times of the year. This information can be used to elucidate the life cycle of the animal. It can, in conjunction with other population data, indicate when recruitement is occurring in the population and can indicate changes in spider distribution and periods when heavy mortality is occurring.

Methods

M. mengei and L. peltata densities were estimated by sampling in Area 6 from August 1980 to November 1981. This area was dominated by blaeberry (Vaccinium myrtillus) and a general view of the area is given in Fig.10.1. A grid of 280 (2X1m) units was measured out in July 1980 and hand samples were taken at approximately 4-week intervals. Sampling was only carried out on fine days, so that density estimates would not be affected by variable weather conditions. On some occasions the weather deteriorated after sampling had started and when this occurred the sampling was terminated and fewer units were sampled. Thus on each sampling occasion 8-10 randomly selected units were sampled. As both L. triangularis and M. segmentata were found in small numbers in Area 6 (see chapter on Spider Distribution) these spiders were sampled in two other areas. In both of these blaeberry was still the dominant vegetation but they were more open sites than Area 6. M. segmentata was sampled in Area 13. The blaeberry in this area was taller than in Area 6 and was considerably defoliated and small rowan and birch trees

Fig.10.1: General view of Area 6, which was sampled for density estimates of *Metellina mengei* and *Linyphia peltata* in 1980-1981.

were scattered through the area (Fig.10.2). *L. triangularis* was sampled in Area 10. Besides being more open the vegetation in this site was shorter than in Area 6 (Fig.10.3). Both these areas were considerably smaller than Area 6. Area 10 consisted of 30 (2x1m) units and Area 13 of 45 (2X1m) units. Both areas were sampled from late May / early June 1982 at approximately 2-3 week intervals. Ten randomly selected units were sampled by hand collecting.

All the sampling areas had transverse paths between the sampling units to reduce trampling on the vegetation during sampling. In the case of *M. segmentata* and *L. triangularis* the number of spiders in each sample was recorded and the spiders were then released back into the sampling area. With samples of *M. mengei* and *L. peltata* the spiders were retained and used for other purposes. It was not thought this proceedure significantly affected subsequent density estimates as Area 6 was very large and the number of units sampled on each occasion was small, in relation to the 280 units which comprised the area

Fig.10.2: General view of Area 13, which was sampled for density estimates of <u>Metellina segmentata</u> in 1982.

Fig.10.3: General view of Area 10, which was sampled for density estimates of <u>Linyphia</u> <u>triangularis</u> in 1982.

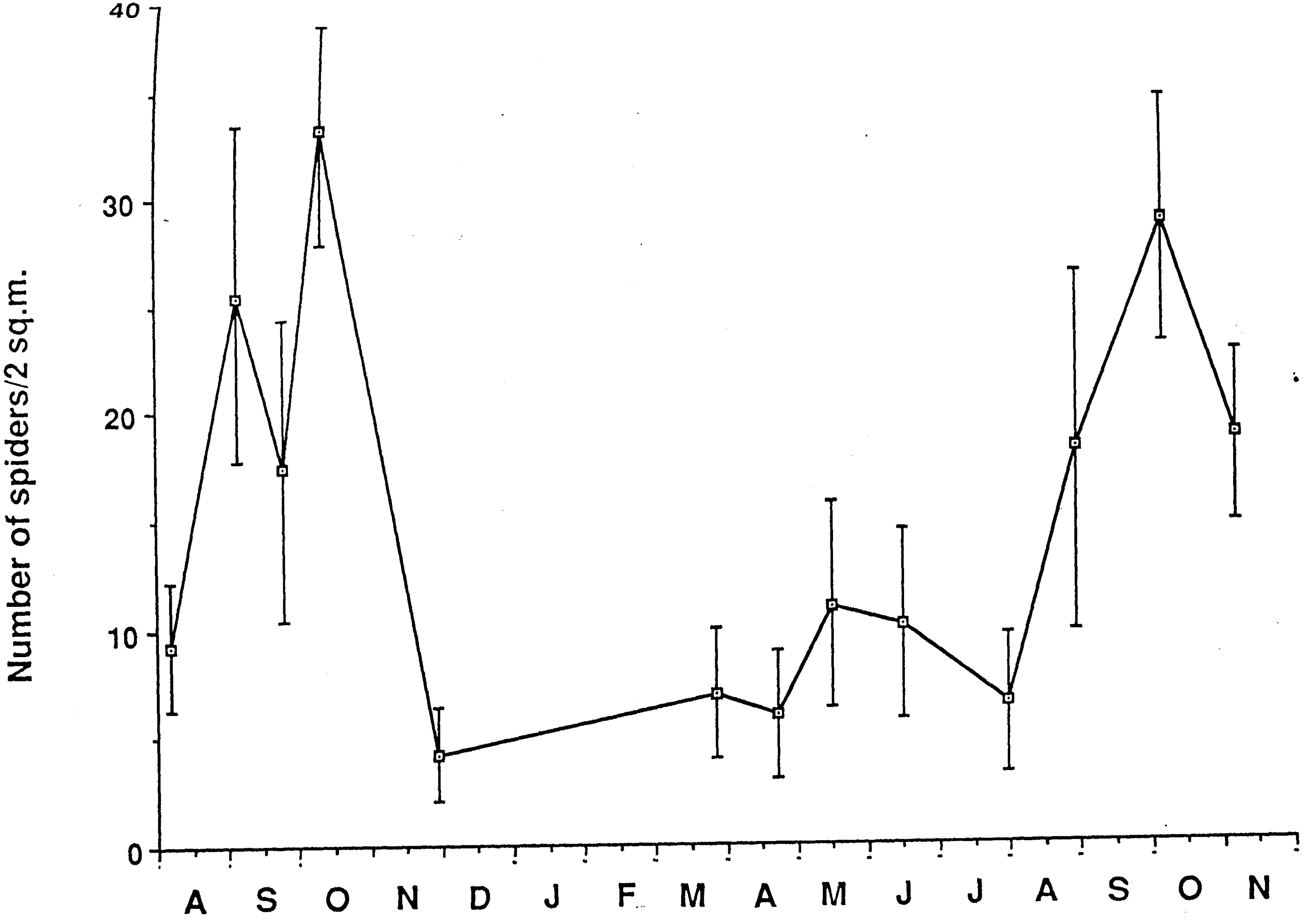
Results

Metellina mengei

Estimates of spider density are given in Fig.10.4. Spiderlings leave the egg sacs in July and this is reflected in a significant increase in spider numbers between early August and early September 1980 (t=3.88, d.f.=9, P<0.01). There was a drop in density between early and late September (although the difference was not significant), followed by a significant increase between late September and early October (t=3.60, d.f.=18, P<0.01). No satisfactory explanation can be offered for the decline towards the end of September.

Peak spider densities were recorded in early October in both 1980 and 1981 and there was no significant difference in spider density, in October, between the two years (t=1.13, d.f.=16, P>0.20). Spider numbers decreased sharply from October to late November (t=10.05, d.f.=7, P<0.001) and remained at a similar level in late March and late April in 1981. This decline in spider density in early winter is probably due to a combination of spider mortality and spider inactivity. The latter is certainly a factor as spider density increases in mid-May and was significantly higher than in the previous November (t=2.61, d.f.=16, P<0.025). As no recruitment occurs over this time it is

Fig.10.4: Density estimates (mean±2SE) of *Metellina mengei* throughout the year 1980-1981 in Area 6.


Number of spiders/2 sq.m.
40
30
20
10
0
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N

assumed that the lower estimates in November, March and April simply reflect a lower level of activity, due to reduced temperatures during this period.

Spider density in mid-May was significantly lower than in the previous October and this is attributed to spider mortality. Spider density decreased from mid-May to late July - but the difference was not significant. There is, however, a significant decline in density from October 1980 to July 1981 ($t=8.56$, d.f.=18, $P<0.001$) and this drop in density, from 16.6 - 3.3m , represents a mortality rate of over 80% over this 9.5 month period. It should be stressed again that this represents overall mortality in a population which comprises more than one year group.

From the minimum level in July, there is a sharp increase in density in late August ($t=2.61$, d.f.=7, $P<0.05$) as the new generation starts to enter the population and this continued to early October ($t=2.11$, d.f.=14, $P<0.05$). Spider numbers decrease sharply from early October to early November ($t=2.55$, d.f=11, $P<0.05$) and this is again attributed to a combination of spider mortality and reduced activity with the approach of winter. Mean spider density, on each sampling occasion, is given in Table 10.1.

Table 10.1: The mean density of the spider *M. mengei* per 2 sq.m in Area 6, from early August 1980 until early November 1981.

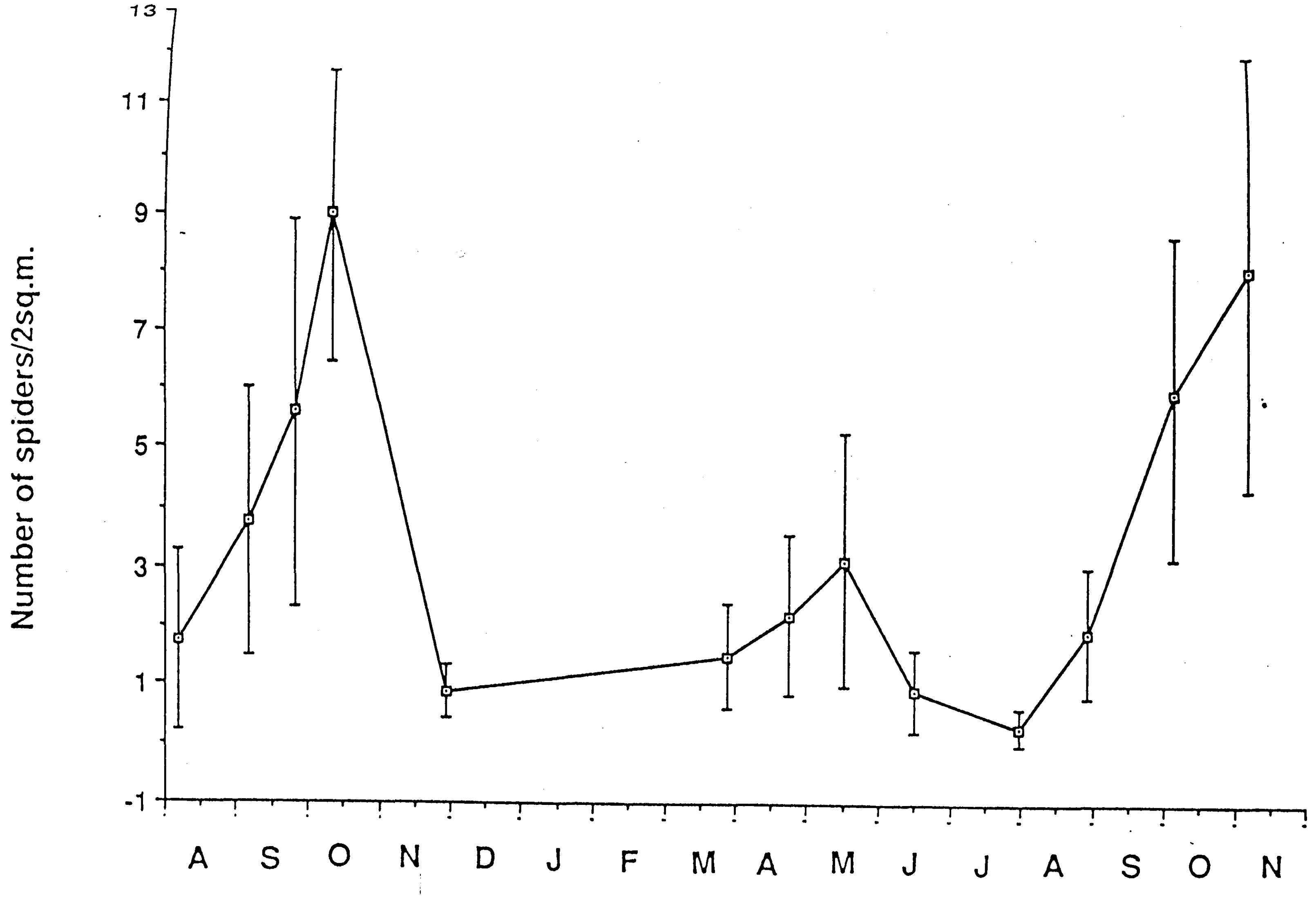
Date of sampling	Number of spiders Mean + S.D.	Number of sampling units
6/8/1980	9.25 + 4.17	8
5/9/1980	25.50 + 11.10	8
24/9/1980	17.40 + 11.03	10
10/10/1980	33.20 + 8.44	10
28/11/1980	4.25 + 3.06	8
26/3/1981	7.00 + 4.71	10
22/4/1981	6.00 + 4.62	10
15/5/1981	11.00 + 7.42	10
15/6/1981	10.10 + 6.76	10
29/7/1981	6.50 + 5.10	10
28/8/1981	18.13 + 11.73	8
4/10/1981	28.75 + 8.07	8
5/11/1981	18.60 + 4.45	5

Linyphia peltata

The results are shown in Fig.10.5. The numbers of spiders increase from early August to mid-October ($t=4.54$, d.f.$=16$, $P<0.001$). This is due to the recruitment of the new generation into the population. The density drops sharply from mid-October to late November ($t=6.24$, d.f.$=7$, $P<0.001$), presumably due to the spiders becoming inactive during the winter. Numbers have increased by late March and a peak occurred in mid-May. No recruitment occurs to the population during this period and this increase is thought to reflect increased activity as the spiders emerge from the overwintering period. Thus the decrease in spider density from mid-October to mid-May is taken as an estimate of spider mortality during this period.

From a peak in May, spider density decreases to a minimum level in late July ($t=2.62$, d.f.$=9$, $P<0.05$). This corresponds to the time when most adult spiders are dying after having reproduced. From the lowest level in late July, spider numbers increase sharply over the autumn as a new generation emerges from the egg sacs. Thus there was a significant increase between late July and late August ($t=2.76$, d.f.$=7$, $P<0.05$) and between late August and early October ($t=2.72$, d.f.$=7$, $P<0.05$). The increase between early October and early November was not significant ($t=0.93$, d.f.$=11$, $P>0.05$). In 1980 the highest recorded

Fig.10.5: Density estimates (mean±2SE) of *Linyphia peltata* throughout the year 1980-1981 in Area 6.


Number of spiders/2sq.m.
13
11
9
7
5
3
1
-1
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N

density was in early October and in 1981 in early November. There is no significant difference between the peak densities in the two years (t=0.45, d.f.=13, P>0.05). Mean spider density, on each sampling occasion, is given in Table 10.2.

Table 10.2: The mean density of the spider *Linyphia peltata* per 2sq.m in Area 6 from early August 1980 until early November 1981.

Date of sampling	Number of spider mean + S.D.	Number of sampling units
6/8/1980	1.75 + 2.19	8
5/9/1980	3.75 + 3.20	8
24/9/1980	5.60 + 5.19	10
10/10/1980	9.00 + 4.06	10
28/11/1980	0.88 + 0.64	8
26/3/1981	1.50 + 1.43	10
22/4/1981	2.20 + 2.15	10
15/5/1981	3.10 + 3.35	10
15/6/1981	0.90 + 1.10	10
29/7/1981	0.30 + 0.48	10
28/8/1981	1.88 + 1.55	8
4/10/1981	5.88 + 3.87	8
5/11/1981	8.00 + 4.18	5

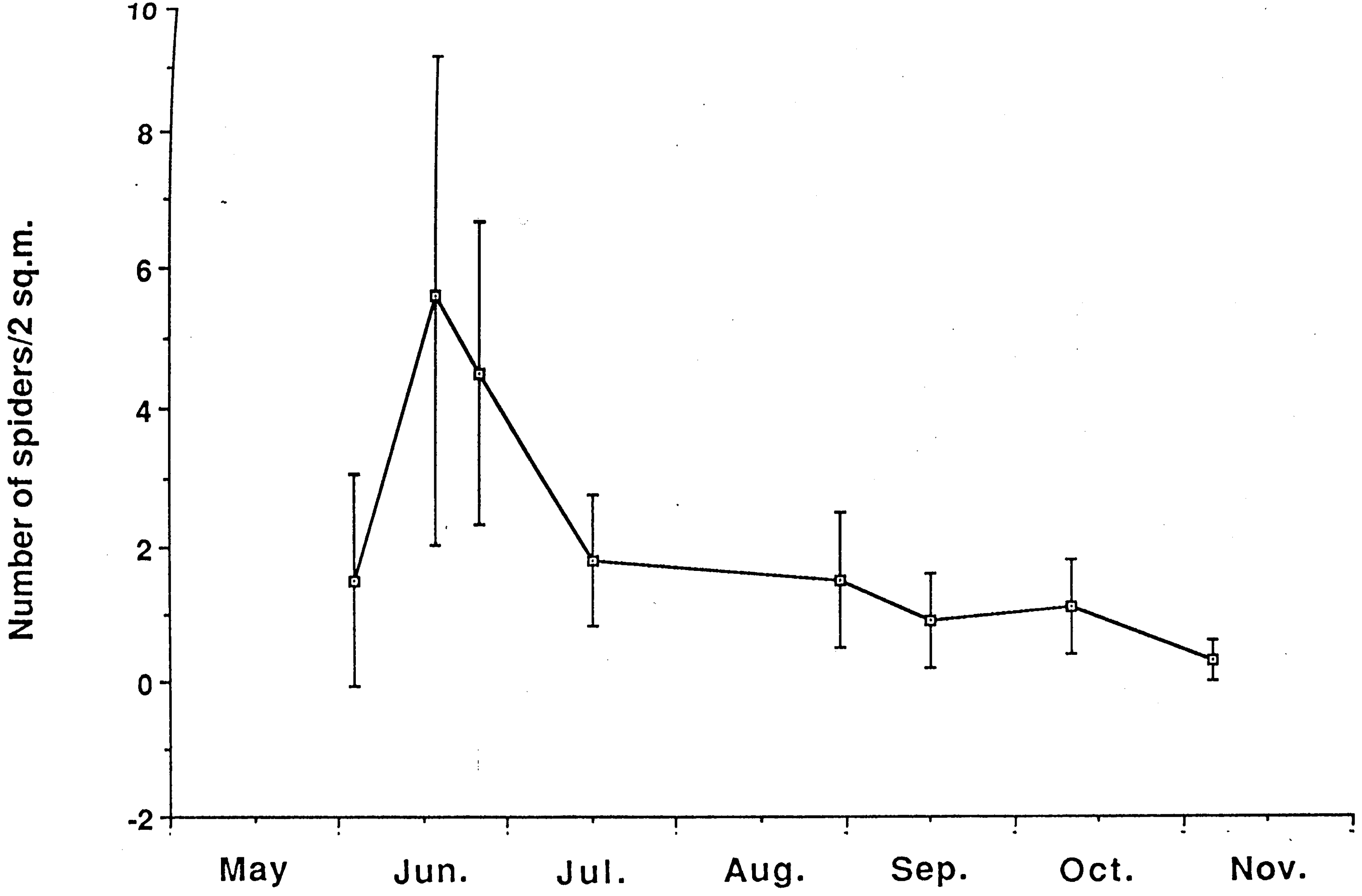
Metellina segmentata

The results are shown in Fig.10.6. The number of spiders increased (but not significantly) from early to mid-June. This is the period when the spiderlings are emerging from the egg sacs. The fact that the increase was not statistically significant is due to the very large standard errors which reflect the clumped dispersion of the spiderlings. There is no significant change in density between mid and late June but numbers decreased towards mid-July ($t=2.28$, d.f.=9, $P<0.05$). There is no significant change in density between mid-July and late August and between late August and mid-September. No significant change in spider numbers occur between mid-September and early October but the numbers decreased significantly between early October and early November ($t=2.52$, d.f.=9, $P<0.05$). This reflects the death of adult spiders after reproducing. The results of the density estimates are summarised in Table 10.3.

Table 10.3: The mean density of the spider *Metellina segmentata* per 2 Sq.m in Area 13 in Ross Wood from early June 1982 until early November 1982.

Date of sampling	Number of spider mean ± S.D.	Number of sampling units
3/6/1982	1.50 ± 2.50	10
17/6/1982	5.60 ± 5.66	10
25/6/1982	4.50 ± 3.41	10
15/7/1982	1.80 ± 1.55	10
29/8/1982	1.50 ± 1.58	10
15/9/1982	0.90 ± 1.10	10
10/10/1982	1.10 ± 1.10	10
5/11/1982	0.30 ± 0.48	10

Fig.10.6: Density estimates (mean±2SE) of *Metellina segmentata* throughout the year 1982 in Area 13.


Number of spiders/2 sq.m.
10
8
6
4
2
0
-2
May
Jun.
Jul.
Aug.
Sep.
Oct.
Nov.

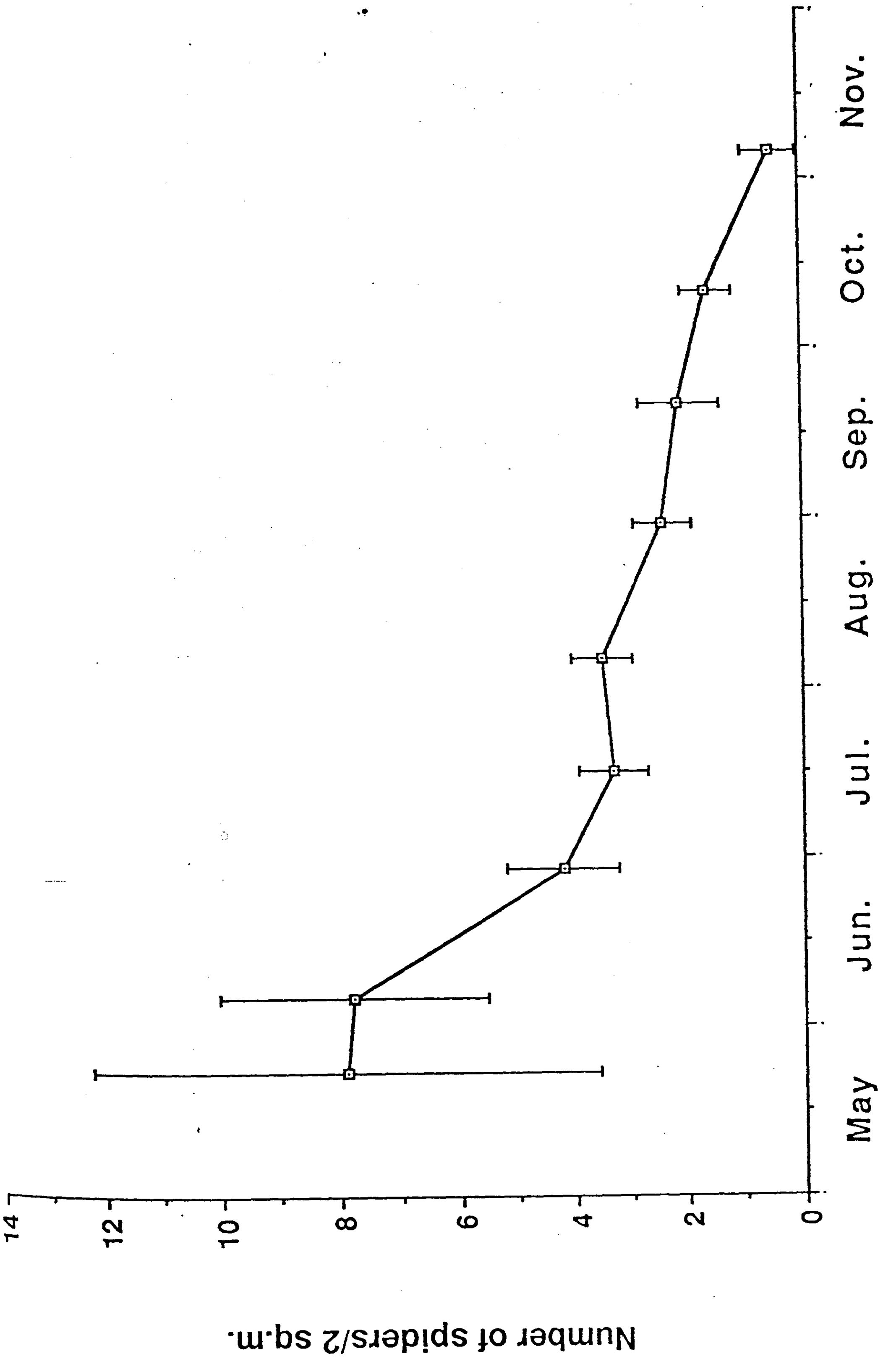
Linyphia triangularis

The results are shown the Fig.10.7. There is no significant change in the density between 22/5/82 and 5/6/82 but numbers decrease significantly during June ($t=2.92$, d.f.=9, $P<0.05$). The decline between late June and early August is not significant but there is a significant drop during August ($t=2.91$, d.f.=18, $P<0.05$). This is thought to reflect the death of adult males during this period. There was no significant decrease between late August and late September or between late September and early October. There was, however, a significant decrease between early October and early November ($t=3.50$, d.f.=18, $P<0.05$). This is attributed to the death of adult females after they have produced egg sacs. The results of the density estimates are summarised in Table 10.4.

Table 10.4: The mean density of the spider Linyphia triangularis per 2sq.m in Area 10 in Ross Wood from late May 1982 until early November 1982.

Date of sampling	Number of spider mean ± S.D.	Number of sampling units
22/5/1982	7.90 ± 6.85	10
5/6/1982	7.80 ± 3.58	10
28/6/1982	4.20 ± 1.55	10
15/7/1982	3.30 ± 0.95	10
5/8/1982	3.50 ± 0.85	10
29/8/1982	2.40 ± 0.84	10
20/9/1982	2.10 ± 1.10	10
10/10/1982	1.60 ± 0.70	10
5/11/1982	0.50 ± 0.71	10

Fig. 10.7: Density estimates (mean±2SE) of *Linyphia triangularis* throughout the year 1982 in **Area 10.**


Number of spiders/2 sq.m.
0
2
4
6
8
10
12
14
May
Jun.
Jul.
Aug.
Sep.
Oct.
Nov.

Discussion

Density estimates were obtained by hand collecting because this was the best sampling method (see chapter on Sampling Comparisons). However it is influenced by spider activity and the low numbers in early winter and early spring may be due, in part, to spiders moving into overwintering sites such as crevices in the bark of trees, in clumps of mosses or in piles of leaf litter.

The patterns of spider density are similar in *M. mengei* and *L. peltata* . Thus peak density occurred in mid-October (16.6 spiders/m^2 for *M. mengei* and 4.5 spiders/m^2 for *L. peltata*). Spider numbers dropped during the late winter and the spring, for the reasons indicated above, and rose to a second peak in mid-May (5.5 spiders/m^2 in *M. Mengei* and 1.6 spiders/m2 in *L. peltata*).

The changes in spider densities are similar for *M. segmentata* and *L. triangularis* . The spiderlings emerge from the egg sacs in early summer and peak densities occur in late May for *L. triangularis* (4.0 spiders/m^2) and in mid-June for *M. segmentata* (2.8 spiders/m^2). The density of spiders in mid-October was 0.8/m^2 for *L. triangularis* and 0.6/m^2 for *M. segmentata* . In the case of *L. triangularis* only adult females are present at this time while both adult males and females of *M. segmentata* are represented.

There are relatively few studies which give density estimates for web spinning spiders. Duffey (1962) gave a value of 1.2 spiders/m^2 for field layer spiders in Wytham Wood in October 1951. This value is low compared with those in the present study. In October 1980 the combined density for *M. mengei* and *L. peltata* was 21.1 spiders/m^2. The average annual densities for the four species were *M. mengei* 6.3/m^2; *L. peltata* 1.3/m^2; *M. segmentata* 1.1/m^2 and *L. triangularis* 2.3/m^2. These results are comparable with those found by Kajak (1967) for three orb web building spiders - *Araneus quadratus* 6.4/m^2; *A. cornutus* 1.9/m^2 and *Singa hamata* 2.4/m^2.

CHAPTER 11

Seasonal Weight Changes in the Four Species

Introduction

The aim of this chapter is to investigate the seasonal weight changes in the four species. This, combined with density estimates, would allow biomass to be calculated throughout the year and would provide additional information on the spider life cycles.

Methods

The sampling areas were the same areas, or similar areas, as those sampled for density estimates. *M.* mengei was sampled from August 1980 to November 1981 in Area 6 by hand collecting. Samples of adult females were taken by sweep netting during this period in Area 7 - which was adjacent to Area 6. Some additional sweep net samples of adult females were taken in 1985. *L. peltata* was sampled, from August 1980 to November 1981 in Area 6, by hand collecting. Additional samples were taken in an adjacent area (Area 7) by sweep netting from August 1980 to July 1981. Although hand searching is the best method for obtaining representative samples (see chapter on Sampling Comparisons), sweep netting can provide samples for comparative purposes, when only one age class is represented - as is the case with *L. peltata* . *L.*

triangularis was sampled from May to October 1982 in Area 9, which was adjacent to Area 10. *M. segmentata* was sampled from Area 12 which was adjacent to Area 13. Additional samples of *M. segmentata* were taken in Dawsholm Park (Area B3) where the dominant vegetation was tall grass with broom bushes (*Cytiscus scoparius*). Both species were collected by hand sampling. The spiders in all the samples were weighed on a Cahn Electromicrobalance.

Results

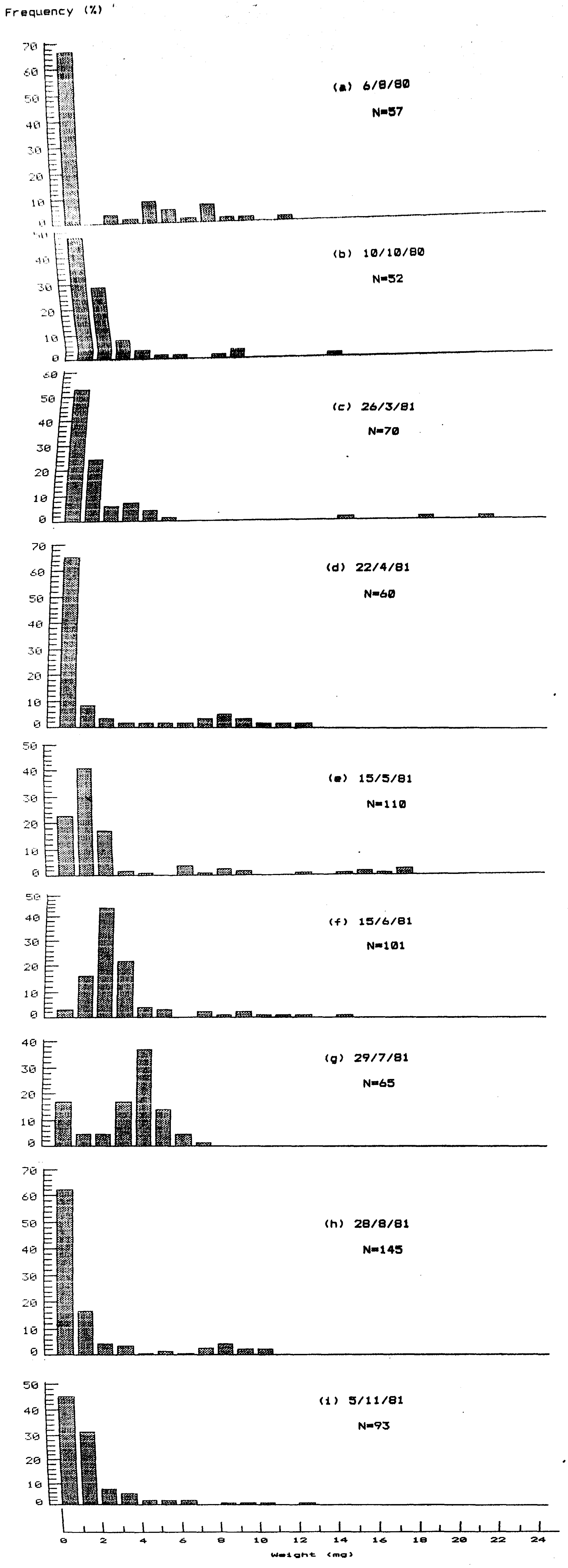
Metellina mengei

Histograms of the weight distribution of the samples are given in Fig.11.1. These are similar in appearance to the histograms presented in the chapter on the Age Structure and Life Cycle of *M. mengei* . Values of mean spider weight on each sampling occasion are given in Fig.11.2. Where more than one year group or cohort is present in a sample then a value for mean spider weight may not be very meaningful with respect to the spiders in the sample. However changes in mean spider weight throughout the year can provide additional information on which to base an account of the life cycle of the spider.

There is no significant change in mean spider weight

Fig.11.1: Weight distribution of *Metellina mengei* throughout the year 1980-1981 in Area 6. Samples were taken by hand collecting.

Fig.11.4: Weight distribution of adult females of *Metellina mengei* throughout the year 1980-1981 in Area 7. Samples were taken by sweep netting.


Frequency (%)
(a) 6/8/80
N=57
(b) 10/10/80
N=52
(c) 26/3/81
N=70
(d) 22/4/81
N=60
(e) 15/5/81
N=110
(f) 15/6/81
N=101
(g) 29/7/81
N=65
(h) 28/8/81
N=145
(i) 5/11/81
N=93
0
2
4
6
8
10
12
14
16
18
20
22
24
Weight (mg)

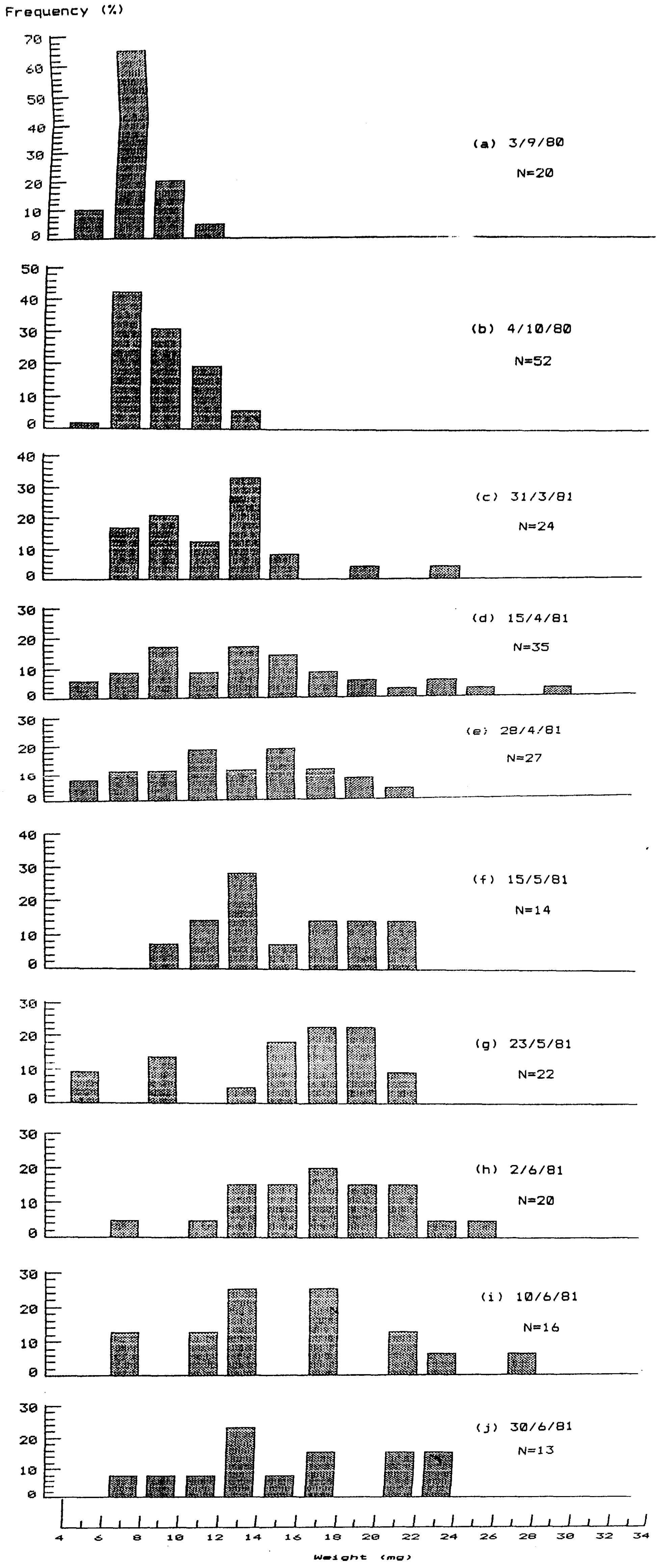
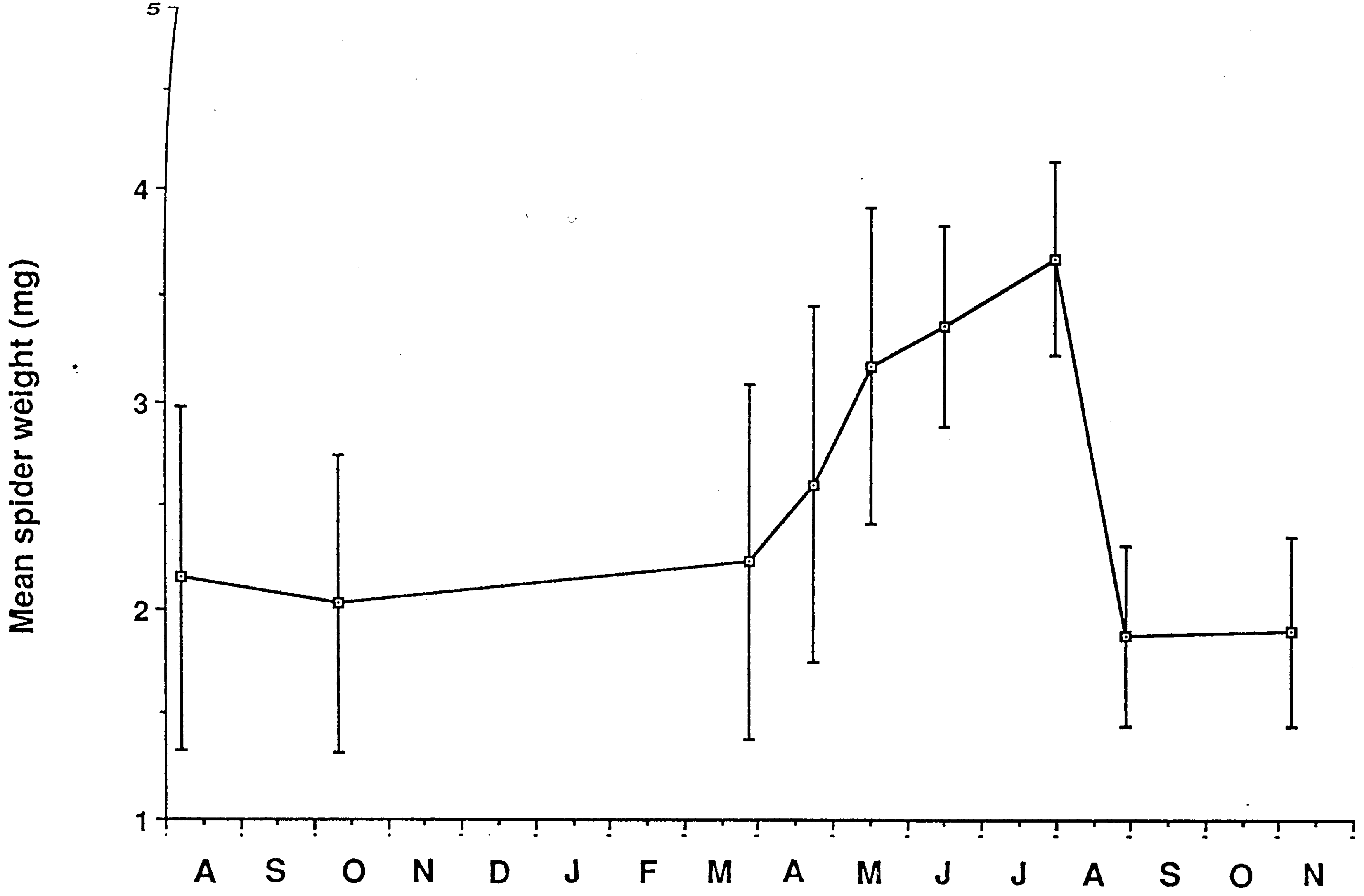

Frequency (%)
(a) 3/9/80
N=20
(b) 4/10/80
N=52
(c) 31/3/81
N=24
(d) 15/4/81
N=35
(e) 28/4/81
N=27
(f) 15/5/81
N=14
(g) 23/5/81
N=22
(h) 2/6/81
N=20
(i) 10/6/81
N=16
(j) 30/6/81
N=13
4
6
8
10
12
14
16
18
20
22
24
26
28
30
32
34
Weight (mg)

Fig. 11.2: Seasonal weight changes (mean±2SE) in *Metellina mengei* throughout the year 1980-1981 in Area 6.


