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ECOLOGICAL RESEARCH ON SPIDERS ASSOCIATED WITH MOORLANDS.

by

J. M. CHERRETT.

St. John's College.

- being a thesis presented in candidature for the Degree of Doctor of Philosophy in the University of Durham, 1961.

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The data for Figures 29 and 30 were collected with the help of Messrs. J. Ford, W. Block and J. Whittaker.

Philosophers more grave than wise
Hunt science down in Butterflies;
Or fondly poring on a Spider,
Stretch human contemplation wider;

...

In such pursuits if wisdom lies,
Who, Laura, shall thy taste despise?

Pope and Gay.

(As quoted in Bronowski, The Common Sense of Science.)

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ECOLOGICAL RESEARCH ON SPIDERS ASSOCIATED WITH MOORLANDS.

I. INTRODUCTION.

Spiders, which constitute the Order Araneae, have attracted attention from ancient times, and have been prominent in the superstition and mythology of the widest range of cultures. Liked, or disliked, they have never been ignored, and as a result, the subject possesses an extensive literature, which is however largely concerned with the taxonomy, morphology and behaviour of the group. Systematic ecological studies have been few, especially in this country, and this has perhaps been partly due to the taxonomic difficulties, which until recently have hindered workers in this field, and to the lack of any stimulus from Applied Biology.

Two detailed, systematic ecological studies have however been made; Duffey (1955, 1956) investigated the spider communities of limestone grassland in Oxford, and Turnbull (1957) examined the ecology of some woodland spiders, also in Oxford.

Other detailed ecological work of particular note has been that of Gabbutt (1956) on the spiders of an oak wood in Devon, Elliot (1930) on the spiders of a beech-maple forest, Lowrie (1948) on the ecological succession of spiders of the Chicago area dunes, and Barnes and Barnes (1953, 1954, 1955) on the ecology of spiders in a variety of habitats, all in America. In Denmark, Nørgaard (1945, 1951, 1952) has worked on the ecology of Lycosids, while in Germany the work of Tretzel (1954, 1955a, 1955b) using seasonal pitfall trapping is of particular importance.

With this work in mind, it was decided to investigate the role of spiders in an area of high Pennine moorland, for three principal reasons, first, because with the exception of casual collecting, very little seems to be known of the spider fauna of British uplands; second because it was hoped that the paucity of species associated with such an area would simplify the relationships being studied, and third because such a study would fill in a gap, and derive much information from, the more comprehensive study of the fauna of this particular area being undertaken for the Nature Conservancy.

As all spiders are predators, they have become adapted to catching their prey in a variety of ways, and in a general review of this sort, the investigation must fall into sections corresponding to the broadly different ways of life exhibited by the group, for each section presents its own peculiar problems, and must be investigated by special methods. Accordingly, the spider fauna has been divided up into orb-web building spiders, wolf spiders, and hammock-web building spiders, and these will be discussed separately.

II. TAXONOMY.

The classical taxonomic works on the British spider fauna are undoubtedly those of Blackwell (1861-4) "A History of the Spiders of Great Britain and Ireland", and the Rev. O. Pickard - Cambridge who published taxonomic papers from 1852 to 1914, and his only book, "The Spiders of Dorset" in 1879 and 1881. The need for an up to date and comprehensive key to the order has however only been fulfilled in the last few years by the publication of a two volume work entitled "British Spiders" by G. H. Locket and A. F. Millidge for The Ray Society, and it is on this excellent work that all the taxonomy in this study has been based.

A comprehensive account of the development of British Araneology by W. S. Bristowe can be found in an introductory chapter to the above work, and in it he says "We can, however, "make bold to say" that, in all probability, knowledge of the British spider fauna compares favourably with that of any other country in the world". It is some measure of the truth of this statement, that during the three years of the present, detailed investigation of a rather remote area, no species new to Science, Britain, or even England have been recorded.

With only one or two exceptions, the species are readily determined in both sexes by an examination of the sex organs, but the limitations of such a system are obviously the necessity of killing the animals for examination, and the inability to distinguish immature forms. This latter drawback is particularly serious in ecological studies, and in common with others, it has been found necessary to pool all the immature forms in families.

III. THE STUDY AREA.

This work was carried out at the Moor House National Nature Reserve 80, in Westmorland (Nat. Grid Ref. NY 758329). This is an area of high Pennine moor which includes parts of both the western scarp, and the eastern dip slopes of its three principal fells, Little Dun Fell (2,701 ft.), Great Dun Fell (2,780 ft.), and Knock Fell (2,604 ft.) and covers an area of approximately 4,000 hectares. The more gentle eastern slope upon which the Field Station (1,800 ft.) is built is bounded by the River Tees, which is the principal river on the Reserve, into which drain such tributaries as Troutbeck, Moss Burn, and Rough Sike, which will be referred to later. (See Figure 1).

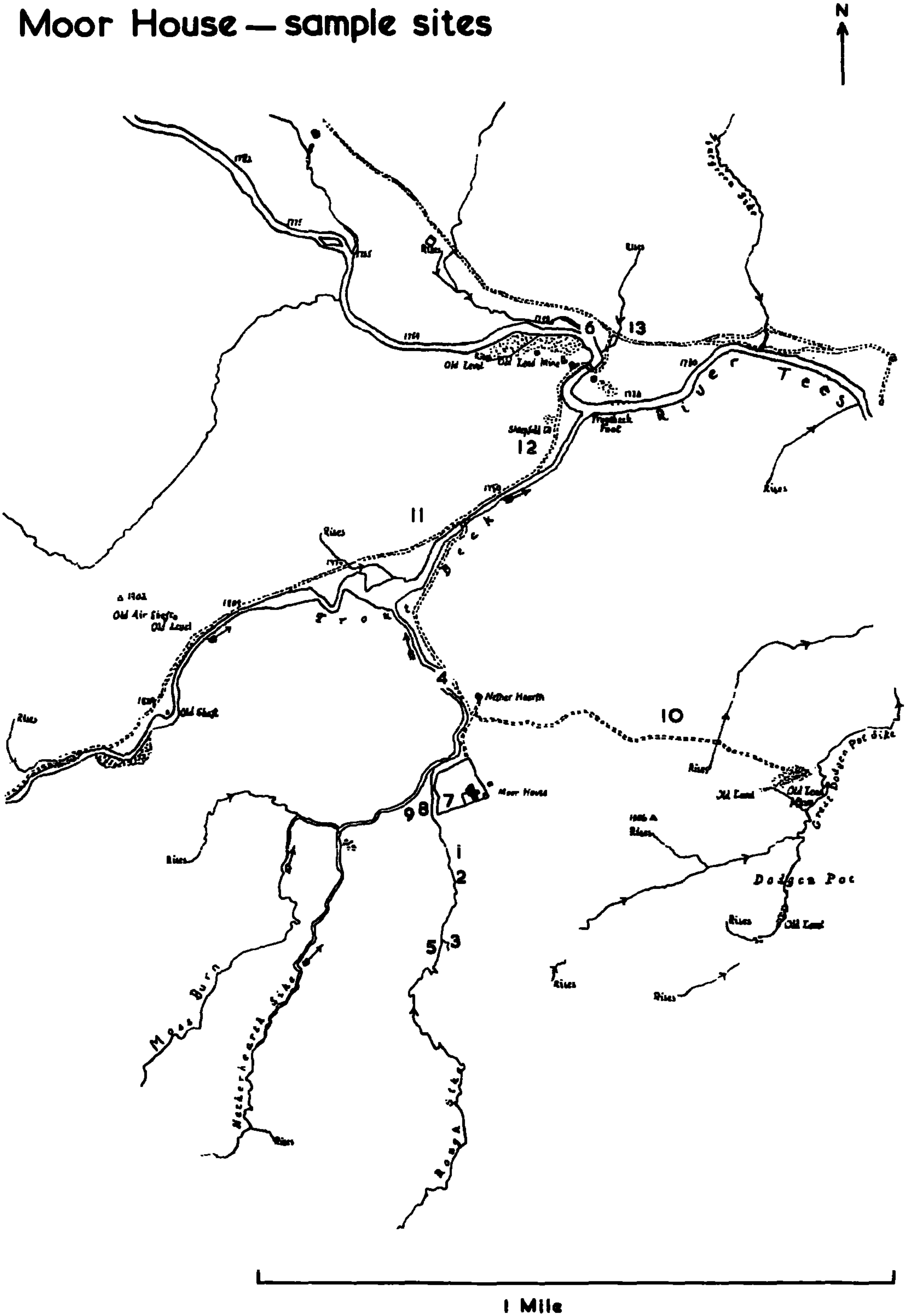
Whilst general descriptions of the Reserve have been made by Conway (1955), and Nicholson (1957), the geology of the area has been studied by Dunham (1948) and Johnson (1958). The area lies on the Yordale series of Carboniferous sandstones, shales and limestones, and this series with its associated flora which in turn is greatly affected by erosion, presents a most complex series of plant communities.

Typically, the area is covered with blanket bog peat, 2 - 3 metres deep which can either be actively growing, or eroding. In the former case, the 'Mixed Moor' Calluna vulgaris, Eriophorum vaginatum plant cover is underlain with actively growing Sphagnum sp. and the peat is very wet, while in the latter case the blanket of peat is cut through with erosion channels, leaving well drained peat hags upon which there is typically Calluna, but very little Eriophorum, underlain here by Cladonia sp. In the areas of disturbed, or redeposited peat, which are especially to be found at the edges of the deep peat, Juncus squarrous is characteristically the dominant plant.

Where peat is absent, in most cases due to erosion,

Fig. 1.

Moor House — sample sites



From Ordnance Survey
1911.

Figures refer to sample sites for explanation see text.

the plant communities depend upon the nature of the underlying substrate; thus the limestone outcrops support a relatively rich flora characterised by *Festuca ovina*, *Agrostis tenuis*, and *Thymus drucei*, with *Potentilla erecta* and *Trifolium repens* occurring commonly, whilst on the more acid sandstones, solifluxion clays, drift, and alluvial terraces, as Pearsall (1950) has pointed out, an impoverished flora dominated by the mat grass, *Nardus stricta* is to be found.

The climate of Moor House was first studied by Manley (1936, 1943, 1952), and in 1952 it was established as an "Auxiliary Climatological Station" under the Meteorological Office.

Summarising the data collected at Moor House, Manley (1936) wrote "As a whole, the figures confirm the prevailing impression of bleakness associated with a windy and damp upland and correspond well with records at sea level in Southern Iceland", and this impression can be substantiated by all who have worked in the area.

More specifically, July is the warmest month, and January the coldest, the temperature is known to have fallen below freezing point in every month of the year, whilst 80 days of snow cover with over 150 days of frost, and an average of only 3 - 4 hours sunshine daily are representative annual measurements.

IV. THE SPIDER FAUNA OF MOOR HOUSE AND ITS SIGNIFICANCE.

71 species of spiders have been recorded from the Reserve, of which 17 are thought to be additions to the published records for Westmorland, and a check list is given below.

Family Dictynidae.

1. Dictyna arundinacea (Linnaeus)

Family Clubionidae.

2. Clubiona trivialis C.L. Koch
3. C. diversa O.P.-Cambridge

Family Thomisidae.

4. Xysticus cristatus (Clerck)
5. Oxyptila trux (Blackwall)

Family Lycosidae.

6. Lycosa tarsalis Thorell
7. L. pullata (Clerck)
8. L. amentata (Clerck)
9. L. nigriceps Thorell
10. Tarentula pulverulenta (Clerck)
11. Trochosa terricola Thorell
12. Pirata piraticus (Clerck)

Family Agelenidae.

13. Antistea elegans (Blackwall)

Family Theridiidae.

14. Robertus lividus (Blackwall)
15. R. arundineti (O.P.-Cambridge)

Family *Tetragnathidae*.

16. *Tetragnatha extensa* (Linnaeus)

Family *Argiopidae*.

17. *Meta segmentata* (Clerck)

18. *M. merianae* (Scopoli)

19. *Araneus cornutus* Clerck

Family *Linyphiidae*.

* 20. *Ceratinella brevipes* (Westring)

21. *C. brevis* (Wider)

22. *Walckenaera acuminata* Blackwall

23. *Wideria antica* (Wider)

24. *Trachynella nudipalpis* (Westring)

25. *Cornicularia karpinskii* (O.P.-Cambridge)

* 26. *C. cuspidata* (Blackwall)

* 27. *Dicymbium tibiale* (Blackwall)

28. *Gonatium rubens* (Blackwall)

29. *Peponocranium ludicrum* (O.P.-Cambridge)

* 30. *Hypselistes jacksoni* (O.P.-Cambridge)

31. *Oedothorax gibbosus/tuberosus*

32. *O. fuscus* (Blackwall)

33. *Trichopterna mengei* (Simon)

34. *Silometopus elegans* (O.P.-Cambridge)

* 35. *Tiso vagans* (Blackwall)

* 36. *Monocephalus fuscipes* (Blackwall)

* 37. *Jacksonella falconeri* (Jackson)

* 38. Gongylidiellum vivum (O.P.-Cambridge)

* 39. G. latebricola (O.P.-Cambridge)

40. Micrargus herbigradus (Blackwall)

41. Erigonella hiemalis (Blackwall)

42. Savignia frontata (Blackwall)

43. Diplocephalus permixtus (O.P.-Cambridge)

44. Erigone dentipalpis (Wider)

* 45. E.atra (Blackwall)

46. Eboria fausta (O.P.-Cambridge)

47. Drepanotylus uncatus (O.P.-Cambridge)

48. Phaulothrix hardyi (Blackwall)

49. Porrhomma montanum Jackson

* 50. Agyneta decora (O.P.-Cambridge)

* 51. Meioneta rurestris (C.L. Koch)

52. M. saxatilis (Blackwall)

53. M. beata (O.P.-Cambridge)

* 54. Maro minutus (O.P.-Cambridge)

55. Centromerus prudens (O.P.-Cambridge)

* 56. C. arcanus (O.P.-Cambridge)

57. Centromerita bicolor (Blackwall)

58. C. concinna (Thorell)

59. Oreonetides abnormis (Blackwall)

60. O. vaginatus (Thorell)

* 61. Bathyphantes gracilis (Blackwall)

62. *Tapinopa longidens* (Wider)
* 63. *Stemonyphantes lineatus* (Linnaeus)
64. *Bolyphantes luteolus* (Blackwall)
65. *Lepthyphantes tenuis* (Blackwall)
66. *L. zimmermanni* Bertkau
* 67. *Lepthyphantes cristatus* (Menge)
68. *L. mengei* Kulczynski
69. *L. ericaeus* (Blackwall)
70. *L. angulatus* (O.P.-Cambridge)
71. *Mengea scopigera* (Grube)

* Probable addition to the published county records.

It can be seen at once from this list that the Family Linyphiidae is the most important, with 52 species, and it is of interest to examine the family composition of the fauna in more detail. In Figure 2, the comparative family structures of 5 faunas are shown, and it would appear that the structure of the Moor House fauna is similar to that of Iceland, that is to say that it shows a sub-arctic pattern. It is atypical of the British fauna as a whole because of the increased importance of the Linyphiidae and the Lycosidae and the absence of several groups, in particular the Salticidae which eventually become of great importance in tropical countries.