Mean spider weight (mg)
5
4
3
2
1
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N

between early August and late March (Fig.11.2). This might be interpreted as indicating that no growth takes place during this period but an examination of Fig.11.1 indicates that this is not the case. Thus the sub-adults present in August, which represent about 35% of the sample, are represented by a small number of adults in the March sample - where the bulk of the animals are those which were very small spiders in August. Mean spider weight shows a significant increase from late March to late July ($t=2.96$, $d.f.=133$, $P<0.005$) - which reflects spider growth throughout the spring and summer. There is a significant decrease in spider weight between late July and late August ($t=5.73$, $d.f.=208$, $P<0.001$). As can be seen from Fig.11.1, this reflects the fact that emergence of spiderlings from egg sacs starts in early August and there is an influx of small spiders into the population at this time. There is no significant change in spider weight between late August and early November.

Changes in the mean weight of adult females, from September 1980 to June 1981, are shown in Fig.11.3 and changes in the weight distribution, over the same period, are shown in Fig.11.4. Changes in the weight distribution from April to June 1985 are shown in Fig.11.5. From Fig.11.3 it is seen that mean adult weight is at its lowest in early September - which is the time when moulting to adult of the 2 year animals occurs. The mean weight has increased significantly

Fig.11.3: Seasonal weight changes (mean±2SE) of adult females of Metellina mengei throughout the year 1980-1981 in Area 7.

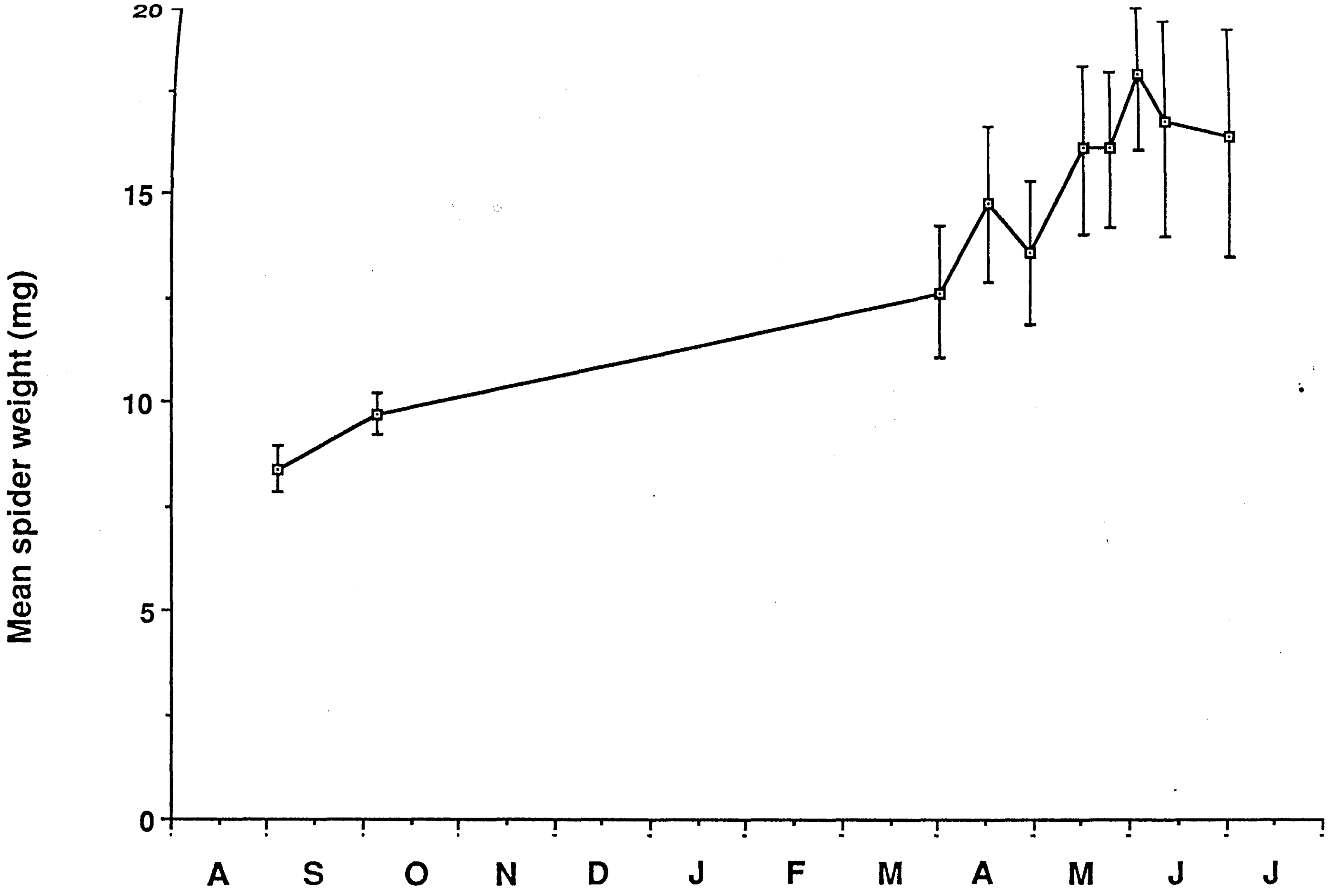
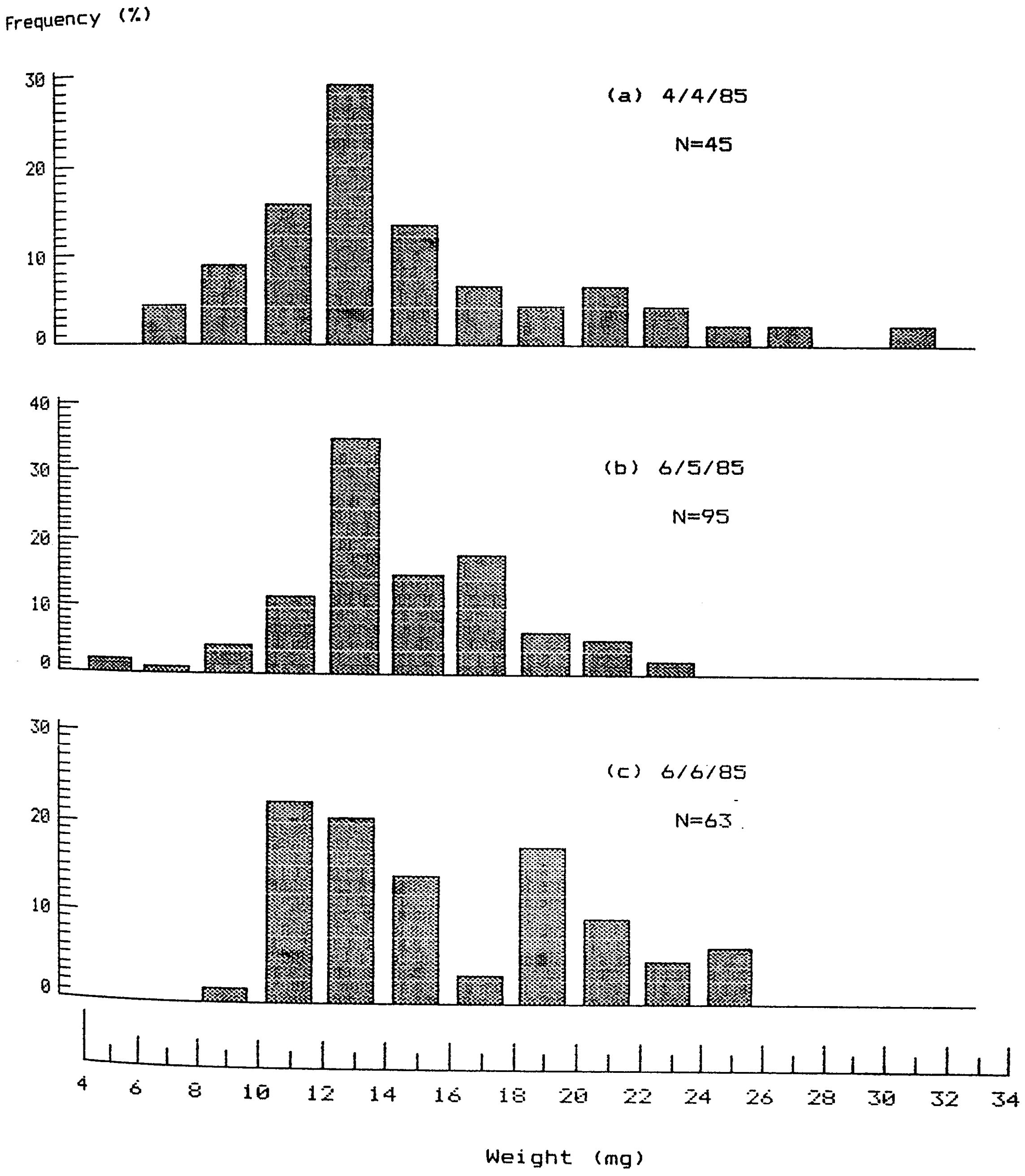

Mean spider weight (mg)
20
15
10
5
0
A
S
O
N
D
J
F
M
A
M
J
J

Fig.11.5: Weight distribution of adult females of *Metellina mengei* in 1985 in Area 7. Samples were taken by sweep netting.


Frequency (%)
(a) 4/4/85
N=45
(b) 6/5/85
N=95
(c) 6/6/85
N=63
0
10
20
30
40
4
6
8
10
12
14
16
18
20
22
24
26
28
30
32
34
Weight (mg)

by early October ($t=3.37$, d.f.$=70$, $P<0.001$) and there is also a significant increase between October and March ($t=3.53$, d.f.$=74$, $P<0.001$). Between March and early June the weight again increases significantly ($t=4.31$, d.f.$=42$, $P<0.001$). This is interpreted as an increase in spider weight prior to the production of egg sacs. Spider weight declines during the rest of June - although the decline is not significant. This decline presumably reflects the fact that some spiders have produced egg sacs. Support for this interpretation comes from the fact that there is a significant correlation between spider size and weight in May (Fig.11.6) but the relationship is not significant in June (Fig.11.7), possibly because of the presence of both gravid females and large "spent" females in the June sample.

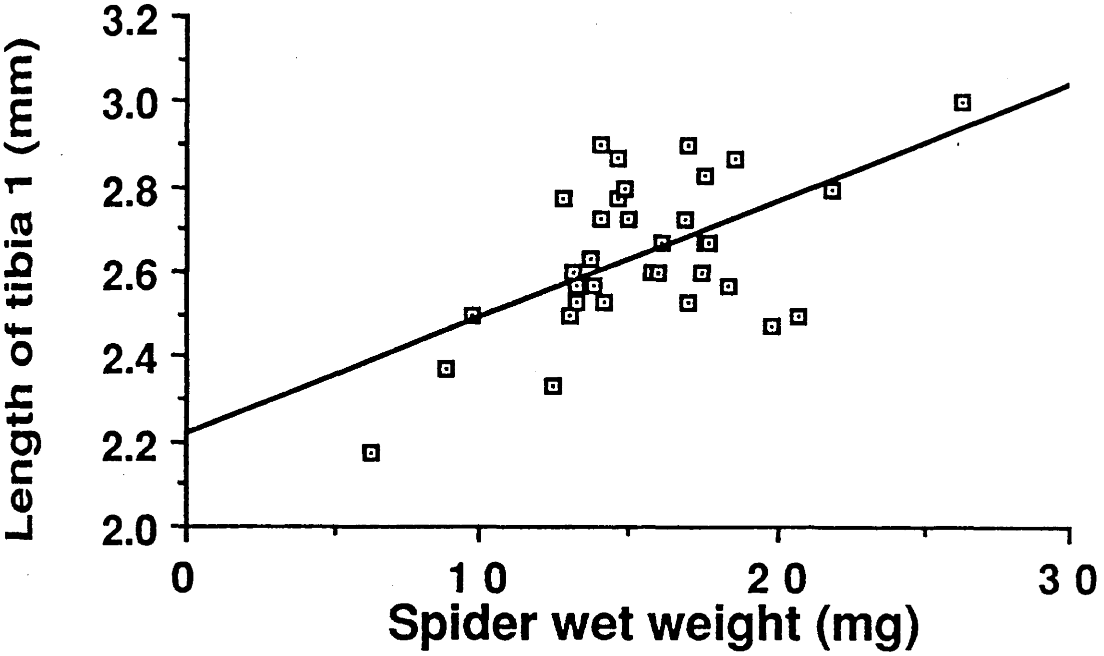
The range in the weight distribution is indicated in Table Table 11.1. It can be seen that the range is large in all samples, except in the autumn. In both 1981 and 1985 the greatest range occurs in April, with spiders covering a weight range of 24mg. The extension at the lower end of the range is interpreted as a reflection of the fact that small one year animals are just entering the population. No satisfactory explanation can be offered for the very heavy females present at this time, as it is not a time when egg sacs are produced.

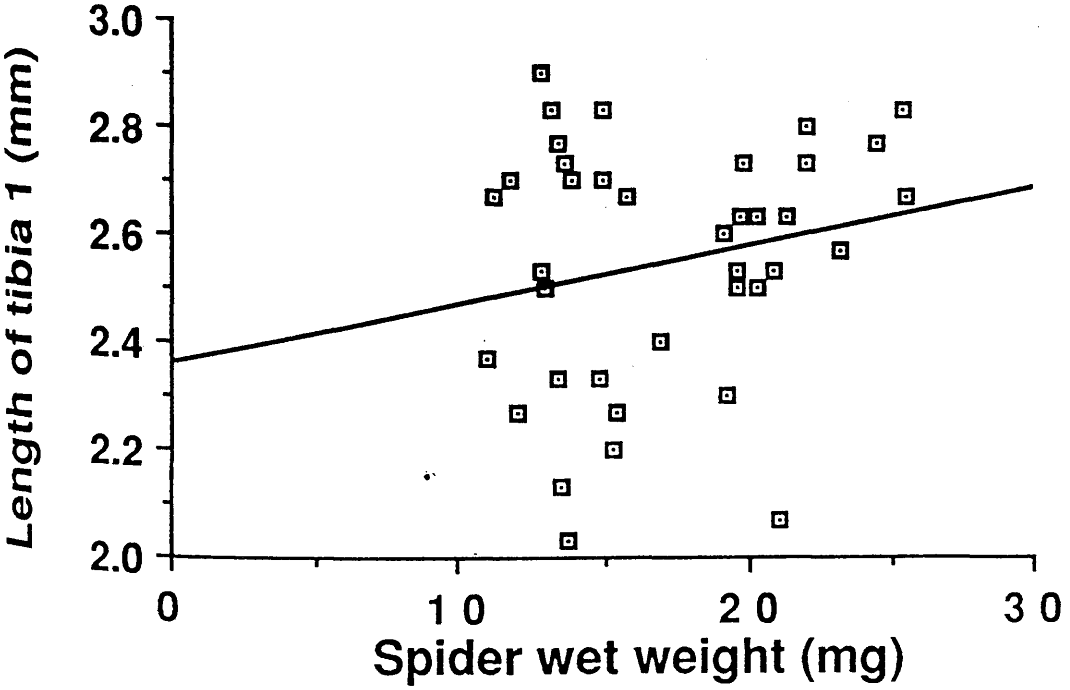
Table 11.1: Range of weights of adult females of *M. mengei* in 1980-1981 and in 1985.

Date of sampling	Range of spider weight (mg)	Total weight range (mg)
3 Sept. 1980	6 - 12	6
9 Oct. 1980	6 - 14	8
31 March 1981	8 - 24	16
15 April 1981	6 - 30	24
28 April 1981	6 - 22	16
15 May 1981	10 - 22	12
23 May 1981	6 - 22	16
2 June 1981	6 - 26	20
10 June 1981	8 - 28	20
30 June 1981	8 - 24	16
4 April 1985	8 - 32	24
6 May 1985	6 - 24	18
6 June 1985	10 - 26	16

Fig.11.6: Relationship between wet weight and the length of tibia 1 in adult females of <u>Metellina</u> <u>mengei</u> on 6/5/1985.

Fig.11.7: Relationship between wet weight and the length of tibia 1 in adult females of <u>Metellina</u> <u>mengei</u> on 6/6/1985.


Length of tibia 1 (mm)
3.2
3.0
2.8
2.6
2.4
2.2
2.0
0
1 0
2 0
3 0
Spider wet weight (mg)


Length of tibia 1 (mm)
3.0
2.8
2.6
2.4
2.2
2.0
0
1 0
2 0
3 0
Spider wet weight (mg)

Linyphia peltata

Histograms, displaying the changes in seasonal weight in the samples from Areas 6 and 7, are given in Fig. 11.8 & 11.9 respectively. The patterns of the changes in the weight distribution are similar in the two areas and the histograms are similar to those presented in the section on the age structure of L. peltata . Change in mean spider weight, for Areas 6 and 7, is given in Fig.11.10

There is no significant difference in mean spider weight between the two areas on any comparable date. In both areas there is a significant increase in weight between early August and early October 1980 - because of the rapid growth of the small spiders which emerged from egg sacs in July. No significant increase in mean weight was found between early October and late March. There is a significant weight increase between late March and late April 1981, prior to moulting to adult. Mean spider weight increased sharply towards June and this is interpreted as being due mainly to an increase in weight of adult females, prior to the production of egg sacs. Mean weight decreases in July, as the females have produced egg sacs and a new generation of small spiders is entering the population. Mean spider weight increases towards October, as these young spiders grow rapidly. There is no significant increase between early October and early November.

Fig.11.8: Weight distribution of *Linyphia peltata* throughout the year 1980-1981 in Area 6. Samples were taken by hand collecting.

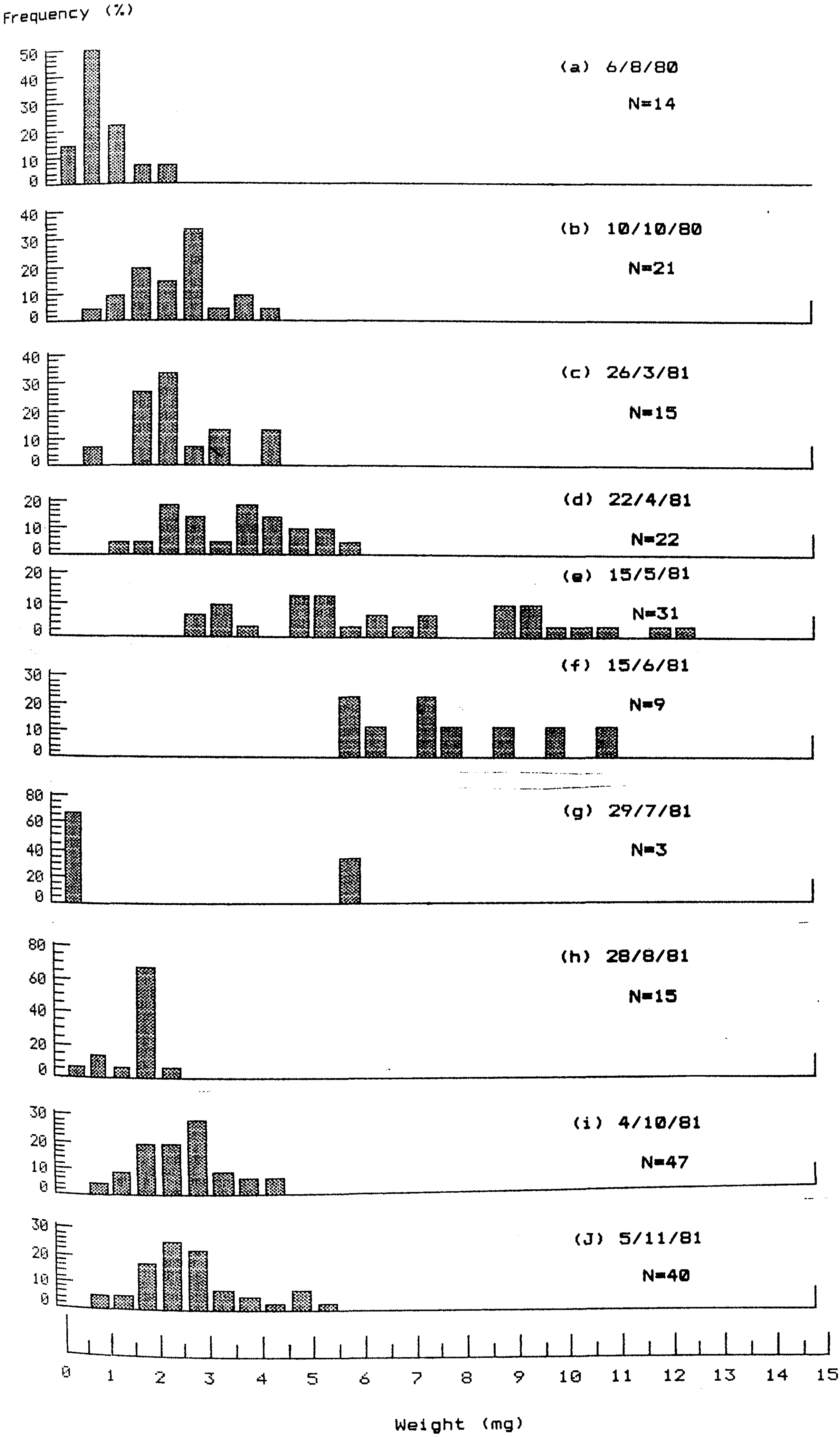
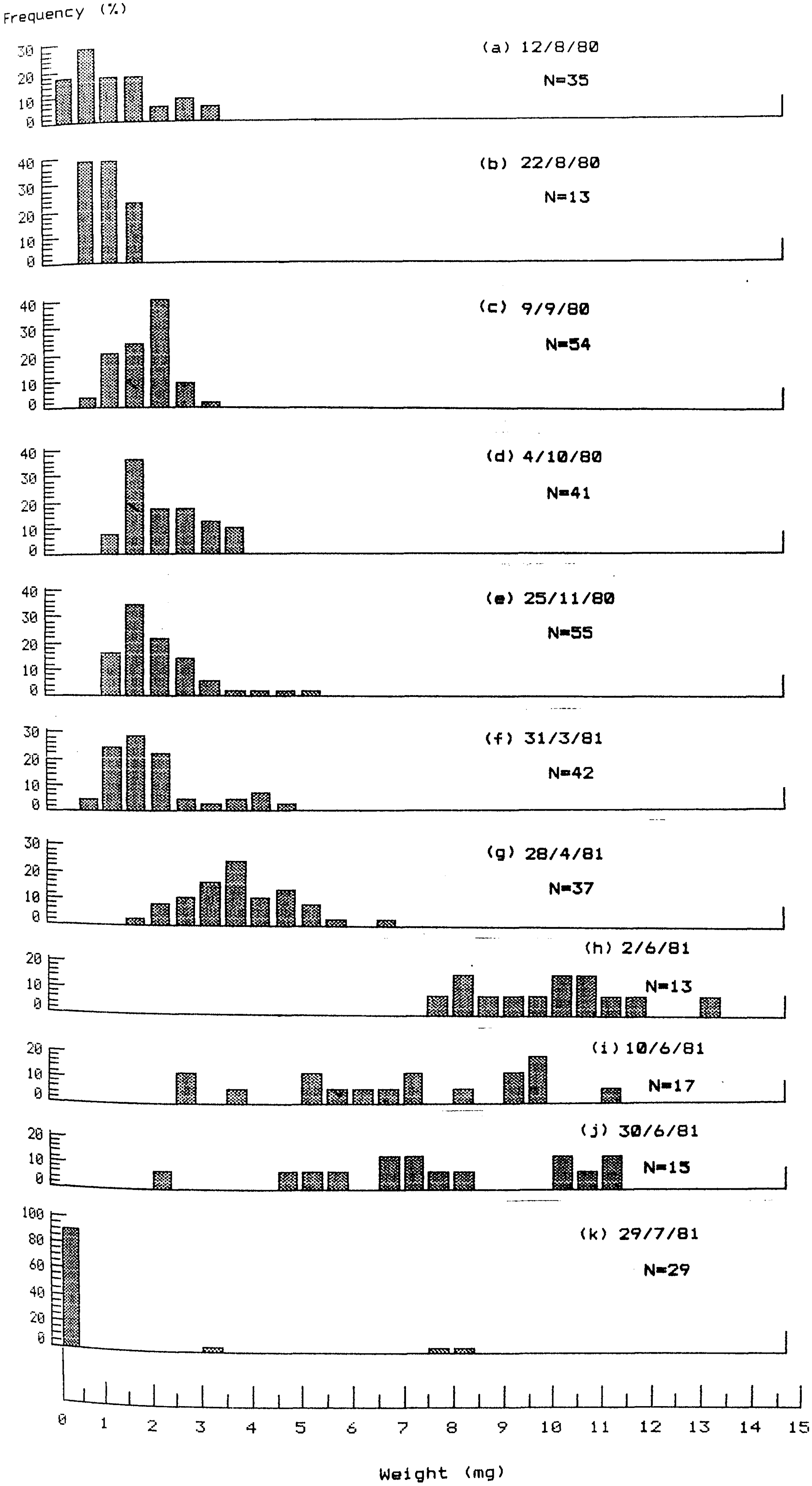
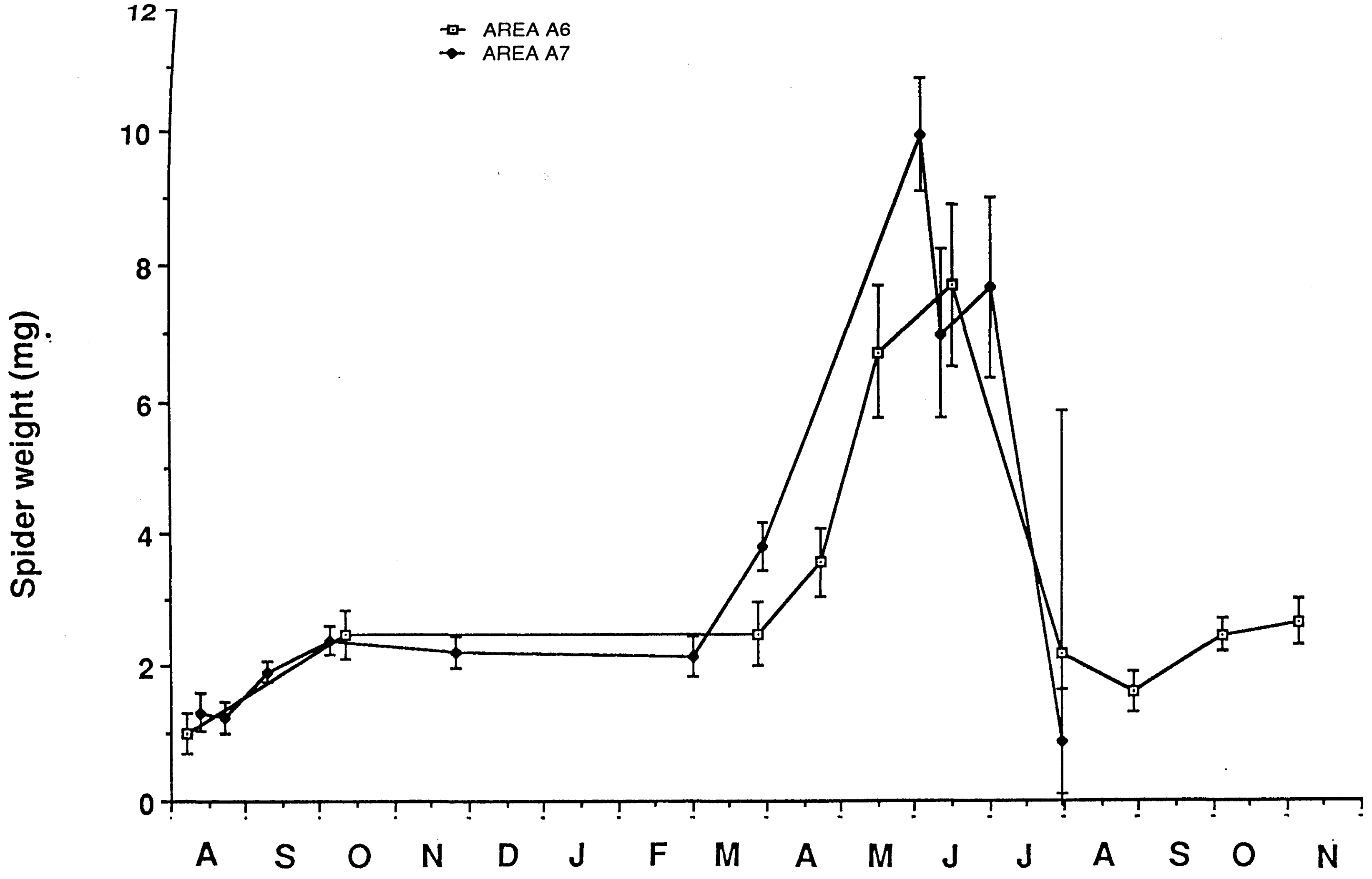

Frequency (%)
(a) 6/8/80
N=14
(b) 10/10/80
N=21
(c) 26/3/81
N=15
(d) 22/4/81
N=22
(e) 15/5/81
N=31
(f) 15/6/81
N=9
(g) 29/7/81
N=3
(h) 28/8/81
N=15
(i) 4/10/81
N=47
(J) 5/11/81
N=40
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
Weight (mg)

Fig.11.9: Weight distribution of *Linyphia peltata* throughout the year 1980-1981 in Area 7. Samples were taken by sweep netting.



Frequency (%)
(a) 12/8/80
N=35
(b) 22/8/80
N=13
(c) 9/9/80
N=54
(d) 4/10/80
N=41
(e) 25/11/80
N=55
(f) 31/3/81
N=42
(g) 28/4/81
N=37
(h) 2/6/81
N=13
(i) 10/6/81
N=17
(j) 30/6/81
N=15
(k) 29/7/81
N=29
0
10
20
30
40
60
80
100
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15
Weight (mg)

Fig.11.10: Seasonal weight changes (mean±2SE) of Linyphia peltata throughout the year 1980-1981 in Area 6 & 7.

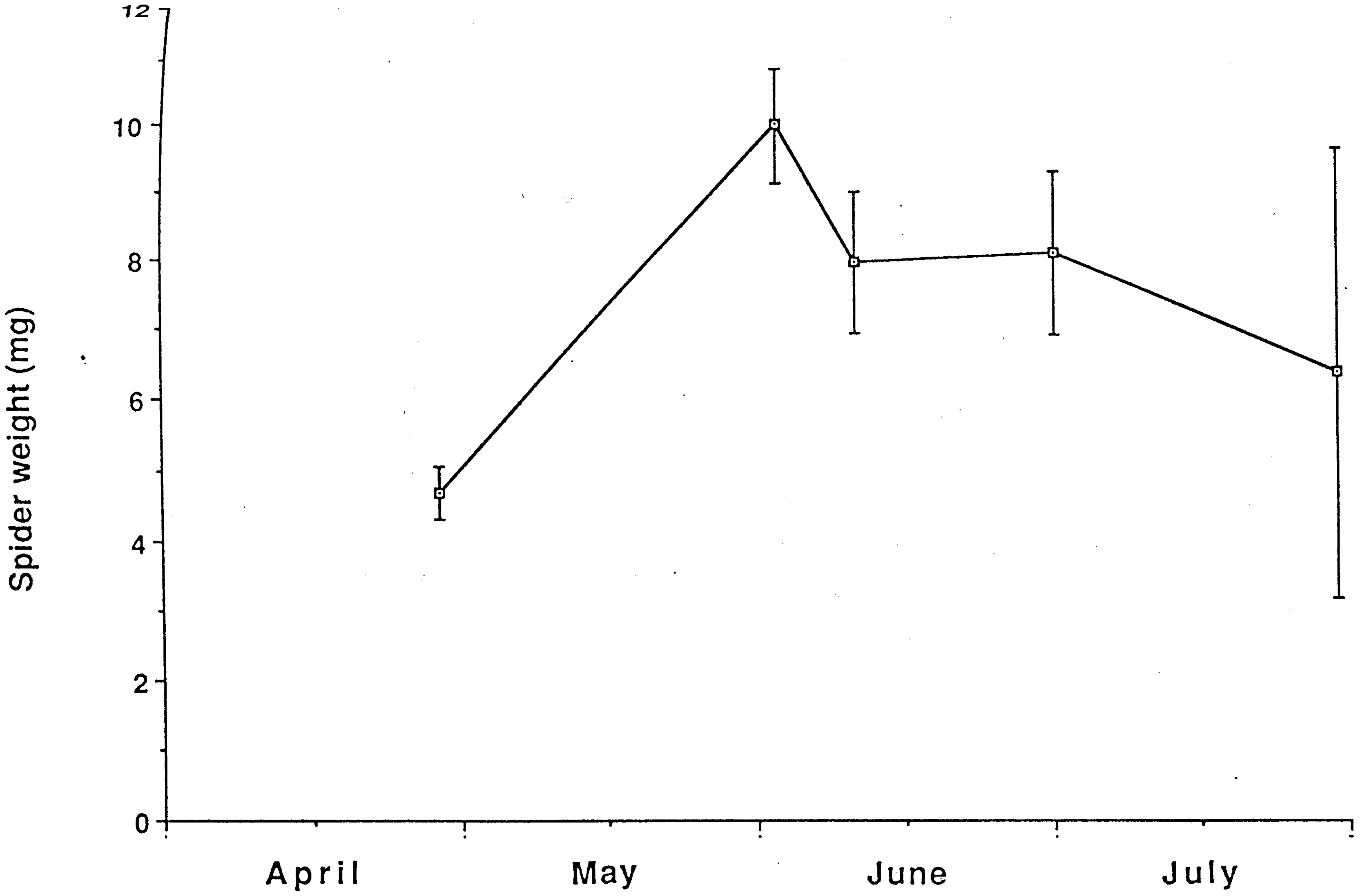

AREA A6
AREA A7
Spider weight (mg)
12
10
8
6
4
2
0
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N

Although there is no change in mean spider weight between early October and early March (Fig.11.10), the mean weight of sub-adult males increases from the autumn to the following spring (Table 11.2). Casual observation has indicated that the spiders are active in the early spring and some feeding probably occurs at that time. Weight changes in adult females in Area 7 are indicated in Fig.11.11. Adult females show a sharp increase in weight between late April and early June ($t=11.35$, d.f.=17, $p<0.05$). This is attributed to feeding prior to egg sac production. The mean weight of females declines during the remainder of June ($t=3.02$, d.f.=25, $P<0.05$). This is due to the production of egg sacs by some of the females.

Table 11.2: The mean weight of sub-adult males of *L. peltata* in autumn and spring 1980/81 in Area 6 and Area 7.