The Comparative Family Structure of 5 Faunas.

After Bristowe 1939.

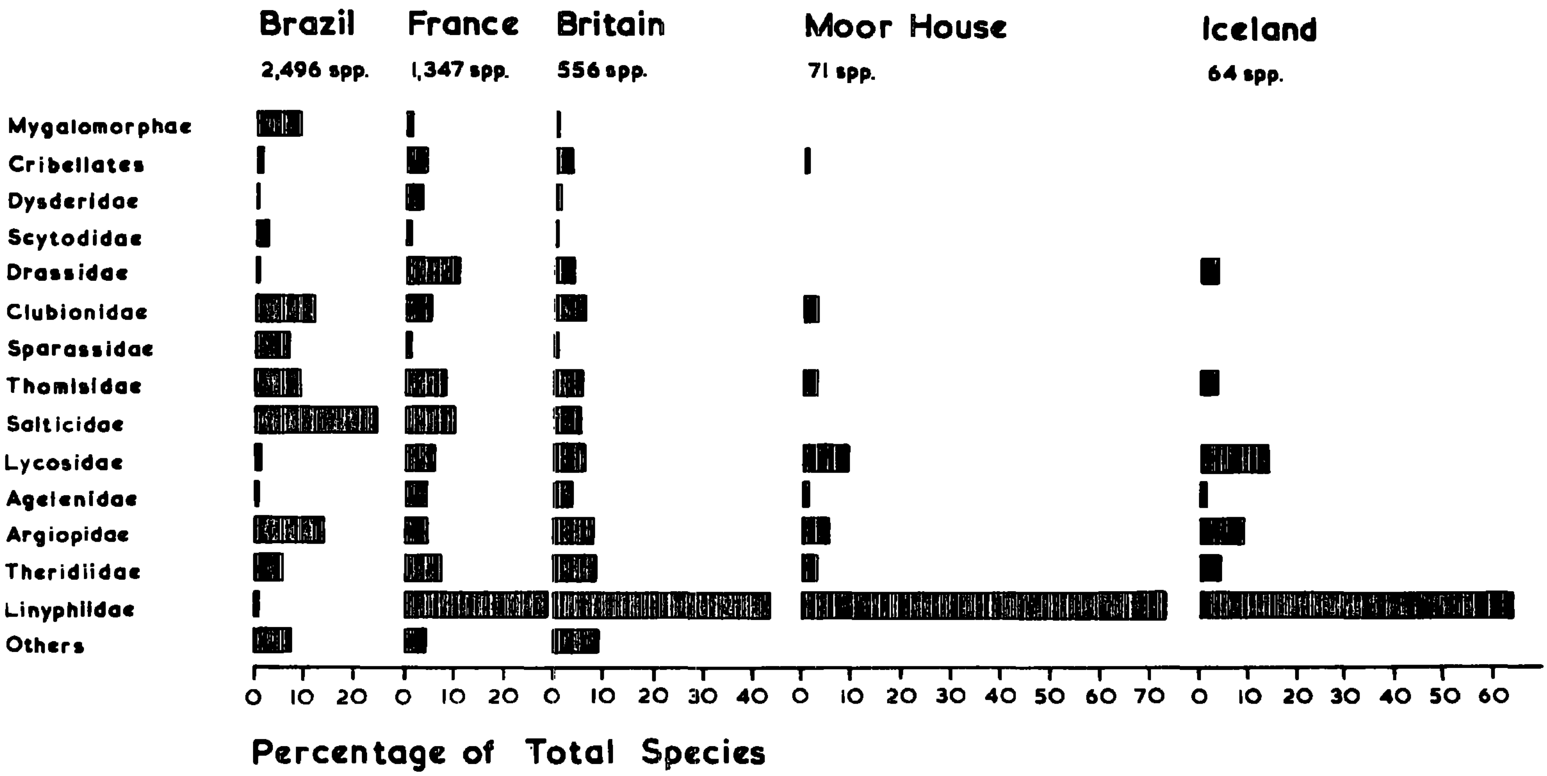


Fig. 2.

A comparison can be made with the species list obtained by Duffey (1955) from a lowland limestone grassland area in Oxford where, he recorded 141 species of which 58, or 41% were Linyphiids, compared with the 52 out of 71 or 73% at Moor House; a difference which is significant at the .05 level by a χ^2 test.

This predominance of the Linyphiidae supports the contention of Bristowe (1939) that this family reaches its greatest importance in Arctic and Sub-Arctic regions which fits in well with what is known of the climate of the area.

As over 560 species are known to occur in Britain, the Moor House spider fauna can be said to be as impoverished in its number of species, as it is in the variety of families represented.

V. THE ORB-WEB BUILDING SPIDERS.

1. General Habits.

This group builds the familiar orb-web, cart-wheel, or geometric web, an example of which can be seen in Plate 1., and in Britain, is composed of three families, the Argiopidae, Tetragnathidae, and Uloboridae.

The web is roughly circular, and consists of a variable number (11 - 66) of radius threads, attached at their periphery to a series of bridge threads, which

Plate 1.

Orb-web of Meta merianae spun amongst stones in a drainage channel.

anchor the whole structure to the substratum, and at their centre, to a hub surrounded by a short strengthening zone. Upon this basic framework, a viscid spiral is laid, and this is the only sticky thread in the whole structure. This can be seen in Plate 1. where powder, dusted on to the web to make it more visible for photographic purposes, has stuck only on this thread.

From the hub a signal thread is often spun to the animal's retreat, and serves to give the alert when anything strikes the web. Comprehensive descriptions of the structure of the orb-web are to be found in Savory (1952), Tilquin (1942) and McCook (1889, 1890).

The general structure of these webs, and the fact that they are normally hung vertically, suggests that they are especially suited for capturing flying insects, and this concentration upon a particular prey type has meant that the group must be considered separately.

2. Notes on the Orb-Web Building Species Recorded.

Only 4 species have been recorded from the Reserve.

Family Tetragnathidae

Tetragnatha extensa (Linnaeus)

This species has only been taken infrequently, when it has been found with its web on heather, and in drainage channels, characteristically near to water.

Family Argiopidae

Meta segmentata (Clerck)

Only one specimen, which was found migrating across an area of heather, has ever been taken.

M. merianae (Scopoli)

This is a widespread and common form, found in large numbers. The web could be distinguished from that of the other common species by having an Open Hub, Bristowe (1941), McCook (1889).

Araneus cornutus (Clerck)

This again is a widespread and common form, but with a web having a meshed hub.

As there are 9 species belonging to the Tetragnathidae, and 41 to the Argiopidae in the British list, it would appear that this group is poorly represented. As the distribution of the existing forms, will indicate, this could be due to lack of suitable places in which these webs can be constructed, a situation arising largely from the low herbaceous nature of the plant cover.

3. The Habitats of this Group, and the Significance of its Distribution.

The only two species of any importance are Meta merianae, and Araneus cornutus, and it is the distribution of these which will be discussed.

Both species are virtually confined to what might be termed "breaks in the blanket bog cover" i.e. erosion channels, stream edges, rocky outcrops, and old mine workings, and this is borne out by the results in Table 1, for *A. cornutus* obtained while searching for webs. Although both species are restricted in this way, their detailed ecology is markedly different.

A. cornutus lives in a silken retreat constructed in the vegetation, and this takes the form of a thimble-shaped cell, in which the animal sits, holding on to the signal thread running from the nearby web. In the study area, this retreat is normally spun amongst the tips of *Calluna* shoots which overhang an erosion channel, but

TABLE 1.

Number of Araneus cornutus webs seen during a 100 pace transect -

	Along the edges of eroded peat.	Across open Calluna/ Eriophorum Bog
1.	6	0
2.	10	0
3.	10	0
4.	13	0
5.	9	0
6.	2	0
7.	10	0
8.	6	0
9.	7	0
10.	2	0

they have also been found amongst the seed capsules of *Juncus effusus*, and even on a tuft of *Festuca ovina* within the erosion gully. These observations are in agreement with those of Pickard-Cambridge (1881) who writes (P.276) "*Epëira cornuta* is generally distributed throughout Great Britain, and is particularly abundant in marshy places, among furze, heather, coarse grass, and rushes, especially on the banks of streams", and Thomas (1927) who says that a habitat near water is characteristic.

Plate 2 shows a retreat spun on a *Calluna* shoot, with the owner, a sub-mature male resting on the central hub of the web, after wrapping up an insect.

M. merianae on the other hand does not spin any retreat, and the adults are only to be found in damp, dark places. Plate 3 shows a female hanging from her threads. This habitat preference is confirmed by Bristowe (1929, 1958) who says that the species is found in shady situations under overhanging banks, or in the corners of damp outhouses. At Moor House, this spider is most commonly found on the underside of eroding peat edges, which have been undercut by water. Here, the spider is protected by the overhanging vegetation from sun, wind and predators, is in constant contact with the damp peat, and has adequate vertical space in which to

Plate 2.

Orb-Web of Araneus cornutus spun amongst Calluna shoots, showing the Retreat, together with animal and its prey.

Plate 3.

Meta merianae, - Female hanging from threads.

sling its web.

The only other places in which this species has been found, are the entrances to disused mine shafts, and the cracks in the limestone walls of the larger streams.

The habitat differences are summarised in Figure 3, A and B being typical A. Cornutus situations, whilst C is the position most frequently occupied by M. merianae. It is interesting to note however, that differences in habitat preference are much less marked in the early instars, where the young of M. merianae are often found high up amongst the heather on the sides of the erosion channels. These differences in the distribution of young and old animals are important, and will be referred to later.

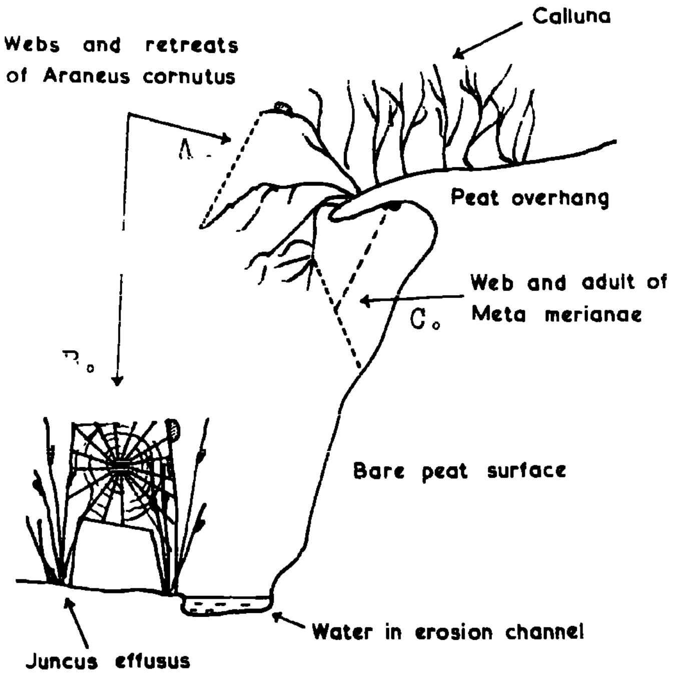
The differences already mentioned between the two species, together with the observation that the range of A. cornutus extended to drier and more exposed erosion channels than were ever colonised by M. merianae suggested that the species may differ in their water relations, and this was accordingly tested by desiccation experiments performed on the adults of both species.

(a) Humidity Reactions

Six individuals of each species were kept in corked 2 x 1 specimen tubes containing moist filter paper, at

Figure 3.

EROSION CHANNEL THROUGH DEEP PEAT



For explanation of letters, see text.

room temperature, and the number of days that each lived was recorded. See Table 2.

TABLE 2.

Survival in days under Humid Conditions

M. merianae	A. cornutus
9	11
44	44
24	24
8	24
32	32
29	18
Mean 24.3	Mean 25.5

t = .1632 with 10 df

A random 't' test showed a probability $> .8$, and it may be concluded, that in damp conditions, the mean survival time of the two species is similar.

Under desiccating conditions however, the situation was found to be different. Here, the animals were kept in uncorked tubes at room temperature, and no water was provided. The results are shown in Table 3.

A random 't' test showed a probability $< .001$, and this was confirmed by a 2 x 2 contingency test upon whether or not the animals were alive on the 15th day after the start of the experiment, where $\chi^2 = 16.9$ with 1 df, again a probability of $< .001$. This second test takes into account the fact that an animal can only die once, and hence it eliminates the factor of 'Accidental

TABLE 3.

Survival in days under Desiccating Conditions.

M. merianae		*A. cornutus*	
5	7	30	16
5	10	18	14
10	9	18	18
5	10	32	27
11	11	18	18
20	7	9	19
11	10	24	10
7	7	24	14
24	8	18	30
10	8	15	
8			
Mean 9.7		Mean 19.6	

t = 5.5667 with 38 df

Death', which is not taken into account in tests involving the survival period.

All this suggests that adults of *A. cornutus* are able to withstand desiccation longer than adults of *M. merianae*.

These experiments had to be carried out at room temperature in the Field Station, and consequently no details of the experimental conditions are available, although it is known that they fluctuated considerably, though less violently than they would in the field. Lack of information about these experimental conditions was not considered to be a serious drawback, in view of the aim of the work, which was simply to obtain a comparative picture of the reactions of 2 species to an unfavourable environmental factor, other factors, as in the field, remaining inconstant.

Such differences in ability to withstand desiccation do not of themselves explain the different distribution of the two species, and a further experiment was carried out, to see if *M. merianae* could survive in an *A. cornutus* environment. Adults of both species were imprisoned in net sleeves, which were tied over *Calluna* shoots, the whole experiment being set up within an existing colony of *A. cornutus*. In addition to *M. merianae* adults free in their sleeves, an equal number were corked up in damp tubes, also within sleeves. As before, the survival time in days was recorded. Unfortunately during the experiment, some of the sleeves were torn, probably by sheep, and the animals escaped. The results are in Table 4.

TABLE 4.