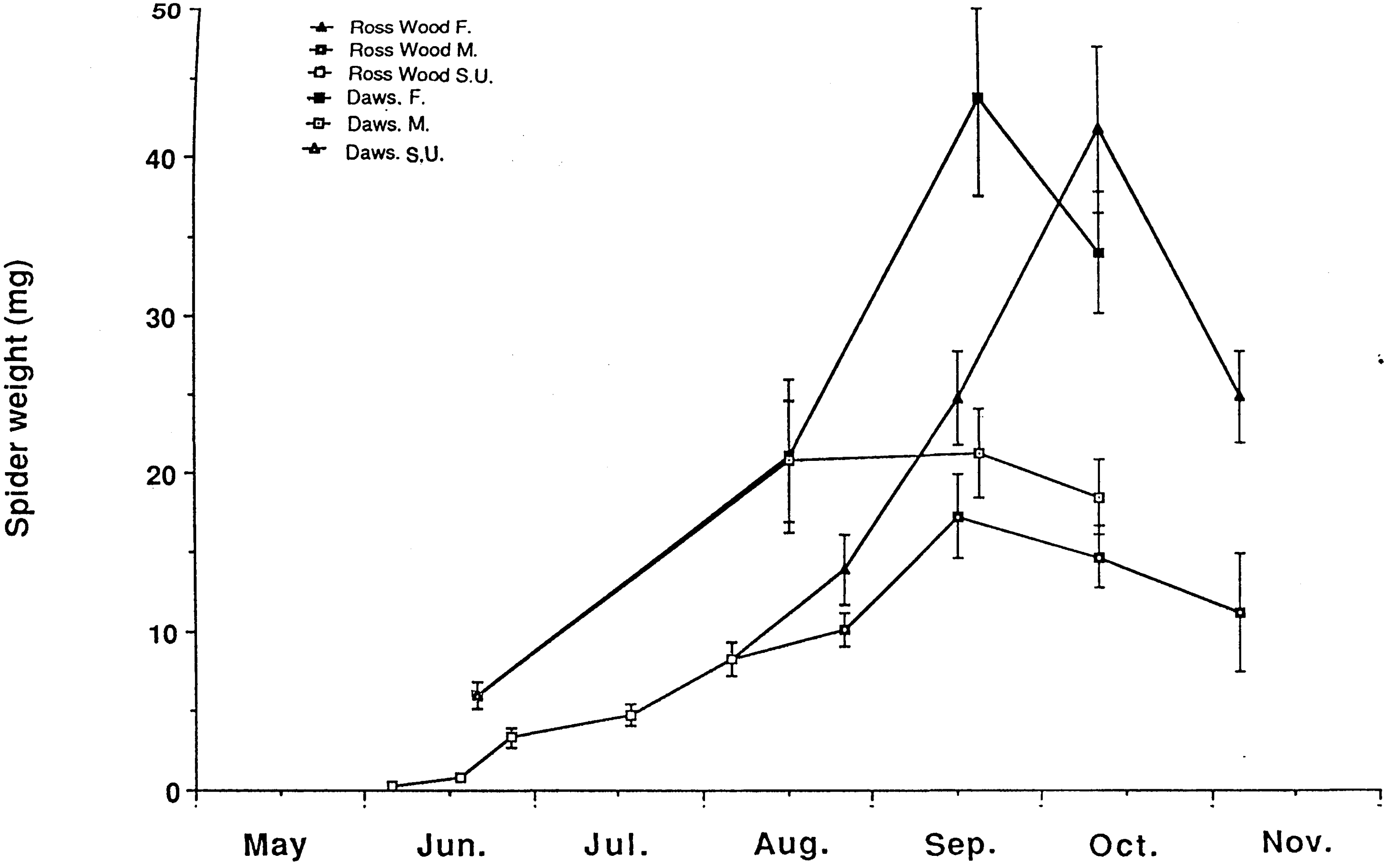
	Early October	Late March
Area 6	3.06 ± 0.73 (8)	3.98 ± 0.58 (3)
Area 7	3.04 ± 0.60 (15)	3.94 ± 0.80 (7)

Fig.11.11: Seasonal weight changes (mean±2SE) of adult females of <u>Linyphia peltata</u> in 1981 in Area 7.


Spider weight (mg)
0
2
4
6
8
10
12
April
May
June
July

Metellina segmentata

The changes in seasonal weight are shown in Fig.11.12. In the Ross Wood spiders emerge from the egg sacs in early to mid-June (see chapter on Egg Sac Production). They grow very rapidly and there is a significant increase in mean weight beween 5/6/82 and 17/6/82 ($t=5.81$, d.f.=51, $P<0.05$). There is also a sharp increase between 17/6/82 and 26/6/82 ($t=6.61$, d.f.=59, $P<0.05$). The mean weight increases towards mid-July ($t=3.07$, d.f.=77, $P<0.05$) and continues to increase between mid-July and early August ($t=5.59$, d.f.=69, $P<0.05$). At this time the spiders start to reach the sub-adult stage. The mean weight increases between early and late August for both males ($t=2.47$, d.f.=64, $P<0.05$) and females ($t=5.12$, d.f.=47, $P<0.05$). In late August, just before moulting to adult, the females are heavier than males ($t=3.10$, d.f.=53, $P<0.05$). The mean weight increases between late August and mid-September for both males ($t=5.95$, d.f.=47, $P<0.05$) and females ($t=5.27$, d.f.=45, $P<0.05$). By mid-September most of the spiders are adult. There is a sharp increase in the weight of adult females between mid-September and mid-October ($t=5.19$, d.f.=61, $P<0.05$). Adult males did not show any increase in weight during the same period. These differences are to be expected as the adult females are feeding actively, prior to producing egg sacs, whereas males feed little after they reach the adult stage. The weight of females decreases


Spider weight (mg)
50
40
30
20
10
0
May
Jun.
Jul.
Aug.
Sep.
Oct.
Nov.
Ross Wood F.
Ross Wood M.
Ross Wood S.U.
Daws. F.
Daws. M.
Daws. S.U.

markedly between 10/10/82 and 5/11/82 as the spiders produce egg sacs.

In Dawsholm Park the development pattern of the spiders is similar but the rate of development is more rapid. Thus the spiders, which emerge from the egg sacs in May, grow more rapidly than in the Ross Wood. By mid-June the spiders from Dawsholm Park are significantly heavier than those from the Ross Wood in late June (t=5.18, d.f.=69, P<0.05). By mid-August some spiders have reached the adult stage. The mean weight of adult females reached a maximum on 19/9/82 and at this time the females are much heavier than those in the Ross Wood (t=5.30, d.f.=57, P<0.05). The mean weight of adult females decreases sharply towards mid-October as some females produce egg sacs.

Linyphia triangularis

The changes in the seasonal weight are shown in Fig.11.13. The spiders emerge from the egg sacs in late May (see chapter on Egg Sac Production). They grow very rapidly and there is a significant increase in mean weight between 23/5/82 and 3/6/82 (t=4.11, d.f.=58, P<0.001) and also between 3/6/82 and 25/6/82 (t=6.37, d.f.=72, P<0.001). A very sharp increase occurs between 25/6/82 and 5/7/82. Males and females can be distinguished at this stage. The increase continued until 20/7/82 and was significant for both males (t=17.24, d.f.=55, P<0.001) and females (t=16.30, d.f.=61, P<0.001). Between 20/7/82 and 25/8/82 the adult males show no significant weight change (t=0.88, d.f.=32, P>0.05). This is to be expected as males feed little after they reach the adult stage. By contrast, there is a sharp increase in weight of adult females between 20/7/82 and 25/8/82 (t=7.38, d.f.=57, P<0.001). This increase continued from late August to early October (t=9.01, d.f.=58, P<0.001). This is to be expected as the females moult to adult in early August and feed activly thereafter before producing egg sacs in October. The mean weight of females decreases from early to late October (t=4.96, d.f.=49, P<0.001) as the spiders produce egg sac.

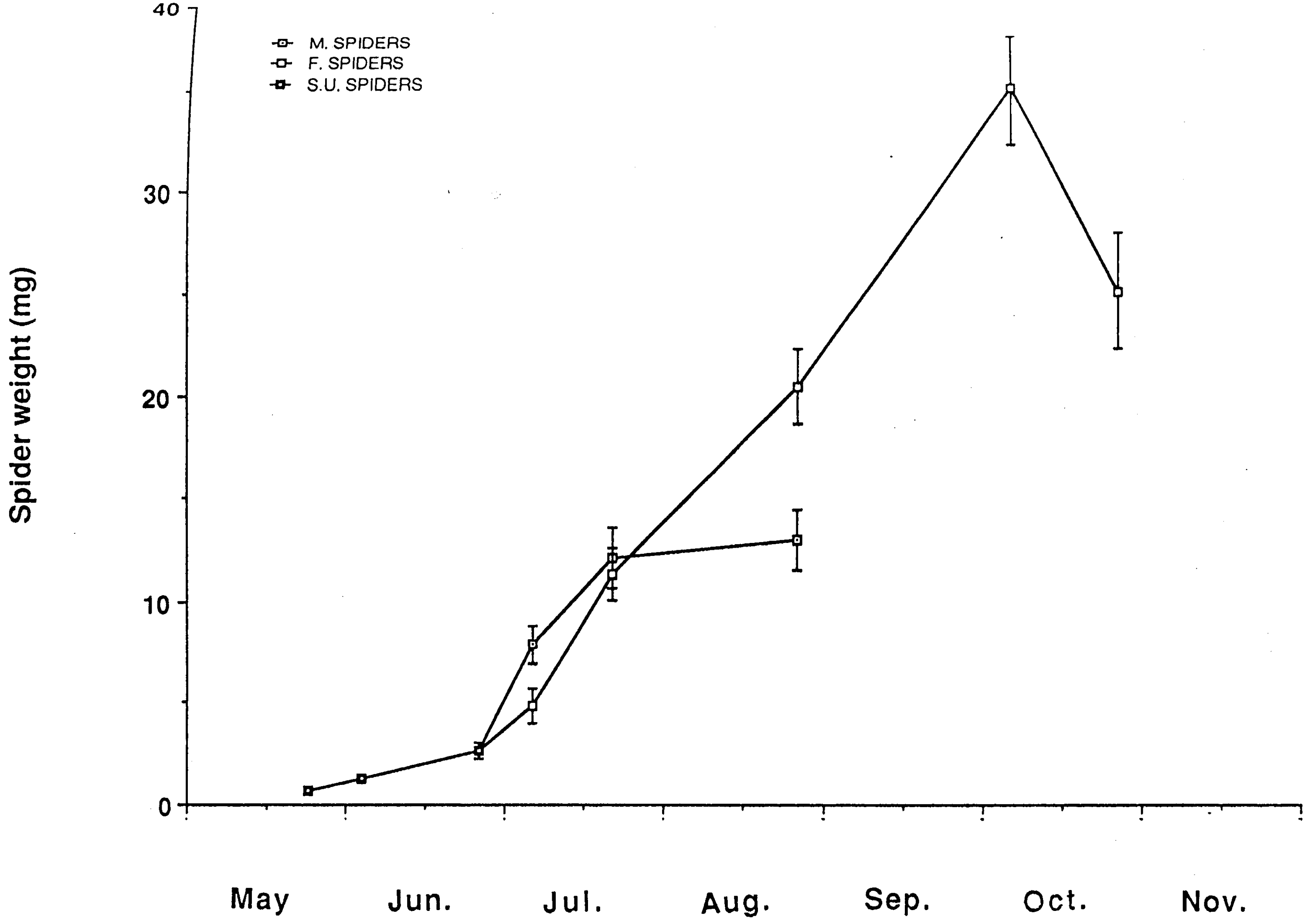
Discussion

The seasonal weight changes of M. mengei and L. peltata are similar in the two years they were studied. Edgar (1971) found that seasonal weight changes were similar in the two years of a study of the wolf spider Pardosa lugubris but Kajak (1967) found that in a two year study of Araneus quadratus the spiders were lighter throughout their life cycle in one of the years. This year was a particularly cold and wet one.

In M. mengei and L. peltata there is little change in spider weight over the winter. Edgar (1971) found a similar situation for the wolf spider Pardosa lugubris . This is to be expected as the spiders are relatively inactive, and presumably feed little, during the winter.

The small instars of M. segmentata and L. triangularis grow very rapidly over the summer months. Thus in early June M. segmentata has a mean weight of 0.26 mg and L. triangularis 1.23 mg. By the end of July the mean weight of M. segmentata is 8.18 mg and L. triangularis is 11.34 mg. This represents a percentage increase, from the weight at the beginning of June, of 3046% for M. segmentata and 822% for L. triangularis . The much higher growth rate of M. segmentata reflects the fact that the adults of M.

Fig.11.13: Seasonal weight changes (mean±2SE) of *Linyphia triangularis* in 1982 in Area 9. (F-females; M-males; S.U.-sexually undifferentiated)


40
30
20
10
0
Spider weight (mg)
M. SPIDERS
F. SPIDERS
S.U. SPIDERS
May
Jun.
Jul.
Aug.
Sep.
Oct.
Nov.

segmentata are heavier than the those of L. triangularis .

The sub-adult females of M. segmentata are heavier than the males while the reverse is true in L. triangularis . In the latter case this may reflect that the males reach the adult stage earlier than the females.

The adult females of M. segmentata have a four fold increase in body weight during the adult stage while adult females of L. triangularis triple their body weight. These large increases in body weight are associated with high feeding rates prior to the production of egg sacs. Rapid growth rates of adult females have been reported for a variety of spiders (Kajak 1967; Edgar 1971; Steigen 1975; Fritz & Morse 1985).

After moulting to adult the males exhibit little change in body weight and this has been noted for other spiders (Kajak 1967; Edgar 1971)

CHAPTER 12

Mortality Rates in *Metellina segmentata*, *Linyphia triangularis* and *L. peltata*

Introduction

The results from this section are based on information from the sections on density estimates, age structure, egg sacs and birth rates.

Methods

Mortality rates can be calculated from successive density estimates provided it can be assumed that the drop in spider numbers is due solely to mortality and that the spiders involved belong to the same cohort. The chapters of the age structure and life cycle of *M. segmentata* and *L. triangularis* indicate that these spiders have a one year life cycle with one cohort present in the population. *L. peltata* also has a one year life cycle but two cohorts, of very unequal size, are present in the population. Density estimates have been recalculated using the age structure histograms for the larger of these cohorts.

Results

Linyphia peltata

The density estimates (spiders/m^2) in Area 6 are presented in Table 12.1. Peak spider density, of 4.35/m^2, occurred in 10/10/80. As indicated in the chapter on spider density, spider numbers are lower in November, March and April than in May and this is thought to reflect reduced activity during the winter and early spring. The density in May is 1.55/m^2. This represents a mortality rate of 64% between October and May. By mid-June the density is 0.45/m^2, a mortality rate of 70% between May and June and of 90% between October and June.

Looking at the sexes separately: At the sub-adult stage males can be distinguished from females by their clubbed pedipalps. In the sample on 10/10/80 there are 77 sub-adult animals (26 males and 51 females) giving a sex ratio of 1:1.96 i.e. almost 1:2 in favour of females. An analysis of the age structure histogram from 4/10/81 shows that the sex ratio was 13 males to 25 females i.e. 1:1.92. Hence in both years the sex ratio in October was almost 1:2 in favour of females. Assuming a 1:1 sex ratio at the time of hatching, this implies high differential male mortality.

The density of adult females in mid-May, the period before

Table 12.1: Density estimates for the larger cohort of *Linyphia peltata* /m² in Area 6 from August 1980 to June 1981.

Sampling date	Spider density
6/8/1980	0.88
5/9/1980	1.62
24/9/1980	2.80
10/10/1980	4.35
28/11/1980	0.44
26/3/1981	0.70
22/4/1981	1.05
15/5/1981	1.55
15/6/1981	0.45

Table 12.2: The average number of spiderlings produced by female, *Linyphia peltata* .

Average number of eggs produced	42.2
Loss of egg sacs in the field	22.2 %
Average number of eggs survived	32.8
Mortality of eggs within the egg sac	14.1 %
Average number of spiderlings which survived to emerge in the field	28.2
Average number of female spiderlings assuming 1:1 sex ratio	14.0

egg sac production, is 1.15/m^2 and declines to 0.45/m^2 by mid-June. This represents a mortality rate of 61% during this one month period. In a sample taken on 29/7/81 there were no adults females still alive in this cohort.

Taking the value of 1.15/m^2 to be the density of reproducing females, an estimate of recruitment into the population can be made. From the section on the egg sac and birth rate it is known that 22.2% of egg sacs in the field disappear. In addition, in egg sacs which survived to hatching there was a mortality rate of 14.1% among the eggs and developing spiderlings. The average number of eggs/egg sac is 42.2. Applying these egg sac mortalities to this value, indicates that, on average, 28.2 spiderlings emerge from each egg sac (Table 12.2). Taking a female density of 1.15/m^2, this means that 28.2X1.15 i.e. 32.4 spiderlings, are produced per m^2. If we assume that the sex ratio amongst spiderlings is 1:1 then we can say that 16.1 female spiderlings are produced per m^2. Most spiderlings have emerged by late July and one can probably take peak emergence to be in mid-July.

By mid-October spider density is 4.35/m^2. Assuming a sex ratio of 1:2 in favour of females, then this represents a density of 1.45 males and 2.90 females /m^2. Thus between mid-July and mid-October male density dropped from 16.2 to 1.45 - a mortality rate of 91%. Female density dropped from 16.2 to 2.90 during the same period - a mortality rate of 82%.

Metellina segmentata

The density estimates (spiders/m^2) in Area 13 are presented in Table 12.3. Peak spider density, of 2.80m^2 occurred in 17/6/82. This drops to 0.90m^2 in 15/7/82. This represents a mortality rate of 60.0% between mid-June, the time when the egg sacs have hatched, and mid-July, when some spiders have reached the third instar. No significant change of spider density occurs between mid-July and late August and and between late August and early October. However there is a significant decrease between mid-July and early October.

Looking at the sexes separately: At the sub-adult stage males can be distinguished from females by their clubbed pedipalps. In the sample on 29/8/82 the density of female spiders is 0.40m^2 while that of male spiders is 0.35 giving a sex ratio of 1:1.14 i.e. almost 1:1. Assuming a 1:1 sex ratio at the time of hatching, this implies similar mortality of both sex.

The density of adult females on 10/10/1982, the period when they are producing egg sacs, is 0.35m^2 and declines to 0.15m^2 by 5/11/1982. This represents a mortality rate of 57.1% during this period.

Taking the value of 0.35m^2 to be the density of

Table 12.3: Density estimates of the spider Metellina segmentata per m^2 in Area 13 in 1982.

Sampling Date	Spider Density
3/6/1982	0.75
17/6/1982	2.80
25/6/1982	2.25
15/7/1982	0.90
29/8/1982	0.75
15/9/1982	0.45
10/10/1982	0.55
5/11/1981	0.15

Table 12.4: The average number of spiderlings produced by female, Metellina segmentata .

Average number of eggs produced	78.7
Loss of egg sacs in the field	14.3 %
Average number of eggs survived	67.4
Mortality of eggs within the egg sac	22.0%
Average number of spiderlings which survived to emerge in the field	52.6
Average number of female spiderlings assuming 1:1 sex ratio	26.3

reproducing females, an estimate of recruitment into the population can be made. From the section on the egg sac and birth rate it is known that 14.3% of egg sacs in the field disappear. In addition, in egg sacs which survived to hatching there was a mortality rate of 22.0% among the eggs and developing spiderlings. The average number of eggs/egg sac is 78.65. Applying these egg sac mortalities to this value, indicates that, on average, 52.6 spiderlings emerge from each egg sac (Table 12.4). Taking a female density of $0.35m^2$, this means that 52.6 X 0.35 i.e. 18.4 spiderlings, are produced per m^2. If we assume that the sex ratio amongst spiderlings is 1:1 then we can say that 9.20 female spiderlings are produced per m^2. Most spiderlings have emerged by mid-June and one can probably take peak emergence to be in mid-June. By late August spider density is $0.75/m^2$. Assuming a sex ratio of 1:1, then this represents a density of 0.38 $females/m^2$ and 0.38 males. Thus between mid-June and late August male density dropped from 9.20 to 0.38 - a mortality rate of 96.0%. A similar female mortality occurs during the same period.

Linyphia triangularis

The density estimates (spiders/m^2), in Area 10 in the Ross Wood, are presented in Table 12.5. Peak spider density, of 3.95/m^2 occurred in 22/5/82. This drops to a density of 2.10/m^2 in 28/6/82. This represents a mortality rate of 46.8% between late May, the time when the egg sacs have hatched, and late June. By mid-July the density is 1.65/m^2 - a mortality rate of 21.4% between late June and mid-July, the time when third and fourth (sub-adult) instars are present.

Looking at the sexes separately. At the sub-adult stage males can be distinguished from females by their clubbed pedipalps. In the sample on 15/7/82 the density of female spiders is 1.05/m^2 while that of male spiders is 0.60 giving a sex ratio of 1:1.75 i.e. almost 1:2 in favour of females. Assuming a 1:1 sex ratio at the time of hatching, this implies high differential male mortality.

The density of adult females on 10/10/1982, the period when they are producing egg sacs, is 0.80/m^2 and declines to 0.25/m^2 by 5/11/1982. This represents a mortality rate of 68.8% during this period.

Taking the value of 0.80/m^2 to be the density of reproducing females, an estimate of recruitment into the

Table 12.5: Density estimates of Linyphia triangularis per m^2 in Area 10 in 1982.

Sampling Date	Spider Density
22/5/1982	3.95
5/6/1982	3.90
28/6/1982	2.10
15/7/1982	1.65
5/8/1982	1.75
29/8/1982	1.20
20/9/1982	1.05
10/10/1982	0.80
5/11/1981	0.25

Table 12.6: The average number of spiderlings produced by female, Linyphia triangularis .

Average number of eggs produced	67.7
Loss of egg sacs in the field	27.3 %
Average number of eggs survived	49.2
Mortality of eggs within the egg sac	8.5 %
Average number of spiderlings which survived to emerge in the field	45.0
Average number of female spiderlings assuming 1:1 sex ratio	22.5

population can be made. From the section on the egg sac and birth rate it is known that 27.3% of egg sacs in the field disappear. In addition, in egg sacs which survived to hatching there was a mortality rate of 8.5% among the the eggs and developing spiderlings. The average number of eggs/egg sac is 67.7. Applying these egg sac mortalities to this value, indicates that, on average, 45.0 spiderlings emerge from each egg sac (Table 12.6). Taking a female density of 0.80/m^2, this means that 45.0X0.80 i.e. 36.0 spiderlings, are produced per m^2. If we assume that the sex ratio amongst spiderlings is 1:1 then we can say that 18.0 female spiderlings are produced per m^2. Most spiderlings have emerged by early June and one can probably take peak emergence to be in late May.

By mid-July spider density is 1.65/m^2. Assuming a sex ratio of 1:2 in favour of females, then this represents a density of 1.05 females per m^2 and 0.55 males. Thus between late May and mid-July male density dropped from 18.0 to 0.55 - a mortality rate of 96.9%. Female density dropped from 18.0 to 1.10 during the same period - a mortality rate of 93.9%.

Discussion

In all three species the natality is less than fecundity due to egg sac loss in the field and mortality within the egg sac.

Most studies on spiders have indicated that high mortality occurs in early instars (Kajak 1967; Breymeyer 1967; Hagstrum 1970; Edgar 1971; Steigen 1975; Humphreys 1976). Thus Edgar (1971a) found that 85% of the year group of Pardosa lugubris had died by the third/fourth instar and Humphreys (1976) estimated a mortality of 64.4% between the spiderlings and the second size class in Geolycosa godeffroyi . In the current study the calculations indicated that in M. segmentata and L. triangularis over 93% mortality had occurred by the time the spiders had reached third/fourth instar while 82.0% of the year group of L. peltata had died by the time the spiders had reached the sub-adult stage. After the high initial mortality, the mortality rates fall to low levels until the adult stage. Thus Edgar (1971a) found mortality rates of 4-6% in the larger instars of P. lugubris and 16% in sub-adults while Humphreys (1976) found that after the second size class, mortality in G. godeffroyi levelled off to a rate of 15.3% per month. Similar reduced levels of mortality were found for the larger instars of the three species in the current study. Thus survivorship curves, which could be constructed on the basis of these studies, would approximate to the concave type III curve (Deevey 1947).

In L. peltata there was a 64% mortality in the period from October to May. Duffey (1962) found a high overwintering mortality (57.6%) in field layer spiders in Wytham Wood. He attributed this to predators, particularly birds, and to the cold weather. He found overwintering mortality rates of 13-45% in spiders in the ground vegetation. Edgar (1971a) considered that little mortality occurred in P. lugubris during the winter.

The current study indicates that there is high differential male mortality in the two Linyphia species and this results in an adult sex ratio which is biased in favour of females. In M. segmentata mortality in the sexes is similar and this results in a 1:1 adult sex ratio.

Most spider studies (Kajak 1967; Hagstrum 1970; Edgar 1971a; Steigen 1975) have shown that adult spiders die off very suddenly - the males after mating and the females after producing egg sacs. This was also found in the current study. Thus survivorship curves for the adult stages, which could be constructed on the basis of these studies, would approximate the convex type I curve (Deevey 1947).

CHAPTER 13

Standing Crop of the Four Species

Introduction

The aim of this section is to determine the standing crop of the four species throughout the year. This information, combined with the results of feeding experiments, will allow energy flow through the spider populations to be estimated.

Methods and results

Values for spider biomass can be obtained by combining estimates of spider density with information on mean spider weight throughout the year. This can, in turn, be combined with energy equivalent values, obtained by combusting samples in a microbomb calorimeter, to express the standing crop of the spiders in terms of Joules/m^2.

In order to obtain wet weight/dry weight conversion values for spider tissues, samples were obtained throughout 1982. These samples were of adult and sub-adult animals, in the case of M. mengei and L. peltata , but covered all stages of the life cycle in the case of M. segmentata and L. triangularis . The spiders were weighed individually dried to a constant value in a vacuum oven at 60C and then reweighed. Wet weight/dry weight regression equations were calculated for the various categories of the four species and the results are given in Tables 13.1-13.4. In all cases there was a significant linear relationship between spider wet and dry weights. For *L. peltata* and *M. mengei* a regression equation was calculated for the combined samples (Tables 13.1 & 13.2) and these were used to convert wet weights to dry weights. In the case of *L. triangularis* and *M. segmentata* the individual equation for the various size categories (Tables 13.3 & 13.4) were used to make the appropriate wet weight/dry weight conversions.

Density estimates of *L. peltata* and *M. mengei* came from Area 6, for *L. triangularis* from Area 10 and for *M. segmentata* from Area 13 (see chapter on Density Estimates).

Seasonal weight changes for the four species were estimated in adjacent areas to the areas of density estimates. Seasonal weight changes of *L. peltata* and *M. mengei* came from Areas 6 & 7, for *L. triangularis* from Area 9 and for *M. segmentata* from Area 12 (see chapter on Seasonal Weight Changes).

Energy equivalents were obtained by combusting samples in Phillipson Microbomb Calorimeter. For *L. triangularis* and *M. segmentata* energy equivalents were obtained for

Table 13.1: Regressions of dry weight against wet weight of *M. mengei* .

Category	Number	Y = b X + a	r
Sub-adult males	19	Y = 0.34 X - 0.55	0.94
Sub-dult females	11	Y = 0.34 X - 0.66	0.98
Adult males	25	Y = 0.30 X - 0.03	0.93
Adult females	33	Y = 0.36 X - 0.91	0.93
Total	88	Y = 0.32 X - 0.43	0.94

Table 13.2: Regressions of dry weight against wet weight of the spider *Linyphia peltata* .

Category	Number	Y = b X + a	r
Sub-adult males	43	Y = 0.39 X - 0.15	0.95
Sub-adult females	76	Y = 0.37 X - 0.13	0.89
Adult males	12	Y = 0.30 X + 0.14	0.94
Adult females	18	Y = 0.32 X + 0.26	0.97
Total	149	Y = 0.36 X - 0.08	0.99

Table 13.3: Regressions of dry weight against wet weight of the spider M. segmentata .

Category	Number	Y = b X + a	r
1st - 2nd instars	23	Y = 0.31 X + 0.01	0.99
2nd - 3rd instars	41	Y = 0.26 X + 0.02	0.99
Sub-adult females	21	Y = 0.26 X - 0.34	0.98
Sub-adult males	36	Y = 0.27 X - 0.30	0.97
Adult females	28	Y = 0.26 X - 0.69	0.97
Adult males	22	Y = 0.25 X + 0.23	0.96
Gravid females	35	Y = 0.36 X - 1.91	0.99
Spent females	29	Y = 0.26 X - 0.70	0.97

Table 13.4: Regressions of dry weight against wet weight of the spider L. triangularis .

Category	Number	Y = b X + a	r
1st - 2nd instars	18	Y = 0.29 X - 0.03	0.99
2nd - 3rd instars	28	Y = 0.27 X + 0.06	0.99
Sub-adult females	14	Y = 0.26 X + 0.12	0.99
Sub-adult males	16	Y = 0.28 X + 0.05	0.99
Adult females	35	Y = 0.36 X - 1.63	0.97
Adult males	16	Y = 0.27 X + 0.21	0.88
Gravid females	25	Y = 0.36 X - 2.07	0.98

the various categories of spiders and these are given in Table 13.5. For L. peltata and M. mengei averaged values were calculated from energy equivalents which were obtained for adult and sub-adult animals (see chapter on Energy Content). The conversion values used were 25.68 Joules/mg ash free dry weight for L. peltata and 24.81 for M. mengei .

Biomass values for the four species were obtained by multiplying density estimates by values for mean spider weight. Wet weight/dry weight regression equations were used to convert wet biomass values into dry weight. The values for energy equivalents were then used to express the standing crop in terms of energy equivalents (Tables 13.6-13.9)

The seasonal changes in spider density, mean spider weight and standing crop, for the four species, are shown in in Fig.13.1-13.8.

Table 13.5: Energy equivalents (Joules/mg ash free dry weight ± standard deviations; (n) number of samples) of various categories of *L. triangularis* and *M. segmentata* .

Category	*L. triangularis*	*M. segmentata*
	Mean ± S.D. (n)	Mean ± S.D. (n)
Early instars	22.72 ± 0.42 (4)	23.96 ± 0.18 (3)
Sub-adults	23.42 ± 0.47 (4)	23.61 ± 0.35 (4)
Adult females	25.59 ± 0.98 (5)	26.09 ± 0.42 (4)
Adult males	24.85 ± 0.57 (4)	26.57 ± 0.43 (4)
Gravid females	26.70 ± 0.72 (5)	27.39 ± 0.82 (5)

Table 13.6: Standing crop of a population of *M. mengei* in Area 6 in 1980/1981.

Date of sampling	Density spiders /m^2	Mean weight (mg)	Total weight mg/m^2	Total dry weight mg/m^2	Standing crop J/m^2
Early August 80	4.63	2.15	9.95	2.80	69.47
Mid-October 80	16.60	2.03	33.70	10.49	260.26
Late March 81	3.50	2.23	7.81	2.10	52.10
Late April 81	3.00	2.60	7.80	2.10	52.10
Mid-May 81	5.50	3.16	17.38	5.20	129.01
Mid-June 81	5.05	3.35	16.92	5.05	125.29
Late July 81	3.25	3.67	11.93	3.44	85.35
Late August 81	9.06	1.87	16.94	5.06	125.54
Early November 81	9.30	1.89	17.58	5.27	130.75

Table 13.7: Standing crop of a population of <u>Linyphia peltata</u> in Area 6 in 1980/1981.

Date of sampling	Density spiders /m^2	Mean weight (mg)	Total weight mg/m^2	Total dry weight mg/m^2	Standing crop J/m^2
Early August 80	0.88	1.31	1.15	0.33	8.47
Early Sept. 80	1.88	1.91	3.59	1.21	31.07
Mid-October 80	4.50	2.37	10.67	3.76	96.56
Late November 80	0.44	2.20	0.97	0.27	6.93
Late March 81	0.75	2.47	1.85	0.59	15.15
Late April 81	1.10	3.55	3.91	1.33	34.15
Mid-May 81	1.55	6.73	10.43	3.67	94.25
Mid-June 81	0.45	7.52	3.38	1.14	29.28
Late July 81	0.15	2.15	0.32	0.04	1.03
Late August 81	0.94	1.58	1.49	0.46	11.81
Early October 81	2.94	2.44	7.17	2.50	64.20
Early November 81	4.00	2.64	10.56	3.72	95.53

Table 13.8: Standing crop of a population of *M. segmentata* in Area 13 in 1982.

Date of sampling	Density spiders /m^2	Mean wet weight (mg)	Mean dry weight mg/m^2	Total dry weight mg/m^2	Standing crop J/m^2
Early June 82	0.75	0.26	0.09	0.07	1.68
Mid-June 82	2.80	0.74	0.24	0.67	16.05
Late June 82	2.25	3.33	1.04	2.34	56.07
Mid-July 82	0.90	4.75	1.26	1.13	27.07
Late August 82	0.73	12.22	2.90	2.12	50.05
Mid-September 82	0.45	21.42	5.22	2.35	61.76
Mid-October 82	0.55	31.93	9.76	5.37	146.44
Early November 82	0.15	24.84	5.76	0.86	22.44

Table 13.9: Standing crop of a population of *L. triangularis* in Area 10 in 1982.

Date of sampling	Density spiders /m^2	Mean wet weight (mg)	Mean dry weight mg/m^2	Total dry weight mg/m^2	Standing crop J/m^2
Late May 82	3.95	0.72	0.18	0.71	16.13
Early June 82	3.90	1.23	0.33	1.29	29.13
Late June 82	2.10	2.62	0.76	1.60	36.35
Mid-July 82	1.65	11.62	3.20	5.28	123.66
Late August 82	1.20	17.95	6.14	7.37	187.50
Early October 82	0.80	35.03	10.98	8.78	234.43

Fig.13.1: Seasonal changes in standing crop (Joules/sq.m.) and density estimates (spiders/sq.m.) throughout the year 1980-1981 for *Metellina mengei* in Area 6.

Fig.13.2: Seasonal changes in standing crop (Joules/sq.m.) and mean spider weight throughout the year 1980-1981 for *Metellina mengei* in Area 6.

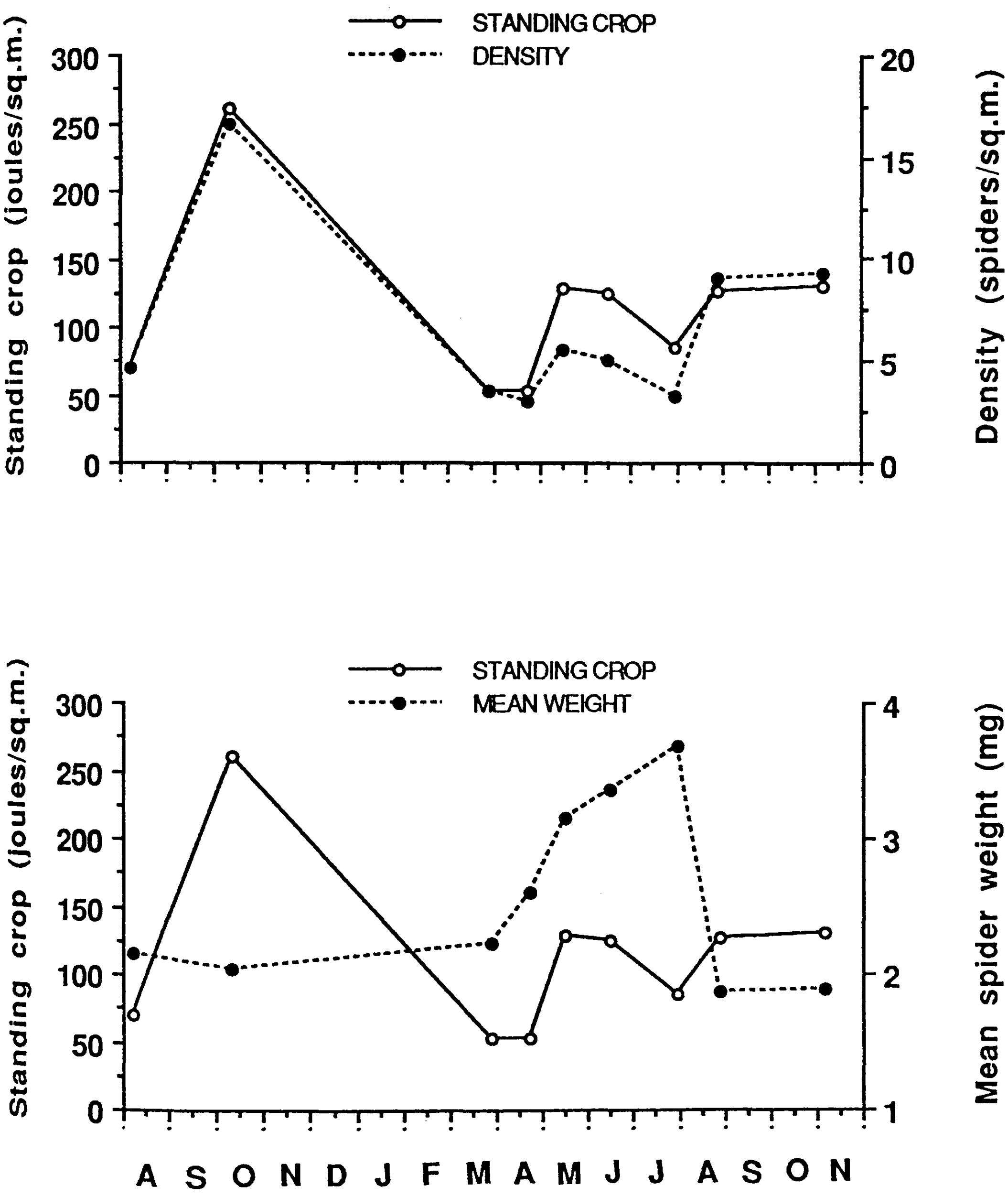

STANDING CROP
DENSITY
Standing crop (joules/sq.m.)
Density (spiders/sq.m.)
300
250
200
150
100
50
0
20
15
10
5
0
STANDING CROP
MEAN WEIGHT
Standing crop (joules/sq.m.)
Mean spider weight (mg)
300
250
200
150
100
50
0
4
3
2
1
A S O N D J F M A M J J A S O N

Fig.13.3: Seasonal changes in standing crop (Joules/sq.m.) and density estimates (spiders/sq.m.) for *Linyphia peltata* throughout the year 1980-1981 in Area 6.

Fig.13.4: Seasonal changes in standing crop (Joules/sq.m.) and mean spider weight throughout the year 1980-1981 for *Linyphia peltata* in Area 6.

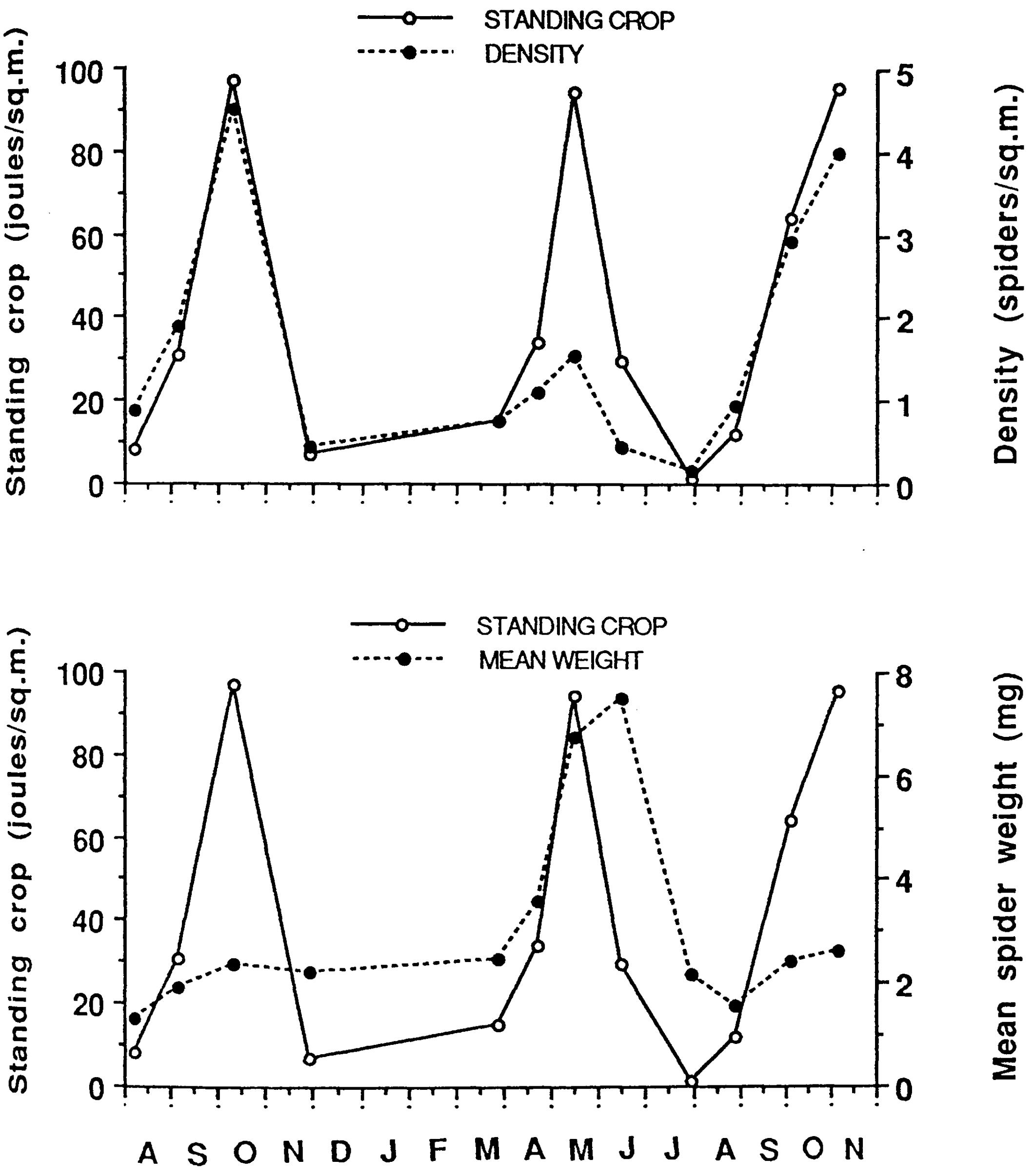
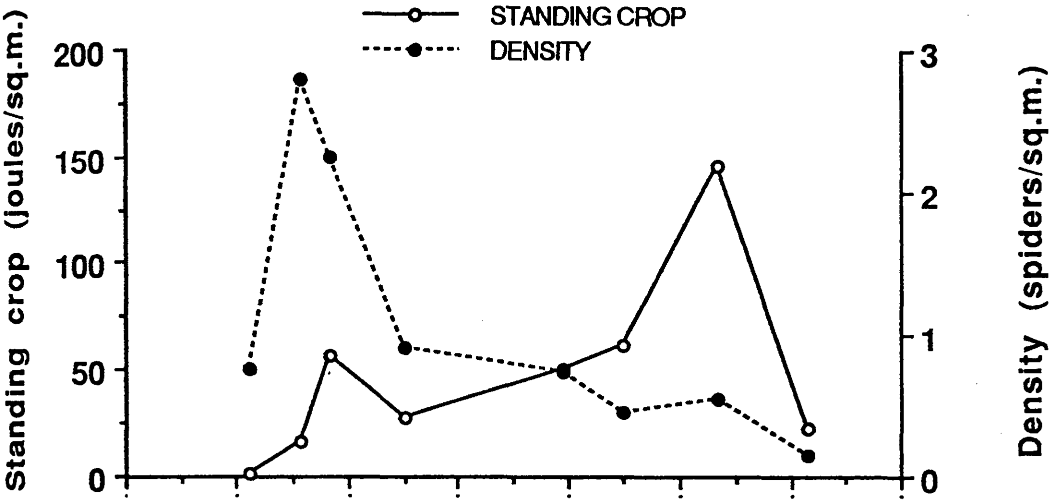

STANDING CROP
DENSITY
Standing crop (joules/sq.m.)
Density (spiders/sq.m.)
0
20
40
60
80
100
0
1
2
3
4
5
STANDING CROP
MEAN WEIGHT
Standing crop (joules/sq.m.)
Mean spider weight (mg)
0
20
40
60
80
100
0
2
4
6
8
A S O N D J F M A M J J A S O N

Fig.13.5: Seasonal changes in standing crop (Joules/sq.m.) and density estimates (spiders/sq.m.) throughout the year 1982 in *Metellina segmentata*.

Fig.13.6: Seasonal changes in standing crop (Joules/sq.m.) and mean spider weight throughout the year 1982 in *Metellina segmentata*.


STANDING CROP
DENSITY
Standing crop (joules/sq.m.)
200
150
100
50
0
Density (spiders/sq.m.)
3
2
1
0

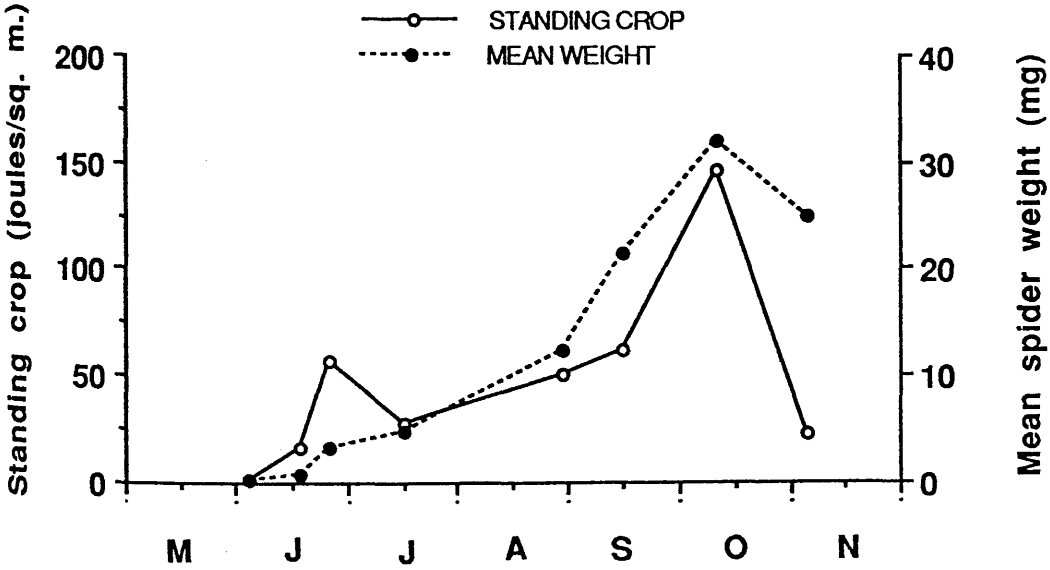
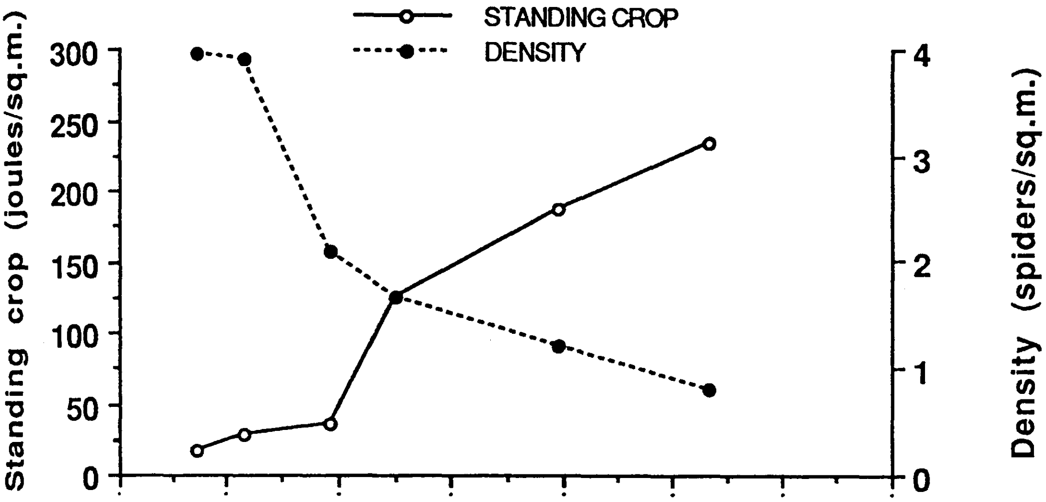
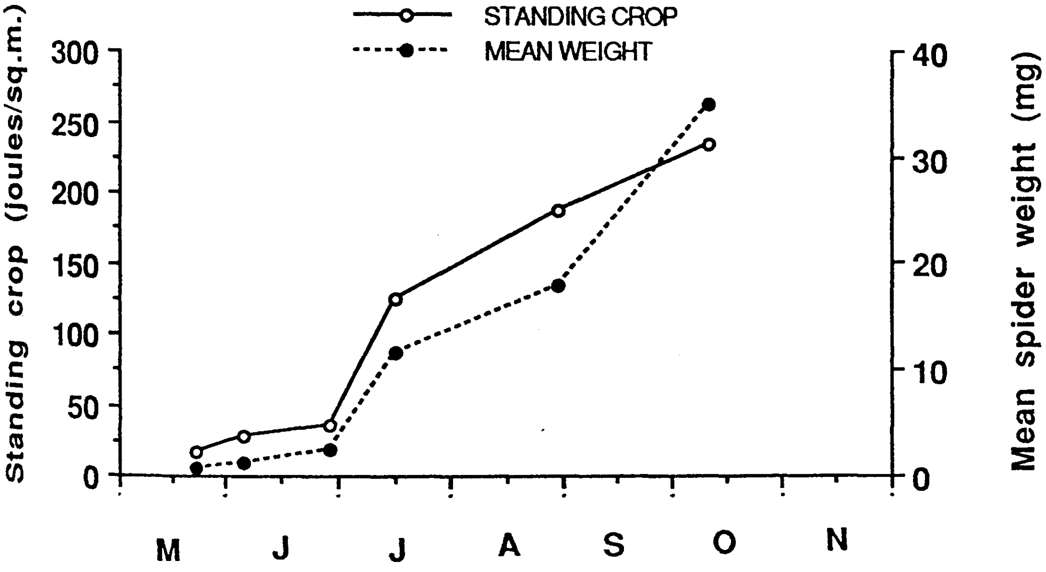

STANDING CROP
MEAN WEIGHT
Standing crop (joules/sq. m.)
200
150
100
50
0
Mean spider weight (mg)
40
30
20
10
0
M
J
J
A
S
O
N

Fig.13.7: Seasonal changes in standing crop (Joules/sq.m.) and density estimates (spiders/sq.m.) throughout the year 1982 in *Linyphia triangularis* .

Fig.13.8: Seasonal changes in standing crop (Joules/sq.m.) and mean spider weight throughout the year 1982 in *Linyphia triangularis* .


STANDING CROP
DENSITY
Standing crop (joules/sq.m.)
300
250
200
150
100
50
0
Density (spiders/sq.m.)
4
3
2
1
0


STANDING CROP
MEAN WEIGHT
Standing crop (joules/sq.m.)
300
250
200
150
100
50
0
Mean spider weight (mg)
40
30
20
10
0
M
J
J
A
S
O
N

Discussion

Changes in standing crop will reflect changes in both spider density and mean spider weight. Because of low body weight of the small spiders and their high mortality rates one would expect, in a spider with a highly synchronised one year life cycle, that the standing crop would be at its lowest at the period after the adult females have died off and when the population is represented only by small spiders. Conversely, standing crop would be at its highest when the population consisted of adult animals, and the females were about to produce egg sacs. This is seen to be the case for M. segmentata and L. triangularis where there is a highly synchronised one year life cycle. Thus peak standing crop occurs in October when adult animals make up the population and the majority of these are females, and is at its lowest in May, when the population comprises of small spiders. Hence in these two species standing crop tends to mirror changes in mean spider weight (Fig.13.6 & 13.8).

In M. mengei there is a wide spread of size categories present at most times and consequentley mean spider weight varies relatively little throughout the year and standing crop tends to mirror changes in spider density (Fig.13.1). In L. peltata changes in the standing crop in autumn tend to reflect changes in spider density (Fig.13.3) but in the spring and early summer they tend to reflect changes in mean spider weight, as the spiders are growing very rapidly at this time (Fig.13.4)

There are relatively few studies which give values for spider biomass. Some values, giving biomass in terms of dry weight, are given in Table 13.10 and values, in energetic equivalents, are given in Table 13.11. The biomass values in the current study were lower than the published values for either web spinning or wolf spiders.

Table 13.10: Biomass values of spiders in mg dry weight/m^2.

Spider	Auther	Mean annual biomass
Araneus quadratus	Kajak (1967)	158.3
Araneus cornutus	Kajak (1967)	13.0
Singa hamata	Kajak (1967)	6.5
Metellina mengei	Current study	4.5
Metellina segmentata	Current study	1.9
Linyphia triangularis	Current study	4.2
Linyphia peltata	Current study	1.4

Table 13.11: Biomass values of spiders in Joules/m^2.

Spider	Auther	Mean annual biomass
Metellina segmentata	Geyer (1971)	849.2
Pardosa lugubris	Edgar (1971)	734.0
Geolycosa godeffroyi	Humphreys (1978)	214.0
Metellina mengei	Current study	107.8
Metellina segmentata	Current study	47.8
Linyphia triangularis	Current study	104.5
Linyphia peltata	Current study	35.2

CHAPTER 14

The Sex Ratio of the Four Species

Introduction

The sex ratio in any species presumably evolves to maximise the number of offspring produced. In many species the sex ratio at birth is approximately 1:1 and the ratio is also near unity at maturity. However, in some species the ratio may deviate markedly from unity and there may be marked differential mortality in the sexes between birth and the attainment of sexual maturity.

With regard to spiders, a number of studies have suggested an adult sex ratio close to unity (Deevey 1949; Hackman 1957; Turnbull 1965; Edgar 1968; Humphreys 1974) but other studies have suggested sex ratios which deviate considerably from 1:1 (Brown et al 1985; Vollrath 1986). In some animals it is fairly easy to determine the sex at birth but in others the external sexual features only become evident as the adult stage is approached. Male spiders can normally be distinguished from females by the fact that the terminal segments of the pedipalps are swollen and males usually have "clubbed" pedipalps in the sub-adult stage and possibly also in earlier instars. Claims have been made that spiders can be distinguished at, or before, birth (Montgomery 1908) but this has been disputed (Bonnet 1938; Deevey 1949).

The present study presents information on the sex ratio of the four spider species. In all the species the sub-adult males have swollen pedipalps and in the Linyphia species the third instar males also have slightly swollen pedipalps. The sex ratio was examined to see if it varied with different sampling methods, varied from year to year, varied in different vegetation types or in different localities or varied at different stages in the spider life cycle.

Methods

The information on the sex ratios was obtained during sampling programms to elucidate various aspects of the biology of the spiders.

Results

The sex ratio of L. peltata , in a number of samples, is shown in Table 14.1. These samples are all from the Ross Wood and are either of sub-adult or adult animals or a mixture of both. Some samples were taken by hand collecting. It can be seen that the sex ratio is quite variable - ranging from 0.74 to 3.07. These two samples were taken within two weeks of each other in April 1980. This suggests that some caution may be required in

Table 14.1: Sex ratios in samples of L. peltata (* Sex ratio significantly different from 1:1, P<0.05).

Date	Females	Males	Sex ratio
28/3/80	26	19	1.37
31/3/80	11	7	1.57
11/4/80	46	15	3.07 *
11/4/80	7	5	1.40
11/4/80	23	9	2.57
11/4/80	52	23	2.26 *
14/4/80	21	19	1.11
18/4/80	27	33	0.82
24/4/80	17	23	0.74
30/4/80	78	39	2.00 *
10/10/80	69	31	2.23 *
10/10/80	51	27	1.89
10/10/80	43	24	1.79
28/11/80	104	45	2.31 *
28/11/80	28	17	1.65
4/10/81	25	13	1.92
5/11/81	24	13	1.85
14/11/82	51	22	2.32 *
14/11/82	28	16	1.75
15/11/82	23	18	1.28
15/11/82	92	49	1.88 *

attempting to draw conclusions from the samples. However, in almost all the samples females predominated and in seven out of total of 21 samples the sex ratio differed significantly from 1:1.

These samples were examined in more detail to see whether the sex ratio was affected by (a) sampling method (b) vegetation type (c) the year the samples were taken. The sex ratios in samples taken by sweep netting and hand collecting are given in Tables 14.2 & 14. 3. The sex ratios in samples from three different vegetation types are given in Tables 14.4 & 14.5. The sex ratios in samples from blaeberry in 1980 and 1981 is given in Table 14.6. The sex ratios do not differ between sampling methods, vegetation types or between the the two years.

The sex ratio in samples of <u>L. triangularis</u> is given in Table 14.7. The ratio ranges from 0.81 to 15.5. In all but one of the 28 samples females predominate but the ratio is only significantly different from 1:1 on four occasions and those are in the autumn when adult males are dying off after mating.

The sex ratio in samples from conifer and blaeberry is given in Table 14.8. There is no signifaicant difference in the sex ratio in the two vegetation types. The sex ratio in samples from the Ross Wood and Dawsholm Park on 8 August

Table 14.2: Sex ratios in samples of L. peltata from heather, collected by hand collecting and sweep netting, in November 1980.

Date	Females	Males	Sex ratio	Sampling method
28/11/80	104	45	2.31	Sweep
28/11/80	28	17	1.65	Hand

Table 14.3: Sex ratios in samples of L. peltata from blaeberry, collected by hand collecting and sweep netting, in April 1980.

Date	Females	Males	Sex ratio	Sampling method
11/4/80	7	5	1.40	Sweep
11/4/80	52	23	2.26	Hand

Table 14.4: Sex ratios in samples of L. peltata from three vegetation types in April 1980.

Date	Females	Males	Sex ratio	Vegetation
11/4/80	7	5	1.40	Blaeberry
11/4/80	23	9	2.57	Conifer
11/4/80	46	15	3.07	Heather

Table 14.5: Sex ratios in samples of _L. peltata_ from three vegetation types in November 1982.

Date	Females	Males	Sex ratio	Vegetation
14/11/82	28	16	1.72	Blaeberry
14/11/82	51	22	2.32	Conifer
15/11/82	92	49	1.88	Heather

Table 14.6: Sex ratios in samples of _L. peltata_ from blaeberry in 1980 and 1981.

Date	Females	Males	Sex ratio
10/10/80	51	27	1.89
4/10/81	25	13	1.92
5/11/81	24	13	1.85

Table 14.7: Sex ratios in samples of *L. triangularis*
(* Sex ratio significantly different from 1:1, P<0.05).

Date	Females	Males	Sex ratio
24/6/80	8	7	1.14
9/7/80	20	13	1.54
16/7/80	24	14	1.71
26/7/80	20	16	1.25
8/8/80	20	18	1.11
8/8/80	22	5	4.40 *
2/9/80	31	2	15.50 *
9/9/80	23	9	2.56
12/10/80	18	0	
8/8/80	22	5	4.40 *
2/9/80	31	2	15.50 *
15/10/80	12	0	
28/6/81	20	16	1.25
28/6/81	35	29	1.21
7/7/81	15	8	1.88
22/7/81	15	9	1.67
22/7/81	48	28	1.71
30/7/81	16	11	1.45
29/8/81	20	10	2.00
15/7/82	21	12	1.75
16/7/82	17	15	1.13
16/7/82	13	11	1.18
15/7/82	17	21	0.81
19/7/82	32	21	1.52
19/7/82	52	37	1.41
5/8/82	19	16	1.19
29/8/82	16	8	2.00
20/9/82	21	0	
10/10/82	16	0	
5/11/82	5	0	

Table 14.8: Sex ratios in samples of L. triangularis in two vegetation types in June 1981.

Date	Females	Males	Sex ratio	Vegetation
28/6/81	20	16	1.25	Conifer
28/6/81	35	29	1.21	Blaeberry

Table 14.9: Sex ratios in samples of L. triangularis in Ross Wood and at Dawsholm Park in August 1980.

Date	Females	Males	Sex ratio	Locality
8/8/80	20	18	1.11	Ross Wood
8/8/80	22	5	4.40	Dawsholm

Table 14.10: Sex ratios in samples of L. triangularis in blaeberry in July in 1980, 1981 and 1982.

Date	Females	Males	Sex ratio
16/7/80	24	14	1.71
22/7/81	15	9	1.61
22/7/81	48	28	1.71
19/7/82	32	21	1.52
19/7/82	52	37	1.41

1980 is given in Table 14.9. There are significantly ($\chi^2=5.75$, d.f.=1 , $P<0.05$) more females in the sample from Dawsholm Park. The sampling site at Dawsholm Park is much more open than that in the Ross Wood and it is thought that the difference in the sex ratio reflects the fact that development is more rapid at Dawsholm Park and that males are already dying off by early August. The sex ratio in samples from 1980, 1981 and 1982 is given in Table 14.10. The ratio is similar in the three years.

The sex ratio in samples of *M. mengei* is given in Table 14.11. These samples were collected from various habitats by either hand collecting or sweep netting. The sex ratio ranges from 0.88 to 4.50. In all but one of the 18 samples females predominate. However, the difference is significantly different from 1:1 in only six samples.

The sex ratio in samples collected by hand collecting and by sweep netting is compared in Septembrer 1980 (14.12) and in October 1980 (Table 14.13). The sex ratio do not differ significantly between the two methods.

The sex ratio in samples of *M. segmentata* is given in Table 14.14. These samples collected from various habitats by either hand collecting or sweep netting. The sex ratio ranges from 0.53 to 3.63. In all but one of the 13 samples females predominate. However, the difference is

Table 14.11: Sex ratios in samples of *M. mengei* (* Sex ratio significantly different from 1:1, $P<0.05$).

Date	Females	Males	Sex ratio
31/3/80	23	13	1.77
15/5/80	20	18	1.11
6/8/80	11	7	1.54
5/9/80	20	19	1.05
23/9/80	12	5	2.40
24/9/80	18	23	0.88
30/9/80	43	19	2.26 *
10/10/80	13	13	1.00
14/10/80	83	50	1.66 *
10/6/81	40	20	2.00
19/11/84	45	10	4.50 *
19/11/84	10	0	
3/4/85	90	46	1.96 *
3/4/85	48	20	2.40 *
6/5/85	103	53	1.94 *
6/5/85	38	31	1.23
6/6/85	79	52	1.52
6/6/85	10	10	1.00

Table 14.12: Sex ratios in samples of M. mengei collected from blaeberry, by hand collecting and sweep netting, in September 1980.

Date	Females	Males	Sex ratio	Sampling method
23/9/80	12	5	2.40	Sweep
24/9/80	18	23	0.88	Hand

Table 14.13: Sex ratios in samples of M. mengei collected from blaeberry, by hand collecting and sweep netting, in October 1980.

Date	Females	Males	Sex ratio	Sampling method
14/10/80	83	50	1.66	Sweep
14/10/80	13	13	1.00	Hand

Table 14.14: Sex ratios in samples of *M. segmentata* (* Sex ratio significantly different from 1:1, $P<0.05$).

Date	Females	Males	Sex ratio
8/8/80	19	13	1.46
10/8/80	19	13	1.46
9/9/80	25	14	1.79
16/9/80	42	25	1.68
15/10/80	16	7	2.29
25/8/82	19	36	0.53
29/8/82	8	7	1.14
15/9/82	5	4	1.25
15/9/82	28	13	2.15
10/10/82	7	4	1.75
10/10/82	35	11	3.18 *
5/11/82	3	0	
5/11/82	29	8	3.63 *

significantly different from 1:1 in only two samples in the late autumn, when adult males are dying off after mating.

Discussion

As indicated in the introduction, some studies on spiders have suggested that the sex ratio is close to unity while others have indicated a ratio which deviates considerably from 1:1. There are a number of factors which make the determination of the true sex ratio difficult. Perhaps the most important of these is where the behaviour of the sexes differ and consequently the sampling method used is biased with respect to one sex. For example, if the sexes differed in their positions in the vegetation then this might bias the sex ratio in the samples. It was for this reason that samples were taken in different vegetation types using various sampling methods. The results indicated that there were no significant differences in the sex ratios, in different vegetation types, or in using different sampling methods. There is considerable variability in the sex ratios for the four species - although females normally predominate. Thus this study, in part, agrees with studies which suggest a sex ratio close to unity and agrees, in part, with others which found ratios which deviated considerably from unity. A more detailed study would be required to resolve this situation.

CHAPTER 15

The Distribution and Abundance of the Four Spider Species

The distribution and abundance of animals can be influenced by physical and biological factors. Some insight into the factors influencing distribution may be obtained by making general observations on where the animal is abundant and where it is absent. It is to be expected that spider density would be highest in the most suitable habitat. Further insight into the distribution of spiders may be obtained by studying, in the laboratory, the responses to environmental variables like light and temperature. This may give an indication of the preferred environment of the spider.

Bristowe (1939) argued that the geographical distribution of spider families was determined by climatic factors. With regard to more local distribution, vegetation structure is thought to be a key factor because it can greatly influence suitability of a habitat for web building spiders (Bristowe 1939 ; Lowrie 1964; Enders 1973, 1977; Colebourn 1974; Stratton et al 1974; Reichert & Tracy 1975)

The aim of this section is to examine the distribution and abundance of the four species of web building spiders. This involves looking at the abundance of the spiders in different locations in west central Scotland and also in different areas of the Ross Wood. The microdistribution of the spiders was also studied in certain vegetation types in the Ross Wood and this was supplemented by laboratory experiments on the thermal death points of spiders and their reaction to light.

Abundance of spiders in six localities in west central Scotland in 1981

Spiders were collected from six localities in west central Scotland in 1981 and 1982. These areas comprised of one woodland site in the Ross Wood (NS 374956) and five open sites. These were; (a) Dawsholm Park (NS 558697); (b) On the Stockiemuir (NS 511809); (c) near Aberfoyle (NN 518037); (d) near Arrochar (NN 295050); (e) near Arden on Loch Lomond side (NS 379821). These sites are indicated in Fig.15.1.

In 1981 each area was sampled in the spring (mid-March to mid-May), summer (mid-May to mid-September) and autumn (mid-September to late November). Each area was sampled, by hand collecting, for a period of one hour. The results from the five open areas were combined and compared with those from the Ross Wood. The results are given in Tables 15.1, 15.2 & 15.3.

Table 15.1: The number of spiders of the four species which were collected in Ross Wood and five open areas in spring 1981.

Location	*Metellina segmentata*	*Metellina mengei*	*Linyphia triangularis*	*Linyphia peltata*	Total
Ross Wood	0	113	0	86	199
Five Open Areas	64	60	133	12	269
Total	64	173	133	98	468

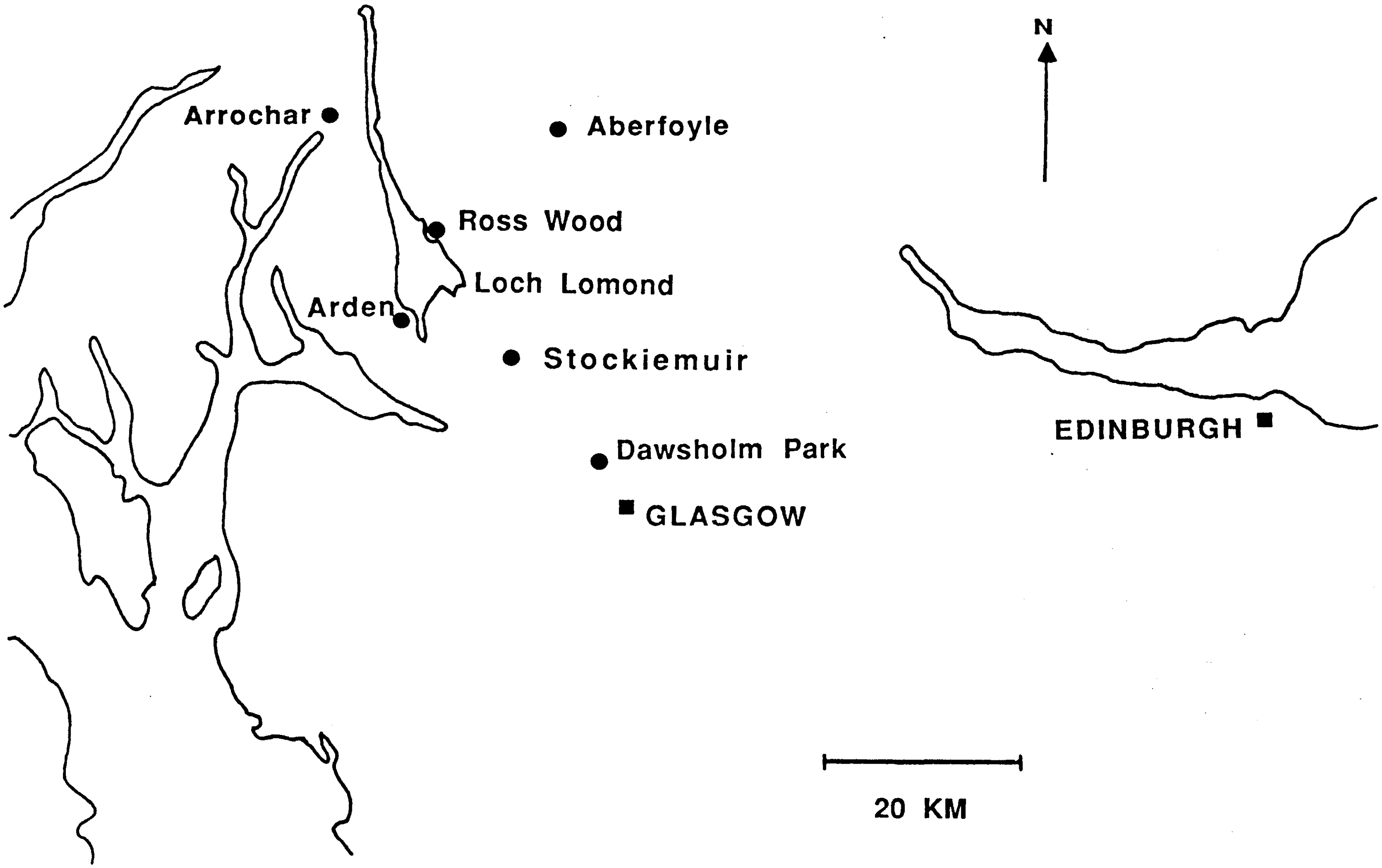
Table 15.2: The number of spiders of the four species which were collected in Ross Wood and five open areas in summer 1981.

Location	*Metellina segmentata*	*Metellina mengei*	*Linyphia triangularis*	*Linyphia peltata*	Total
Ross Wood	124	360	105	232	821
Five Open Areas	271	25	355	19	670
Total	395	385	460	251	1491

Table 15.3: The number of spiders of the four species which were collected in Ross Wood and five open areas in autumn 1981.

Location	*Metellina segmentata*	*Metellina mengei*	*Linyphia triangularis*	*Linyphia peltata*	Total
Ross Wood	67	214	56	82	419
Five Open Areas	156	84	135	26	401
Total	223	298	191	108	820

Fig.15.1: The distribution of the localities in Central Scotland sampled in 1981- 1982.


N
Arrochar
Aberfoyle
Ross Wood
Loch Lomond
Arden
Stockiemuir
Dawsholm Park
GLASGOW
EDINBURGH
20 KM

These indicated that *M. segmentata* and *L. triangularis* are more abundant in open areas while *M. mengei* and *L. peltata* are more abundant in woodland areas. Bearing in mind that the results for the "Open Areas" represent five hours of sampling and those of the "Ross Wood" only one hour, then it is evident that the spiders were, in general, more abundant in the woodland area than in the open areas.

Abundance of spiders at six open and three shaded areas in 1982

In 1982 more detailed studies were carried out at the five open areas and some additional sites adjacent to these, which were in small areas of woodland. All these sampling areas measured $36m^2$ and they were searched in a systematic fashion and all spiders were collected by hand from the vegetation.

The area at Dawsholm Park, Area 31, had vegetation dominated by broom bushes (*Sorothamnus scoparius*) and grass and was bounded on one side by a stone wall. The area at Stockiemuir which was sampled in 1981, Area 32A, had vegetation dominated by gorse (*Ulex europaelus*) and grass and was also bounded on one side by a stone wall

(Fig.15.2). An adjacent area, Area 32B, was in a small patch of woodland and the dominant ground vegetation was bracken (Pteridium aquilinum). The area at Aberfoyle, Area 33, was a flat area (Fig.15.3) where the dominant ground vegetation was heather (Calluna vulgaris). A second area close by, Area 34, was sampled in 1982. This was located in a depression and again heather was the dominant vegetation. Area 36A was located near Arrochar and was dominated by gorse bushes. Area 36B was an additional site sampled in 1982. It was close to Area 36A but was in a small area of woodland and a variety of shrubs and grasses formed the ground vegetation. Area 37A near Arden (Fig.15.4) on Loch Lomond side was dominated by gorse bushes and Area 37B, which was an additional site sampled in 1982, was in a patch of woodland where grasses and shrubs formed the ground vegetation.

These nine areas, six open and three shaded sites, were sampled in July, August, September and October in 1982. For the present purposes these monthly samples for each area are combined and presented in Table 15.4.

The results confirm the general picture for 1981 in that M. mengei and L. peltata are more abundant in the shaded areas while L. triangularis is more abundant in the open areas. The situation for M. segmentata is less clear-cut. In general it is more abundant in the open areas

Table 15.4: The number of spiders of the four species which were collected in nine sampling areas in 1982. * shaded area.

Location, Area	*Metellina segmentata*	*Metellina mengei*	*Linyphia triangularis*	*Linyphia peltata*
Dawsholm, 31	295	2	81	0
Stockiemuir, 32A	117	10	200	3
Stockiemuir, 32B*	23	165	22	125
Aberfoyle, 33	0	3	145	1
Aberfoyle, 34	0	0	240	0
Arrochar, 36A	105	19	150	3
Arrochar, 36B*	115	151	19	70
Arden, 37A	65	7	90	0
Arden, 37B*	92	36	25	10

Fig.15.2: Open area (Area 32A) in Stockiemuir.

Fig.15.4: Open area (Area 37A) and shaded area (37B) near Arden.

Fig.15.3: Open area (Area 33) in moorland near Aberfoyle.

but it is absent from the Aberfoyle sites, which differ from the other open sites in that that they are fairly exposed moorland sites and they have short vegetation. At Arrochar and Arden M. segmentata is more abundant in the shaded areas. It will be argued later that these results are influenced by seasonal movement of this spider.

Temperature and wind speed measurements at an open and shaded site at Stockiemuir

At the Stockiemuir sites measurements were made of temperature and wind speed. Temperatures were recorded on 4/8/1982 and 8/8/1982 using a thermister with six probes. The probes were placed in the vegetation and covered to give a shade temperature. Readings were taken alternately in the two areas giving a total of 24 readings in each area on each occasion. The results are given in Table 15.5 and indicate, as might be expected, that the temperatures were significantly higher in the open area than in the shaded area. Wind speed were recorded on 18/8/1982, which was a windy day, using a Westen anemometer. The anemometer readings were taken at a height of 0.5m. Four alternate five minute readings were taken in each area. The results are given in Table 15.6 and these indicate that windspeeds are higher in the open areas.

Table 15.5: Mean temperatures (n=24) at open and shaded areas at Stockiemuir in August 1982

Date	Shaded Area (32A)	Open Area (32B)
4/8/82	22.77 ± 0.24	23.93 ± 0.16
18/8/82	15.22 ± 0.40	15.91 ± 0.23

Table 15.6: Mean wind speeds (m/sec.) at open and shaded areas at Stockiemuir in August 1982. Each value is mean of four observation periods, each of five minutes duration.

Date	Shaded Area (32A)	Open Area (32B)
18/8/82	6.59 ± 1.23	10.11 ± 1.39

Samples from different vegetation types in the Ross Wood

The Ross Wood comprised the main sampling area for the spider study and spiders were sampled from a variety of different vegetation types in, or close to, the Ross Wood. In all these samples the area sampled was 36m^2 and spiders were collected by systematically searching the vegetation. Mean vegetation heights were also measured in each area.

In July and September 1982 spiders were sampled from an area of tall rushes (*Juncus* species), Area 23 (Fig.15.5), just inside the wood and from an area of tall gorse, Area 24 (Fig.15.6), and an area of bog myrtle (*Myrica gale*), Area 25, just outside the wood. The results are given in Tables 15.7 & 15.8.

As will be seen later the numbers of spiders in these areas are less than in blaeberry - which is the dominant ground vegetation within the Ross Wood. *L. peltata* is rare or absent in these three areas while *M. mengei* is rare or absent from gorse or bog myrtle. *L. triangularis* is most abundant in gorse while *M. segmentata* is most abundant in rushes in July and gorse in September.

While blaeberry is the dominant ground vegetation within

Table 15.7: The number of spiders of the four species which were collected from three vegetation types in July 1982.