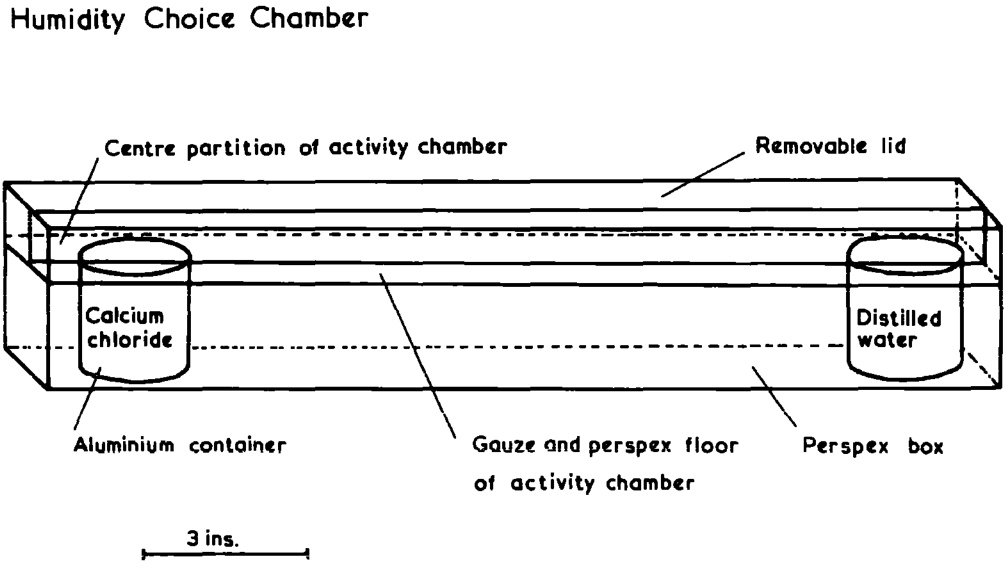
Survival time in days; Animals confined in net sleeves on *Calluna* shoots

M. merianae free in sleeve	*M. merianae* in moist tube in sleeve	*A. cornutus* free in sleeve
>42	19	>19
>19	19	42
19	14	42
14	19	19
Mean A 23.5	Mean B 17.7	Mean C 30.5

A random 't' test between Means A and B gave a probability >.4, which, being not significant, suggests that lack of moisture in an invironment normally inhabited by A. cornutus did not affect the longevity of M. merianae. Applying the same test to Means A and C, a probability $>.4$ resulted, suggesting that under the conditions of the experiment, which involved starvation, M. merianae was able to live as long as A. cornutus in the latter's preferred habitat. This is not, of course, surprising in view of even M. merianae's ability to withstand desiccation, when it is remembered that the average annual rainfall at Moor House is in the region of 70 inches.

Although the animal's ability to withstand certain conditions gives a general clue to its possible range of habitats, the actual habitat in which an animal is found has, as a rule, been selected by that animal, and hence it is the preferred conditions which must be examined, if reasons for distribution are to be found. Accordingly, humidity preference experiments were carried out, using the simple choice chamber shown in Figure 4. This consisted of a long narrow perspex box, with a container of calcium chloride at one end, and a container of distilled water at the other. Just above these containers was the gauze floor to the activity chamber, which was divided longitudinally into two. The whole was closed by a tight-fitting lid. The humidity of the air inside the apparatus was measured with cobalt chloride, and

Figure 4.



Choice chamber apparatus for determining humidity preferences.

cobalt thiocyanate papers, after a technique described by Solomon (1945, 1951, 1957), as indeed were all humidity measurements made, in the present investigations. It was found that a humidity gradient was soon established between the containers at each end, ranging from about 85% R.H. over the distilled water, to <40% over the calcium chloride. Difficulties were soon experienced once the spiders were introduced as they seemed to be very easily frightened, and would lie in a defensive position at the spot where they were put in, and would not move for long periods of time. As a result, all attempts to measure the length of time spent in various parts of the apparatus were abandoned, and instead, an adult of each species was put into the activity chamber, the 2 being separated by the longitudinal partition. The animals were then left over-night, and the position in which each was first found the next morning was marked, and the humidity at that spot recorded. This was done, on the assumption that the animals would have settled down during the night in their optimum position, and as a rule, the number of drag-threads in the activity chamber suggested that their movements had indeed been extensive.

Different animals were used on each occasion, and care was taken to ensure that the positions of the apparatus, chemicals, and animals within, were all adequately randomised. As before, conditions during the experiments were variable, and the same arguments apply. The results appear in Table 5.

TABLE 5.

Humidity preferences - choice chamber analysis.

Results expressed in % Relative Humidity.

M. merianae		A. cornutus	
<40	74	<40	<40
72	80	<40	<40
72	80	<40	<40
<40	<40	<40	<40
<40	<40	<40	<40
80	85	<40	<40
76	<40	45	<40
<40	<40	80	<40
<40	<40	<40	<40
77	<40	<40	<40

The most obvious point to emerge from these results is that whatever else may be influencing the animals, they show a marked preference for the ends of the apparatus, and accordingly the analysis was simplified and made on a 'Wet and Dry End' basis.

M. merianae. In 20 replicates, the animal was found at the dry end 11 times, and at the wet end 9 times; with a χ^2 of .2 and a probability >.5, this showed that within the limits of the experiment no response to a humidity gradient could be detected.

A. cornutus, on the other hand, with 19 observations at the dry end, and only 1 at the wet end had a χ^2 of 16.2 and a probability of <.001, strongly suggesting that individuals of this species actively sought out the dry end of the apparatus, i.e. the region where the R.H. was normally <40%.

Measurements were made in the field to see if there were humidity differences between the two habitats occupied by the adults of the two species, and they were performed on two exceptionally hot and dry days in May 1959, when any differences could be expected to be at their greatest. The met. data for these days are as follows.

Air temp. 60/56°F; Mean wind <6 knots; Rain, - non for at least the previous 5 days; Sunshine, - 10.7/14.9 hrs. In all cases, the measuring papers were placed as near to the actual adult animals in the field as was practicable. Table 6 records the results.

It would then appear to be confirmed, that <u>M. merianae</u> inhabits damper places than does <u>A. cornutus</u>. It has already been pointed out that <u>M. merianae</u> selects dark, damp habitats, whilst <u>A. cornutus</u> selects light drier ones, and it was decided to examine the light reactions of the two species.

(b) Light Reactions

Corked, inch diameter test tubes containing a strip

TABLE 6.

Humidity measurements in the field

Results expressed in % Relative Humidity.

M. merianae habitat	A. cornutus habitat
100	62
100	60
100	55
97	57
95	63
97	45
100	47
100	52
100	

In a random 't' test, t = 18.76 with 15 df, and so the probability was <.001.

of wet filter paper were used for this experiment, some of which had their top, and others their bottom halves painted black. 5 adult females of both species were placed in these at random, and the tubes were laid in an east facing window. The "light" or "dark" position of each animal was recorded at 2 hourly intervals, and after each observation, the animal was shaken into the other section of the tube. Tubes, animals and positions were all adequately randomised throughout the experiment. See table 7.

As was suggested previously the habitat differences between the species appear to break down in the young stages, because the early instars of M. merianae are

TABLE 7.

Light Reactions of M. merianae and A. cornutus Adults

	M. merianae		A. cornutus	
	Dark	Light	Dark	Light
1.	4	1	1	4
2.	3	2	0	5
3.	4	1	0	5
4.	5	0	1	4
5.	5	0	1	4
6.	5	0	1	4
7.	4	1	1	4
8.	4	1	0	5
9.	5	0	1	4
10.	5	0	0	5
11.	5	0	1	4
12.	5	0	1	4
	54	6	8	52

A 2 x 2 contingency test gave a χ^2 of 67.5 which with 1 df gave a probability of <.001, showing that <u>A. cornutus</u> was strongly photopositive, whilst <u>M. merianae</u> was strongly photonegative.

found much higher up amongst the heather on the sides of the erosion channels, and a very similar phenomenon has been recorded by Nielsen (1932) p. 182 for the closely related species <u>M. menardi</u> which is normally found in even darker situations than <u>M. merianae</u>. He says that the young are not so dependent on moisture and darkness. as the full grown animals, and are often found along stream sides, and he concludes that, "<u>M. menardi</u> must disperse from the darkness of the grottos and come out into the daylight, and when the young have undergone a few moults here, they must, though still of very tender age, exchange their life in the daylight for an existence in darkness". In view of the field observations on M. merianae, the light reactions of 9 animals belonging to the first 3 instars were tested in a similar manner to that described above. See Table 8.

TABLE 8.

Light reactions of Young M. merianae

	Light	Dark
1.	10	0
2.	6	4
3.	10	0
4.	8	2
5.	9	1
6.	6	3
7.	8	1
8.	8	1
9.	6	2
	71	14

A χ^2 test gave a χ^2 of 38.2, and a probability $<.001$ indicating significant photopositivity, and this is to be compared with the 6 Light, 54 Dark photonegativity of the adults (χ^2 38.4 $p <.001$); Montgomery (1908a) reports similar observations on A. marmoreus, and (1908b) Latrodectus mactans. The less 'retiring' nature of the early instars of M. merianae is then certainly correlated with, and quite possibly caused by a positive reaction to light.

4. The Colonies Under Investigation.

(a). Sites.

In September 1957, three stretches of eroding peat edge near Rough Sike were selected for study, and called "Peat Edges A, B and C". For their positions, see Figure 1, sample site numbers 1, 2 and 3. Figure 5 shows maps of these three areas. For a description of the structure and formation of erosion channels at Moor House see Bower (1959)

PEAT EDGE A. See Plate 4.

In this area, the peat is 6 to 10 ft. deep, and consequently there is a long, sloping bare peat surface below the heather overhang. As the stream is undercutting the peat at this point, there is considerable variation in the amount of overhang, a point which will be referred to later, and considerable danger of peat collapses, three of which have been observed.

A pure colony of *M. merianae* inhabits this region, with the exception of one specimen of *A. cornutus*, which lived here from July 28th. to September 28th. 1958.

PEAT EDGE B. See Plate 5.

Again, a deep peat edge, about 10 to 12 ft. undercut by the water of Rough Sike. As can be seen from Figure 5, it falls into two different regions. The North Westerly end has a large peat overhang, but above this the peat

Plate 4.

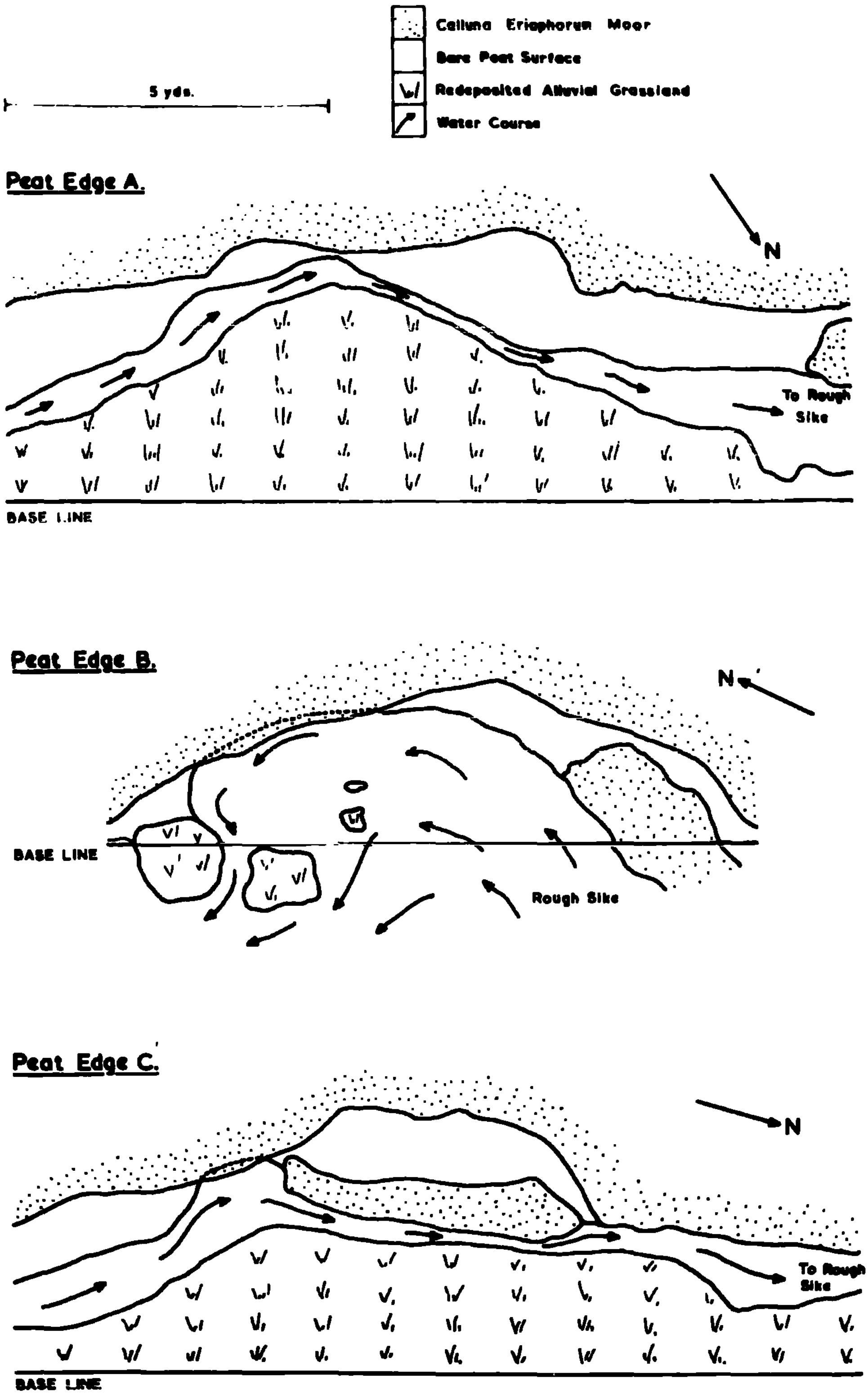
Peat Edge A.

Plate 5.

Peat Edge B.

Fig. 5.

Peat Edge Study Areas



surface is very exposed. Whilst the space under the overhang was much used by M. merianae, it was not a very permanent site, as a rise in the stream level washes the whole area out. The South Easterly end is different in character, as a large section of the bank has fallen into the stream, diverting it, and leaving a deep sheltered fissure behind it.

The whole site is very wet, and in winter, large areas of the exposed peat are covered with a sheet of ice.

Again, this site supports a pure colony of M. merianae with the exception of one specimen of A. cornutus seen on the 11th August 1959.

PEAT EDGE C. See Plate 6.

This area is rather different from the other two, in that there is only a thin layer of peat, from 2 to 5 ft. deep. As a result of this, the overhanging vegetation shields most of the peat surface, making the whole area more sheltered. As in Peat Edge B, the undercutting action of the small drainage stream has caused the fall of a large piece of the bank, and this in its turn has produced an area of broken peat behind it.

The site supports a mixed colony of M. merianae and A. cornutus, and the presence of the latter species may be explained by the luxuriant overhanging growth of Calluna.

Plate 6.

Peat Edge C.

Although the generalisations previously made about the different habitat requirements of the two species are believed to be true, observations on this site suggest that it is a complex area, where their territories overlap, in the sense that here, webs of the two species are often as little as 5 to 10 cms. apart.

(b). Methods Employed.

Web counts were made on every visit to the area, and every morning during a prolonged stay.

The usual procedure was to work up each Peat Edge in turn, recording the number and position of all the webs seen. During the first season, the position of each web was marked with a plant label, but in the second season, each Peat Edge was divided up into foot intervals with plant labels, and the correct position of each web along the Edge was noted, by estimating the number of inches from the nearest foot interval.

Webs of all sizes, corresponding to all stages of maturity were found, and though it was felt that counts of the large webs could be made with confidence, the smaller webs, being much more difficult to see would be estimated less accurately.