Vegetation, Area	Metellina segmentata	Metellina mengei	Linyphia triangularis	Linyphia peltata	Total
Rushes, 23	46	23	2	0	71
Gorse, 24	0	0	17	0	17
Bog myrtle, 25	0	0	12	0	12
Total	46	23	31	0	100

Table 15.8: The number of spiders of the four species which were collected from three vegetation types in September 1982.

Vegetation, Area	Metellina segmentata	Metellina mengei	Linyphia triangularis	Linyphia peltata	Total
Rushes, 23	14	12	0	0	26
Gorse, 24	34	0	28	2	64
Bog myrtle, 25	6	3	0	4	13
Total	54	15	28	6	103

Fig.15.5: Area 23 inside Ross Wood.

Fig.15.6: Open area (Area 24) on the edge of Ross Wood.

the Ross Wood other types of vegetation can be common in certain areas within the oak woodland. On 3/8/1982 samples were taken from three vegetation types - namely small coniferous trees, bracken and heather. For comparison, an area of blaeberry of medium height (30-40 cm.) was also sampled. On an area basis, the amount of blaeberry and conifers sampled was similar while the area of heather sampled was about 2/3, and of bracken about 1/3, of the areas of conifer and blaeberry. The results (Table 15.9) indicate that M. mengei and L. peltata are, in general, more abundant than the other two species. As all these sites are within the Ross Wood, and are shaded to a greater or lesser extent, this is what one might expect on the basis of earlier results. M. segmentata is less abundant in heather than in other vegetation while L. triangularis is more abundant on blaeberry than in other vegetation. L. peltata is less abundant in blaeberry and more abundant on heather while M. mengei is abundant on all the vegetation types.

Although blaeberry is the dominant ground vegetation in the Ross Wood there are areas where there are substantial numbers of small deciduous trees - namely rowan (Sorbus aucuparia) and birch (Betula pubescens). In some areas a number of these trees had been killed, probably as a result of damage by Roe Deer, and these defoliated, skeletal trees seemed to provide a suitable structure for

Table 15.9: The number of spiders of the four species which were collected from four vegetation types on 3/8/1982.

Vegetation	*Metellina segmentata*	*Metellina mengei*	*Linyphia triangularis*	*Linyphia peltata*	Total
Blaeberry	12	51	17	8	88
Conifer	14	43	2	25	84
Bracken	8	33	3	13	57
Heather	3	35	6	38	82
Total	37	162	28	84	311

web building spiders.

In July and September 1982 extensive samples were taken from three vegetation types - namely medium height blaeberry (30-40 cm.), intact deciduous trees and dead trees. The areas sampled for each of the vegetation types were approximately the same. The results are summarized in Tables 15.10 & 15.11.

In both July and September the spiders are, in general, more abundant on blaeberry than on dead trees while, with the exception of L. triangularis , which is absent from trees, they are much more abundant on dead trees than on living ones. M. mengei was the most abundant spider on blaeberry while M. segmentata and L. peltata were the most abundant species on dead trees.

Samples from areas of blaeberry within the Ross Wood

As the samples in 1981 and 1982 had indicated that all four spiders could be abundant in woodlands, and blaeberry was the dominant ground vegetation in the Ross Wood, samples were taken in eight areas in the Ross Wood in July and September 1982. These areas comprised mainly of blaeberry of varying heights and all had an area of $36m^2$. Areas 15

Table 15.10: The number of spiders of the four species which were found in samples from medium blaeberry, intact deciduous trees and dead deciduous trees in July 1982.

Vegetation	Metellina segmentata	Metellina mengei	Linyphia triangularis	Linyphia peltata	Total
Blaeberry	41	149	36	55	281
Intact trees	4	5	0	0	9
Dead trees	117	35	1	38	191
Total	162	189	37	93	481

Table 15.11: The number of spiders of the four species which were found in samples from medium blaeberry, intact deciduous trees and dead deciduous trees in September 1982.

Vegetation	Metellina segmentata	Metellina mengei	Linyphia triangularis	Linyphia peltata	Total
Blaeberry	72	188	30	57	347
Intact trees	4	2	0	0	6
Dead trees	35	15	0	65	115
Total	111	205	30	122	468

and 16 had tall blaeberry (+50 cm) and some of the blaeberry in Area 16 was defoliated. The reasons for this defoliation were not obvious. Areas 17 and 19 had medium blaeberry (+40 cm) and in Area 17 there were some dead birch or rowan trees. Areas 18, 20, 21 and 22 had short blaeberry (18-28 cm). Area 21 had some dead birch or rowan trees while Area 22 had some clumps of bracken and was more densely shaded than the other areas.

The results of the sampling are indicated in Tables 15.12 & 15.13, where the areas are arranged in ascending vegetation height, which was measured in July. In general, M. segmentata is less abundant in blaeberry than the other three species. It is the most abundant species in Area 17, which has a number of dead deciduous trees. Area 21, which is the only other area with dead deciduous trees, has the second highest number of M. segmentata . L. triangularis is most abundant in short blaeberry. The only exception to this is Area 22 which was heavily shaded. M. mengei and L. peltata were more abundant in tall blaeberry.

Four of these areas, namely Areas 15,16,17 and 18, were sampled monthly from July to October in 1982 and the results of this more detailed sampling programme are given in Tables 15.14-15.17. Table 15.14 gives the results for area 15 which had tall intact blaeberry. This vegetation

Table 15.12: The number of spiders of the four species in samples, in July 1982, from eight areas of the Ross Wood where blaeberry was the dominant ground vegetation (vegetation height the mean of 36 measurements).

Area	Vegetation height (cm)	Metellina segmentata	Metellina mengei	Linyphia triangularis	Linyphia peltata	Total
21	18.3	26	33	78	12	149
20	22.1	7	20	54	0	81
22	23.8	7	41	29	31	108
18	28.0	15	31	68	22	136
19	37.3	8	48	35	27	118
17	44.6	65	48	33	21	167
15	48.3	21	96	9	54	180
16	50.5	14	48	22	69	153
Total		163	365	328	236	1092

Table 15.13: The number of spiders of the four species in samples, in September 1982, from eight areas of the Ross Wood where blaeberry was the dominant ground vegetation (vegetation height the mean of 36 measurements).

Area	Vegetation height (cm)	Metellina segmentata	Metellina mengei	Linyphia triangularis	Linyphia peltata	Total
21	18.3	18	24	39	27	108
20	22.1	6	22	42	9	79
22	23.8	6	30	19	12	67
18	28.0	8	27	46	15	96
19	37.3	4	39	20	19	82
17	44.6	48	37	17	26	128
15	48.3	5	143	6	43	197
16	50.5	12	94	9	84	199
Total		107	416	198	235	956

Table 15.14: The number of spiders of the four species which were collected from area 15 (tall blaeberry) in 1982. Abundance ranking for each monthly sample is shown in parentheses.

Month	*Metellina segmentata*	*Metellina mengei*	*Linyphia triangularis*	*Linyphia peltata*	Total
July	21 (3)	96 (1)	9 (4)	54 (2)	170
August	11 (4)	132 (1)	14 (3)	61 (2)	228
September	5 (4)	143 (1)	6 (3)	43 (2)	197
October	1 (4)	185 (1)	2 (3)	32 (2)	220
Total	38	556	31	190	815

Table 15.15: The number of spiders of the four species which were collected from area 16 (tall blaeberry with some defoliation) in 1982. Abundance ranking for each monthly sample is shown in parentheses.

Month	*Metellina segmentata*	*Metellina mengei*	*Linyphia triangularis*	*Linyphia peltata*	Total
July	14 (4)	48 (2)	22 (3)	69 (1)	153
August	11 (4)	62 (2)	15 (3)	105 (1)	193
September	12 (3)	94 (1)	9 (4)	84 (2)	199
October	8 (3)	66 (1)	7 (4)	58 (2)	139
Total	45	270	53	316	684

type seemed to be the preferred habitat for M. mengei in that it was the most abundant species on all four months and comprised 68.2% of the total number of spiders collected in the area. Table 15.15 gives the results for area 16 which had tall blaeberry which was considerably defoliated. L. peltata was the most abundant species in the area, representing 46.2% of the total spider catch and was commonest species on two of the four monthly samples. Table 15.16 gives the results for Area 17 which had medium blaeberry and which had a number of dead birch and rowan trees. M. segmentata is the most abundant species in the area and was commonest in three of the monthly samples and represents 31.4% of the total spider catch. Table 15.17 gives the results for Area 18 which was an area of short blaeberry. L. triangularis is the dominant spider in this area. It is the commonest in each monthly sample and comprises 46.3% of the total spider catch. These results confirm the findings of the previous section.

Measurements of light intensity, temperature and wind speed from the four "optimum" areas in the Ross Wood

As each of the four areas, dealt with in the previous section, appeared to be an optimum habitat for one of the four spider species i.e. Area 15 for M. mengei , Area 16

Table 15.16: The number of spiders of the four species which were collected from area 17 (medium blaeberry with dead trees) in 1982. Abundance ranking for each monthly sample is shown in parentheses.

Month	*Metellina segmentata*	*Metellina mengei*	*Linyphia triangularis*	*Linyphia peltata*	Total
July	65 (1)	48 (2)	33 (3)	21 (4)	167
August	42 (2)	54 (1)	27 (4)	30 (3)	153
September	48 (1)	37 (2)	17 (4)	26 (3)	128
October	37 (1)	29 (2)	11 (4)	22 (3)	99
Total	172	168	88	99	547

Table 15.17: The number of spiders of the four species which were collected from area 18 (short blaeberry) in 1982. Abundance ranking for each monthly sample is shown in parentheses.

Month	*Metellina segmentata*	*Metellina mengei*	*Linyphia triangularis*	*Linyphia peltata*	Total
July	15 (4)	31 (2)	68 (1)	22 (3)	136
August	13 (4)	36 (2)	59 (1)	31 (3)	139
September	8 (4)	27 (2)	46 (1)	15 (3)	96
October	6 (4)	22 (2)	31 (1)	11 (3)	70
Total	42	116	204	79	441

for L. peltata , Area 17 for M. segmentata and Area 18 for L. triangularis , physical factors were measured in August 1982. This involved measuring temperature, light and wind speed. Short term variations can occur with respect to these factors, particularly in the case of wind speed and light intensity, and measurements were taken on overcast days were the wind speed fairly constant, so as to make comparisons between areas more valid.

Temperatures were recorded on 6/8/1982 and 23/8/1982. Recordings were made at points just within the vegetation - at levels at which spiders webs are found. On 6/8/1982 a total of 24 readings were taken and 12 on 23/8/1982. The results are given in Table 15.18. On both dates there were significant differences in mean temperature between the four areas. On both dates temperatures were higher in areas 17 and 18 than in 15 and 16.

Light measurements were taken in the four areas on 18/8/1982 using an EEC Photometer. The photocell was held in a horizontal position just above the vegetation. 35 measurements were taken in each area in the morning (11.00-12.00 hours) and in the afternoon (15.00-16.00 hours). The results are given in Table 15.19. These indicate that the light intensity is higher in Areas 17 and 18 than in 15 and 16.

Table 15.18: Temperatures (C) in four sampling areas (mean±S.D.). 24 measurements were taken in each area on 6/8/82 and 12 on 23/8/82. Temperature ranking on each date in parentheses.

Date	Area 15	Area 16	Area 17	Area 18
6/8/82	20.98 ± 0.25 (4)	21.20 ± 0.31 (3)	21.83 ± 0.21 (1)	21.56 ± 0.39 (2)
23/8/82	14.38 ± 0.28 (4)	14.61 ± 0.25 (3)	15.13 ± 0.30 (2)	16.00 ± 0.33 (1)

Table 15.19: Light intensity (in Kilolux) in the four sampling areas on 18/8/82. The figures are mean±S.D. of 35 readings. Illumination ranking on each occasion in parentheses.

Time	Area 15	Area 16	Area 17	Area 18
11.00-12.00	22.69 ± 14.11 (3)	22.07 ± 15.17 (4)	30.09 ± 14.87 (1)	28.50 ± 14.85 (2)
15.00-16.00	30.34 ± 15.34 (3)	24.69 ± 14.65 (4)	34.88 ± 13.51 (2)	35.26 ± 13.01 (1)

Table 15.20: Mean wind speeds (m/sec) in the four sampling areas. Wind speed ranking for the two heights are given in parentheses.

Height	Area 15	Area 16	Area 17	Area 18
0.5m	6.34 (3)	5.28 (4)	6.84 (2)	7.26 (1)
1.5m	6.94 (3)	5.73 (4)	7.20 (2)	8.12 (1)

Wind speeds were measured in the four areas on 12/8/1982 using a rotating cup anemometer. Windspeeds were measured at heights of 0.5m and 1.5m. Readings were made for two 15 minute periods in each area and the mean values for these are presented in Table 15.20. Windspeeds were higher in Areas 17 and 18 than in Areas 15 and 16.

The results of the measurements of these physical factors indicate that the two areas of tall blaeberry (Areas 15 and 16) have lower temperatures, lower light intensities and lower wind speeds than the areas with medium or low blaeberry (Areas 17 and 18)

Web height and vegetation height in the four "optimum" areas

An investigation was made of web height and vegetation height in the four areas in July and September 1982 - with the exception of Area 18 which was only sampled in July. The vegetation was measured at 36 fixed points within each area and spider web heights were measured to the nearest centimetre. The results are shown in Tables 15.21 and 15.22.

The height of the vegetation in each area did not change

Table 15.21: Height in cm (mean±S.D.) of vegetation and of spider webs in the four sampling areas in July 1982. (n) numbers of spiders webs or vegetation measurements. [n] ranking of web height.

Area	Vegetation height (cm)	*Metellina segmentata*	*Metellina mengei*	*Linyphia triangularis*	*Linyphia peltata*
15	48.3 ± 11.7 (36)	48.4 ± 7.4 (21) [1/2]	43.3 ± 5.1 (25) [3]	34.9 ± 5.7 (9) [4]	48.4 ± 4.6 (25) [1/2]
16	50.5 ± 10.5 (36)	53.4 ± 6.6 (14) [1]	41.8 ± 5.3 (25) [3]	34.1 ± 6.3 (22) [4]	44.2 ± 4.1 (25) [2]
17	44.6 ± 38.3 (36)	69.4 ± 36.4 (25) [1]	40.3 ± 4.0 (25) [3]	31.8 ± 3.8 (25) [4]	48.8 ± 22.7 (21) [2]
18	28.0 ± 9.8 (36)	39.4 ± 12.4 (15) [1]	34.6 ± 6.7 (25) [3]	22.7 ± 3.9 (25) [4]	35.4 ± 5.8 (22) [2]

Table 15.22: Height in cm (mean±S.D.) of vegetation and of spider webs in the four sampling areas in September 1982. (n) numbers of spiders webs or vegetation measurements. [n] ranking of web height.

Area	Vegetation height (cm)	*Metellina segmentata*	*Metellina mengei*	*Linyphia triangularis*	*Linyphia peltata*
15	48.1 ± 11.3 (36)	50.2 ± 1.8 (5) [1]	40.9 ± 3.3 (25) [3]	32.0 ± 3.0 (6) [4]	47.2 ± 5.0 (25) [2]
16	49.3 ± 13.4 (36)	55.4 ± 5.0 (12) [1]	44.4 ± 6.1 (25) [2]	31.4 ± 4.9 (9) [4]	42.8 ± 6.4 (25) [3]
17	46.8 ± 32.7 (36)	49.5 ± 13.6 (25) [1]	43.8 ±14.6 (25) [3]	29.7 ± 4.2 (17) [4]	48.5 ± 22.3 (26) [2]

significantly between July and September. The very large standard deviation about the mean in Area 17 reflects the fact that this area had small deciduous trees in it and some of these contributed to the measurement of vegetation height.

The results of the web measurements indicate that the four spider species tend to display vertical stratification. Thus on all occasions *M. segmentata* has the highest, or highest equal, web height. On all occasions the mean web height of *M. segmentata* is higher than mean vegetation height. This reflects the fact that this spider is found in the highest points of the vegetation. The difference is particularly striking in Area 17, where *M. segmentata* is the most abundant species, which has a number of dead deciduous trees. These appear to provide ideal web building sites for *M. segmentata* .

On all but one occasion *L. peltata* has the second highest web height or better. On all but one occasion *M. mengei* has the third highest web height and on all occasions *L. triangularis* has the lowest web height.

Seasonal changes in spider web height

Additional samples suggested that spider web heights changed at different times of the year. Samples of *L. triangularis* and *L. peltata* were taken from Area 29A from April to October. This was an area of medium blaeberry. The results are presented in Table 15.23.

From April to July the webs of *L. peltata* are low in the vegetation while from August to October they are located on the highest parts of the blaeberry. This change reflects the recruitment of the new generation into the population and these small spiders are found high in the vegetation. *L. triangularis* occurs higher in the vegetation than *L. peltata* in May and June but by July, when the spiders of the two species are of a similar size, they occur at the same level in the vegetation. In August, September and October *L. triangularis* is again found higher in the vegetation but not as high as *L. peltata* at this time.

Less extensive samples of spider web height were made in Area 29B, which was also an area of medium blaeberry, although this was somewhat shorter than in Area 29A. Samples of *L. peltata* were taken in April, May, August and September. At the same time samples were taken of the

Table 15.23: Height in cm (mean±S.D.) of vegetation and of spider webs of *L. triangularis* and *L. peltata* in Area 29A in 1982. (n) numbers of spiders webs or vegetation measurements.

Date	Vegetation height (cm)	*Linyphia triangularis*	*Linyphia peltata*
16/4/82	42.0 ± 17.8 (25)		22.6 ± 7.5 (25)
17/5/82	42.6 ± 15.1 (25)	34.7 ± 4.9 (17)	21.4 ± 6.9 (25)
7/6/82	43.0 ± 17.2 (25)	27.2 ± 4.7 (22)	20.3 ± 6.2 (25)
12/7/82	43.9 ± 14.6 (25)	19.2 ± 6.1 (21)	21.0 ± 8.1 (25)
7/8/82	40.0 ± 16.3 (25)	26.0 ± 5.0 (25)	47.5 ± 6.5 (25)
18/9/82	40.7 ± 19.5 (25)	34.7 ± 4.7 (25)	45.0 ± 7.8 (25)
15/10/82	34.9 ± 16.7 (25)	28.4 ± 4.4 (16)	44.0 ± 6.9 (25)

Table 15.24: Height in cm (mean±S.D.) of vegetation and of spider webs of *L. peltata* and *M. mengei* (large and small) in Area 29B in 1982. (n) numbers of spiders webs or vegetation measurements.

Date	Vegetation height (cm)	*Metellina mengei* (L)	*Metellina mengei* (S)	*Linyphia peltata*
16/4/82	35.9 ± 18.2 (25)	42.7 ± 16.8 (14)	31.1 ± 9.3 (16)	23.9 ± 7.7 (20)
17/5/82	37.2 ± 17.1 (25)	41.7 ± 8.4 (15)	35.9 ± 6.3 (15)	23.6 ± 4.7 (20)
7/8/82	35.6 ± 14.9 (25)	45.9 ± 7.4 (15)	33.3 ± 7.5 (15)	42.0 ± 7.0 (20)
18/9/82	35.0 ± 16.1 (25)	43.0 ± 7.8 (20)	36.7 ± 7.1 (20)	35.5 ± 5.5 (20)

web heights of *M. mengei* . This species is represented by two distinct size groups and large and small spiders were examined separately. The results are given in Table 15.24.

These indicate that *L. peltata* and the two size groups of *M. mengei* tend to occur at different levels in the vegetation. Thus large specimens of *M. mengei* occur high in the vegetation - with an average web height higher than average vegetation height. The small specimens of *M. mengei* occur lower in the vegetation than the large ones but are still quite high in the vegetation. In April and May *L. peltata* occurs much lower in the vegetation than *M. mengei* but in August and September, when the new generation is present, *L. peltata* is now found high in the vegetation. A comparison of the results for *L. peltata* in August and September in Areas 29A and 29B shows the spider has a lower mean web height in Area 29B. This probably reflects the fact that the vegetation is lower in this area and in both areas in August the mean web height of *L. peltata* is about 7cm higher than the mean vegetation height.

Seasonal movement of the spiders

The results of the two previous sections suggest that in blaeberry there is some degree of stratification of the spiders within the vegetation and also that there are seasonal changes with respect to this. Other samples suggested that seasonal movement occurred in other vegetation types and also that there was seasonal movement from one vegetation type to another.

Area 30 comprised of stand of 15 small conifers (1.5-2.0m) in a small clearing in the Ross Wood. In 1982 these trees were sampled monthly from June to September for L. triangularis . The webs were simply recorded as to whether they were in the inner or outer layers of the trees or at the top or bottom of the tree. Webs above 1m were considered to be in the top of the tree while if the web touched the trunk of the tree it was regarded to be on the inside of the tree. The results are given in Table 15.25.

Initially in June the majority of the spiders are on the outside at the bottom of the tree but during July and August the situation changes and the majority of spiders are found near the top of the tree close to the trunk. The conical shape of the small conifer, plus the fact that the web sizes increase during the summer, means that there is a

Table 15.25: Numbers of spiders of L. triangularis which were collected from different positions in small conifer trees in Area 30 in 1982.

Date	Inside	Outside	Top	Bottom
7/6/82	16	75	29	62
12/7/82	45	32	52	25
7/8/82	59	11	42	28
18/9/82	42	2	28	16
Total	162	120	151	131

Table 15.26: Location of the spider L. triangularis in bog myrtle at Area 35 in 1982.

Date	Bottom	Top
12/5/82	4	42
17/6/82	29	4

Table 15.27: Abundance of the spider L. triangularis on bog myrtle and grass at Area 35 in 1982.

Date	Bog myrtle	Grass
29/5/82	51	28
9/7/82	14	46
13/8/82	0	42

high probability that most webs in mid-summer in the top part of the tree will touch the trunk. Hence the results probably reflect mainly a movement up the tree rather than an inward movement.

A different type of movement was found with respect to *L. triangularis* in Area 35. This area was located near Aberfoyle and was dominated by bog myrtle and short grass. The area was sampled from mid-May to mid-August in 1982. Spiders were recorded as to whether they were on the grass or the bog myrtle. Those on the bog myrtle were subdivided as to whether they were on the "top" or "bottom" of the plant. The results are summarized in Tables 15.26 & 15.27.

Table 15.26 indicates that there is a movement of the spider from the top to the bottom of the bog myrtle between May and June while Table 15.27 indicates a movement of the spider from bog myrtle to grass during the period from late May mid-August.

M. segmentata was also found to display seasonal movement. Area 28 comprised of medium blaeberry with intact and dead deciduous trees. Samples of spiders were taken in July and September 1982. The results for *M. segmentata* are given in Table 15.28. Looking at the numbers on blaeberry and dead trees there is a significant difference between July and September which suggests a downward

Table 15.28: Numbers of *M. segmentata* collected from Area 28 in July and September 1982.

Vegetation	July	September
Blaeberry	41	72
Intact trees	4	4
Dead trees	117	35

Table 15.29: Numbers of *M. segmentata* in four shaded and four open sites in 1982.

	Ross Wood		Stockiemuir		Arrochar		Arden	
Month	Shade	Open	Shade	Open	Shade	Open	Shade	Open
July	46	0	12	65	52	0	46	0
August	22	2	7	49	39	3	38	5
September	14	34	4	37	21	64	8	36
October	0	22	0	26	3	41	0	24
Total	82	78	23	177	115	108	92	65

movement of spiders to the lower vegetation in the autumn.

In addition to vertical seasonal movement there is also evidence for horizontal seasonal movement for *M. segmentata* . This can be seen by looking at the results obtained from the open and shaded areas at Arrochar (Areas 36A & 36B), Arden (Areas 37A & 37B) and Stockiemuir (Areas 32A & 32B) and also from Area 23, an area of rushes just within the Ross wood and Area 24, an area of gorse just outside the Ross Wood. The results of sampling these areas from July-September 1982 are given in Table 15.29.

The results in the Ross Wood, Arrochar and Arden sites are similar. In the shaded areas the numbers drop from a maximum in July while in the open areas the numbers increase to a peak in September. This suggests that in the autumn *M. segmentata* is moving from shaded areas to open areas. The pattern at Stockiemuir is different. This area does differ in certain respects from the other areas but it is not clear to what extent these differences could account for the results obtained. A somewhat different pattern of seasonal movement for *M. segmentata* was found in Area 31, which was located in Dawsholm Park. This area consisted mainly of tall broom with short grass and the area was bounded on one side by a stone wall. *M. segmentata* was found on both vegetation types and webs were also found on, and in, the stone wall. Systematic searches of the area were made from May to December 1982 and the results of these are given in Table 15.30.

The results indicate that early in the year the spiders are most abundant in the wall. These are small spiders which have recently emerged from the egg sac. Egg sacs are deposited in large numbers in crevices within the walls. A similar situation was found at Stockiemuir and temperature recordings there indicated that the temperature within the wall was significantly higher than in the surrounding vegetation. At Area 31 the numbers of spiders in the grass reach a peak in June - suggesting a movement of spiders from the wall to the grass. Peak numbers of spiders on broom occur in August and September and, as numbers are becoming low in the grass at this time, this suggests a movement of the spider onto taller vegetation. In October and November the majority of spiders are again found in the wall. This suggests a movement of adult females into the wall to deposit their egg sacs.

Thus M. segmentata appears to display both vertical and horizontal movement although the pattern of the latter is not consistent in all areas. It seems likely that these seasonal movements reflect changes in the requirements of the spider at different stages in its life cycle but that the precise pattern of the movement may differ from habitat

Table 15.30: The numbers of the spider *M. segmentata* collected from Area 31 in 1982.

Date	Wall	Grass	Broom
17/5/82	25	0	0
3/6/82	253	48	0
18/6/82	174	264	11
5/7/82	36	65	23
2/8/82	12	31	42
16/9/82	2	5	41
5/10/82	23	0	15
15/11/82	28	2	2
16/12/82	2	0	0

to habitat and may be influenced by the structure of the vegetation.

Conclusions on the distribution of the four spider species

From this chapter we can draw some conclusions about the distribution of the four species. The sections which deal with the abundance in woodland and open areas indicate that all four species are abundant in woodland areas but *M. mengei* and *L. peltata* are relatively more abundant in woodlands than *M. segmentata* and *L. triangularis* . This is reflected in samples from rushes, gorse and bog myrtle in, or near, the Ross Wood. *L. peltata* is rare in all these habitats which suggests that it is the species most restricted to woodland. *M. mengei* is common in the rushes which is just inside the woodland but is rare in the two vegetation types just outside the wood. *L. triangularis* is common on gorse while *M. segmentata* is common in grass in June and in gorse in September. This latter result may reflect a horizontal seasonal movement of *M. segmentata* into open areas as it reaches maturity in the autumn.

The samples from conifers, heather and bracken within the Ross Wood indicate that *M. mengei* and *L. peltata* are commoner on these vegetation types than the other two species. This again probably reflects the fact that *M. mengei* and *L. peltata* are more abundant in woodlands. *M. mengei* seems to be common on all these vegetation types as well as on blaeberry while *L. triangularis* is much commoner on blaeberry than on the other vegetation types. The reverse is the case for *L. peltata* which is relatively more common on the other vegetation types than on blaeberry.

M. segmentata is very abundant on dead deciduous trees in the Ross Wood as is *L. peltata* . *L. triangularis* is virtually absent from deciduous trees.

Samples from blaeberry of different heights in the Ross Wood suggest that *M. segmentata* is less abundant on blaeberry than the other three species and tends to occur on dead deciduous trees. *M. mengei* and *L. peltata* prefer tall blaeberry with *L. peltata* preferring tall blaeberry which is defoliated. *L. triangularis* prefers short blaeberry.

Measurements of web heights in blaeberry suggests that *M. segmentata* has the highest webs, followed by *L. peltata* with *M. mengei* next. *L. triangularis* has the lowest web height.

From all these results conclusions can be drawn about where these four species are most likely to be abundant. *M. mengei* and *L. peltata* appear to be most restricted to woodland. *M. mengei* seems to be common on all vegetation types within woodland but tends not to occur on trees and is found fairly low in the vegetation. *L. peltata* seems to be the species most restricted to woodland. It is more common on the other vegetation types within the woodland than it is on blaeberry and can be quite abundant on small dead deciduous trees. There is evidence of seasonal movement with the small specimens occuring higher up the vegetation than the adults. *L. triangularis* is less restricted to woodland than *L. peltata* or *M. mengei* . It can occur on both high and low vegetation outwith woods and on coniferous trees within woods. It is found on short blaeberry within woods but is not common on other vegetation types within woods and is almost absent from deciduous trees. It displays seasonal movement, but the pattern of this may vary in different vegetation types. *M. segmentata* is less common in woods than the other three species and appears to show a seasonal movement - both horizontal and vertical movement. With regard to vertical movement; in woodland areas the spider appears to move from high to low vegetation between July and September whereas in open areas the movement, during the same period, is from low to high vegetation. With regard to horizontal movement, there is a tendancy for the spiders to move from shaded to open areas in the autumn. This species is relatively rare in blaeberry and is particularly abundant in small dead deciduous trees.

Discussion

Bristowe (1939) indicated that vegetation type and structure could affect the local distribution of spiders. The vegetation could provide a structure on which the spiders could build their webs and it could also influence the microclimate. The vegetation type and structure might also influence the prey available to the spider.

With regard to the latter point; some studies have indicated that areas of high prey density normally have high densities of spiders (Bristowe 1929; Turnbull 1964; Wise 1979; Olive 1982) while others have suggested that no such relationship exists (Cherrett 1964; Lindley 1974; Gritten 1979; Middleton 1984). All four species in the current study appear to feed on a wide variety of insects and other arthropods and it seems unlikely that differences in the local distribution are due to differences in prey availability.

With regard to vegetation influencing spider distribution by affecting the microclimatic conditions or by providing a structure for web building: vegetation type and structure has been shown to influence spider distribution (Bristowe 1929, 1939; Lowrie 1964; Enders 1973, 1977; Colebourn 1974; Lindley 1974; Riechert 1974; Riechert & Tracy 1975; Middleton 1984). The effect of vegetation on microclimatic conditions has also been considered to influence spider distribution. Norgaard (1956) and Riechert (1974) found that the spiders they studied were more abundant in depressions in the ground. These provided favourable microclimatic conditions. In the present study *L. triangularis* was significantly more abundant, in heather moorland near Aberfoyle, in a depression than it was in an adjacent flat area. Wind is considered to be an important factor in the distribution of web building spiders (Lowrie 1948; Chew 1961; Pointing 1965; Enders 1973, 1977; Gritten 1979) and Enders (1975) indicated that the vegetation acted as a windbreak and influenced the distribution of *Argiope aurantia* . Studies by Norgaard (1951), Duffey (1966) and Utez & Dillary (1974) suggest that both vegetation structure and microclimate can affect spider distribution.

The current study indicates that the four species have preferred habitats which differ slightly in vegetation type and structure. The areas which are optimum for *L. triangularis* and *M. segmentata* have higher windspeeds, temperature and light intensities than the optimum areas for the other two species. These microclimatic differences may be a factor in those differences in spider abundance, as laboratory experiments have shown that *L. triangularis* and *M. segmentata* prefer higher temperatures and light intensities than *M. mengei* and *L. peltata* . Middleton (1984) found that in the field the light intensity was higher in the habitat of *L. triangularis* than in that of *L. peltata* . He found that, in field experiments, *L. triangularis* had a higher light preference than *L. peltata* . He measured temperatures in the preferred habitats of the two species but did not find a significant difference. The study on the distribution has not been sufficiently detailed to allow any definitive statement to be made on how habitat structure or microclimate influences the distribution of the individual species, but it does provide some pointers.

Thus *M. segmentata* shows a preference for dead trees rather than living ones. There may be a number of reasons for this. The dead trees provide a more open habitat for building webs than do living ones and might thus facilitate the catching of prey. Also, intact trees might offer greater wind resistance and consequently move more in strong winds, with resultant web damage. The leaves themselves, of living trees, might damage the webs during strong winds. *L. peltata* shows a preference for defoliated blaeberry and similar arguments might hold.

The movement of *L. triangularis* to the lower reaches of bog myrtle (*Myrica gale*) plants, as the spider becomes older, may reflect the fact that the lower part of the plant provides greater space for the larger webs of the older instars and is also more sheltered from the wind. The preference of L. triangularis for short blaeberry may reflect the fact that webs in shorter vegetation are less likely to be damaged by wind.

In looking at the distribution of an animal it must be borne in mind that different stages in the life cycle may have different habitat preferences. This has been shown for web building spiders (Duffey 1968; Enders 1973, 1974) and for wolf spiders (Edgar 1971b; Edgar & Loenen 1974). The current study also indicates that immature spiders may have different habitat preferences from that of adult animals.

All four species in the current study are widely distributed - which suggests that they possess good mechanisms for dispersal. Dispersal of spiders by ballooning is a wide spread phenomenon (Braendegard 1937; Bristowe 1939, 1958; Duffey 1956, 1962; Wingerden & Vugts 1974; Vugts & Wingerden 1976; Tolbert 1977; Coyle 1983; Greenstone et al 1985, 1987). Although the current study did not look at ballooning behaviour, it seems likely that this mode of dispersal will occur in the immature stages. The movement of spiderlings of L. peltata onto high vegetation may be a mechanism to facilitate ballooning.

CHAPTER 16

Light/dark Preference of Spiders

The response of the four species to light was tested by introducing individual spiders into a choice chamber. These choice chambers were constructed using a similar method to that used by Cherrett (1964) but by using two 7.5x2.5 cm tubes. These were joined together at the open ends using clear sellotape. One of the tubes was darkened using black tape. The choice chambers were placed in a horizontal position and were exposed to natural light from a south facing window. Individual spiders were introduced into the chamber and their location was noted at the end of one hour. The experiments involved small instars, sub-adults and adults of the four species. The results are given in Tables 16.1-16.4.

Some additional experiments were carried out on other spiders - namely sub-adults of Metellina merianae and small instars of Meta menardi . Both these spiders are found in situations of low light intensity. Thus according to Locket and Millidge (1953) M. menardi occurs "In caves, damp cellars or out buildings, well away from light" while M. merianae occurs "In cellars, culverts and caves (not far from entrances), also on trees and low plants, and amongst rocks, especially when close to water". The results of experiments on these two species are given in Table 16.5. These indicate, as might be expected, that these two species have a strong preference for dark conditions.

With regard to the other four species. Both M. segmentata and L. triangularis (Tables 16.1 & 16.2) show a strong preference for light conditions at all stages in their life cycles. The situation for M. mengei (Table 16.3) is less clear-cut. In all cases there is a preference for the light conditions but this is statistically significant in only three of the seven experiments. With regard to L. peltata (Table 16.4), there is no significant preference for either dark or light at any stage in the life cycle. No clear pattern emerges with respect to preference at different stages in the life cycle.

These results are in broad agreement with the results for the distribution of the four species in that the two species which are most common outside woods, M. segmentata and L. triangularis , show a significant preference for light conditions while L. peltata , which appears to be the species most closely tied to woodlands, shows no preference. M. mengei occupies an intermediate position in that in some occasions it shows a preference for light conditions.

Table 16.1: Light/dark preference for *Metellina segmentata* in 1982.

Month	Stage	No. in light	No. in dark	χ^2
June	2nd instar	58	2	33.40
July	3rd instar	60	12	18.00
August	Sub-adult	63	9	23.59
September	Adult	54	18	9.60

Table 16.2: Light/dark preference for *Linyphia triangularis* in 1982.

Month	Stage	No. in light	No. in dark	χ^2
June	3rd instar	60	0	40.00
July	Sub-adult	57	15	13.39
August	Adult	67	5	32.77
September	Adult	62	10	21.59

Table 16.3: Light/dark preference for _Metellina mengei_ in 1982.

Month	Stage	No. in light	No. in dark	χ^2
May	Adult	41	19	4.17
June	4th instar	47	13	10.47
July	Sub-adult	47	25	3.41
July	Small instars	41	31	0.70
August	Sub-adult	56	16	12.04
September	Adult	46	26	2.83
September	Small instars	38	34	0.11

Table 16.4: Light/dark preference for _Linyphia peltata_ in 1982.

Month	Stage	No. in light	No. in dark	χ^2
May	Adult	37	23	1.66
July	Adult	44	28	1.80
July	Small instars	37	35	0.03
September	3rd/4th instar	43	29	1.37

Table 16.5: Light/dark preference for small instars of _Meta menardi_ and young spiders of _Metellina merianae_ in 1982.

Spider	Month	No. in light	No. in dark	χ^2
Meta menardi	May	0	15	10.00
	June	0	15	10.00
Metellina merianae	July	1	23	12.76
	August	1	17	8.86
	September	0	12	8.00

CHAPTER 17

Thermal Death Point

The upper temperature limit of an animal may give some insight into its distribution. Upper thermal limits were determined for various stages in the life cycles of the four species. Spiders were collected from the Ross Wood and kept overnight before the experiment. Each experiment consisted of 24 spiders of each species unless otherwise indicated. Any spiders which had just moulted were excluded from the experiment. Spiders were placed individually into tubes (7.5x2.5cm) which were stoppered and placed in a temperature controlled water bath. Two tubes, with thermometers in them, were used to monitor the temperatures to which the spiders were exposed. Preliminary experiments indicated that the thermal death points of all the spiders were above 33C, hence the temperature of the water bath was raised to 33C and then raised by 1C every 30 minutes. Spiders were examined at each temperature and it was recorded whether the spiders were alive or dead.

The detailed results of these experiments are given in Appendix 5. What might be of interest, with respect to the distribution of the four species, would be to compare thermal death points of different stages of the life cycle within a species and the same stages in the life cycle in different species.

The results for the four species are summarized in Tables 17.1–17.4. Clearly numerous comparisons could be made, but only those which seem to be most significant, from a biological point of view, will be discussed. Comparisons were made using the Kolmogorov-Smirnov two samples test for small samples (Siegel 1956).

For L. triangularis (Table 17.1) there is no significant difference between adult females at different times of the year. The first instars had a significantly higher thermal death point than the adult females.

For M. segmentata (Table 17.2) similar results were obtained, with the first instars having a higher thermal death point than the adult females.

For L. peltata (Table 17.3) there was no significant difference between adult females at different times of the year. The first instars had, however, a significantly lower thermal death point than the adult females.