For this reason, distinction was made between 'large' and 'small' webs, and measurements of the radii of webs from these two categories, showed that 'large' webs were as a rule those with a radius of more than 5.1 cms. A value judgment of this sort, must, to a certain extent be variable, but in practice this concept of 'large' and 'small' webs usually remained clear in the mind, and the two categories could be assigned with little difficulty.

Observations on the animals of a colony, as distinct from their webs, whilst relatively easy in the case of *A. cornutus* where the retreat is readily found, and the spider in it observed, and if necessary marked, present a serious problem in *M. merianae*. This species is nocturnal, and is very difficult to locate when hiding under a peat overhang. As it will emerge in daylight, to kill and remove any prey, caught in the web, an electric vibrator, or 'artificial fly' was used in trying to count and mark the animals. Nørgaard (1943). This consisted of an electric bell with the gong removed, and a steel point soldered to the armature, which was touched on to the web and buzzed, as a result of which the spider would emerge, and bite the vibrating steel tip. However, the success of this apparatus in 'calling out' spiders was so variable, that it was abandoned as an impracticable census method.

The method finally adopted, was to search after dusk with a powerful paraffin light, when the animals were normally active. The heat and light usually disturbed them, and their movements made them at once conspicuous. Individual colour marking was carried out by catching the animal in a 3 x 1 glass cylinder, one end of which was covered by net. A cork plunger was then slid in at the other end, and the animal was forced up against the net. Animals were always released at the point from which they had been taken.

(c). The Distribution of Individuals.

Table 9 shows the recapture data for 7 marked adult ♀s, together with the maximum length of peat edge traversed, as measured by the points of recapture.

TABLE 9.

Movement Within the Colony as Indicated by the Recapture of Marked Individuals.

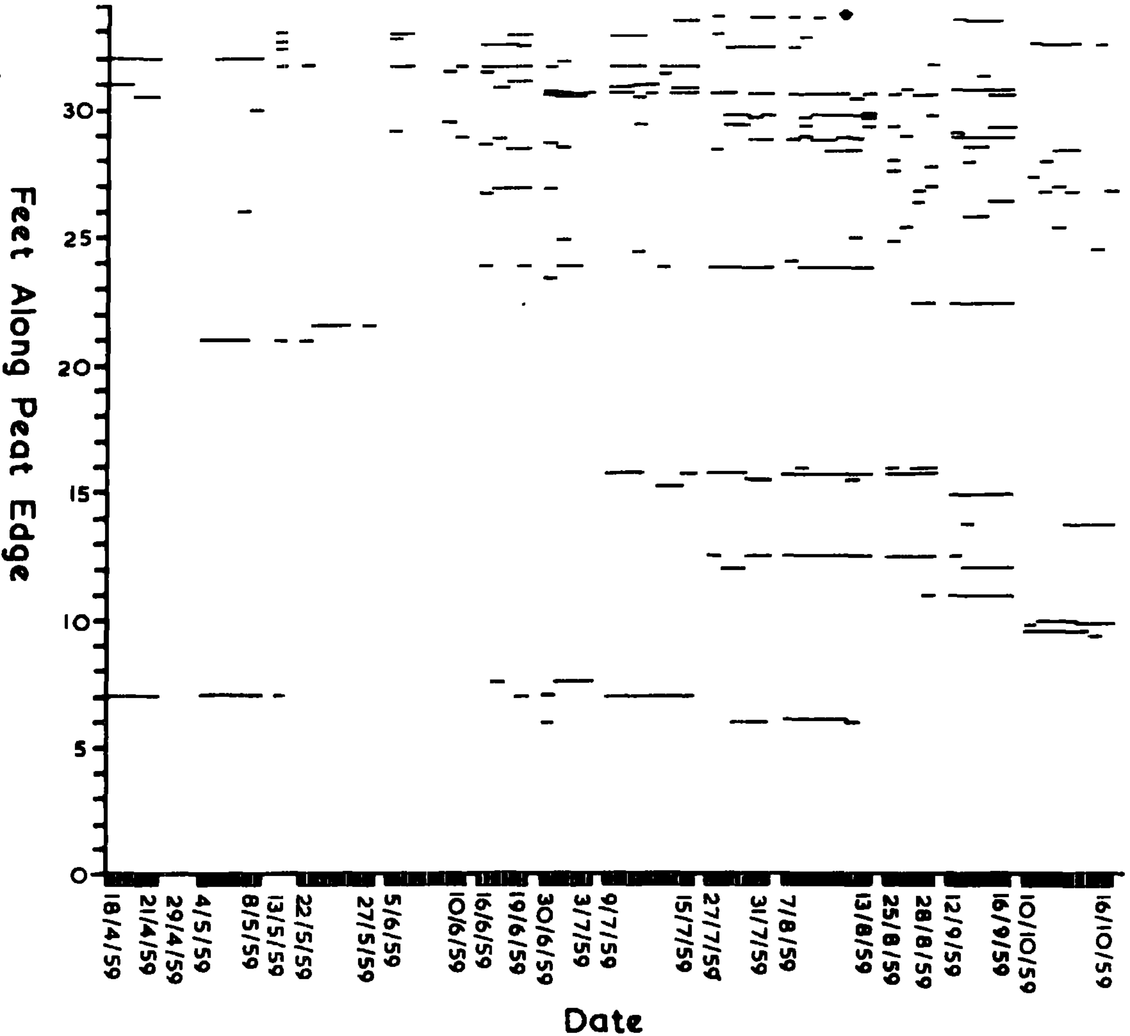
Peat Edge A.

	Length of Peat Edge between extreme Capture points.	No. of Recaptures	Dates
1.	52'0"	6	-/10/57 - 6/ 5/59
2.	4'4"	2	22/ 9/58 - 17/10/58
3.	0'0"	2	22/ 9/58 - 21/10/58
4.	7'0"	2	22/ 9/58 - 21/10/58
5.	27'4"	2	22/ 9/58 - 17/10/58
6.	8'4"	3	22/ 9/58 - 21/10/58
7.	5'4"	2	22/ 9/58 - 21/10/58

Although the numbers are small, and there is no means of knowing what happened to the animals which are not recaptured, the results do suggest that whilst the animals are capable of moving considerable distances along the peat edge (at least 52 ft. in 1½ years), many, even after intervals of up to a month, are recaptured relatively close to their previous release point. This is not surprising, because as Figure 6 shows, there is a tendency for webs to appear in the same place day after day; thus to cite an example, a single web in the rather isolated position of foot intervals 6 - 8 Peat Edge B, was present on most days for 4 months of theyear, and in general, the overall impression of long periods of occupation in a given position, suggest a high degree of 'site tenacity'. This is particularly true of <u>A. cornutus</u>, where females have been observed to remain in the same position all summer, but here, where a complicated retreat is spun it is more understandable. In <u>M. merianae</u> however, it is probably the existence of foundation lines for the web which makes the animal disinclined to move unless it must. These represent a sound labour investment, because as many writers have pointed out, they are usually the most difficult part of the web to construct, and once spun, the same foundation lines are used as long as circumstances permit. Savory (1928, 1952). Gertsch (1949), Crompton (1950), Bristowe (1947, 1951), McKeown (1952), Fabre (1912).

Fig. 6.

Web Occurrence at Peat Edge B During 1959



— Presence of M. merianae Web on Day Shown

● Ditto A. cornutus

18/4/59 21/4/59 Readings on Consecutive Days Between Dates Shown

To investigate the spatial distribution of <u>M. merianae</u> webs, the total number of different (i.e. new) 'large' webs, spun in each foot interval was calculated. This was done for each peat edge, for all the observation days of the 1959 season. The foot intervals of peat edge were then classified according to the number of webs which had been spun in them, and knowing the total number of webs seen, and the possible number of foot intervals in which they could have been spun, a theoretical average was calculated, together with its expected Poisson distribution of class frequencies, - Snedecor (1937).

Table 10 shows the observed number of foot intervals in each class frequency compared with the calculated number assuming random distribution.

In the case of each peat edge, there is a highly significant difference between the observed and expected distributions, indicating in this case that the distribution is not random, but aggregated; that is to say that during the season, an unexpectedly large number of foot intervals have fewer, and also of course larger, numbers of webs in them, than could be accounted for purely by chance. In particular, Peat Edge A had 9 foot intervals within which a web had never been spun, compared with an expected number of <1; Peat Edge B. had 12 foot intervals, - expected <1, whilst Peat Edge C had no foot

Table 10.

Meta merianae. Distribution of Web Numbers Throughout 1959. - 'Large Webs'.

Peat Edge A (44ft.)

No. Webs/Ft.	Observed No. Ft. Showing this.	Expected No. Ft. from Poisson.	χ^2
<3	19	7.4193	18.07 ***
3	4	7.316	1.31
4	3	8.314	3.4
5	3	7.558	2.75
6	2	5.725	2.42
>6	13	7.6677	3.71

Total χ^2 = 31.66

with 4 df. P <.001

(9ft. had no webs, expected = .4673)

Peat Edge B (34ft.)

No. Webs/Ft.	Observed No. Ft. Showing this.	Expected No. Ft. from Poisson.	χ^2
<6	20	8.2112	16.92 ***
6/7	2	9.6270	6.04 *
8/9	1	8.5580	6.67 **
>9	11	7.6038	1.52

Total χ^2 = 31.16

with 2 df. P <.001

(12ft. had no webs, expected = .0188)

Peat Edge C (44ft.)

No. Webs/Ft.	Observed No. Ft. Showing this.	Expected No. Ft. from Poisson.	χ^2
<15	17	5.5261	12.38 ***
15/16	4	5.68	.5
17/18	1	7.456	5.63 *
19/20	4	7.855	1.89
21/22	2	6.792	3.38
>22	16	10.6866	2.64

Total χ^2 = 26.43

with 4 df. P <.001

(There were no ft. without webs, as expected.)

Distribution of Web Numbers, after Removal of Sections 'Unsuitable for Spinning'.

Peat Edge A

No. Webs/Ft.	Observed No. Ft. Showing this.	Expected No. Ft. from Poisson.	χ^2
<4	14	6.2502	9.61 **
4	3	5.128	.88
5	3	5.859	1.39
6	2	5.578	2.29
>6	13	12.1848	.55

Total χ^2 = 14.73

with 3 df. P <.01

Peat Edge B

No. Webs/Ft.	Observed No. Ft. Showing this.	Expected No. Ft. from Poisson.	χ^2
<10	11	6.1599	3.8
10/11	1	5.043	3.24
>11	10	10.7971	.06

Total χ^2 = 7.10

with 1 df. P <.01

Peat Edge C

No Sections 'Unsuitable for Spinning'.

intervals without any webs, more or less as expected. The most obvious explanation is that Edges A and B contained areas unsuitable for web-spinning, whilst there were no such areas in Edge C, and this fits in very well with the descriptions of the sites already given.

As certain sections of Edges A and B have been considered unsuitable for spinning, so far as the spiders are concerned, the effective length of the edges is less than the actual length, and so the distribution has been recalculated on the basis of effective length (i.e. neglecting the unoccupied areas). These results are also shown in Table 10, and still they reveal highly significant aggregation.

As it is now known that webs could be spun in all the sections under review, the aggregation must have been due to one of the 3 following reasons.

1. Some form of social interaction which made the animals aggregate in respect of one another.

2. The presence of exceptionally favourable, and correspondingly unfavourable areas.

3. Site tenacity, which, because the figures are based on the total number of newly spun webs in any foot interval throughout the season, would tend to increase disproportionally the number of webs in any foot inter-

val once an individual had become settled there.

Whilst the importance of the first of these can be analysed quite simply, the relative importance of the last two cannot be fully disentangled, although certain indications can be revealed.

The interaction of M. merianae individuals, as indicated by the positions of their webs, can be studied by comparing the number of webs per foot interval with the expected, assuming random distribution, on any given day. As one would expect that any interactions would be most clearly demonstrated when there were many webs, the spatial distribution of 'large' webs has been examined for the one day in each month, when the maximum number was present. Ten was the minimum number of webs on which calculations were made.

It should perhaps be added at this point, that there is some doubt about the sensitivity of this statistical test, when the expectation per sample is low - Dice (1952), Rao and Chakravarti (1956) and Cole (1946), although the latter author used this for very small expectations. With this in mind, it is hoped that the data may be reanalysed in the future, using the spacing measurement system of Dice (1952).

As can be seen in Table 11, with the exception of one occasion in June at Peat Edge C. which is inexpli-

Meta merianae. Distribution of the Maximum Number of 'Large Webs' on Any Day in the Month. - Data corrected for 'Unsuitable Areas'.

Peat Edge A (35ft.)

	No. Webs/Ft.	Observed No. Ft. Showing this.	Expected No. Ft. from Poisson.	χ^2
AUGUST	0	24	25.57	.10
	>0	11	9.43	.26
	Total χ^2 = .36 P>.5			
SEPTEMBER	0	23	24.14	.05
	>0	12	10.86	.12
	Total χ^2 = .17 P >.5			

Peat Edge B (22ft.)

	No. Webs/Ft.	Observed No. Ft. Showing this.	Expected No. Ft. from Poisson.	χ^2
JULY 30.	0	14	13.96	.00
	>0	8	8.04	.00
	Total χ^2 = .00 P >.95			
JULY 31.	As above.			
AUGUST 8.	As above.			
AUGUST 12.	As above.			
AUGUST 28.	0	13	13.96	.07
	>0	9	8.04	.11
	Total χ^2 = .18 P >.5			
SEPTEMBER	0	12	13.35	.14
	>0	10	8.65	.21
	Total χ^2 = .35 P >.5			

Peat Edge C (44ft.)

	No. Webs/Ft.	Observed No. Ft. Showing this.	Expected No. Ft. from Poisson.	χ^2
MAY	0	27	28.58	.09
	1	15	12.34	.57
	>1	2	3.08	.38
	Total χ^2 = 1.04 P >.3			
JUNE	0	11	18.13	2.81
	1	28	16.07	8.86 **
	>1	5	9.8	2.35
	Total χ^2 = 14.01 P<.001			
JULY 28.	0	18	17.34	.25
	1	12	16.15	1.07
	>1	14	10.51	1.16
	Total χ^2 = 2.48 P>.1			
JULY 31.	0	14	17.34	.64
	1	21	16.15	1.46
	>1	9	10.51	.22
	Total χ^2 = 2.32 P>.1			
AUGUST	0	21	20.32	.23
	1	16	15.7	.06
	>1	7	7.98	.12
	Total χ^2 = .40 P >.5			
SEPTEMBER	0	26	26.69	.02
	>0	18	17.31	.03
	Total χ^2 = .05 P >.8			
OCTOBER	0	35	33.51	.07
	>0	9	10.49	.21
	Total χ^2 = .28 P >.5			

cable, and may be due to sampling error, the spatial distribution of webs along a peat edge on a given day corresponded closely with that predicted by a Poisson distribution, when intervals of one foot are considered. That is to say that considering the numbers found within a foot length of peat edge, there is no evidence for suggesting mutual attraction or repulsion between individuals of *M. merianae*. This is of interest, because it might have been thought that animals which rely on a net to filter food from the air would have evolved some territorial system which would ensure the spacing of snares with its consequent increase in efficiency, by reduction of competition. The results correspond well with observations however, as 4 webs, one behind the other have been seen stretched across the mouth of a small burrow in peat, and Duncan (1949) also notes, that two big orb webs were frequently built, one behind the other, their cables intermingling, and the faces of the orbs only an inch apart, and she concludes that only the outer one would 'get the flies'.