With regard to M. mengei (Table 17.4) many more experiments were carried out than on the other three species. Adult females in the spring of 1983 had a lower thermal death point than those in the autumn of 1982. First and second instars in July had a lower thermal death point than adult females at the same time.

Table 17.1: Numbers of different stages of *L. triangularis* alive and dead at 41C in thermal death point experiments.

Date	Stage	Alive	Dead
15/7/1982	Sub-adult	0	24
14/8/1982	Adult male	9	15
17/8/1982	Adult female	1	23
20/10/1982	Adult female	1	23
6/11/1982	Adult female	0	24
22/5/1983	1st instar	12	12

Table 17.2: Numbers of different stages of *M. segmentata* alive and dead at 39C in thermal death point experiments.

Date	Stage	Alive	Dead
14/7/1982	3rd instar	0	24
14/8/1982	Sub-adult	1	23
7/9/1982	Adult female	0	24
7/9/1982	Adult male	0	24
21/10/1982	Adult female	0	24
7/11/1982	Adult female	0	24
22/5/1983	1st instar	10	14

Table 17.3: Numbers of different stages of L. peltata alive and dead at 37C in thermal death point experiments.

Date	Stage	Alive	Dead
15/7/1982	Adult female	21	3
28/7/1982	1st instar	0	24
17/8/1982	2/3rd instar	20	4
20/10/1982	3/4th instar	24	0
6/11//1982	Sub-adult	21	3
22/4/1983	Sub-adult	13	11
15/5/1983	Adult female	17	7

Table 17.4: Numbers of different stages of M. mengei alive and dead at 38C in thermal death point experiments.

Date	Stage	Alive	Dead
14/7/1982	4th instar	19	5
15/7/1982	Adult female	23	1
28/7/1982	1/2nd instar	0	24
14/8/1982	Sub-adult	2	22
17/8/1982	2/3rd instar	0	24
7/9/1982	Adult female	24	0
7/9/1982	Adult male	16	8
21/10/1982	Adult female	22	2
21/10/1982	2/3rd instar	0	24
7/11/1982	Adult female	16	8
7/11/1982	2/3rd instar	2	22
22/4/1983	Adult female	9	15
15/5/1983	Adult female	3	21
22/5/1983	3/4th instar	0	24

With regard to comparisons between species, the most appropriate comparisons might be between stages at the extremes of the life cycle. Thus comparisons of thermal death points were made for first/second instars of the four species and also for adult females.

The results for first / second instars are given in Table 17. 5. At 36C there is no significant difference in the numbers dead and alive for *M. mengei* , *M. segmentata* and *L. triangularis* but significantly more *L. peltata* are dead at this temperature than for the other three species. At 37C there is no significant difference in the numbers dead and alive for *M. segmentata* and *L. triangularis* but significantly more *M. mengei* are dead at this temperature than are individuals of the two former species. At 38C significantly more *M. segmentata* are dead than is the case for *L. triangularis* .

The results for adult females are given in Table 17.6. At 38C there is no significant difference in the numbers dead and alive between *M. mengei* and *L. triangularis* but significantly more *L. peltata* and *M. segmentata* are dead at this temperature than is the case for the two former species.

The trend demonstrated from the results of Tables 17.5 & 17.6 is further illustrated by looking at the total numbers

Table 17.5: Comparisons of thermal death points of first/second instars of the four species.

Date	28/7/1982		28/7/1982		22/5/1983		22/5/1983	
Species	L. peltata		M. mengei		M. segmentata		L. triangularis	
Temp. (c)	Alive	Dead	Alive	Dead	Alive	Dead	Alive	Dead
34	24	0	24	0	24	0	24	0
35	16	8	24	0	24	0	24	0
36	3	21	22	2	24	0	24	0
37	0	24	6	18	22	2	24	0
38	0	24	0	24	10	14	23	1
39	0	24	0	24	0	24	20	4
40	0	24	0	24	0	24	17	7
41	0	24	0	24	0	24	12	12

Table 17.6: Comparisons of thermal death points for adult females of the four species.

Date	15/7/1982		15/7/1982		7/9/1982		17/8/1982	
Species	L. peltata		M. mengei		M. segmentata		L. triangularis	
Temp. (c)	Alive	Dead	Alive	Dead	Alive	Dead	Alive	Dead
37	21	3	24	0	24	0	24	0
38	7	17	23	1	13	11	24	0
39	0	24	0	24	0	24	24	0
40	0	24	0	24	0	24	24	0
41	0	24	0	24	0	24	1	23

alive and dead, for the four species, at each temperature. These results, which utilize all information presented in Appendix 5, are presented in Table 17.7. Percentage of spiders dead at each temperature are presented in this table. Statistical tests cannot be done on percentages but these values do confirm the trend indicated in Tables 17.5 & 17.6 - that L. peltata has the lowest thermal death point and L triangularis the highest, with M mengei and M. segmentata having intermediate positions. These results are in accord with those from the section on spider distribution, which indicated that L. peltata was the species most tied to woodlands and L. triangularis the species least closely associated with shaded woodland areas.

Table 17.7: Number of the four species alive and dead, and percentages dead, at various temperatures.

Species	*L. peltata*			*M. mengei*			*M. segmentata*			*L. triangularis*		
Temp. (c)	Alive	Dead	%	Alive	Dead	%	Alive	Dead	%	Alive	Dead	%
37	116	52	31.0	272	40	12.8	164	4	2.4	143	1	0.7
38	18	150	89.3	112	200	64.1	94	74	44.0	142	2	1.4
39	0	168	100	6	306	98.1	11	157	93.5	137	7	4.9
40	0	168	100	0	312	100	0	168	100	126	18	12.5
41	0	168	100	0	312	100	0	168	100	23	121	84.0
42	0	168	100	0	312	100	0	168	100	0	144	100

Discussion

There is a considerable literature on the thermal death points of arthropods and of their tolerance to desiccation (Mellanby 1932, 1954, 1958; Solomon 1937; Norgaard 1951, 1956; Davies & Edney 1952; Colhoun 1954; Baldwin & Riordan 1956; House et al 1958; Cherry 1959; Cloudsley-Thompson 1962; Ahearn & Hadley 1969; Almquist 1970; Tolbert 1971, 1979; Seymour & Vinegar 1973; Punzo & Jellies 1983) although relatively few of these studies have dealt with the thermal death points of spiders (Norgaard 1951, 1956; Cloudsley-Thompson 1962; Almquist 1970; Tolbert 1979). Comparisons with the present study are difficult to make because the experimental methods used vary greatly from study to study.

Humidity decreases with temperature and in some cases thermal death can be attributed to desiccation (Almquist 1971; Edney 1971) but this is not always the case (Norgaard 1951; Mellanby 1958; House et al 1958; Cloudsley-Thompson 1962; Seymour & Vinegar 1973). In the current experiments it seems unlikely that humidity changes within the stoppered tubes were a significant factor in the death of the spiders.

Acclimation can affect the thermal death point (Mellanby 1954, 1958; Colhoun 1954; Baldwin & Riordan 1956; House et al 1958; Cherry 1959). In the present study the spiders were kept overnight at room temperature before experimentation and acclimation is not thought to have had a significant effect on the results. In thermal death point experiments the death of the animals occurs over a very short temperature range - perhaps as little as 1C (Mellanby 1932). The current results also displayed this phenomenon and the total thermal death point range for individuals of the four species was only 5C and was less than this for the individual species.

The thermal death points for the four species were lower than most of those quoted in the literature (Mellanby 1932, 1954, 1958; Norgaard 1951, 1956; Cloudsley-Thompson 1962; Almquist 1970; Tolbert 1971), however many of these involved tropical or desert living species. In general, thermal death points seem to correlate with the physical conditions of the habitat in which the arthropod occurs (Norgaard 1951; Davis & Edney 1952; Nemenz 1954; Lagerspetz & Jaynas 1959; Duffey 1962; Almquist 1971; Edney 1971, 1977; Vollmer & MacMahon 1974; Cloudsley-Thompson & Constantinou 1983). The current study confirms this trend in that the two species which are commonest outside woods, _L. triangularis_ and _M. segmentata_ , have higher thermal death points than _L. peltata_ and _M. mengei_ , which are more restricted to woods.

Small spiders tend to become more readily desiccated than larger ones because they have a larger surface area / volume ratio (Hall 1922; Norgaard 1956; Almquist 1971), although there are exceptions to this general rule (Tolbert 1979; Punzo & Jellis 1983). In the current study the fact that the spiderlings of *M. mengei* and *L. peltata* have lower thermal death points than the adults is in line with this trend. The reverse is the case for *L. triangularis* and *M. segmentata* . These two species overwinter in the egg sac and the spiderlings emerge in the spring. It is suggested that these spiderlings may seek out microhabitats with high temperatures and an abundant food supply to facilitate a rapid rate of growth.

Duffey (1962) suggested that spiders in the field layer were more resistant to desiccation than ground living ones. With respect to the four species studied, they are all field layer spiders. There does not appear to be any obvious relationship between the height at which they occur in the vegetation and their thermal death points.

CHAPTER 18

Parasites

The purpose of this section is to review, briefly, the parasites of spiders and to present information on the parasitism of L. triangularis and L. peltata by an inchneumon wasp.

A parasite is normally considered to be an animal which lives on or in another animal or a plant and which obtains its sustenance from its host. It is usually considered that the host is not killed by the parasite although it may be weakened by it - particularly if it carries a heavy parasite burden.

Parasites can be either internal (endoparasites) or external (ectoparasites). Same insects, particularly certain hymenopterans and diperans, lay their eggs on the living bodies or eggs of other arthropods. The larvae from these eggs develop on or in the arthropod, consuming its tissues, and eventually kill it. This "parasitism" is akin to predation and consequently such parasites are termed parasitoids. The majority of parasites of spiders are in fact parasitoids. Hunting wasps, notably those of the family Pompilidae, attack and paralyse spiders which are then buried along with the wasp eggs (Petrunkevitch 1952). The paralysed spiders provide food for the developing wasp larva. Although the spider is not killed at the time of the attack this type of interaction is best considered as a form of predation.

Spiders can be attacked by parasites and parasitoids at various stages in their life cycles. Thus either the spider itself or its eggs can be attacked. When the spider is attacked the parasite can be either an ectoparasite or an endoparasite. When the eggs are attacked individual eggs can be parasitized or the whole egg batch can be destroyed.

With regard to ectoparasites of spiders: An unidentified mite species has been recorded from the wolf spider *Pardosa hortensis* (Parker & Roberts 1974). Fungi have been found growing on spiders and in some cases the death of the spider has been attributed to the fungus (Bristowe 1941; Edgar 1968; Nentwig 1985). Ichneumon wasps of the genus *Acrodactyla* (Sub-F. Pimplinae) have been recorded as ectoparasites of a variety of spiders including *Linyphia* species (Morley 1907; Nielsen 1923; Bristowe 1941). The wasp attaches an egg to the abdomen of the spider and the larva, on emerging from the egg, attaches itself to the abdomen and feeds on the body fluid of the host which it eventually kills.

Internal parasites of spiders include nematode worms of the genus *Mermis* (F. Mermithidae) (Parker & Roberts 1974; Poiner 1985). These worms are normally detected when they emerge from a spider, which is killed in the process (Bristowe 1941). The larvae of certain species of Diptera of the family Acroceridae are endoparasites of spiders (Bristowe 1941; Easton et al 1967). In this case the small larva attaches itself to the spider and penetrates the spider's body where it completes its development. This seems to have no detrimental effect on the spider which is only killed when the larva emerges from spider in order to pupate (Bristowe 1941).

The eggs of spiders are attacked by a variety of insects. Normally one or more eggs is laid in the egg sac and the developing larva destroys all the eggs. The larvae of certain neuropteran species of the family Mantispidae act in this way (Killebrew 1982; Rice 1985) although they are not found in Britain (Bristowe 1941). In Britain the parasites (parasitoids) of spider egg sacs are usually ichneumon wasps (Sub. F. Pimplinae) of the genera _Gelis_ and _Tromatobia_ (Bristowe 1941; Horstmann 1970; Edgar 1971d; Kessler & Fokkinga 1973).

The minute wasps of the family Proctotrypidae parasitize individual eggs and not all the eggs in an egg sac are affected (Bristowe 1941; Kessler & Fokkinga 1973).

During the course of the present study an external parasite was found to attack _L. triangularis_ and _L._

peltata . This was identified by Mr. I. Gauld (British Museum of Natural History) as *Acrodactyla Degener* (Hal.) an ichneumon hymenopteran of the tribe Polysphinctini.

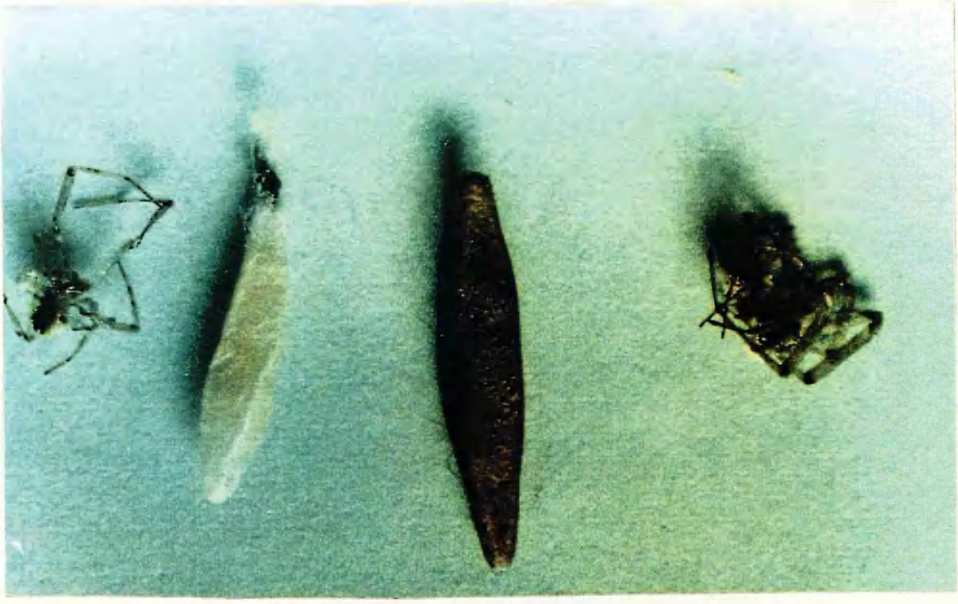
The life cycle of the *Linyphia* species has been described in detail in Chapter 7. Both have a one year life cycle and pass through five instars. *L. triangularis* emerges from egg sacs, which overwinter in the leaf letter, in mid-May, reaches the adult stage in early August, and starts laying egg sacs in early October. The adults die before the winter. *L. peltata* starts to emerge from the egg sac in mid-July and overwinters as immature animals (mainly sub-adults). Moulting to adult occurs in late April and egg sacs are produced in early June.

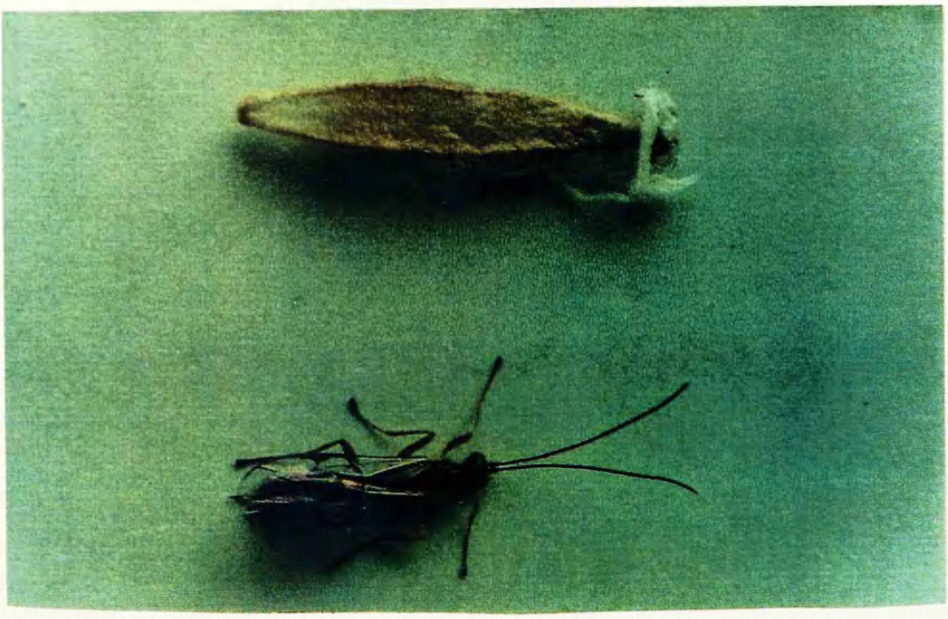
The ichneumon parasite *A. degener* lays an egg on the spider and the larva from this remains attached to the abdomen of the spider (Fig.18.1). As a result of the presence of the parasite, the spider dies just prior to the pupation of the parasitic larva. The larva consumes most of the spider and leaves only the hard integument (Fig.18.2). The larva has a white colour early in its development but later turns to yellow . After killing and consuming the spider the larva starts to build a cocoon which takes approximately 24 hours ($X=21.0\pm5.6$ hours, n=5, range 14-28 hours). The cocoon first has a white colour which later

Fig.18.1: Parasitic larva of *Acrodactyla degener* on *Linyphia triangularis* in early June 1981.

Fig.18.2: Pupae of *Acrodactyla degener* from larvae which fed on different sizes of spiders. (a) a white colour pupa on small spiders (left) (b) a dark brown pupa on large spider. The hard integuments of the spiders are shown beside each pupa.

Fig.18.3: Adult parasite after emerging from the pupa in early August 1981.





becomes darker. This appeared to relate to the level of food consumption prior to pupation as pupae of the larvae which had fed on comparatively small spiders remained white in colour (Fig.18.2). This was not studied systematically but agreed with an observation of Nielsen (1923).

The parasite is bivoltine - the first generation parasitizes mainly *L. triangularis* in late June but a few adult and sub-adult females of *L. peltata* are also attacked. The larvae grow quickly and kill the spiders in late July to early August. In the case of *L. triangularis* the spider dies before attaining maturity but with *L. peltata* most of the females will have laid an egg sac prior to being killed by the larva. Thus seven adult females of *L. peltata* were collected from the field on 10/7/81 and reared in the laboratory. Five of them laid egg sac prior to being killed by the parasite. Spent females, carrying parasites, were also found in the field. The larvae pupate for approximately two weeks (X=14.1±1.5 days, n=10, range 12-17 days) before the adult emerges (Fig.18.3)

The second generation parasitizes the spiderlings of *L. peltata* from mid-August to late September. The larva overwinters on the spider - which it kills in April. Pupation lasts for around four weeks (X=28.8±4.3 days, n=10, range 22-36 days) and the parasite emerges in late

May and early June. A summary of the life cycle of A. degener is given in Fig.18.4.

Degree of parasitism

In order to obtain a valid estimate of the degree of parasitism it was necessary to collect spiders at a time when all the spiders which would be parasitized had been attacked by A. degener and before the time when the parasitic larvae started to kill the spiders. For L. triangularis this period was from late June to late July and for L. peltata from early October to late November and in the spring up until early April.

In 1981 the degree of parasitism for L. triangularis was estimated for four different areas in the Ross Wood. This species is found in a variety of habitats in both wooded and non-wooded sites. In 1982, in addition to estimating the degree of parasitism in two areas in the Ross Wood, samples were taken in three open areas (Dawsholm Park, Aberfoyle and Stockiemuir). The results are shown in Tables 18.1 and 18.2. In Table 18.1 the results are given in chronological order and in Table 18.2 are arranged in order of increasing degree of parasitism.

In 1981 there is no significant difference in the degree of parasitism in any of the four samples. In 1982 the degree

Fig.18.4: Life cycle of *Acrodactyla degener*.

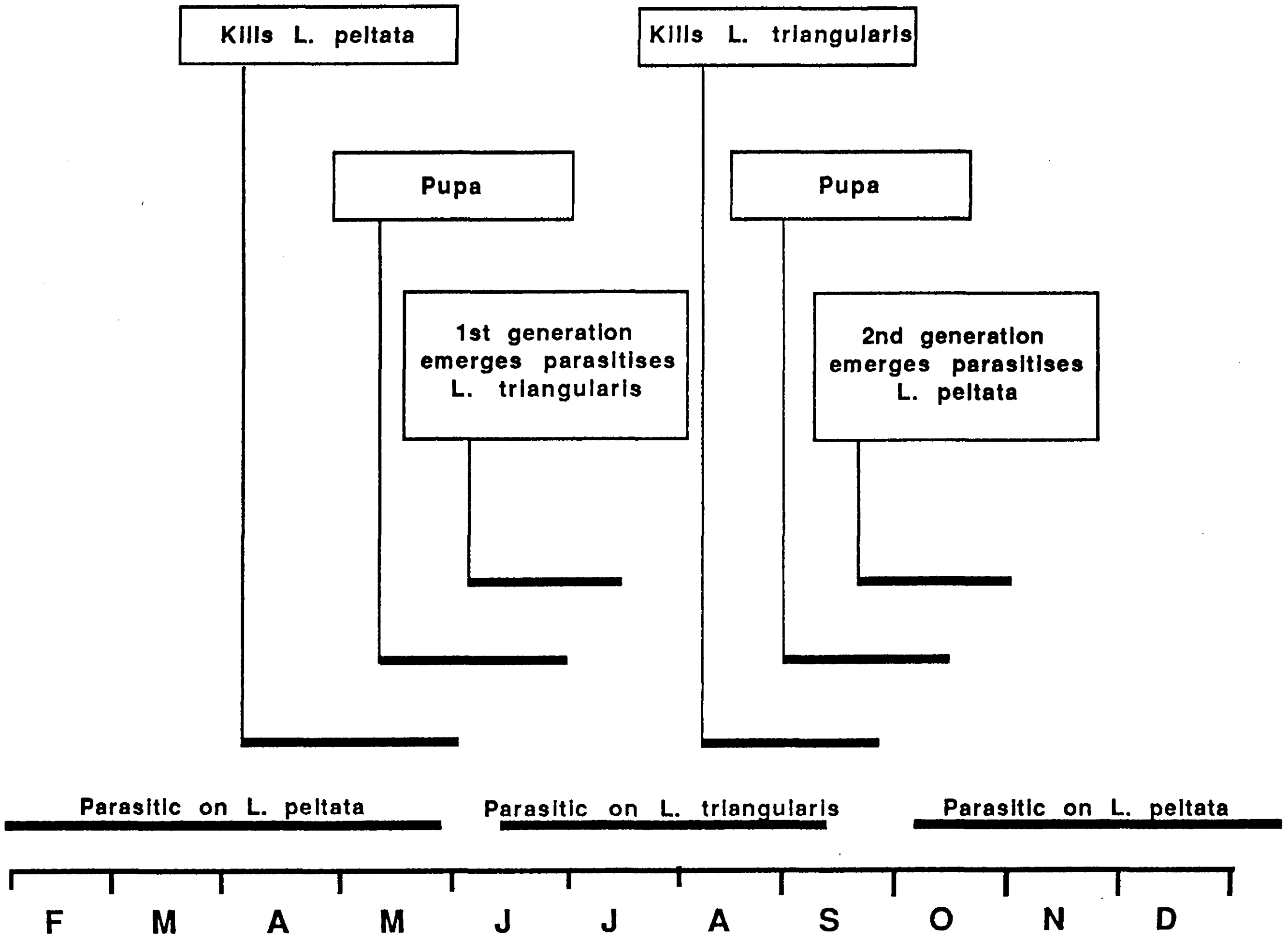

Kills L. peltata
Kills L. triangularis
Pupa
Pupa
1st generation emerges parasitises L. triangularis
2nd generation emerges parasitises L. peltata
Parasitic on L. peltata
Parasitic on L. triangularis
Parasitic on L. peltata
F
M
A
M
J
J
A
S
O
N
D

Table 18.1: Incidence of parasitism of *Linyphia triangularis* by *Acrodactyla degener* at different times in different localities.

Date of sampling	Location	Vegetation Type	Number of spiders examined	Number parasitized	% parasitized
28/6/81	Ross Wood	Conifer	36	5	13.9
28/6/81	Ross Wood	Blaeberry	64	4	6.3
22/7/81	Ross Wood	Blaeberry	24	1	4.2
22/7/81	Ross Wood	Blaeberry	76	7	9.2
16/7/82	Dawsholm park	Grass	32	1	3.1
16/7/82	Stockiemuir	Grass	24	0	0
15/7/82	Aberfoyle	Heather	38	0	0
19/7/82	Ross Wood	Blaeberry	53	6	11.3
19/7/82	Ross Wood	Blaeberry	89	7	7.9

Table 18.2: Incidence of parasitism of *Linyphia triangularis* by *Acrodactyla degener* at different times in different localites (samples joined by lines are not significantly different).

Date of sampling	Location	Vegetation type	Number of spiders examined	Number parasitized	% parasitized	Significance	
15/7/82	Aberfoyle	Heather	38	0	0		¦
16/7/82	Stockiemuir	Grass	24	0	0	¦	¦
16/7/82	Dawsholm park	Grass	32	1	3.1	¦	¦
22/7/81	Ross Wood	Blaeberry	24	1	4.2	¦	¦
28/6/81	Ross Wood	Blaeberry	64	4	6.3	¦	¦
19/7/82	Ross Wood	Blaeberry	89	7	7.9	¦	¦
22/7/81	Ross Wood	Blaeberry	76	7	9.2	¦	¦
19/7/82	Ross Wood	Blaeberry	53	6	11.3	¦	
28/6/81	Ross Wood	Conifer	36	5	13.9	¦	

of parasitism is similar in the three open sites and is significantly lower than in the blaeberry areas (χ^2= 6.64, d.f.=1, P<0.01). There was no significant difference between the degree of parasitism in the blaeberry areas in July 1981 and in July 1982 (χ^2=0.04, d.f.=1, P>0.80). Thus the degree of parasitism of L. triangularis is higher in woodland sites than in open sites.

The degree of parasitism for L. peltata in 18 samples, in a variety of vegetation types in the Ross Wood, between 28/3/80 - 15/11/82 is shown in Tables 18.3 and 18.4. Table 18.3 gives the samples in chronological order and Table 18.4 arranges them in order of increasing degree of parasitism. In the spring of 1980 the degree of parasitism is significantly lower in blaeberry than in the other vegetation types (χ^2=4.12, d.f.=1, P<0.02). In October 1980 the degree of parasitism was lower in blaeberry than in conifer (χ^2=14.43, d.f.=1, P<0.001). In November 1980 there is no significant difference in the degree of parasitism between heather and blaeberry (χ^2=1.37, d.f.=1 P>0.20). There is no significant difference in the degree of parasitism between heather and conifer, both for samples in October and November 1980 (χ^2=1.09, d.f.=1, P>0.20) and November 1982 (χ^2=0.64, d.f.=1, P>0.30).

As indicated in Table 18.4, overall blaeberry has a lower degree of parasitism than either heather or conifer. The

Table 18.3: Incidence of parasitisim of Linyphia peltata by Acrodactyla degener at different times and in different vegetation types in the Ross Wood.

Date of sampling	Vegetation Type	Number of spiders examined	Number parasitized	% parasitized
28/3/80	Heather & Blaeberry	45	7	15.6
11/4/80	Heather	61	19	31.1
11/4/80	Blaeberry	12	0	0
11/4/80	Conifer	32	10	31.3
10/10/80	Conifer	200	38	19.0
10/10/80	Blaeberry	90	1	1.1
10/10/80	Conifer	85	9	10.6
28/11/80	Blaeberry	7	0	0
28/11/80	Heather	149	26	17.5
28/11/80	Heather	45	6	13.3
26/3/81	Blaeberry	9	0	0
31/3/81	Blaeberry	42	9	21.4
4/10/81	Blaeberry	47	0	0
5/11/81	Blaeberry	40	0	0
14/11/82	Conifer	73	16	21.9
14/11/82	Blaeberry	44	3	6.8
15/11/82	Heather	41	6	14.6
15/11/82	Heather	141	16	11.3

Table 18.4: Incidence of parasitism of *Linyphia peltata* by *Acrodactyla degener* at different times in different vegetation types in the Ross Wood (samples joined by lines are not significantly different).

Date of sampling	Vegetation type	Number of spiders examined	Number parasitized	% parasitized	Significance	
4/10/81	Blaeberry	47	0	0	¦	
5/11/81	Blaeberry	40	0	0	¦	
26/3/81	Blaeberry	15	0	0	¦	
11/4/80	Blaeberry	12	0	0	¦	
28/11/80	Blaeberry	7	0	0	¦	
10/10/80	Blaeberry	90	1	1.1	¦	
14/11/82	Blaeberry	44	3	6.8	¦	
10/10/80	Blaeberry	85	9	10.6		¦
15/11/82	Heather	141	16	11.3		¦
28/11/80	Heather	45	6	13.3	¦	¦
15/11/82	Heather	41	6	14.6	¦	¦
28/3/80	Heather & Blaeberry	45	7	15.6	¦	¦
28/11/80	Heather	149	26	17.5	¦	¦
10/10/80	Conifer	200	38	19.0	¦	¦
31/3/81	Blaeberry	42	9	21.4	¦	¦
14/11/82	Conifer	73	16	21.9	¦	¦
11/4/80	Heather	61	19	31.3	¦	
11/4/80	Conifer	32	10	31.3	¦	

degree of parasitism is consistently low - with the exception of the sample on 31/3/81.

The range in the degree of parasitism is much wider in L. peltata (0-31.3%) than in L. triangularis (0-13.9%) although the average degree of parasitism in blaeberry is higher for L. triangularis (8.2%) than for L. peltata (4.8%) although the difference just fails to be statistically significant (χ^2=3.67, d.f.=1, P>0.05).

The degree of parasitisim of males and females of L. peltata was determined in nine samples taken from a variety of vegetation types (Table 18.5). The overall degree of parasitism was similar (20.5% for males and 17.2% for females) and in seven of the samples there was no significant difference in the degree of parasitism between males and females. In two of the samples (11/4/80 and 15/11/82) significantly more males were parasitized.

Multiple Parasitism

Although parasitized spiders normally only carry one larva, two parasitic larvae may occasionally be found. The two larvae appear to grow at the same rate (Fig.18.5). Attempts were made to rear spiders with two parasites but none of the parasites pupated and eventually the larvae died (Fig.18.6).

Table 18.5: Degree of parasitism of males and females of Linyphia peltata by Acrodactyla degener .

Date of sampling	Vegetation Type	Number of spiders examined		Number of spiders parasitized		χ^2
		Male	Female	Male	Female	
28/3/80	Heather & Blaeberry	19	26	2	5	0.46
11/4/80	Heather	15	46	8	11	4.56
11/4/80	Conifer	9	23	2	8	0.47
10/10/80	Conifer	31	169	5	33	0.19
28/11/80	Heather	45	104	8	18	0.00
28/11/80	Heather	17	28	3	3	0.44
31/3/81	Blaeberry	7	35	2	7	0.26
15/11/82	Heather	18	23	5	1	4.47
15/11/82	Heather	49	92	8	8	1.85

Fig.18.5: Two larvae of similar size on the spider *Linyphia peltata* .

Fig.18.6: Two larvae died before pupation.

Parasitisim of other spider species

A. degener was not found to attack either Metellina segmentata or M. mengei but it was found on Tetragnatha montana , an orb web spinner which inhabits the field layer, and on Lepthyphantes zimmermanni , a sheet web species from the ground layer. Both these species overwinter as immature stages.

A sample of M. segmentata on 1/8/81 revealed that three of the 31 spiders were parasitized by a parasite which looked similar to, but darker than, A. degener . The parasitized spiders were lighter (X=3.82±0.97 mg; n=31 than the unparasitized ones (X=5.48±2.72 mg; n=28). Two of these larvae pupated in late August and the cocoons had a different shape from those of A. degener . The cocoons were retained in the laboratory until the following year but no parasites emerged. It was therefore not possible to identify the parasite. However, it may have been Polysphincta clypeata , another member of the tribe Polysphinctini, which has been found to parasitize M. segmentata in Denmark (Nielsen 1923).

M. mengei is the most abundant spider in the study area but of all the specimens collected only one, in October 1983, was parasitized (Fig.18.7). The species involved could not be determined as the spider died before the larva

Fig. 18.7: Parasitic larva of an unknown species on *Metellina mengei* .

pupated.

The effect of parasitism on spider growth

The parasitic larva retards spider growth and on only one occasion was a parasitized spider observed to moult. The effect on spider growth is seem most strikingly for _Linyphia triangularis_ in July, as at this time of the year the spider normally grows very quickly. Thus parasitized spiders collected in July are significantly lighter than unparasitized ones (Table 18.6) ($t=14.3$, d.f.$=65$, $P<0.05$).

Parasite energy budget

Energy flow studies have been carried out on insect parasites of spiders (Edgar 1971d; Prakash & Pandian 1978) but these have involved parasites of egg sacs. Carrying out an energy flow study of the parasites of spider egg sacs is technically much easier than that of a parasite of the spider as it is fairly straightforward to estimate the amount of energy laid down in an egg sac and to estimate the energy equivalent of the emerging parasites. The technical problems of trying to estimate the amount of energy, passing through a spider, which goes into its ectoparasite, were such that no attempt was made to estimate the energy flow to the parasite population.

Table 18.6: Mean weight of parasitized and unparasitized specimens of Linyphia triangularis collected in July 1981.

	Parasitized spiders	Unparasitized spiders
Mean weight (mg) ± S.D.	4.21 ± 1.27	11.67 ± 2.96
Number of spiders	25	42

Table 18.7: Mean weights (mg ± S.D.) of a sample (n=14) of the first generation of Acrodactyla degener, reared from Linyphia triangularis, giving wet weights of pupa, emergent adult parasite and pupal remains and dry weight of adult parasite.

Pupa (Wet. Wt.)	Pupa remains (wet. Wt.)	Adult parasite (Wet. wt.)	Adult parasite (dry wt.)
3.45 ± 1.43	0.75 ± 0.39	1.24 ± 0.84	0.45 ± 0.30

Table 18.8: Mean weights (mg ± S.D.) of a sample (n=16) of the second generation of Acrodactyla degener, reared from Linyphia peltata, giving wet weights of pupa, emergent adult parasite and pupal remains and dry weight of adult parasite.

Pupa (Wet. Wt.)	Pupa remains (wet. Wt.)	Adult parasite (Wet. wt.)	Adult parasite (dry wt.)
2.54 ± 0.73	0.74 ± 0.28	1.02 ± 0.33	0.37 ± 0.13

However information is presented on the weights of the parasite pupae and emerging parasites in Tables 18.7 & 18.8.

From these figures an estimate of the growth efficiency during the pupal stage can be obtained by expressing the weight of the emerging parasite as a percentage of the initial weight of the pupa. This gives a value of 36% for the first generation of _A. degener_ and 40% for the second generation. Prakash and Pandian (1978) give a mean value of 48% for the "pupal efficiency" of _Sarcophaga banksi_ , a dipteran parasite of spider egg sacs.

CHAPTER 19

Predators

The aim of this section is to discuss, briefly, the predators of spiders and to present some observations on cannibalism and interspecific predation involving the species under study. Information is also given of a red mite (*Anystis* species) which may be an important predator of the early instars of *Metellina mengei* and *Linyphia peltata* .

Relatively little information is available on the predators of spiders and this tends to be in the form of casual observations (Bristowe 1941; Edgar 1969). Similarly, in the present study, no systematic attempt was made to assess the predators of the four spiders species but some casual observations were made during the course of regular field sampling - particularly when collecting food items from webs. Cannibalism is known to occur in spiders (Bristowe 1941; Edgar 1969) and Bristowe (1941) has suggested that the most important predators of spiders may be other spiders. Some cannibalism was found in the present study: In a few cases adult females of *M. mengei* were found feeding on adult males in late July and adult females of *M. segmentata* were found eating adult males of the species in October. Adult females of *M. segmentata* were also found eating other adult females (Fig.19.1). Some

Fig.19.1: Female of *Metellina segmentata* eating other female.

Fig.19.2: A red mite eating a spiderling of *Metellina mengei* .

interspecific predation was also noted, with adult females of L. peltata feeding on immatures of M. mengei in the spring.

Another arthropod predator of the spiders was a red mite of the genus Anystis (F. Anystidae). This was found to feed on small instars of M. mengei and L. peltata during the summer (Fig.19.2). Sweep netting in 1981 indicated that the mites appeared to reach a peak in abundance in late July (Table 19.1), at the time when the small instars of M. mengei and L. peltata were present in large numbers. In early August 1982 mites were again found feeding on small spiders (Table 19.2). All the mites found to be feeding in the sweep net samples were feeding on small specimens of either M. mengei or L. peltata which suggests that these spiders form an important part of the diet of the mite in mid-summer. The mite is larger than the small instars of M. mengei and L. peltata present in mid-summer (Table 19.3) but there was no evidence of the mite feeding on the larger spider instars.

Edgar (1969), in his study of the wolf spider Pardosa lugubris in the oakwoods near the University Field Station, concluded that vertebrates, in the form of amphibians and reptiles, were probably of minor importance as predators of this wolf spider. The habits of frogs, toads and lizards would suggest that they are even less

Table 19.1: Numbers of mites and spiders collected by sweep netting in an area 10X1m in 1981.

Date	No. of *Anystis*	No. of *M. mengei*	No. of *L. peltata*	No. of mites feeding on spiders	% of mites feeding
Early July	3	0	0	0	0
Mid-July	18	7	3	0	0
Late July	29	82	37	2	7
Early August	12	67	52	0	0

Table 19.2: Numbers of *Anystis* collected during casual sweep netting between 5-7 August 1982.

No. of *Anystis*	No. of mites feeding-on spiders	% of mites feeding
117	3	2.6

Table 19.3: Mean weights (mg) of the mite *Anystis* and small instars of the spiders *M. mengei* and *L. peltata* in late July 1981.