If then, social aggregation can be discounted as a factor in the aggregation effect seen when the number of webs in each section over the whole year is examined, site tenacity and/or favourable sections must account for it.

If a certain foot length of peat edge is peculiarly suitable for web spinning, and there is no particular repulsion between spiders, then it might be expected that on any given day, more than one spider would be found there with a web, and during the course of a season, such suitable areas should reveal, themselves, by having an unexpectedly high number of 'multiples'.

Table 12 shows this analysis performed on the data from Peat Edge C, and due to the small number of 'multiples', and the amount of calculation required, no attempts were made to continue this demonstration on the other two peat edges.

TABLE 12.

M. merianae.

PEAT EDGE C.

Analysis of Multiple Web Occupation 1959. Large Webs.

No. of multiples/ft.	Obs.No/ft.	Expt.	χ^2
<2	18	8.468	10.73**
2	6	9.707	1.416
3	4	9.854	3.478
4	4	7.501	1.634
>4	12	8.47	1.471

Total $\chi^2 = 18.729$

3 df $p < .001$

As can be seen, there is a highly significant difference between the observed and the calculated random distribution of 'multiple' web occurrences, suggesting that within the terms of the analysis there is considerable aggregation of 'multiples'. In other words, certain foot sections do in fact have an exceptionally large number of days in which there is more than one web, and it is suggested that these areas are particularly favoured by M. merianae final instars as sites for web spinning.

Plate 7 shows the 'best' and 'worst' web sections for each peat edge, as judged by the greatest number of 'multiples' on the one hand, and the complete absence of webs on the other, and it seems clear that as a rule the favourable sites are characterised by an extensive protective overhang of luxuriant heather growth, whilst the unfavourable sites are bare, bleak and unprotected.

Site tenacity however is charactérised by webs in a particular area appearing time after time, that is to say by an unusually large number of 'web days'.

TABLE 13.

M. merianae

PEAT EDGE C.

Analysis of 'Web Days' during 1959.			Large Webs
No. of 'Web Days'/ft.	Obs.No/ft.	Expt.	χ^2
<12	15	6.013	13.43***
12/13	2	6.772	3.362
14/15	5	8.636	1.531
16/17	4	8.466	2.356
18/19	2	6.575	3.184
<19	16	7.538	9.499**

Total $\chi^2 = 33.362$

4 df $p < .001$

Plate 7.

<u>Peat Edge A</u>. Favourable and Unfavourable Sites. <u>M. merianae</u>.

UNFAVOURABLE.

Multiples = 0.
Webs = 0.

FAVOURABLE.

Multiples = 2.
Webs = 20.

Multiples = 2.
Webs = 16.

Peat Edge B.

UNFAVOURABLE.

Multiples = 0.
Webs = 0.

FAVOURABLE.

Multiples = 7.
Webs = 34.

Plate 7. (Cont.)

Peat Edge C.

M. merianae - UNFAVOURABLE. **A. cornutus** - FAVOURABLE.

	M.m.	A.c.
Multiples =	0.	1.
Webs =	2.	7.

M. merianae - FAVOURABLE. **A. cornutus** - UNFAVOURABLE.

	M.m.	A.c.
Multiples =	12.	0.
Webs =	44.	0.

	M.m.	A.c.
Multiples =	12.	0.
Webs =	43.	0.

Table 13 shows this analysis for Peat Edge C. only, in which the number of 'web days' observed (days during which a web or webs were found in the given foot interval) per foot are compared with the random expectation. Again, there is a highly significant difference, indicating that many foot intervals possess webs on an unexpectedly large number of days, a situation which supports the hypothesis of 'site tenacity'.

It should be emphasised that these two analyses only indicate favourable areas, and site tenacity as both being important contributing factors to the overall seasonal web aggregation effect, as their relative contributions cannot be accurately separated. Thus, multiple occupation of any foot interval would tend to increase its record of 'web days', because although one animal did not spin on a particular day, the other might well do so. Again, the fact of 'site tenacity' would tend to increase the number of 'multiples' in any area, once more than one animal had become established there. Despite this however, these analyses probably do serve a useful purpose in giving reason to suppose that both favourability and 'site tenacity' are important, by virtue of their two highly significant results.

Similar calculations were performed on 'small' M. merianae webs from Peat Edge C, - see Table 14.

TABLE 14.

M. merianae.

PEAT EDGE C.

Distribution of Small Webs Throughout 1959

No. of Webs/ft.	Obs. No./ft.	Expt.	χ^2
<9	19	6.2664	25.86***
9/10	7	8.114	.1529
11/12	0	9.973	9.973**
13/14	3	8.833	3.852*
>14	15	10.8136	1.949

Total $\chi^2 = 41.7869$
3 df $p < .001$

and the picture appears to be the same, with 'unsuitable areas', and aggregation of web records in certain foot intervals. Consequently, the analysis was not pursued. When the distribution of 'small' webs during a given day was examined however, 3 significant aggregations were obtained, compared with 1 for the 'large' webs. - see Table 15, and this does suggest that aggregations seem more likely to occur in the early instars. Observations in the field suggest that this may often be due to an emergence of spiderlings from a nearby cocoon, and their tendency to spin their first webs close to this point before they disperse more widely.

So far, this examination of distribution has been restricted to M. merianae, but although the numbers are smaller, some analysis has been attempted for A. cornutus, all of course on Peat Edge C.

Meta merianae. Distribution of the Maximum Number of 'Small Webs' on Any Day in the Month. - Data corrected for 'Unsuitable Areas'.

Peat Edge A (34ft.)

No. Webs/Ft.	Observed No. Ft. Showing this.	Expected No. Ft. from Poisson.	χ^2
AUGUST			
0	22	23.89	.15
>0	12	10.11	.35

Total χ^2 = .5 P >.3

Peat Edge B (29ft.)

No. Webs/Ft.	Observed No. Ft. Showing this.	Expected No. Ft. from Poisson.	χ^2
AUGUST			
0	17	10.67	3.75
1	5	10.67	3.01
>1	7	7.66	.06

Total χ^2 = 6.82 P <.01

No. Webs/Ft.	Observed No. Ft. Showing this.	Expected No. Ft. from Poisson.	χ^2
SEPTEMBER			
<2	15	9.991	2.51
2	4	7.741	1.81
3	1	5.782	3.95 *
>3	9	5.486	2.25

Total χ^2 = 10.53 P <.01

No. Webs/Ft.	Observed No. Ft. Showing this.	Expected No. Ft. from Poisson.	χ^2
OCTOBER			
0	19	14.06	1.74
>0	10	14.94	1.63

Total χ^2 = 3.37 P >.05

Peat Edge C (44ft.)

No. Webs/Ft.	Observed No. Ft. Showing this.	Expected No. Ft. from Poisson.	χ^2
MAY			
0	27	23.29	.59
1	10	14.82	1.57
>1	7	5.89	.21

Total χ^2 = 2.37 P >.1

No. Webs/Ft.	Observed No. Ft. Showing this.	Expected No. Ft. from Poisson.	χ^2
JUNE			
0	27	20.32	2.2
1	10	15.7	2.07
>1	7	7.98	.12

Total χ^2 = 4.39 P <.05

No. Webs/Ft.	Observed No. Ft. Showing this.	Expected No. Ft. from Poisson.	χ^2
JULY			
0	30	27.94	.15
>0	14	16.06	.26

Total χ^2 = .42 P >.5

No. Webs/Ft.	Observed No. Ft. Showing this.	Expected No. Ft. from Poisson.	χ^2
AUGUST			
0	33	32.75	.00
>0	11	11.25	.00

Total χ^2 = .01 P >.9

No. Webs/Ft.	Observed No. Ft. Showing this.	Expected No. Ft. from Poisson.	χ^2
SEPTEMBER			
0	35	34.27	.01
>0	9	9.73	.05

Total χ^2 = .07 P >.7

Table 15.

TABLE 16.

A.cornutus.

PEAT EDGE C.

Distribution of Large Webs Throughout 1959.

No. of Webs/ft.	Obs.No./ft.	Expt.	χ^2
0	21	11	9.0909**
1	9	15.25	2.563
2	5	10.57	2.936
>2	9	7.18	.4614

Total χ^2 = 15.0513
2 df p <.001

Distribution of Web Numbers after Removal of Sections 'Unsuitable for Spinning'.

0	11	5.653	5.058*
1	9	10.14	.1281
2	5	9.102	1.849
>2	9	9.105	.0012

Total χ^2 = 7.0363
2 df p <.05

Table 16 shows again the familiar pattern of aggregated web counts both before and after the removal of 'unsuitable areas' for 'large webs', but it is of interest to compare the most, and least favourable areas along Peat Edge C for the two species.

As judged by 'multiples', the most favourable foot intervals for M. merianae were numbers 31 and 33 equally; A. cornutus had no webs in these two sections at all. Conversely, the most favourable site for A. cornutus was number 41, while two webs only were recorded from this section for *M. merianae*, - the lowest number for the whole 43 feet of the peat edge! This gives some measure of the differences in habitat of the two species.

The picture of 'small' web distribution for *A. cornutus* as it appears in Table 17., is the usual one, until the 'unsuitable' areas are removed, when aggregation seems to disappear. No explanation can be given for this, except to say that the numbers are rather low, and that web tenacity is less noticeable in the young

TABLE 17

A. cornutus.

PEAT EDGE C.

Distribution of Small Webs Throughout 1959.

No. of Webs/ft.	Obs. No/ft.	Expt.	χ^2
<2	26	14.602	8.9**
2	3	11.68	6.449*
3	3	8.932	3.940*
>3	9	8.7860	.0052

Total χ^2 = 19.2942
2 df p <.001

Distribution of Web Numbers after Removal of Sections 'Unsuitable for Spinning'.

No. of Webs/ft.	Obs. No/ft.	Expt.	χ^2
<3	15	10.384	2.053
3	3	6.583	1.951
4	3	5.54	1.164
>4	8	7.493	.0343

Total χ^2 = 5.2023
2 df p >.05

which appear to be much more mobile. This latter point may well account for the fact that Table 18 does not show the tendency for aggregation in the young which was seen in the case of *M. merianae*.

TABLE 18.

PEAT EDGE C.

A. cornutus.

Distribution of Maximum Nos. of 'Small Webs' on any day in the Month. - Data corrected for 'unsuitable' areas.

July.

No.of Webs/ft.	Obs.No./ft.	Expt.	χ^2
0	22	20.09	.1816
>0	8	9.91	.3681

Total χ^2 = .5497
1 df $p > .3$

August.

No.of Webs/ft.	Obs.No./ft.	Expt.	χ^2
0	22	20.79	.0704
>0	8	9,21	.159

Total χ^2 = .2294
1 df $p > .5$

All this latter analysis of the distribution of spiders along peat edges, has been based upon the position of the webs which the animals have spun, but no mention has been made of the distribution of the animals during periods when they are not spinning.

During the months of September 1957 to February 1958, the position along Peat Edge A of all animals seen during the night counts was noted, and the distribution of the maximum numbers for each month is shown in Figure 7 together with the positions of any webs, the following morning. An examination of Figure 7 suggests a change in the distribution of the animals during the months of September, October and November, and to show this, the figures have been treated in Table 19.

The numbers of spiders seen in each of 4, 10 ft. lengths of peat edge for each of the 3 months shown (the figures for December and February were not used, as the totals were too small for analysis) were subjected to a J x J contingency χ^2 test. Moroney (1951).

TABLE 19.

M. merianae.

The Distribution of Spiders along Peat Edge A during September, October and November 1957.

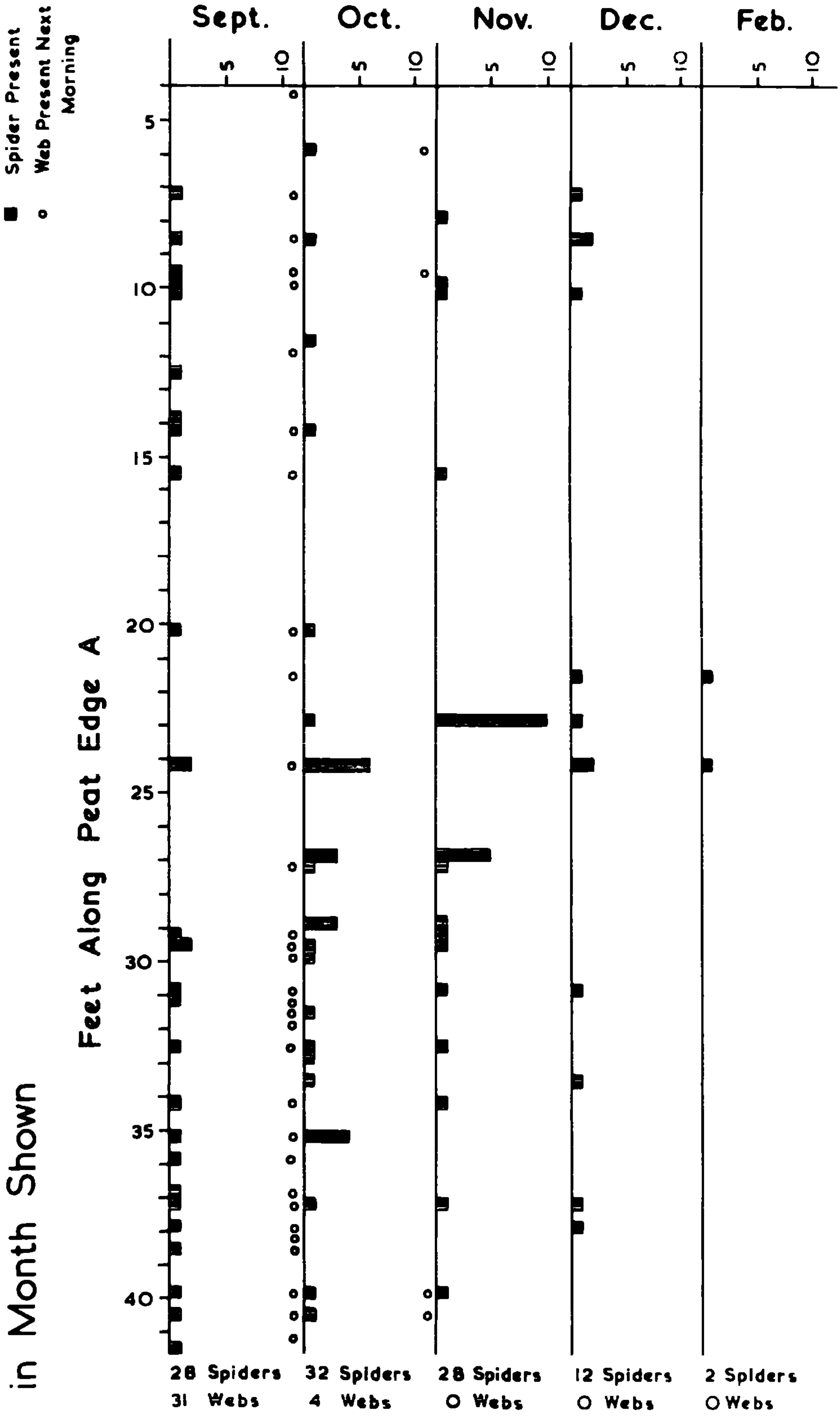
Section of Peat Edge	Sept.	Oct.	Nov.	Σ
1 - 11ft.	5	2	3	10
11 - 21ft.	5	3	1	9
21 - 31ft.	6	16	20	42
31 - 41ft.	11	11	4	26
Σ	27	32	28	87

$\chi^2 = 15.62$ with 6 df
$p < .02$

As these figures are heterogeneous, it means that the number of spiders in the 4 sections of peat edge are NOT independent of the month of examination, and it seems that a concentration of animals developed in the 21 - 31ft.

Fig. 7.

M. merianae. Max. No. and Posit. of Spiders Seen During One Night in Month Shown



region as Winter approached, and web spinning ended for the season. Now this region is characterised by a very large overhang, further protected by <u>Calluna</u>, and it is concluded that when the weather became unfavourable for web building, the animals congregated in a sheltered position to overwinter.

5. The Life Histories of Meta merianae, and Araneus cornutus.

(a). Qualitative Investigations.

(i) Period of Egg Laying, with Notes on Nests and Cocoons.

M. merianae.

The eggs of this species are enclosed in silken cocoons, which are hidden in crevices in the peat overhang, - Blackwall (1864) p 354, Nielsen (1932) p 181, making them very difficult to find, without doing extensive damage to the habitat. This increases the difficulties of discovering laying and hatching times. Judging from animals brought into the laboratory, cocoons are produced from May to August, and the young can take up to 6 weeks to emerge.

A. cornutus.

As previously mentioned, this species lives in a silken retreat spun amongst foliage, and as the animal may remain here for a very long time, the egg cocoons are incorporated into the structure. - Blackwall (1864) p 327, Nielsen (1932) p 171. As can be seen in Plate 8, the first cocoon is built into the bottom of the retreat and sealed off by a silken partition, and then the whole retreat is lengthened so as to provide a new resting place for the spider. The whole structure is enlarged to accommodate subsequent cocoons in a similar manner, and in the example shown, two cocoons have been produced and the female spider remains in a third cell. The first cocoon of the season was recorded in May, and production continued until August, by which time some of the first cocoons had hatched, 4 - 6 weeks having elapsed between egg-laying and the emergence of the young from the cocoon.

(ii) Hatching and the First Instar.

M. merianae.

After hatching, the young live communally inside the cocoon for some time before escaping, and the fact that measurements made on young, still in the cocoon are identical with those on young taken from small orb-webs, shows that they emerge, and begin spinning webs at once without an intervening moult. Careful examination of a cocoon from which the young had just emerged, revealed some unhatched eggs, and many spent egg cases, but no cast skins, indicating that in this species, the young emerge and begin spinning, during their first instar.

Plate 8.

Retreat of Araneus cornutus cut open, to show the Two Cocoons, and the Adult Female, within.

In the field, this emergence is most noticeable in September and October.

A. cornutus.

Examination of the empty cocoons of this species produced unhatched eggs, spent egg cases, and large numbers of cast skins, light fawn, and almost transparent. In this case, measurements indicated that emergence, and the beginning of spinning activity took place in the second instar, and they have been observed in the field from August to October.

(iii). The Number of Instars in the Two Species, as Determined from Body Measurements.

To discover the number of instars through which both species pass, attempts were made to culture the animals in the laboratory, but these failed, due to their refusal, (particularly M. merianae) to spin webs in captivity, and so the method of measuring various parts of the bodies of individuals for all size ranges was attempted.

It is not normally possible to identify immature spiders, and it was here that the paucity of orb-web spinning spiders in the area proved so useful. In any group of immature animals collected from orb-webs in this area, it was only necessary to distinguish between individuals of M. merianae and A. cornutus, and this could be done easily, as the former species has long legs relative to its body, whilst the latter's legs are shorter, and give a more squat appearance to the animal.

Animals were collected at random throughout 1958 and 1959, and 4 measurements were made on each specimen as follows:-

1. The width of the carapace at its widest point.
2. The length of the sternum at its longest point.
3. The length of femur 1.
4. The length of tibia 1.

It was hoped that with the application of Dyar's growth law (1890) it would be possible to deduce the number of instars in each species from the above measurements, and although this has been attempted in the following section it should perhaps be noted that two serious difficulties attend any such analysis.

1. At least the first and last instars should be known by direct observation, as interpolation cannot show when a series should begin and end.

2. As the range of measurements, particularly for the final instars, usually overlap, it is important that the appropriate growth law should be applied, because as Ghent (1956) has shown, some species follow a linear growth curve, and not the exponential curve of Dyar.

Harding (1948) has developed a method of analysing polymodal distributions by means of probability paper, and Gabbutt (1959) has used this technique for assessing the instars of the Wood Cricket, but even he resorted to the number of antennal segments in order to confirm his head width measurements. In view of the many uncertainties which surround theuse of this method (which is the only practicable one in very many cases), the present author agrees with Ghent (1956) who writes, "In any event, the investigator should place his greatest reliance upon direct inspection of the measurements, to see if in relation to the general rate of increase of the series, there is at any point a discontinuity sufficiently great to indicate that a moult may have been entirely missed".

To obtain the clearest graphical evidence of the differences between instar measurements, it was decided not to rely on any one of the four measurements made, because as Blackith (1958) has said, "Multivariate analyses are more sensitive than univariate ones". This it was hoped would reduce the errors which always appear, when whole pickled specimens are measured, due to inaccuracies in the measuring, and slight abnormalities in parts of the animal.

M. merianae.

Figure 8 shows width of carapace plotted against length of tibia 1, and length of sternum against length of femur 1. As can be seen, there is a constant relationship between the 2 measurements, in both cases, and as a result, each pair has been summed.

In Figure 9, where the width of the carapace plus the length of tibia 1 has been plotted against the length of the sternum plus the length of femur 1, all fouf measurements contribute towards the separation of the instars.

This graph shows that whilst the measurements from small animals fall fairly readily into the typical 'cluster of points', the points for the larger animals form a more continuous series. The mature animals could be recognised as such, by their sex organs, as could sub-mature males, where the palpal tarsus is greatly swollen. These 2 instars were marked accordingly, but for the rest, the suggested groupings were drawn in by inspection. Some overlap will at once be noticed between the larger sub-mature males, and the smaller mature females, whilst the constant relationship between the two pairs of summed measurements, indicates that further summing is permissible when another factor needs to be correlated with this 'best available' description

Fig. 8.

M. merianae. Growth Relationships of Paired Measurements

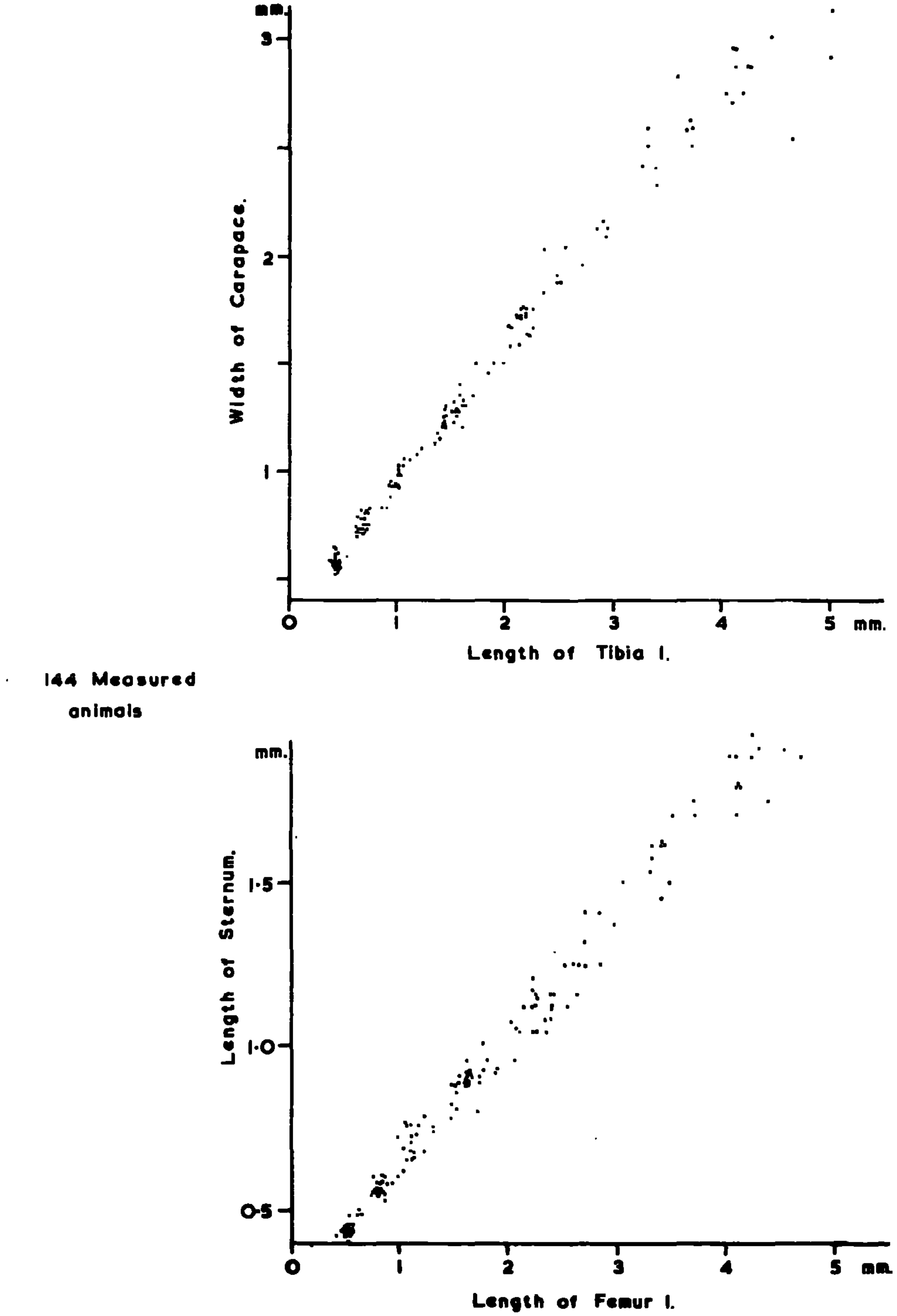
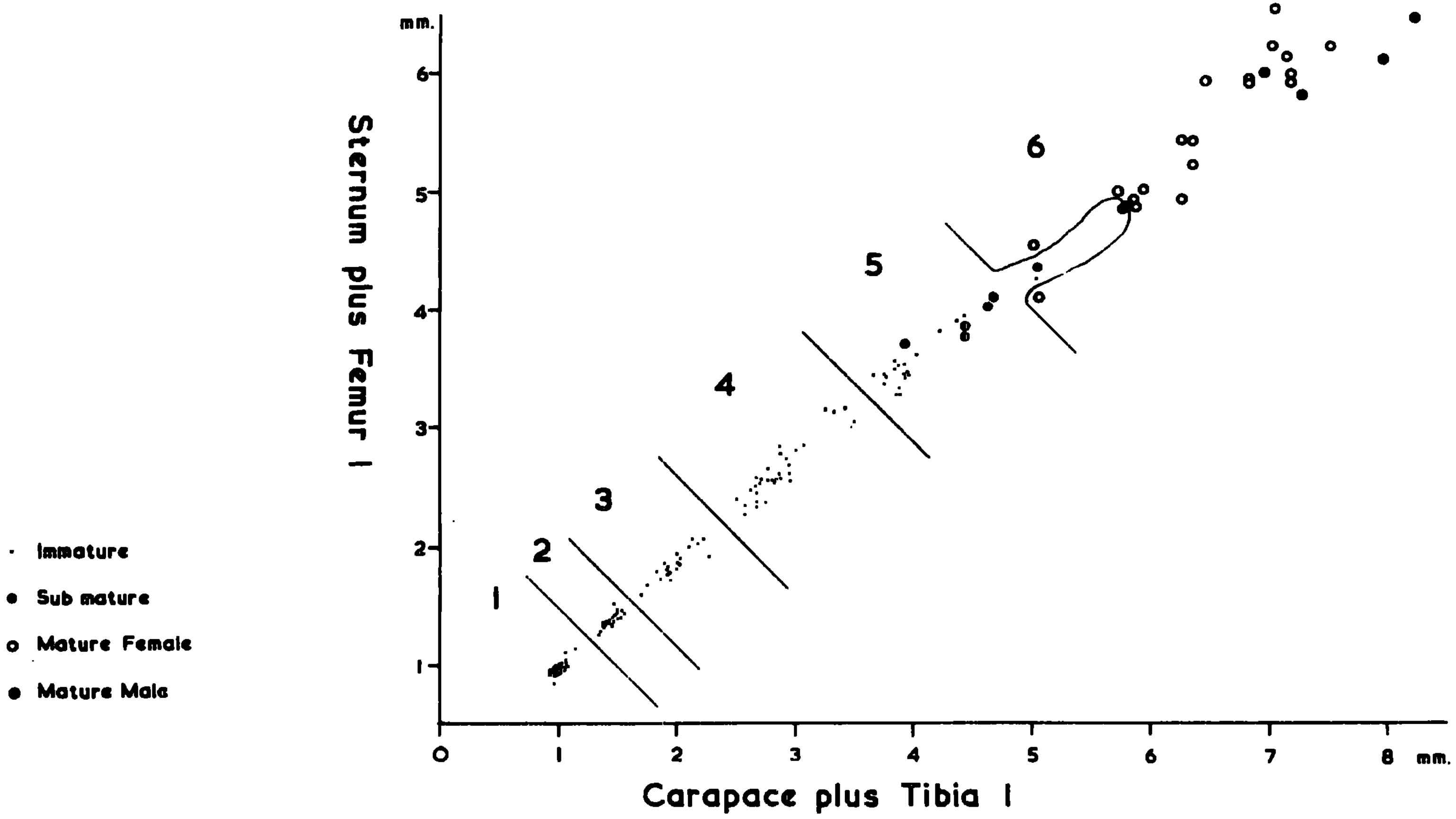


Fig. 9.