	Anystis	*M. mengei*	*L. peltata*
Mean ± S.D.	0.48 ± 0.04	0.25 ± 0.04	0.19 ± 0.02
Number of animals	28	29	30

likely to be feeding on web spinning spiders which occupy the field layer vegetation. Betts (1955), in her study of the feeding behaviour of titmice in oakwoods, found that spiders constituted a small part of the diet of these birds. Thus blue tits (Parus caeruleus) fed on spiders of the families Theridiidae and Linyphiidae while great tits (Parus major) fed on those of the families Lycosidae and Argiopidae. Great tits and blue tits occur in the Ross Woods. Although they are versatile feeders it would appear most likely that they would be taking spiders from the woodland canopy and ground layers rather than from the field layer (Elton & Miller 1954).

CHAPTER 20

Mating Behaviour in *Metellina segmentata*, *M. mengei*, *Linyphia triangularis* and *L. peltata*

Introduction

Before describing mating behaviour in the four species a brief account will be given of spider reproduction. In spiders the sexes are always separate and females are normally larger than males. This sexual dimorphism is particularly marked in certain tropical orb web spiders (Robinson and Robinson 1978) and the much smaller males may reach the adult stage in fewer instars, and in a shorter time, than the females (Foelix 1982). The internal sexual organs release the sperm or eggs through a genital opening situated on the ventral side of the abdomen. The external copulatory organ in the female is the epigyne, which consists of a slightly raised sclerotized plate with several cuticular infoldings. The male copulatory organs are the pedipalps. Sperm is deposited into a small sperm web and the sperm is then drawn into the hollow terminal bulb of the pedipalp (Bristowe 1958). During copulation the pedipalp is inserted into the epigyne and the sperm is expelled into the female from the pedipalp bulb. The structure of the terminal part of the palp matches that of the epigyne. This "Lock and Key" mechanisim may prevent copulation between different species (Foelix 1982). The pedipalps of the adults of the four species are shown in

Fig.20.1-20.3. The structure of both pedipalp and epigyne are useful characters in the identification of spider species.

There have been a number of studies of the mating behaviour of spiders - most of them dealing with courtship in wolf spiders (Bristowe 1929; Rovner 1966, 1968; Hallander 1967; Harrison 1969; Hegdekar and Dondale 1969; Vogel 1970; Sadana 1972; Farley and Shear 1973). There have been fewer studies on web building spiders. Locket (1926) made some observations on the mating habits of web building spiders, including Linyphia triangularis and L. clathrata . Bristowe (1929) gave an account of the mating habits of spiders - with particular reference to sexual dimorphism. Rovner (1967, 1968) studied sperm induction and copulation in L. triangularis and also territoriality and web reduction in relation to mating behaviour. Proszynski (1961) gave an account of copulation in L. marginata while Bourne (1978) made observations on the Linphiid spider Porrhomma egeria .

The aim of this chapter is to give an account of the mating behaviour of the four spider species and to comment on the significance of sexual dimorphism with respect to this behaviour.

Fig.20.1: The pedipalps of the adult males of *Metellina mengei* (left) and *M. segmentata* .

Fig.20.2: The pedipalps of the adult males of *Linyphia triangularis* .

Fig.20.3: The pedipalps of the adult males of *Linyphia peltata* .

A major difference between *Metellina* and *Linyphia* species is that the former build orb webs which are normally renewed daily while *Linyphia* species build sheet webs which are more permanent structures. As mentioned in Chapter 8, *Linyphia* males reach maturity approximately two weeks earlier than females. In *Metellina* the females mature slightly earlier than males. Mating in *L. triangularis* occurs in August and September and in *L. peltata* it occurs in May and June. The mating period in *M. segmentata* is from September to November and in *M. mengei* from early May until late July. On reaching the adult stage the males of all four species cease building webs and start to search for adult females - whose webs they then share. This behaviour occurs in most web building spiders (Foelix 1982).

Materials and Methods

Observations on the mating habits of the four species, and in particular the courtship behaviour, were carried out in both the field and in the laboratory. In the laboratory the spiders were housed in cages as described in Chapter 6.

Sexual dimorphism was measured in terms of the length of tibia 1, cephalothorax length and breadth and cheliceral length (excluding the fang). These were measured using a binocular microscope - as described in Chapter 4.

Measurement was facilitated by supporting the spiders with glass beads, as suggested by Butler (1973).

Results

Mating Behaviour

Linyphia species

Mating behaviour will be considered under three headings: (a) Agonistic behaviour (b) Web reduction (c) Courtship and copulation.

(a) Agonistic Behaviour

As mentioned earlier, males of the *Linyphia* species reach the adult stage approximately two weeks earlier than females. On becoming adult they abandon their webs and start searching for females webs. Of the 36 webs of adult females of *L. triangularis* examined on 16/8/1981, 25 (69%) were found to contain adult males and by 29/8/1981 all the female webs examined contained adult males and two of these webs had two adult males. After arriving at the female´s web the male defends the web, in territorial fashion, against any other male. If another male enters the web its presence is detected by the vibrations it causes in the web and the resident male rushes towards it and shakes and plucks the web vigorously. This behaviour was observed in all 36 of such male-male incounters. Shaking and plucking the web appears to deter the intruder and in 21 cases (58%) the intruder moved off, or was thrown off, the web as a result of such behaviour. In 12 (33%) of the cases the intruder moved off only after additional aggressive behaviour on the part of the resident male. This appeared to take the form of a threat display which consisted of vibrating the abdomen and flexing the chelicerae. This was usually followed by the resident male moving towards the intruder, with outstretched front legs, and pursuing it to the periphery of the web. In only 3 cases did fighting take place, in the manner described by Rovner (1968), with the males interlocking their chelicerae.

Systematic observation of male agonistic behaviour is difficult to study in the field and in some field situations interactions may be very intense due to high spiders density. Thus on 30/8/82 nine webs of L. triangularis were observed on a single gorse (Ulex europaeus) bush (Fig.20.4). In one of the webs the following sequence was observed: Three males were present on the web and they differed in the size of their chelicerae. The male with the largest chelicerae, which appeared to be the resident one, started to shake the web vigorously. This caused one of the other males to leave the web. The remaining intruder engaged the larger male in a

Fig.20.4: Gorse bush with several webs of *Linyphia trinagularis* .

threat display which involved vibrating the abdomen, flexing the chelicerae and stretching out the front legs. The large male then moved towards the female and the intruder followed. The resident male then rushed towards the intruder and the spiders engaged in fighting - with their chelicerae interlocked. The smaller male broke off the contest and was pursued to the periphery of the web. It left the web and moved along a twig to another web which was occupied by a large resident male. This male rushed towards the intruder and shook the web vigorously and the smaller spider immediately left the web.

(b) Web Reduction

Adult males of L. triangularis perform what is known as "Web Reduction" (Rovner 1968) in which the male rolls up the web of the female and restricts her to a small stretch of web. The mean size of webs of adult females, just prior to the breeding period, was significantly larger than that during the breeding season ($t=6.47$, d.f.$=48$, $p<0.05$) (Table 20.1). Web reduction was also observed in the laboratory. The webs of 15 adult females of L. triangularis were reduced to small areas within two days of the introduction of adult males.

Table 20.1: Mean size of webs of adult females of *Linyphia triangularis* just prior to, and during, the breeding period.

	Pre-breeding period 27/7/1982	Breeding period 14/8/1982
Size of web (cm^2) ±.S.D.	178.8±76.7	56.4±55.5
Numbers of webs measured	25	25

Table 20.2: Number of matings which occur on reduced and on normal webs of *Linyphia triangularis* and *Linyphia peltata* .

Species-	Reduced webs	Normal webs	Total
L. triangularis	35	17	52
L. peltata	10	15	25

(c) Courtship and Copulation

The majority of courtship and copulatory behaviour occurred in webs which had undergone web reduction. Thus of a total of 52 matings observed for L. triangularis in the field and the laboratory, 35 occurred on reduced webs ($\chi^2=6.21$, $p<0.05$).

Courtship in L. triangularis starts with the male approaching the female while vibrating his abdomen and shaking the web gently. He then touches the female with his front legs and if she runs away he will repeat the performance. During the 52 courtships observed no instance of female aggression towards the male was recorded. If the female is not receptive the only way she can avoid courtship is by running to the periphery of the web. If the female is receptive she does not run away. In this case the male temporarily retreats to the periphery of the web and then approaches the female again vibrating his abdomen and cleaning his palps between his chelicerae. He then touches the female who immediately takes up a copulatory position (Fig.20.5). During copulation the spiders hang, inverted, beneath the web with the male above the female (Fig.20.5). The front of the cephalothorax of the male pivots on the female's sternum just behind her chelicerae. The male inserts his palp alternately into the female epigyne. Each insertion lasts 10-20 minutes and the palp is cleaned

Fig.20.5: Copulation in *Linyphia triangularis* .

between the chelicerae after each insertion. The inflation of the palp, which occurs prior to the expelling of sperm into the female, is readily observed (Fig.20.5). Copulation lasts for an average of 90 minutes (X=90±27, n=12, range 40-140 minutes). Copulation may be accidentally interrupted. For example, this occurred on one occasion when a twig fell on the web and in another instance when an insect landed on the web.

Mating behaviour in *L. peltata* is essentially similar to that of *L. triangularis* . However the following differences were noted: Web reduction is less frequent in *L. peltata* (Table 20.2). Thus of a total of 25 matings observed in the field and the laboratory only 10 took place on reduced webs ($\chi^2=1.0$, $p>0.05$). Thus with respect to web reduction, this is significantly less frequent in *L. peltata* than in *L. triangularis* ($\chi^2=5.18$, $p<0.050$). Another difference is that in *L. peltata* no fighting behaviour, involving the interlocking of chelicerae, was observed in males.

Metellina species

Mating behaviour will be considered under four headings (a) Arrival of males (b) Food sharing (c) Embracing (d) Copulation

(a) Arrival of males

As mentioned earlier, males and females in the *Metellina* species mature at approximately the same time - with the females perhaps slightly earlier than the males. On moulting to adult the males abandon their webs and set off in search of females. On entering the web of a female the male plucks on a radial line with his front legs. The female reacts by facing in the direction of the male. The male then advances slowly towards the female, vibrating his abdomen and with his front legs outstretched. On approaching the female the male touches her lightly with his front legs. In all the cases observed the female reacted threateningly and the male retreated to the periphery of the web. While at the periphery of the web, or at any stage in the courtship, the male will defend the web against any other male which enters it. The next phase of courtship occurs when an insect is caught in the female's web.

(b) Food Sharing

As soon as an insect becomes entangled in the web the female rushes from the hub to seize it and starts to feed. In almost all the cases observed (39 out of 40 for *M. segmentata* and 58 out of 60 for *M. mengei*) this initiated the next phase in the mating behaviour. The male approaches the feeding female as before - gently shaking and plucking the web and vibrating his abdomen and with outstretched front legs. He then touches the female with his front legs and if she does not react threateningly then he also starts to feed on the prey item (Fig.20.6 & 20.7). During this phase the male carries out what appears to be part of the courtship behaviour - in the form of slight vibrations and gentle touching of the female with his front legs. In most cases this takes place between bouts of feeding by the male, however in 15 of the 60 observations for M. mengei the male, although in close proximity to the food, did not in fact feed. By contrast, in 3 instances, the male seemed more interested in feeding than in mating in that he did not vibrate or touch the female and continued to feed after the female had left the prey.

(c) Embracing

After the touching of the female, which occurs during food sharing, the male initiates the next phase of the mating behaviour. He retreats from the prey and circles the still-feeding female and then moves rapidly towards her. The female responds by orientating herself beneath the web (Fig.20.8). The male comes into close contact with the female and faces her. He then places his outstretched front legs across her cephalothorax and under her abdomen. This gives an impression as if the male is weighing the female

Fig.20.6: Food sharing in *Metellina segmentata* .

Fig.20.7: Food sharing in *Metellina mengei* .

Fig.20.8: Female of *Metellina segmentata* orientating herself beneath the web.

Fig.20.9: Male spider of *Metellina segmentata* holding the female.

Fig.20.10: Male of *Metellina segmentata* "wraps" the female by circling her with silk.

or assessing the size of her abdomen (Fig.20.9). He retreats again and then returns towards her vibrating his palps and abdomen and cleaning his palps between his chelicerae in a manner similar to that described for the *Linyphia* species. He then makes a final rush towards the female and attempts to copulate. An additional form of behaviour was observed on several occasions for *M. segmentata* where the male built a strong line close to the food item and he then began to wrap the female to the line by circling her with silk several times (Fig.20.10). The female became passive and the male touched her several times before copulating with her.

(d) Copulation

In 11 out of the 40 observations (27.5%) for *M. segmentata* and 27 out of 60 (45.0%) cases for *M. mengei* , the female accepted the male. If the female was not receptive she indulged in "spar fighting" with the male. This involved interlocking of the front legs, and possibly the chelicerae, and resulted in the male being driven to the periphery of the web. Thus behaviour contrasted with that found in *Linyphia* species where the females never displayed any hostility towards the males.

Copulation is very brief and involves the insertion of only one palp. The mean duration for *M. segmentata* was 86 seconds (X=86±34, n=8, range 20-130 seconds) and 111 seconds for *M. mengei* (X=111±31, n=10, range 40-150 seconds).

Sexual Dimorphism

All the body dimensions measured for the four species are significantly larger in the males than in the females - with the exception of cheliceral lengths for the *Metellina* species (Table 20.3 & 20.4). The greater length of tibia 1 in males indicates the fact that the front legs in males are strikingly longer than those of females. The larger cheliceral in the males of the *Linyphia* species is particularly striking in *L. triangularis* (Fig.20.11).

Cephalothorax dimensions, which reflect overall body size, are more significantly different in the *Linyphia* species than in the *Metellina* species.

These results indicate that sexual dimorphism occurs in all four species but is more striking in the *Linyphia* species.

Table 20.3: Mean size (mm)±S.D. of tibia 1, cephalothorax breadth and length and chelicera length in the four spider species.

Species	sex	Tibia 1	Cephalothorax breadth	Cephalothorax length	Chelicera length
Linyphia triangularis	Female	3.05±0.18 (45)	1.66±0.12 (45)	2.37±0.17 (45)	0.96±0.09 (11)
	Male	3.65±0.12 (12)	1.88±0.10 (12)	2.60±0.16 (12)	1.63±0.09 (10)
Linyphia peltata	Female	1.56±0.07 (28)	1.02±0.09 (28)	1.31±0.14 (28)	0.52±0.04 (14)
	Male	2.10±0.17 (9)	1.23±0.11 (9)	1.53±0.15 (9)	0.69±0.05 (14)
Metellina segmentata	Female	2.94±0.36 (37)	1.94±0.22 (37)	2.41±0.24 (37)	0.95±0.11 (10)
	Male	3.93±0.35 (25)	2.13±0.15 (25)	2.60±0.20 (25)	0.99±0.07 (10)
Metellina mengei	Female	2.41±0.16 (18)	1.51±0.06 (18)	1.90±0.09 (18)	0.89±0.10 (10)
	Male	3.50±0.21 (22)	1.57±0.07 (22)	1.99±0.09 (22)	0.94±0.09 (10)

Table 20.4: The values for t-tests, t(degree of freedom) on the size differences between adult males and females of the four spider species, ** highly significant $P<0.001$, * significant $P<0.05$, NS not significant $P>0.05$.

Species	Tibia 1	Cephalothorax breadth	Cephalothorax length	Chelicera length
Linyphia triangularis	13.24 (58) **	6.48 (55) **	4.37 (55) **	17.02 (19) **
Linyphia peltata	9.28 (35) **	5.20 (35) **	3.89 (35) **	9.94 (26) **
Metellina segmentata	10.78 (60) **	4.04 (60) **	3.38 (60) *	0.97 (18) Ns
Metellina mengei	18.62 (38) **	2.92 (38) *	3.15 (38) *	1.18 (18) NS

Fig.20.11: Male of *Linyphia triangularis* with large chelicera.

Discussion

In general terms the mating behaviour of the four species is similar, and typical of web building spiders, in that the males cease web building on moulting to adult and take up a vagrant life in search of mature females. Mating takes place on the female's web and courtship involves the male vibrating the web of the female and touching her with his front legs. There are, however, differences both between and within genera with regard to the details of the mating behaviour. Some of these differences are indicated in Table 20.5 and their significance will be discussed - particularly with respect to sexual dimorphism. The four species are exceptions to the general trend in spiders in that although sexual dimorphism occurs it is the reverse of the general trend in that the males are larger than the females (Tables 20.3 & 20.4).

It is an obvious fact that to effect mating in web spinning spiders one of the sexes has to take up a vagrant life style and search for a mate. Energy requirements for gamete production are much higher in females and hence it is to be expected that the female will continue to construct a food catching web while the male devotes his energies to finding mature females. Adult males die soon after the mating period and feed infrequently (if at all) and their body weight declines during the breeding season (Chapter 11).

Table 20.5: Differences in the mating behaviour of spiders of the genera Metellina and Linyphia .

	Metellina	Linyphia
Web reduction	Absent	Present
Food sharing	Present	Absent
Duration of copulation	Short	Long
"Functional" sex ratio	Males = Females	Males > Females
Female to male aggression	High	Low
Male to male aggression	Moderate	High

Table 20.6: Female sizes, of four features, expressed as a percentage of the size of the same feature in the males of the four species.

Species	Tibia 1	Cephalothorax breadth	Cephalothorax length	Chelicera length
Linyphia triangularis	83.6	88.3	91.2	58.9
Linyphia peltata	74.3	82.9	85.6	75.4
Metellina segmentata	74.8	91.1	92.7	96.0
Metellina mengei	68.9	96.2	95.5	94.7

The sex ratio of both Linyphia and Metellina species is approximately 1:1 (Chapter 14). Males of the Linyphia species tend to moult to adult in advance of the females and this result in a bias in the sex ratio in favour of males in the early stages of the courtship period. In a functional sense this probably extends to the whole mating period as L. triangularis females are reported to mate only once (Rovner 1968) and hence the number of receptive females will always be outnumbered by the number of courting males. A consequence of this is that there is intense competition amongst males. This manifests itself in the form of territorial behaviour displayed by resident males on female webs. In all four species the male will defend a female's web even if the female is absent from the web. It is widely accepted, on the basis of evolutionary theory, that conflict between conspecifics is reduced by the substitution of ritulized threat behaviour for fighting (Maynard Smith & Price 1973). This behaviour allows the individuals to assess their potential competitors and to resolve conflict before physical damage occurs. Very often this involves assessing the size of an opponent and on the basis of this deciding whether to continue, or to break off, the confrontation.

In the case of Linyphia males, casual observation indicated that larger individuals were more likely to drive off smaller ones. The conspicuous chelicerae, which play an important part in male fighting, may be a good indicator of spider size or strength. In this respect they may serve the same function as antlers in male deer (Clutton-Brock et al 1982).

In Metellina species the sexes mature at approximately the same time and hence competition amongst males is likely to be less intense than in Linyphia . Observations confirmed that although males did compete for female webs this was less intense than in Linyphia . This reduced level of male conflict may be reflected in the fact that males of Metellina do not show sexual dimorphism with regard to the chelicerae (Table 20.3).

Although sexual dimorphism occurs in all four species, with the males being larger than the females, it is more marked in Linyphia than in Metellina . This is indicated in Table 20.6, where the size of the structure in the female is expressed as a percentage of the same structure in the male. Thus the difference in body size (cephalothorax dimensions) between the sexes is greater in Linyphia than in Metellina and the difference is even more striking with respect to chelicerae. With regard to the length of the front legs (as reflected by the length of tibia 1) the trend is reversed with Metellina males tending to show a greater difference than those for Linyphia . The front legs play an important role in tactile stimulation of the female and also in "Spar fighting" in the *Metellina* species and also play a part in aggressive displays between males. The longer front legs are clearly advantageous in reducing the possibility of injury in encounters with conspecifics. It is noteworthy that female aggression towards males occurs in *Metellina* but not in *Linyphia* (Table 20.5). The longer front legs of *Metellina* males, compared with those of *Linyphia* , may reflect the need for *Metellina* males to keep as much distance as possible between themselves and the females while indulging in tactile stimulation. The larger body size and chelicerae in *Linyphia* males might account for the fact that there is no female aggression towards the male.

Web reduction is present in the *Linyphia* species but not in *Metellina* and it is more prevalent in *L. triangularis* than in *L. peltata* . Four possible functions have been postulated for this behaviour: (a) It restricts the female's movements during courtship (b) It reduces the territorial area which the resident male has to defend against rivals (c) It reduces the likelihood of copulation being interrupted by prey becoming ensnared in the web. (d) It reduces the release of male attracting pheromone from the female's web (Van Helsdingen 1965; Rovner 1968; Watson 1986). These explanations are not mutually exclusive, but Watson (1986) has presented convincing evidence that emanation of pheromone from the web of a receptive female is the proximate factor which triggers the behaviour.

The absence of web reduction in *Metellina* species is not surprising as such behaviour would be a high risk strategy for the male in the light of the level of female aggression towards the male. Web reduction and sexual dimorphism is more marked in *L. triangularis* than in *L. peltata* . It may be that species with relatively larger males are more likely to indulge in web reduction. A comparative study of a number of species in the genus, with regard to these two features, might prove illuminating.

Food sharing in *Metellina* was first recorded by Menge (1866). It would appear to be a strategy to inhibit female aggression towards the male. It is perhaps significant that it does not occur in *Linyphia* species - where the sexual dimorphism is greater than in *Metellina* . In the orb web spider *Nephila edulis* , where the male is very much smaller than the female, the male copulates with the female while she is feeding. An extension of this type of behaviour is found in the non-web building spider *Pisaura mirabilis* where the male catches a prey item and presents it to the female. Copulation occurs while the female is consuming this meal (Bristowe 1926; Austad & Thornhill 1986).

The duration of copulation is strikingly shorter in *Metellina* than in *Linyphia* and this may reflect the higher level of aggression displayed by *Metellina* females.

Appendix 1: The results of laboratory feeding experiments on *Metellina segmentata*

Table 1: Results of laboratory feeding experiments on 1st instar of the spider *Metellina segmentata* (expressed as joules unless otherwise indicated).

Spider Number	Initial Weight (mg)	Final Weight (mg)	Weight Increase (mg)	Weight Increase	Exuvia	Food Killed	Food Remains	Food Consumed	Growth Efficiency (%)	Ingestion Efficiency (%)	Duration (days)
S2	0.35	0.73	0.38	2.95	0.14	17.84	10.80	7.04	43.9	39.5	7
S3	0.39	0.89	0.50	3.81	0.21	23.69	12.57	11.12	36.2	46.9	8
S5	0.38	0.90	0.52	3.95	0.23	19.81	10.84	8.97	46.6	45.3	7
S9	0.36	0.88	0.52	3.95	0.21	17.94	7.92	10.02	41.5	55.9	7
S13	0.29	0.93	0.64	4.84	0.21	24.08	13.42	10.66	47.4	44.3	8
S19	0.31	1.22	0.91	6.81	0.25	30.85	17.20	13.65	51.7	44.3	10
S21	0.33	0.78	0.45	3.45	0.16	23.49	13.54	9.95	36.3	42.4	9
S22	0.28	0.88	0.60	4.55	0.19	27.03	14.89	12.14	39.0	44.9	8
S25	0.33	0.75	0.42	3.24	0.21	16.52	9.12	7.40	46.6	44.8	7
S26	0.37	1.19	0.82	6.16	0.25	27.88	14.48	13.40	47.8	48.1	9
S28	0.29	0.80	0.51	3.88	0.16	24.66	14.99	9.67	41.8	39.2	7
S29	0.34	0.92	0.58	4.41	0.25	26.98	15.70	11.28	41.3	41.8	7
S4	0.32	0.57	0.25	1.99	0.16	18.64	13.97	4.67	46.0	25.1	11
S7	0.34	0.87	0.53	4.05	0.19	22.57	12.96	9.61	44.1	42.6	8
S17	0.33	0.69	0.36	2.80	0.16	19.35	12.11	7.24	40.9	37.4	10
S24	0.32	0.87	0.55	4.19	0.19	25.66	15.06	10.60	41.3	41.3	9
Mean	0.33	0.87	0.53	4.06	0.20	22.94	13.10	9.85	43.24	42.75	8.25
±S.D.	± 0.03	± 0.16	± 0.16	± 1.19	± 0.04	± 4.21	± 2.47	± 2.39	± 4.28	± 6.33	±1.29

Table 2: Results of laboratory feeding experiments on 2nd instar of the spider <u>Metellina segmentata</u> (expressed as joules unless otherwise indicated).

Spider Number	Initial Weight (mg)	Final Weight (mg)	Weight Increase (mg)	Weight Increase	Exuvia	Food Killed	Food Remains	Food Consumed	Growth Efficiency (%)	Ingestion Efficiency (%)	Duration (days)
S2	0.73	2.12	1.39	10.33	0.43	34.73	11.63	23.10	46.6	66.5	13
S3	0.89	1.78	0.89	6.66	0.31	25.91	7.55	18.36	38.0	70.9	12
S5	0.9	1.86	0.96	7.19	0.37	29.15	11.14	18.01	42.0	61.8	13
S9	0.88	1.94	1.06	7.91	0.43	33.22	13.51	19.71	42.3	59.3	15
S13	0.93	2.25	1.32	9.80	0.41	46.52	19.71	26.81	38.1	57.6	16
S19	1.22	2.59	1.37	10.18	0.45	47.72	17.91	29.81	35.7	62.5	14
S21	0.78	2.08	1.35	9.66	0.41	44.77	21.66	23.11	43.6	51.6	13
S22	0.88	2.54	1.66	12.29	0.43	57.73	23.85	33.88	37.5	58.7	16
S25	0.75	2.92	2.17	16.03	0.49	72.09	31.15	40.94	40.4	56.8	15
S26	1.19	2.12	0.93	6.97	0.41	44.52	22.70	21.82	33.8	49.0	14
S28	0.80	2.51	1.71	12.65	0.49	68.96	31.49	37.47	35.1	54.3	14
S29	0.92	1.89	0.97	7.26	0.35	37.26	18.12	19.14	39.8	51.4	12
S4	0.57	1.34	0.77	5.80	0.35	28.66	12.39	16.27	37.8	56.8	14
S7	0.87	2.57	1.70	12.58	0.39	60.49	26.43	34.06	38.1	56.3	13
S17	0.69	1.85	1.16	8.65	0.33	38.48	13.84	24.64	36.4	64.0	15
S24	0.87	1.92	1.05	7.84	0.39	38.90	17.75	21.15	38.9	54.4	13
Mean ±S.D.	0.87 ± 0.16	2.14 ± 0.40	1.28 ± 0.38	9.49 ± 2.78	0.40 ± 0.05	44.32 ±14.09	18.80 ± 7.09	25.52 ± 7.56	39.03 ± 3.32	58.24 ± 5.82	13.88 ±1.26

Table 3: Results of laboratory feeding experiments on 3rd instar of the spider <u>Metellina</u> <u>segmentata</u> (expressed as joules unless otherwise indicated)

Spider Number	Initial Weight (mg)	Final Weight (mg)	Weight Increase (mg)	Weight Increase	Exuvia	Food Killed	Food Remains	Food Consumed	Growth Efficiency (%)	Ingestion Efficiency (%)	Duration (days)
S2	2.12	6.65	4.53	28.85	1.46	122.41	40.51	81.90	37.0	66.9	27
S3	1.78	5.12	3.34	21.42	0.97	71.50	16.09	55.41	40.4	77.5	24
S5	1.86	5.15	3.29	21.11	1.07	76.21	15.19	61.02	36.3	80.1	21
S9	1.94	5.67	3.73	23.86	1.07	91.02	22.93	68.09	36.6	74.8	20
S13	2.25	5.66	3.41	21.85	1.39	93.31	26.80	66.51	34.9	71.3	22
S19	2.59	4.62	2.03	13.25	0.86	64.63	21.36	43.27	32.6	67.0	19
S21	2.08	4.69	2.61	16.87	0.88	68.41	17.45	50.96	34.8	74.5	23
S22	2.54	6.22	3.68	23.55	1.32	99.16	32.07	67.10	37.1	67.7	22
S25	2.92	5.43	2.51	16.25	0.98	78.84	25.55	53.29	32.1	67.6	24
S26	2.12	6.48	4.36	27.79	1.07	116.71	31.56	85.15	33.9	73.0	22
S28	2.51	4.44	1.93	12.63	0.78	71.72	20.37	51.35	26.1	71.6	21
S29	1.89	4.28	2.39	15.50	0.86	70.23	21.29	48.94	33.4	69.7	23
S4	1.34	1.81	0.47	3.52	0.23	79.89	37.78	42.11	8.9	52.7	24
S7	2.57	4.02	1.45	9.63	0.99	75.23	21.27	53.96	19.7	71.7	26
S17	1.85	3.58	1.73	11.38	0.84	94.56	39.62	54.94	22.2	58.1	23
S24	1.92	2.14	0.22	1.97	0.51	25.76	14.11	11.65	21.3	45.2	25
Mean ±S.D.	2.14 ± 0.40	4.75 ± 1.39	2.61 ± 1.27	16.84 ± 7.90	0.95 ± 0.31	81.22 ±22.49	25.25 ± 8.68	55.98 ± 17.04	30.47 ± 8.47	68.08 ± 9.11	22.88 ±2.13

Table 4: Results of laboratory feeding experiments on 4th instar (sub-adult females) of the spider <u>Metellina segmentata</u> (expressed as joules unless otherwise indicated).

Spider Number	Initial Weight (mg)	Final Weight (mg)	Weight Increase (mg)	Weight Increase	Exuvia	Food Killed	Food Remains	Food Consumed	Growth Efficiency (%)	Ingestion Efficiency (%)	Duration (days)
S2	6.65	14.21	7.56	38.74	3.76	151.85	47.66	104.19	40.8	68.6	33
S5	5.15	14.20	9.05	47.95	3.02	175.03	51.13	123.90	41.1	70.8	28
S13	5.66	12.49	6.83	34.24	2.92	102.53	17.85	84.68	43.9	82.6	28
S19	4.62	8.59	3.97	16.57	2.55	91.31	29.31	62.00	30.8	67.9	29
S21	4.69	11.71	7.02	35.42	2.88	141.59	36.03	105.56	36.3	74.6	34
S22	6.22	14.31	8.09	42.03	3.25	145.25	30.57	114.68	39.5	79.0	28
S26	6.49	12.11	5.63	26.82	2.80	98.28	20.87	77.41	38.3	78.8	29
S29	4.28	12.26	7.98	41.34	2.98	130.99	25.13	105.86	41.9	80.8	32
S1a	4.88	13.97	9.09	48.19	3.43	166.86	45.27	121.59	42.5	72.9	31
S7a	6.72	15.73	9.03	47.83	4.09	169.71	40.83	128.88	40.3	75.9	25
S10a	5.81	14.58	8.77	46.23	3.00	121.19	17.38	103.81	47.4	85.7	29
S12a	3.96	11.45	7.49	38.32	2.76	144.34	30.4	113.94	36.1	78.9	28
Mean ±S.D.	5.43 ± 0.96	12.97 ± 1.92	7.54 ± 1.54	38.64 ± 9.51	3.12 ± 0.44	136.58 ±28.33	32.70 ±11.57	103.88 ± 19.97	40.73 ± 3.46	76.38 ± 5.59	29.50 ±2.54

Table 5: Results of laboratory feeding experiments on 4th instar (sub-adult males) of the spider Metellina segmentata (expressed as joules unless otherwise indicated).

Spider Number	Initial Weight (mg)	Final Weight (mg)	Weight Increase (mg)	Weight Increase	Exuvia	Food Killed	Food Remains	Food Consumed	Growth Efficiency (%)	Ingestion Efficiency (%)	Duration (days)
S3	5.12	11.73	6.61	35.63	2.98	121.22	29.79	91.43	42.2	75.4	31
S9	5.67	14.10	8.43	47.41	3.17	162.13	35.22	126.91	39.9	78.3	32
S25	5.43	12.79	7.36	40.49	3.00	141.22	24.66	116.56	37.3	82.5	28
S28	4.44	11.84	7.47	40.75	3.06	150.14	40.78	109.36	40.1	72.8	29
S8a	5.10	11.46	6.36	34.02	2.96	126.31	33.99	92.32	39.9	73.1	29
S17a	7.38	16.54	9.16	52.13	3.48	185.89	36.76	146.13	38.1	78.6	29
S18a	8.28	16.67	8.39	47.15	3.25	195.96	58.75	137.21	36.7	70.0	30
S20a	5.77	11.45	5.68	29.63	2.84	96.29	17.64	78.65	41.3	81.7	32
Mean ±S.D.	5.90 ± 1.28	13.32 ± 2.21	7.42 ± 1.18	40.90 ± 7.65	3.08 ± 0.21	147.40 ±33.48	35.07 ±12.29	112.39 ± 23.76	39.30 ± 1.96	76.55 ± 4.46	30.00 ±1.51

Table 6: Results of laboratory feeding experiments on 5th instar (adult females), which produced egg sacs, of the spider Metellina segmentata (expressed as joules unless o therwise indicated).

Spider Number	Initial Weight (mg)	Final Weight (mg)	Weight Increase (mg)	Weight Increase	Food Killed	Food Remains	Food Consumed	Growth Efficiency (%)	Ingestion Efficiency (%)	Duration (days)
S2	14.21	53.67	39.46	338.57	771.29	123.19	648.10	52.2	84.0	37
S22	14.31	56.27	41.96	363.33	917.46	137.18	780.28	46.6	85.0	45
S29	12.26	63.20	50.94	452.29	1062.63	139.18	923.45	49.0	86.9	35
S10a	14.58	68.31	53.73	479.90	1037.85	154.52	883.33	54.3	85.1	35
Mean ±S.D.	13.84 ± 1.06	60.36 ± 6.65	46.52 ± 6.88	408.52 ± 68.18	947.31 ±133.38	138.52 ±12.82	808.79 ±122.93	50.53 ± 3.41	85.25 ± 1.21	38.00 ±4.76

Appendix 2: Results of laboratory feeding experiments on *Linyphia triangularis*

Table 1: Results of laboratory feeding experiments on 1st instar of the spider *Linyphia triangularis* (expressed as joules unless otherwise indicated).

Spider Number	Initial Weight (mg)	Final Weight (mg)	Weight Increase (mg)	Weight Increase	Exuvia	Food Killed	Food Remains	Food Consumed	Growth Efficiency (%)	Ingestion Efficiency (%)	Duration (days)
Lt1	0.24	0.80	0.56	3.13	0.22	22.98	16.49	6.49	51.6	28.2	8
Lt2	0.23	0.68	0.45	2.39	0.18	27.08	20.79	6.29	40.9	23.2	7
Lt3	0.19	0.73	0.54	3.00	0.18	18.82	12.43	6.39	49.8	34.0	7
Lt4	0.21	0.63	0.42	2.19	0.16	14.49	10.04	4.45	52.8	30.7	9
Lt5	0.26	0.85	0.59	3.33	0.22	35.15	25.57	9.58	37.1	27.3	6
Lt6	0.22	0.79	0.57	3.20	0.20	24.01	16.73	7.28	46.7	30.3	7
Lt7	0.25	0.67	0.42	2.19	0.10	26.37	20.08	6.29	36.4	23.9	11
Lt8	0.23	0.88	0.65	3.73	0.18	18.46	12.19	6.27	62.4	34.0	9
Lt9	0.20	0.57	0.37	1.86	0.22	20.18	15.30	4.88	42.6	24.2	13
Lt10	0.23	0.73	0.50	2.73	0.14	20.44	14.58	5.86	49.0	28.7	12
Lt11	0.24	0.93	0.69	4.00	0.28	35.66	24.38	11.28	37.9	31.6	7
Lt12	0.22	0.91	0.69	4.00	0.28	30.13	21.99	8.14	52.6	27.0	6
Lt13	0.22	0.78	0.56	3.13	0.24	21.46	14.82	6.64	50.7	31.0	8
Lt14	0.21	0.67	0.46	2.46	0.20	29.39	23.42	5.97	44.6	20.3	7
Lt15	0.23	0.74	0.51	2.79	0.20	21.92	16.49	5.43	55.1	24.8	9
Mean	0.23	0.76	0.53	2.94	0.20	24.44	17.69	6.75	47.3	27.9	8.40
±S.D.	± 0.02	± 0.11	± 0.10	± 0.66	± 0.05	± 6.13	± 4.17	± 1.76	± 7.4	± 4.1	± 2.13

Table 2: Results of laboratory feeding experiments on 2nd instar of the spider <u>Linyphia</u> <u>triangularis</u> (expressed as joules unless otherwise indicated).

Spider Number	Initial Weight (mg)	Final Weight (mg)	Weight Increase (mg)	Weight Increase	Exuvia	Food Killed	Food Remains	Food Consumed	Growth Efficiency (%)	Ingestion Efficiency (%)	Duration (days)
Lt1	0.80	2.31	1.51	9.48	0.49	71.16	40.48	30.69	32.5	43.1	13
Lt2	0.68	2.73	2.05	13.09	0.59	81.80	48.94	32.87	41.6	40.2	12
Lt3	0.73	2.24	1.51	9.49	0.51	89.48	53.97	35.51	28.1	39.7	19
Lt4	0.63	2.11	1.48	9.28	0.55	54.92	31.19	23.74	41.4	43.2	16
Lt5	0.85	2.96	2.11	13.49	0.65	78.92	48.40	30.57	46.3	38.7	15
Lt6	0.79	2.63	1.84	11.68	0.63	88.85	52.25	36.69	33.6	41.3	14
Lt8	0.88	2.34	1.46	9.14	0.47	44.96	21.49	23.47	41.0	52.2	16
Lt9	0.57	1.92	1.35	8.41	0.39	51.36	27.40	23.96	36.7	46.7	11
Lt10	0.73	2.83	2.10	13.42	0.55	72.52	41.82	30.70	45.5	42.3	14
Lt11	0.93	2.34	1.41	8.81	0.47	74.82	43.73	31.09	29.8	41.6	18
Lt12	0.91	1.97	1.06	6.47	0.43	60.77	39.63	21.14	32.7	34.8	16
Lt13	0.78	2.08	1.30	8.07	0.43	51.28	27.36	23.92	35.6	46.7	14
Lt14	0.67	2.13	1.46	9.14	0.71	46.25	21.64	24.62	40.0	53.2	24
Mean ±S.D.	0.77 ± 0.11	2.35 ± 0.34	1.59 ± 0.33	10.00 ± 2.22	0.53 ± 0.10	66.71 ±15.94	38.33 ±11.38	28.38 ± 5.12	37.3 ± 5.8	43.4 ± 5.2	15.54 ± 3.38

Table 3: Results of laboratory feeding experiments on 3rd instar of the spider Linyphia triangularis (expressed as joules unless otherwise indicated).