M. merianae Suggested Instars



of the instars. To test the likelihood of these groupings corresponding with instars, means were taken for each group, and were plotted against equal intervals on the second axis. They seemed to describe the logarithmic growth curve of Dyar, but to test this more critically logs of the means were plotted, and as can be seen in Figure 12 they fit well to a straight line. As the first two and last two instars can be estimated anyway with some confidence, the good straight-line fit lends support to the suggestion that in M. merianae, the adult animal represents the 6th instar.

A. cornutus.

An identical analysis was carried out for this species; Figure 10 shows the constant relationships which permit summing, and Figure 11 the suggested instars and the continuing constant relationship. In this case however, because the epigyne of the mature female has a long scape, sub-mature females as well as sub-mature males could usually be recognised, and here it would appear that the mature and sub-mature do not overlap.

As has already been mentioned, the first instar is passed in the cocoon, the protective effect of which, may account for the animal's exoskeleton never appearing to achieve the hard resistant nature of the later instars.

Fig. 10.

A. cornutus. Growth Relationships of Paired Measurements

128 Measured animals

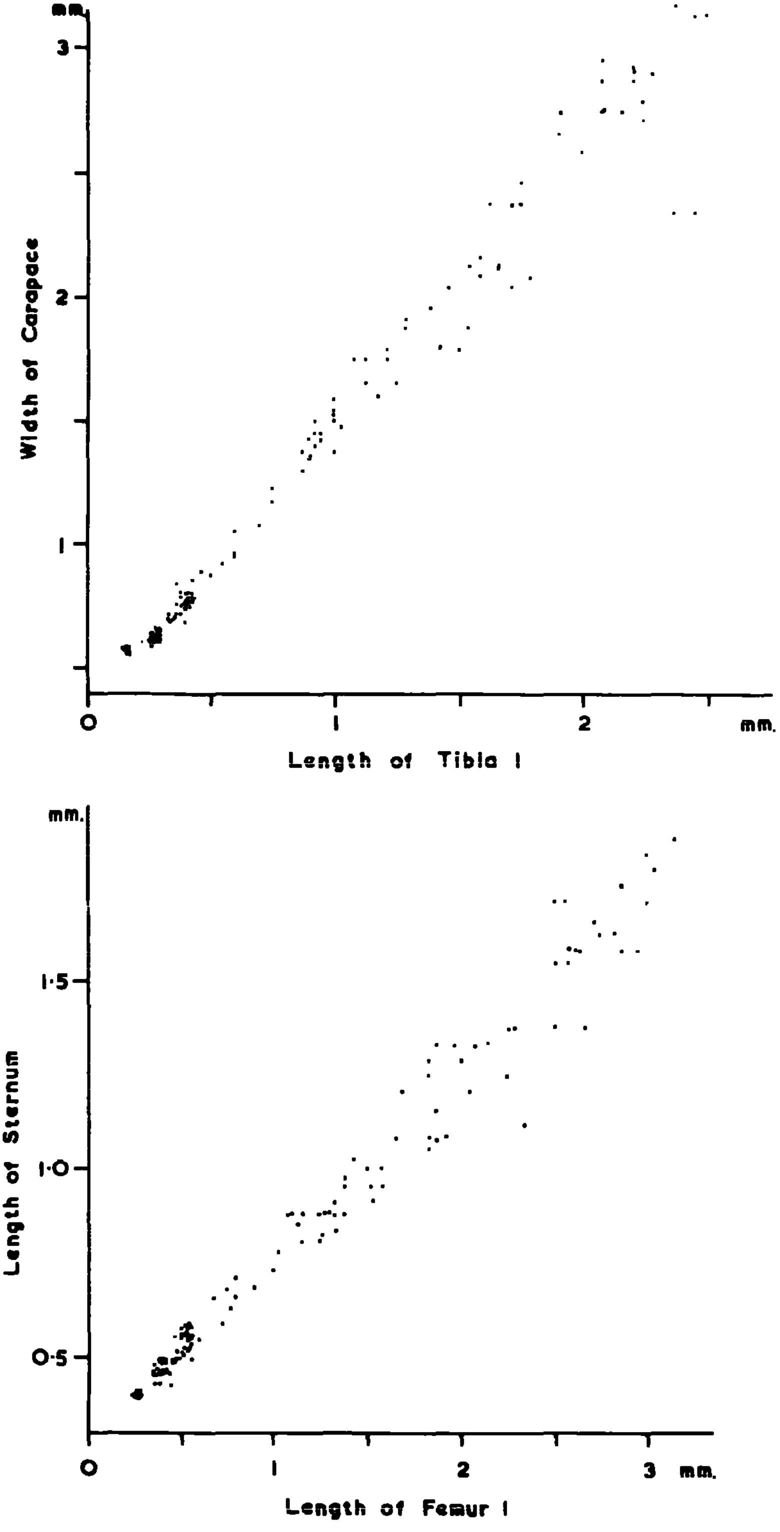


Fig. 11.

A. cornutus Suggested Instars

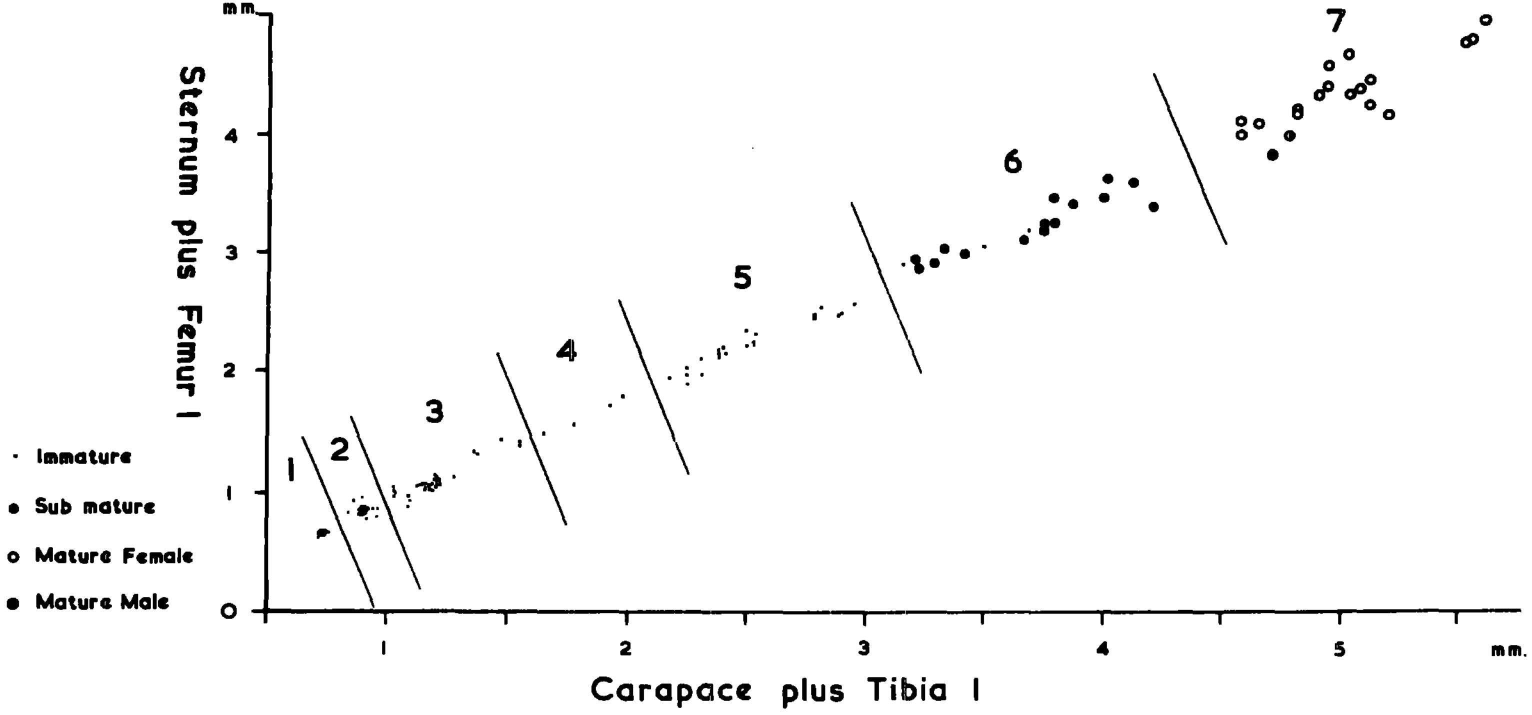
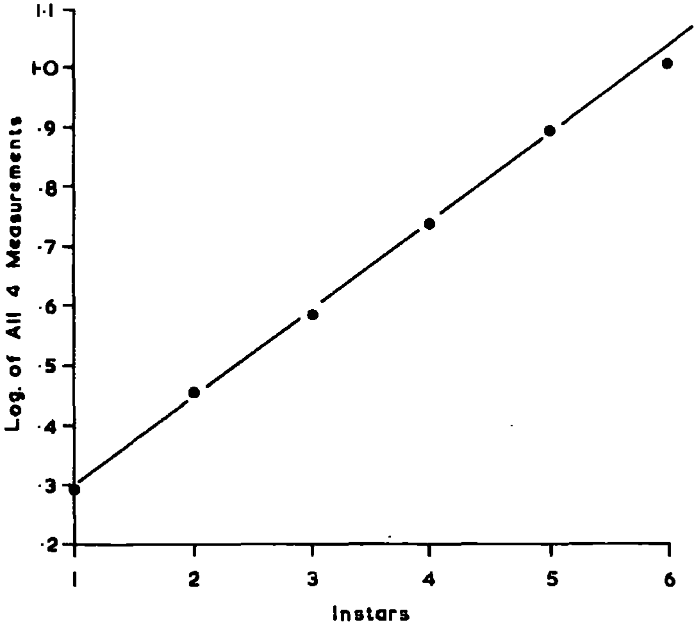


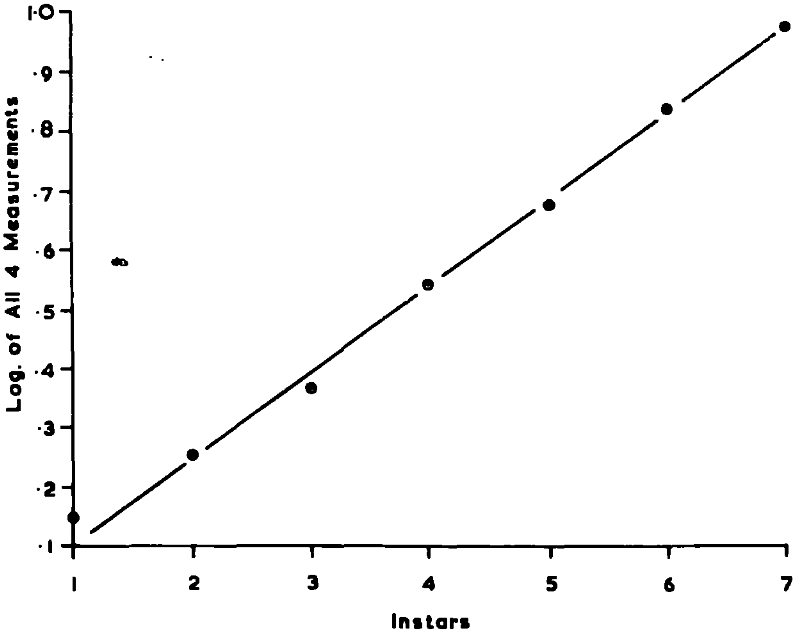
Fig. 12.

Log. Means of the Suggested Instar Groupings

M. merianae



A. cornutus



This may account for the failure of this instar's mean to fit satisfactorily on to the logarithmic growth curve as shown in Figure 12. Given the discrepancy of this rather specialised instar however, a logarithmic growth curve seems to describe the means of the instar groupings perfectly satisfactorily, so that in A. cornutus it is suggested that the adult animal represents the 7th Instar.

These two estimates of 6 and 7 instars respectively, fall well within the range of instar numbers found by other workers on spiders, Savory (1928), Gertsch (1949), Comstock (1940), Bonnet (1926, 1927a). It appears that it is the size of the species which determines the number of moults it will undergo before maturity. Thus, males of Mastophora cornigera require only 2 moults, whilst the male of Eurypelma californica, a tarantula is recorded as having moulted 22 times. Bonnet (1926) rearing spiders in captivity also found some variation within the species. Thus, in A. diadematus 6 females underwent 8 moults, and one 7, whilst 1 male moulted 7 times and 2 six times. For Dolomedes fimbriatus 10 moults are recorded, and it is pointed out that the first moult occurs in the cocoon. In view of these, and other observations, that moulting often occurs after maturity, overlap in the measurements of the later instars is quite understandable, and it may be that the moulting pattern which has emerged, represents only the average situation.

(iv). Overwintering.

In M. merianae, the greatest number of first instar spiderlings was found in September, whilst in A. cornutus, the emergence of second instar individuals continued until October. As small spiders of both species were again present in the May and June of the following year, one can only infer that they overwintered in this stage, a very common situation amongst spiders - Elliott (1930).

As has already been suggested, by the times of egg laying, adults of both species are also found immediately after the winter, and the fact that these animals have indeed overwintered has been shown by adult females of both species, marked during August and September, being subsequently captured the following spring. A marked sub-mature male A. cornutus was also recaptured the following spring.

Whilst it has long been recognised that some adults of A. cornutus overwinter, Thomas (1927), Blackwall (1864) p 321, Nielsen (1932) p 171, Cambridge (1881) p 276, some authors have denied this to be the case in M. merianae Turnbull (1957), Nielsen (1932) p 181 saying that adults only occurred in June and July. This discrepancy is interesting, and it could be, that the less favourable climate of the uplands, reducing the feeding period, serves to lengthen the maximum longevity, (one marked adult female of M. merianae is known to have lived at least 19 months, and overwintered twice) if not the life cycle. On this last point, Cloudsley-Thompson (1955) working on the genus Ciniflo has said that spiderlings hatching in the summer do not reach maturity until the autumn of the following year, that is to say that they first lay eggs when 2 years old, and it is now thought that this may be true of at least some individuals of both species at Moor House. Thus, it is inconceivable that animals of both species which have overwintered in their first or second instars, and have only begun to spin again by mid-May, would be capable of producing the cocoons which are found in early June. Indeed, the young of A. cornutus, which hatched in Mid-August in an artificially established colony, where this species had not previously existed, were still quite small when examined towards the end of the following June, and far from mature by Mid-August, one year after hatching.

It would appear that both species overwinter in at least two stages, as young first or second instar spiderlings, and as mature adults.

(b). Quantitative Investigations.

(i). Fecundity.

As A. cornutus lays its eggs in a conspicuous nest, some material was collected for investigations into its fecundity. Only a little material was taken however, and that, far from the sampling sites, as there was a real danger of decimating the rather sparse population of such an area.

Adult females were taken each month and dissected, and any eggs were counted, and classified as to whether they were 'large but not yet mature' or 'mature and ready to be laid'. The egg-laying condition of the females, as judged by these criteria is shown in Table 20.

TABLE 20.

Seasonal Egg-Laying Condition of A. cornutus Females.