Spider Number	Initial weight (mg)	Final weight (mg)	Weight Increase (mg)	Weight Increase	Exuvia	Food Killed	Food Remains	Food Consumed	Growth Efficiency (%)	Ingestion Efficiency (%)	Duration (days)
Lt1	2.71	5.29	2.58	17.34	1.04	92.59	32.40	60.19	30.5	65.0	20
Lt2	2.20	3.32	1.12	6.87	0.78	56.79	25.62	31.17	24.5	54.9	18
Lt3	2.39	3.76	1.37	8.54	0.92	50.65	16.39	34.26	27.6	67.6	26
Lt4	1.97	4.33	2.36	15.16	1.29	62.76	16.00	46.76	35.2	74.5	20
Lt5	2.36	6.87	4.51	29.52	1.37	176.07	72.52	103.54	29.8	58.8	19
Lt6	2.51	5.27	2.76	17.83	1.13	153.83	46.77	107.07	17.7	69.6	18
Lt7	2.18	4.61	2.43	15.62	1.17	158.54	80.85	77.69	21.6	49.0	26
Lt8	2.58	4.25	1.67	10.55	0.96	83.08	31.82	51.27	22.4	61.7	18
Lt9	2.25	3.93	1.68	10.61	0.78	70.08	28.87	41.21	27.6	58.8	17
Lt10	2.37	5.62	3.25	21.10	1.35	87.25	23.96	63.29	35.5	72.5	15
Lt11	3.38	5.12	1.74	11.01	1.27	57.82	18.15	39.67	31.0	68.6	18
Lt12	2.47	4.36	1.89	12.02	0.88	99.13	39.86	59.27	21.8	59.8	17
Lt13	2.76	6.17	3.41	22.17	1.50	83.99	25.54	58.46	40.5	69.6	17
Lt14	2.15	4.13	1.98	12.62	1.06	100.04	47.09	52.95	25.8	52.9	16
Lt15	2.93	4.67	1.74	11.01	0.98	58.10	17.10	41.01	29.3	70.6	19
Mean ±S.D.	2.54 ± 0.45	4.84 ± 1.02	2.30 ± 0.90	14.80 ± 6.01	1.10 ± 0.22	92.71 ± 39.82	34.86 ±19.79	57.85 ±22.82	28.1 ± 6.1	63.6 ± 7.7	18.93 ± 3.17

Table 4: Results of laboratory feeding experiments on 4th instar (sub-adult females) of the spider <u>Linyphia triangularis</u> (expressed as joules unless otherwise indicated).

Spider Number	Initial Weight (mg)	Final Weight (mg)	Weight Increase (mg)	Weight Increase	Exuvia	Food Killed	Food Remains	Food Consumed	Growth Efficiency (%)	Ingestion Efficiency (%)	Duration (days)
Lt1	5.29	8.68	3.39	23.75	2.01	140.25	46.35	43.90	27.4	67.0	36
Lt2	3.32	11.48	8.16	53.18	2.19	207.51	38.98	168.53	32.9	81.2	35
Lt3	3.76	11.94	8.18	53.30	1.97	211.21	50.22	160.98	34.3	76.2	30
Lt4	4.23	9.23	5.00	33.68	2.03	158.77	43.49	115.28	31.0	72.6	35
Lt5	6.87	12.36	5.49	36.70	2.50	114.99	20.78	94.21	41.6	81.9	32
Lt6	6.27	16.37	10.10	65.14	2.69	222.56	43.99	178.57	38.0	80.2	33
Lt7	4.61	7.98	3.37	23.63	1.91	194.87	79.11	115.72	22.1	59.4	28
Lt8	4.25	11.98	7.73	50.52	2.30	234.25	75.76	158.50	33.3	67.7	34
Mean ±S.D.	4.83 ± 1.23	11.25 ± 2.67	6.43 ± 2.47	42.49 ± 15.24	2.20 ± 0.28	185.55 ± 42.62	49.84 ±19.19	135.71 ± 34.56	32.6 ± 6.0	73.3 ± 8.1	32.88 ± 2.75

Table 5: Results of laboratory feeding experiments on 4th instar (sub-adult males) of the spider <u>Linyphia triangularis</u> (expressed as joules unless otherwise indicated).

Spider Number	Initial Weight (mg)	Final Weight (mg)	Weight Increase (mg)	Weight Increase	Exuvia	Food Killed	Food Remains	Food Consumed	Growth Efficiency (%)	Ingestion Efficiency (%)	Duration (days)
Lt9	3.93	8.96	5.03	34.20	2.03	153.03	36.39	116.64	31.1	76.2	27
Lt10	5.62	14.31	5.69	58.33	2.46	156.07	28.21	127.87	47.5	81.9	33
Lt11	5.12	13.25	8.13	54.63	2.32	202.47	44.08	158.39	36.0	78.2	24
Lt12	4.36	17.24	12.88	85.94	2.75	255.74	50.84	204.90	43.3	81.1	30
Lt13	6.17	13.81	7.64	51.40	2.42	270.86	77.29	193.57	27.8	71.5	31
Lt14	4.13	12.25	8.12	54.57	2.19	219.24	54.22	165.02	34.4	75.3	31
Lt15	4.67	9.26	4.59	31.31	1.82	206.33	72.38	133.95	24.7	64.9	29
Mean ±S.D.	4.86 ± 0.82	12.73 ± 2.91	7.87 ± 2.73	52.91 ±18.00	2.28 ± 0.30	209.11 ± 44.91	51.92 ± 17.95	157.19 ± 33.43	35.0 ± 8.2	75.6 ± 5.9	29.29 ± 2.98

Table 6: Results of laboratory feeding experiments on 5th instar (adult females), which produced egg sacs, of the spider Linyphia triangularis (expressed as joules unless otherwise indicated).

Spider Number	Initial Weight (mg)	Final Weight (mg)	Weight Increase (mg)	Weight Increase	Food Killed	Food Remains	Food Consumed	Growth Efficiency (%)	Ingestion Efficiency (%)	Duration (days)
Lt1	8.68	32.34	23.66	169.49	677.31	122.49	554.82	30.6	81.9	54
Lt2	11.45	27.29	15.81	94.96	328.26	64.39	263.87	36.0	80.4	59
Lt4	9.23	34.95	25.72	189.05	504.56	84.12	420.44	45.0	83.3	57
Lt5	12.36	35.36	23.00	163.22	503.29	98.72	404.57	40.3	80.4	66
Lt6	16.37	39.26	22.89	162.18	463.73	72.77	390.97	41.5	84.3	67
Lt8	11.98	29.24	17.26	108.72	483.13	99.50	383.63	28.3	79.4	59
Mean ±S.D.	11.68 ± 2.74	33.07 ± 4.38	21.39 ± 3.92	147.94 ± 37.24	493.38 ±111.63	90.33 ±21.02	403.05 ± 92.99	36.95 ± 6.52	81.62 ± 1.90	60.33 ± 5.13

Appendix 3: Results of laboratory feeding experiments on *Metellina mengei*

Table 1: Results of laboratory feeding experiments on 1st instar of the spider <u>Metellina mengei</u> (expressed as joules unless otherwise indicated).

Spider Number	Initial Weight (mg)	Final Weight (mg)	Weight Increase (mg)	Weight Increase	Exuvia	Food Killed	Food Remains	Food Consumed	Growth Efficiency (%)	Ingestion Efficiency (%)	Duration (days)
M1a	0.18	0.53	0.35	2.58	0.12	10.48	4.83	5.65	47.8	53.9	8
M2a	0.17	0.47	0.3	2.35	0.12	12.43	6.22	6.21	39.8	50.0	7
M3a	0.14	0.41	0.27	2.11	0.10	10.97	6.22	4.75	46.5	43.3	6
M4a	0.18	0.62	0.44	3.29	0.16	15.84	9.44	6.4	53.9	40.4	9
Mean	0.17	0.51	0.34	2.58	0.13	12.43	6.63	5.72	47.13	46.73	7.50
±S.D.	± 0.02	± 0.09	± 0.07	± 0.51	± 0.03	± 2.42	± 1.95	± 0.72	± 5.33	± 6.08	± 1.29

Table 2: Results of laboratory feeding experiments on 2nd instar of the spider Metellina mengei (expressed as joules unless otherwise indicated).

Spider Number	Initial Weight (mg)	Final Weight (mg)	Weight Increase (mg)	Weight Increase	Exuvia	Food Killed	Food Remains	Food Consumed	Growth Efficiency (%)	Ingestion Efficiency (%)	Duration (days)
M1a	0.53	0.99	0.46	3.52	0.25	19.01	8.98	10.03	37.6	52.8	20
M2a	0.47	1.23	0.76	5.64	0.39	34.12	18.42	15.70	38.4	46.0	15
M3b	0.61	1.16	0.55	3.99	0.35	34.61	20.03	14.58	29.8	42.1	18
M4b	0.67	1.54	0.87	6.34	0.37	34.36	14.96	19.40	34.6	56.5	17
M5b	0.52	1.31	0.79	5.87	0.27	29.24	13.12	16.12	38.1	55.1	22
M6b	0.57	1.33	0.76	5.64	0.29	32.66	11.74	20.92	28.3	64.1	19
M7b	0.50	1.19	0.69	5.17	0.23	28.27	15.19	13.08	41.3	46.3	22
M8b	0.48	1.07	0.59	4.46	0.25	26.81	13.35	13.46	35.0	50.2	18
M9b	0.62	1.35	0.73	5.40	0.35	27.94	12.66	15.28	37.6	54.7	20
M10b	0.53	0.85	0.32	2.35	0.21	25.34	13.12	12.22	20.9	48.2	18
M11b	0.56	0.97	0.41	3.05	0.23	30.22	16.34	13.88	23.6	45.9	19
M12b	0.60	1.61	1.01	7.28	0.29	30.95	12.5	18.45	41.0	59.6	21
M13b	0.55	1.59	1.04	7.51	0.27	35.58	16.57	19.01	40.9	53.4	17
M14b	0.51	1.40	0.89	6.57	0.23	33.39	12.2	21.19	32.1	63.5	19
M15b	0.47	1.27	0.80	5.87	0.25	29.73	13.81	15.92	38.4	53.5	23
Mean ±S.D.	0.55 ± 0.06	1.26 ± 0.23	0.71 ± 0.21	5.24 ± 1.51	0.28 ± 0.06	30.15 ± 4.38	14.20 ± 2.79	15.93 ± 3.26	34.55 ± 6.39	52.73 ± 6.42	19.20 ± 2.18

Table 3: Results of laboratory feeding experiments on 3rd instar of the spider *Metellina mengei* (expressed as joules unless otherwise indicated).

Spider Number	Initial Weight (mg)	Final Weight (mg)	Weight Increase (mg)	Weight Increase	Exuvia	Food Killed	Food Remains	Food Consumed	Growth Efficiency (%)	Ingestion Efficiency (%)	Duration (days)
M1a	0.99	1.89	0.90	6.10	0.35	36.07	14.27	21.8	29.6	60.4	31
M2a	1.23	2.31	1.08	7.28	0.39	37.29	13.35	23.94	32.0	64.2	27
M3b	1.16	1.83	0.67	4.70	0.33	39.24	18.88	20.36	24.7	51.9	25
M4b	1.54	3.12	1.58	10.33	0.51	49.71	21.18	28.53	38.0	57.4	34
M5b	1.31	2.89	1.58	10.33	0.47	51.66	19.57	32.09	33.7	62.1	29
M6b	1.33	3.26	1.93	12.44	0.53	59.71	18.65	41.06	31.6	68.8	35
M7b	1.19	2.45	1.26	8.22	0.39	47.03	17.73	29.3	29.4	62.3	29
M8b	1.07	2.17	1.10	7.28	0.35	44.84	17.03	27.81	27.4	62.0	28
M9b	1.35	3.06	1.71	11.04	0.47	61.90	28.08	33.82	34.0	54.6	32
M10b	0.85	2.99	2.14	13.62	0.47	78.47	31.08	47.39	29.7	60.4	25
M11b	0.97	3.51	2.54	16.20	0.56	94.31	33.61	60.70	27.6	64.4	28
M12b	1.61	2.31	0.70	4.93	0.41	33.14	11.74	21.40	25.0	64.6	25
M13b	1.59	3.63	2.04	13.15	0.51	74.57	23.71	50.86	26.9	68.2	22
M14b	1.40	2.25	0.85	5.87	0.43	31.92	12.89	19.03	33.1	59.6	27
M15b	1.27	2.11	0.84	5.64	0.39	43.62	15.19	28.43	21.2	65.2	30
Mean	1.26	2.65	1.39	9.14	0.44	52.23	19.80	32.43	29.59	61.74	28.47
±S.D.	± 0.23	± 0.59	± 0.59	± 3.59	± 0.07	±18.32	± 6.68	±12.34	± 4.31	± 4.63	± 3.56

Table 4: Results of laboratory feeding experiments on 4th instar (sub-adult females) of the spider Metellina mengei (expressed as joules unless otherwise indicated).

Spider Number	Initial Weight (mg)	Final Weight (mg)	Weight Increase (mg)	Weight Increase	Exuvia	Food Killed	Food Remains	Food Consumed	Growth Efficiency (%)	Ingestion Efficiency (%)	Duration (days)
M8b	2.17	6.74	4.57	21.60	1.85	84.93	16.48	68.45	34.3	80.6	54
M10b	2.99	6.07	3.08	9.39	1.79	43.71	13.05	30.66	36.5	70.1	45
M11b	3.51	7.75	4.24	18.78	2.32	77.60	21.45	x 56.15	37.6	72.4	49
M14b	2.25	6.86	4.61	21.84	1.93	121.07	32.88	88.19	27.0	72.8	46
Mean	2.73	6.86	4.13	17.90	1.97	81.83	20.97	60.94	33.85	73.98	48.50
±S.D.	± 0.64	± 0.69	± 0.72	± 5.84	± 0.24	±31.73	± 8.66	±24.06	± 4.77	± 4.57	± 4.04

Table 5: Results of laboratory feeding experiments on 4th instar (sub-adult males) of the spider Metellina mengei (expressed as joules unless otherwise indicated).

Spider Number	Initial Weight (mg)	Final Weight (mg)	Weight Increase (mg)	Weight Increase	Exuvia	Food Killed	Food Remains	Food Consumed	Growth Efficiency (%)	Ingestion Efficiency (%)	Duration (days)
M6b	3.26	7.71	4.45	23.01	2.18	87.23	22.00	65.23	38.6	74.8	47
M12b	2.31	7.13	4.82	25.83	2.10	110.89	21.29	89.60	31.2	80.8	56
M13b	3.63	6.18	2.55	7.75	1.50	53.76	16.69	37.07	25.0	69.0	39
Mean	3.07	7.01	± 3.94	18.86	1.93	83.96	19.99	63.97	31.60	74.87	47.33
±S.D.	± 0.68	± 0.77	1.22	± 9.73	± 0.37	±28.71	± 2.88	±26.29	± 6.81	± 5.90	± 8.50

Table 6: Results of laboratory feeding experiments on 5th instar (sub-adult females) of the spider <u>Metellina mengei</u> (expressed as joules unless otherwise indicated).

Spider Number	Initial Weight (mg)	Final Weight (mg)	Weight Increase (mg)	Weight Increase	Exuvia	Food Killed	Food Remains	Food Consumed	Growth Efficiency (%)	Ingestion Efficiency (%)	Duration (days)
M1	5.57	11.58	6.01	34.75	3.08	135.74	31.20	104.54	36.2	77.0	32
M5	6.09	13.72	7.63	47.66	3.08	192.04	55.55	136.49	37.2	71.1	32
M7	3.73	10.46	6.72	40.39	3.08	151.58	39.72	111.86	38.9	73.8	40
M8	7.37	14.21	6.84	41.32	3.70	136.23	27.90	108.33	41.6	79.5	35
M17	4.05	8.95	4.90	25.83	2.47	109.18	27.42	81.76	34.6	74.9	23
M18	5.45	9.29	3.84	17.14	3.08	103.33	28.13	75.20	26.9	72.8	25
M19	6.14	13.65	7.51	46.73	3.50	161.33	34.51	126.82	39.6	78.6	29
M21	5.54	12.74	7.20	44.38	3.08	154.99	30.02	124.97	38.0	80.6	36
M23	4.29	10.92	6.64	39.68	2.67	162.30	37.82	124.48	34.0	76.7	29
M24	5.54	10.95	5.41	29.82	2.47	110.15	24.59	85.56	37.7	77.7	23
Mean ±S.D.	5.38 ± 1.10	11.65 ± 1.87	2.27 ± 1.22	36.77 ± 9.86	3.02 ± 0.40	141.69 ±28.30	33.69 ± 9.06	108.03 ±21.10	36.46 ± 4.06	76.30 ± 3.04	30.40 ± 5.70

Table 7: Results of laboratory feeding experiments on 5th instar (sub-adult males) of the spider <u>Metellina</u> <u>mengei</u> (expressed as joules unless otherwise indicated).

Spider Number	Initial Weight (mg)	Final Weight (mg)	Weight Increase (mg)	Weight Increase	Exuvia	Food Killed	Food Remains	Food Consumed	Growth Efficiency (%)	Ingestion Efficiency (%)	Duration (days)
M2	3.97	9.93	5.96	34.28	2.88	159.62	40.19	119.43	31.1	74.8	33
M3	4.77	12.26	7.49	46.49	3.91	171.56	36.64	134.92	37.4	78.6	31
M4	5.92	13.05	7.13	43.67	3.91	172.3	42.32	129.98	36.6	75.4	34
M6	5.82	14.71	8.89	57.67	3.29	216.65	52.72	163.93	37.2	75.7	38
M9	6.57	14.29	7.72	48.37	4.11	212.51	53.43	159.08	33.0	74.9	29
M10	5.51	13.09	7.58	47.43	4.11	192.28	45.39	146.89	35.1	76.4	33
M11	5.12	12.90	7.78	48.84	3.29	165.47	33.81	131.66	39.6	79.6	28
M12	5.56	12.19	6.63	39.68	3.91	145.25	32.39	112.86	38.6	77.7	31
M13	6.03	11.73	5.70	32.17	3.29	130.87	30.50	100.37	35.3	76.7	33
M14	5.45	11.39	5.94	34.05	3.91	133.30	28.37	104.93	36.2	78.7	35
M15	5.27	12.59	7.32	45.32	3.05	161.57	32.86	128.71	37.6	79.7	29
M16	5.16	12.36	7.20	44.38	4.11	147.68	30.26	117.42	41.3	79.5	30
M20	5.70	12.21	6.51	38.74	4.52	150.61	29.55	121.06	35.7	80.4	38
M22	6.30	12.39	6.09	35.22	3.08	167.91	51.30	116.61	32.8	69.4	26
M25	5.52	11.85	6.33	37.33	3.08	153.29	40.42	112.87	35.8	73.6	24
Mean ±S.D.	5.51 ± 0.63	12.46 ± 1.13	6.95 ± 0.90	42.24 ± 7.09	3.63 ± 0.51	165.39 ±25.38	38.81 ± 8.85	126.75 ±18.45	36.22 ± 2.65	76.73 2.92	31.47 ± 4.00

Table 8: Results of laboratory feeding experiments on 6th instar (adult females) of the spider <u>Metellina mengei</u> in autumn 1981 (expressed as joules unless otherwise indicated).

Spider Number	Initial Weight (mg)	Final Weight (mg)	Weight Increase (mg)	Weight Increase	Food Killed	Food Remains	Food Consumed	Growth Efficiency (%)	Ingestion Efficiency (%)	Duration (days)
M1	11.58	18.67	7.09	40.52	127.94	21.82	106.12	38.2	83.0	33
M5	13.72	17.62	3.90	12.25	43.62	8.04	35.58	34.4	81.6	42
M7	10.46	18.78	8.32	51.52	162.55	26.19	136.36	37.8	83.9	37
M8	14.21	29.57	15.36	114.55	378.22	57.65	320.57	35.7	84.8	34
M17	8.95	14.57	5.62	27.51	123.56	19.07	104.49	26.3	84.6	38
M18	9.29	17.16	7.87	47.52	156.70	25.27	131.43	36.2	83.9	39
M19	13.65	21.01	7.36	43.02	128.19	24.81	103.38	41.6	80.6	40
M21	12.74	22.40	9.66	63.53	234.93	38.36	196.57	32.3	83.7	33
M23	10.92	16.98	6.06	31.51	102.84	20.67	82.17	38.3	79.9	39
M24	10.95	20.60	9.65	63.53	212.75	37.90	174.85	36.3	82.2	43
Mean ±S.D.	11.65 ±1.87	19.74 ±4.13	8.09 ±3.11	49.55 ±27.79	167.13 ±91.72	27.98 ±13.64	139.15 ±78.24	35.71 ±4.14	82.81 ±1.68	37.80 ±3.55

Table 9: Results of laboratory feeding experiments on 6th instar (adult females), which produced egg sacs, of the spider <u>Metellina mengei</u> in spring 1982 (expressed as joules unless otherwise indicated).

Spider Number	Initial Weight (mg)	Final Weight (mg)	Weight Increase (mg)	Weight Increase	Food Killed	Food Remains	Food Consumed	Growth Efficiency (%)	Ingestion Efficiency (%)	Duration (days)
M4s	8.92	24.75	15.83	126.54	369.21	67.99	301.22	42.0	81.6	36
M5s	10.11	28.63	18.52	152.11	404.30	68.68	335.62	45.3	83.0	31
Mean ±S.D.	9.52 ±0.84	26.69 ±2.74	17.18 ±1.90	139.33 ±18.08	386.76 ±24.81	68.34 ±00.49	318.42 ±24.32	43.65 ±2.33	82.30 ±0.99	33.50 ±3.54

ppendix 4: Results of hand collecting of the four species in Area 6 in 1980/81.

Table 1: The number of spiders of Metellina mengei, Linyphia peltata, Metellina segmentata, and Linyphia triangularis taken by hand collecting in Area 6 on 6/8/1980.

Site Number	M. mengei	L. peltata	M. segmentata	L. triangularis
42	10	1	1	0
155	17	0	0	0
214	3	2	2	0
17	12	6	0	0
188	8	0	0	0
34	10	0	0	0
210	6	4	0	0
19	8	1	1	0
Total	74	14	4	0

Table 2: The number of spiders of Metellina mengei, Linyphia peltata, Metellina segmentata, and Linyphia triangularis taken by hand collecting in Area 6 on 5/9/1980.

Site Number	M. mengei	L. peltata	M. segmentata	L. triangularis
66	29	9	0	0
22	40	2	1	0
58	28	3	2	0
117	13	7	0	0
190	26	0	0	0
197	6	1	0	0
120	28	2	6	0
47	34	6	8	0
Total	204	30	17	0

Table 3: The number of spiders of *Metellina mengei*, *Linyphia peltata*, *Metellina segmentata*, and *Linyphia triangularis* taken by hand collecting in Area 6 on 24/9/1980.

Site Number	*M. mengei*	*L. peltata*	*M. segmentata*	*L. triangularis*
112	36	17	0	0
21	19	5	0	0
219	21	12	0	0
135	3	2	0	0
175	4	3	0	0
144	10	0	0	0
170	17	4	0	0
192	11	4	0	0
77	33	7	0	0
134	20	2	0	0
Total	174	56	0	0

Table 4: The number of spiders of Metellina mengei , Linyphia peltata , Metellina segmentata , and Linyphia triangularis taken by hand collecting in Area 6 on 10/10/1980.

Site Number	M. mengei	L. peltata	M. segmentata	L. triangularis
274	48	13	1	0
241	19	8	0	1
163	44	11	2	0
251	25	13	0	0
280	40	3	0	0
109	28	3	0	0
229	31	8	1	0
52	34	8	0	0
12	32	8	0	0
184	31	15	0	0
Total	332	90	4	0

Table 5: The number of spiders of *Metellina mengei*, *Linyphia peltata*, *Metellina segmentata*, and *Linyphia triangularis* taken by hand collecting in Area 6 on 28/11/1980.

Site Number	*M. mengei*	*L. peltata*	*M. segmentata*	*L. triangularis*
126	1	0	0	0
74	5	0	1	0
89	5	1	1	0
138	2	1	0	0
137	0	1	0	0
69	8	1	0	0
238	8	2	1	0
260	4	1	0	0
Total	33	7	3	0

Table 6: The number of spiders of *Metellina mengei*, *Linyphia peltata*, *Metellina segmentata*, and *Linyphia triangularis* taken by hand collecting in Area 6 on 26/3/1981.

Site Number	*M. mengei*	*L. peltata*	*M. segmentata*	*L. triangularis*
186	8	1	0	0
225	11	2	0	0
239	11	5	0	0
130	2	1	0	0
27	5	0	0	0
60	5	2	0	0
174	1	2	0	0
259	2	0	0	0
257	15	1	0	0
129	10	1	0	0
Total	70	15	0	0

Table 7: The number of spiders of Metellina mengei, Linyphia peltata, Metellina segmentata, and Linyphia triangularis taken by hand collecting in Area 6 on 22/4/1981.

Site Number	M. mengei	L. peltata	M. segmentata	L. triangularis
185	3	7	0	0
164	4	1	0	0
211	9	5	0	0
156	6	1	0	0
23	6	2	0	0
39	1	1	0	0
178	2	2	0	0
4	4	0	0	0
53	17	1	0	0
183	8	2	0	0
Total	60	22	0	0

Table 8: The number of spiders of *Metellina mengei*, *Linyphia peltata*, *Metellina segmentata*, and *Linyphia triangularis* taken by hand collecting in Area 6 on 15/5/1981.

Site Number	*M. mengei*	*L. peltata*	*M. segmentata*	*L. triangularis*
253	26	4	0	0
246	2	1	0	0
271	17	11	0	0
177	19	5	0	0
181	12	4	2	0
56	11	1	0	0
80	9	1	0	0
194	4	0	0	0
195	5	4	0	0
87	5	0	0	0
Total	110	31	2	0

Table 9: The number of spiders of *Metellina mengei* , *Linyphia peltata* , *Metellina segmentata* , and *Linyphia triangularis* taken by hand collecting in Area 6 on 15/6/1981.

Site Number	*M. mengei*	*L. peltata*	*M. segmentata*	*L. triangularis*
152	21	3	2	3
216	3	0	0	0
277	5	2	2	1
221	11	1	2	0
85	20	2	0	1
108	8	0	3	1
29	15	0	0	1
176	8	0	0	0
147	1	0	0	1
118	9	1	1	1
Total	101	9	10	9

Table 10: The number of spiders of *Metellina mengei*, *Linyphia peltata*, *Metellina segmentata*, and *Linyphia triangularis* taken by hand collecting in Area 6 on 29/7/1981.

Site Number	*M. mengei*	*L. peltata*	*M. segmentata*	*L. triangularis*
11	11	0	5	3
54	2	0	6	1
114	7	0	0	2
107	9	0	0	0
131	18	1	1	1
227	3	0	2	0
250	2	1	0	2
243	6	1	2	0
231	5	0	1	2
189	2	0	0	0
Total	65	3	17	11

Table 11: The number of spiders of *Metellina mengei*, *Linyphia peltata*, *Metellina segmentata*, and *Linyphia triangularis* taken by hand collecting in Area 6 on 28/8/1981.

Site Number	*M. mengei*	*L. peltata*	*M. segmentata*	*L. triangularis*
249	14	1	0	0
122	12	1	0	0
266	10	0	0	0
61	13	2	1	1
140	16	3	1	0
102	21	5	2	0
128	46	1	0	0
153	13	2	0	0
Total	145	15	4	1

Table 12: The number of spiders of Metellina mengei, Linyphia peltata, Metellina segmentata, and Linyphia triangularis taken by hand collecting in Area 6 on 4/10/1981.

Site Number	M. mengei	L. peltata	M. segmentata	L. triangularis
75	41	9	0	0
237	32	2	3	1
115	19	4	0	0
9	34	7	0	0
270	16	1	1	0
10	31	13	0	0
88	27	5	2	1
65	30	6	0	0
Total	230	47	6	2

Table 13: The number of spiders of Metellina mengei, Linyphia peltata, Metellina segmentata, and Linyphia triangularis taken by hand collecting in Area 6 on 5/11/1981.

Site Number	M. mengei	L. peltata	M. segmentata	L. triangularis
228	18	5	0	0
180	14	12	1	0
150	18	13	0	0
110	18	4	0	0
106	26	6	0	0
Total	94	40	1	0

Appendix 5: Results of experiments on the thermal death points of the four species.

Table 1: The number of sub-adult spiders alive and the total dead at different temperature for *L. triangularis* on 15/7/82.

Temperature		35	36	37	38	39	40	41	42
Total number of spiders	Alive	24	24	24	24	23	20	0	0
	Dead	0	0	0	0	1	4	24	24

Table 2: The number of first instar spiders alive and the total dead at different temperatures for *L. peltata* on 28/7/82.

Temperature		35	36	37	38	39	40	41	42
Total number of spiders	Alive	16	3	0	0	0	0	0	0
	Dead	8	21	24	24	24	24	24	24

Table 3: The number of adult female spiders alive and the total dead at different temperature for *L. peltata* on 15/7/82.

Temperature		35	36	37	38	39	40	41	42
Total number of spiders	Alive	24	22	21	7	0	0	0	0
	Dead	0	2	3	17	24	24	24	24

Table 4: The number of 1st/2nd instar spiders alive and the total dead at different temperature for *M. mengei* on 28/7/82.

Temperature		35	36	37	38	39	40	41	42
Total number of spiders	Alive	24	22	6	0	0	0	0	0
	Dead	0	2	18	24	24	24	24	24

Table 5: The number of fourth instar spiders alive and the total dead at different temperature for *M. mengei* on 14/7/82.

Temperature		35	36	37	38	39	40	41	42
Total number of spiders	Alive	24	24	24	19	2	0	0	0
	Dead	0	0	0	5	22	24	24	24

Table 6: The number of adult female spiders alive and the total dead at different temperature for *M. mengei* on 15/7/82.

Temperature		35	36	37	38	39	40	41	42
Total number of spiders	Alive	24	24	24	23	0	0	0	0
	Dead	0	0	0	1	24	24	24	24

Table 7: The number of third instar spiders alive and the total dead at different temperature for *M. segmentata* on 14/7/82.

Temperature		35	36	37	38	39	40	41	42
Total number of spiders	Alive	24	24	24	21	0	0	0	0
	Dead	0	0	0	3	24	24	24	24

Table 8: The number of adult female spiders alive and the total dead at different temperatures for *L. triangularis* on 17/8/82.

Temperature		35	36	37	38	39	40	41	42
Total number of spiders	Alive	24	24	24	24	24	24	1	0
	Dead	0	0	0	0	0	0	23	24

Table 9: The number of adult male spiders alive and the total dead at different temperatures for *L. triangularis* on 14/8/82.

Temperature		35	36	37	38	39	40	41	42
Total number of spiders	Alive	24	24	24	24	24	23	9	0
	Dead	0	0	0	0	0	1	15	24

Table 10: The number of 2nd/3rd instar spiders alive and the total dead at different temperature for *L. peltata* on 17/8/82.

Temperature		35	36	37	38	39	40	41	42
Total number of spiders	Alive	24	24	20	1	0	0	0	0
	Dead	0	0	4	23	24	24	24	24

Table 11: The number of 2nd/3rd instar spiders alive and the total dead at different temperatures for *M. mengei* on 17/8/82.

Temperature		35	36	37	38	39	40	41	42
Total number of spiders	Alive	24	23	17	0	0	0	0	0
	Dead	0	1	7	24	24	24	24	24

Table 12: The number of sub-adult spiders alive and the total dead at different temperatures for *M. mengei* on 14/8/82.

Temperature		35	36	37	38	39	40	41	42
Total number of spiders	Alive	24	24	23	2	0	0	0	0
	Dead	0	0	1	22	24	24	24	24

Table 13: The number of sub-adult spiders alive and the total dead at different temperature for *M. segmentata* on 14/8/82.

Temperature		35	36	37	38	39	40	41	42
Total number of spiders	Alive	24	23	23	22	1	0	0	0
	Dead	0	1	1	2	23	24	24	24

Table 14: The number of adult female spiders alive and the total dead at different temperatures for *M. segmentata* on 7/9/1982.

Temperature		35	36	37	38	39	40	41	42
Total number of spiders	Alive	24	24	24	13	0	0	0	0
	Dead	0	0	0	11	24	24	24	24

Table 15: The number of adult female spiders alive and the total dead at different temperatures for *M. mengei* on 7/9/1982.

Temperature		35	36	37	38	39	40	41	42
Total number of spiders	Alive	24	24	24	24	4	0	0	0
	Dead	0	0	0	0	20	24	24	24

Table 16: The number of adult male spiders alive and the total dead at different temperatures for *M. segmentata* on 7/9/1982.

Temperature		35	36	37	38	39	40	41	42
Total number of spiders	Alive	24	24	24	11	0	0	0	0
	Dead	0	0	0	13	24	24	24	24

Table 17: The number of adult male spiders alive and the total dead at different temperatures for *M. mengei* on 17/9/1982.

Temperature		35	36	37	38	39	40	41	42
Total number of spiders	Alive	24	24	24	16	0	0	0	0
	Dead	0	0	0	8	24	24	24	24

Table 18: The number of adult female spiders alive and the total dead at different temperatures for *M. segmentata* on 21/10/82.

Temperature		35	36	37	38	39	40	41	42
Total number of spiders	Alive	24	24	23	1	0	0	0	0
	Dead	0	0	1	23	24	24	24	24

Table 19: The number of adult female spiders alive and the total dead at different temperatures for *M. mengei* on 21/10/82.

Temperature		35	36	37	38	39	40	41	42
Total number of spiders	Alive	24	23	23	22	0	0	0	0
	Dead	0	1	1	2	24	24	24	24

Table 20: The number of adult female spiders alive and the total dead at different temperatures for *L. triangularis* on 20/10/82.

Temperature		35	36	37	38	39	40	41	42
Total number of spiders	Alive	24	24	24	24	23	22	1	0
	Dead	0	0	0	0	1	2	23	24

Table 21: The number of 3rd/4th instar spiders alive and the total dead at different temperatures for spider *L. peltata* on 20/10/82.

Temperature		35	36	37	38	39	40	41	42
Total number of spiders	Alive	24	24	24	0	0	0	0	0
	Dead	0	0	0	24	24	24	24	24

Table 22: The number of 2nd/3rd instar spiders alive and the total dead at different temperature for *M. mengei* on 21/10/82.

Temperature		35	36	37	38	39	40	41	42
Total number of spiders	Alive	24	19	19	0	0	0	0	0
	Dead	0	5	5	24	24	24	24	24

Table 23: The number of adult female spiders alive and the total dead at different temperatures for *M. segmentata* on 7/11/82.

Temperature		35	36	37	38	39	40	41	42
Total number of spiders	Alive	24	24	22	4	0	0	0	0
	Dead	0	0	2	20	24	24	24	24

Table 24: The number of adult female spiders alive and the total dead at different temperatures for *M. mengei* on 7/11/82.

Temperature		35	36	37	38	39	40	41	42
Total number of spiders	Alive	24	23	23	16	0	0	0	0
	Dead	0	1	1	8	24	24	24	24

Table 25: The number of adult female spiders alive and the total dead at different temperatures for *L. triangularis* on 6/11/82.

Temperature		35	36	37	38	39	40	41	42
Total number of spiders	Alive	24	23	23	23	23	20	0	0
	Dead	0	1	1	1	1	4	24	24

Table 26: The number of sub-adult spiders alive and the total dead at different temperatures for *L. peltata* on 6/11/82.

Temperature		35	36	37	38	39	40	41	42
Total number of spiders	Alive	24	24	21	1	0	0	0	0
	Dead	0	0	3	23	24	24	24	24

Table 27: The number of 2nd/3rd instar spiders alive and the total dead at different temperature for *M. mengei* on 7/11/82.

Temperature		35	36	37	38	39	40	41	42
Total number of spiders	Alive	23	23	19	2	0	0	0	0
	Dead	1	1	5	22	24	24	24	24

Table 28: The number of adult female spiders alive and the total dead at different temperatures for *M. mengei* on 22/4/1983.

Temperature		35	36	37	38	39	40	41	42
Total number of spiders	Alive	24	23	22	9	0	0	0	0
	Dead	0	1	2	15	24	24	24	24

Table 29: The number of adult female spiders alive and the total dead at different temperatures for *L. peltata* on 22/4/1983.

Temperature		35	36	37	38	39	40	41	42
Total number of spiders	Alive	24	19	13	0	0	0	0	0
	Dead	0	5	11	24	24	24	24	24

Table 30: The number of adult female spiders alive and the total dead at different temperatures for *M. mengei* on 15/5/1983.

Temperature		35	36	37	38	39	40	41	42
Total number of spiders	Alive	24	24	24	3	0	0	0	0
	Dead	0	0	0	21	24	24	24	24

Table 31: The number of adult female spiders alive and the total dead at different temperatures for *L. peltata* on 15/5/1983.

Temperature		35	36	37	38	39	40	41	42
Total number of spiders	Alive	24	24	17	9	0	0	0	0
	Dead	0	0	7	15	24	24	24	24

Table 32: The number of 2nd/3rd instar spiders alive and the total dead at different temperatures for *M. mengei* on 22/5/1983.

Temperature		35	36	37	38	39	40	41	42
Total number of spiders	Alive	24	24	15	0	0	0	0	0
	Dead	0	0	9	24	24	24	24	24

Table 33: The number of 1st instar spiders alive and the total dead at different temperatures for M. segmentata on 22/5/1983.

Temperature		35	36	37	38	39	40	41	42
Total number of spiders	Alive	24	24	24	22	10	0	0	0
	Dead	0	0	0	2	14	24	24	24

Table 34: The number of 1st instar spiders alive and the total dead at different temperatures for L. triangularis on 22/5/1983.

Temperature		35	36	37	38	39	40	41	42
Total number of spiders	Alive	24	24	24	23	20	17	12	0
	Dead	0	0	0	1	4	7	12	24

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