Month.	No. of Females examined.	Animals with large but not yet mature eggs.		Animals with large eggs, ready to be laid.	
		No.	%	No.	%
May	7	2	29	1	14
June	15	3	20	4	27
July	12	2	17	2	17
August	7	0		0	
September	4	0		0	
October*	2	0		0	

* Considerable fat stores were noticed, presumably in preparation for overwintering.

Although inadequate, these figures reaffirm field observations that egg maturation begins in May, and that the peak month for egg-laying is June, and this can be compared with work on another insect predator at Moor House, the meadow pipit (Anthus pratensis), by Coulson (1956). He draws attention to the remarkably close relationship between the emergence of Tipula subnodicornis, and the presence of Meadow Pipit nestlings towards the end of May and the beginning of June, and it is interesting that A. cornutus which also preys upon this Tipulid should have its peak period of egg production at about this time.

The numbers of eggs 'ready to be laid' in the appropriate 7 females were 75, 131, 81, 185, 82, 38, but as maturation is presumably progressive, these mean very little. Nests with their cocoons were also collected, and the number of eggs per cocoon was counted. See Table 21.

TABLE 21.

Number of Eggs per Cocoon in A. cornutus.

Month.	No. of Cocoons examined.	Mean	95% Confidence limits
June	5	190	145-235
July	12	119	96-142
August	5	87	75- 99
September	4	106	72-140

The overall mean of 124, with a maximum number of 253, and a minimum of 73 is considerably lower than the numbers of eggs cited by Blackwall (1864) p 327 of 220, and Nielsen (1932) p 172 of 201 - 213, but this is very similar to the means obtained by Bonnet (1927b) for 2 females, each of which produced 10 cocoons, of 117 and 121 respectively.

His figures for the two females are -

I. 202, 165, 148, 164, 106, 95, 84, 88, 78, 45, Σ 1175
II. 234, 218, 182, 140, 112, 87, 81, 72, 51, 33, Σ 1210

and they reflect closely the fall off in numbers of eggs per cocoon observed at Moor House, and so it is now thought that this may be simply due to ageing in the females.

The number of cocoons in each nest was noted in Table 22, which should be compared with Bonnet (1927b),

TABLE 22.

Number of Cocoons per Nest in A. cornutus.

June	1, 1, 1, 1, 1,
July	1, 1, 1, 1, 2, 2, 2, 2, 2, 1, 2,
August	2, 2, 1, 1, 1, 2, 1, 2,
September	1, 1, 3, 4,

who obtained from females reared in the laboratory 6, 10 and 10 cocoons respectively. It would be interesting to examine the reasons for this discrepancy, two of which immediately come to mind.

1. The animals, leave their nests, or are killed before they have produced their full complement of cocoons.

2. The number of cocoons produced, is related to the amount of food which the female has been able to catch, assuming that Bonnet's animals were adequately fed throughout their period in captivity.

No cocoonal parasites were noticed during this study, which is in contrast with observations quoted by Blackwall (1864) p 327 and Neilsen (1932) p 172, but several batches of eggs were found to be attacked by fungus, as is recorded in Table 23.

TABLE 23.

Fungal Attack on the Eggs of A. cornutus.

Month	No. of Cocoons examined.	No. Attacked	% Attacked
June	5	0	0
July	17	0	0
August	12	3	25
September	9	5	55

It was not possible to decide whether this was a parasitic fungus which killed the eggs, and then lived on the remains, or whether it was merely a saprophytic one, living on dead (possibly unfertile) and already decaying ones. In any case, this does mean that cocoons which persist late into the season are less likely to hatch.

Finally, counts of the numbers of young, second instar spiders, which had not yet emerged from the cocoon gave some measure of the hatching success and degree of canabalism, and are set out in Table 24.

TABLE 24.

A Comparison between the Number of Eggs, and Second Instar Spiderlings produced per Cocoon.

Eggs.			2nd Instar Spiders
199	81	87	118
253	140	94	93
181	118	80	110
168	86	100	108
151	144	120	86
88	92	73	100
195	115	128	101
94	175	105	
97	73		
	Σ 3237		Σ 716
	Mean 124.5		Mean 102.3

In a random 't' test, t = 1.24 with 31 df; Thus p >.2. Although the mean number of second instar spiders produced per cocoon is smaller than the mean number of eggs, on the present analysis, this difference is not significant, and so it seems that if the eggs remain healthy, the mortality associated with hatching, the subsequent communal life, and the first moult in this species is quite low.

(ii) Age Distribution Within the Colonies.

Methods.

To study this problem, it was necessary to devise some method of obtaining the data without having to kill and measure the animals, a technique which would have been disastrous with such small numbers. Obviously, second instar animals spin smaller webs than do adults, and the possibilities of this, as a method of estimating age were examined.

Montgomery (1908a) is one of the few people to have studied the changes in the size and nature of the orb-web, with the increasing age of its spinner, and he made comparisons on the following 3 points for the 2 spiders <u>A. sclopetarius</u> and <u>A. marmoreus</u> 1. Number of radii, 2. Number of spiral loops, 3. Greatest diameter of spiral. He concluded that age changes are most clearly reflected in the diameter, and least clearly in the number of radii, and this is supported by Tilquin (1942). MacCann (1936) seems to be one of the few to have used this, even qualitatively, as an ecological tool, when he was making inferences about the life cycle of <u>Nephila maculata</u>.

In the present study, all the animals on which body measurements were made, were taken from orb-webs. This was a rather difficult process, especially in <u>M. merianae</u>, where the signal thread had to be followed up into the peat overhang, and the animal at the end of it captured. In each case, the radius of the web was estimated in cms. by using a pair of compasses as callipers. Estimation was necessary, because rarely was the web a perfect circle, and when this was not the case, an average radius was estimated, i.e. the radius which would have applied if the web could have been pulled into a circle. The radius was measured from the hub to the outermost viscid spiral.

Figure 13 expresses the relation between the 4 body measurements summed, and the radius of the web in cms. for both species. Although the general trend is clear, the scatter of the points is great, but as Montgomery (1908a) has pointed out, this is to be expected, as the size of the web must be related to the size of the space, and the amount of silk available.

In Figure 14, the mean web radii for the suggested instars are plotted, and, with the exception of the point for instar 4 in A. cornutus, they fit a logarithmic curve. The bad fit of this point, is probably due to sampling error, as it is based on only 4 individuals.

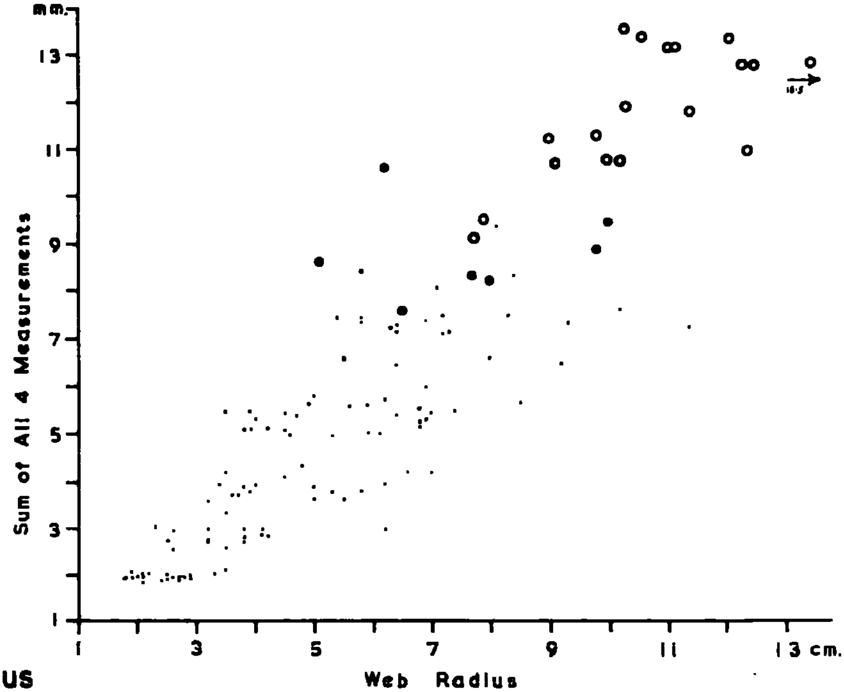
This suggests that the size of the web increases in a linear manner with the size of the animal; that is to say, that it is the area from which food is drawn which bears the constant relationship.

From the two straight-line graphs on Figure 14, the points midway between the instar means were read off, and taken as being the two extreme web radius limits allowed to describe each instar.

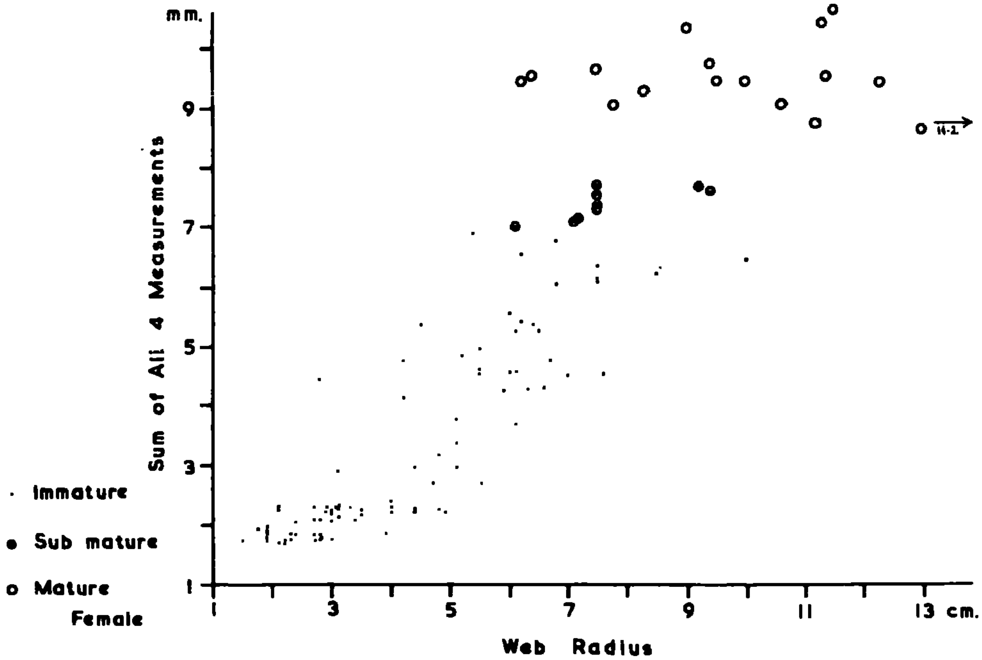
Fig. 13.

Relation of Individual's Size to Web Radius

M. merianae

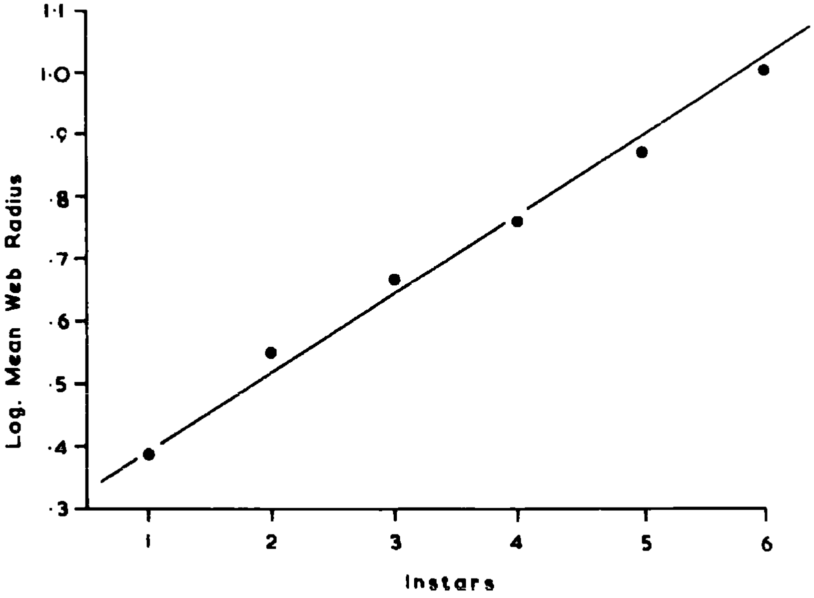


A. cornutus

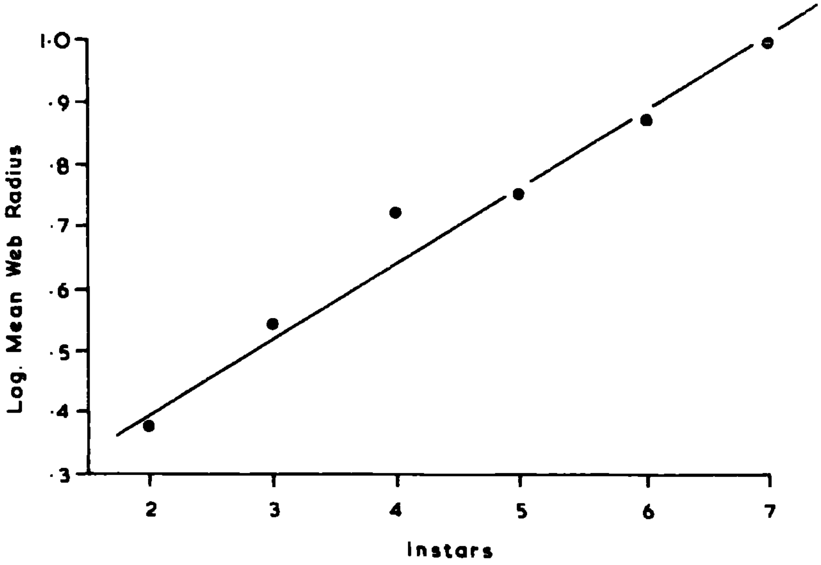


Log. Means of the Web Radii of Suggested Instars

M. merianae



A. cornutus



Basis and Accuracy.

Using the limits set above, the percentage of animals known to belong to the particular instar, which fell within the limits set, was calculated, as was also the percentage falling within the limits of plus and minus one instar. These results for the two species, are summarised in Tables 25 and 26, and it can be seen that on the basis of a given web radius, the spinner can be assigned to an instar, which plus or minus one will be correct with a probability of often well over 90%.

TABLE 25.

M. merianae - Limits set for the web radii of each instar, and the percentage of animals which fall within these limits.

Instar	Log. Values	Radii in cms.	% within Instar	%(±)one Instar
1.	<.45	<2.8	81.0	100.0
2.	>.45 - .58	>2.8 - 3.8	46.7	93.4
3.	>.58 - .71	>3.8 - 5.1	31.6	94.8
4.	>.71 - .83	>5.1 - 6.8	38.7	90.4
5.	>.83 - .96	>6.8 - 9.1	40.7	96.4
6.	>.96	>9.1	79.0	100.0

These are possibly the best results that can be expected from this approach, and while inaccurate, they might be expected to give some guide to the age structure of the colonies under investigation.

TABLE 26.

A. cornutus - Limits set for the web radii of each instar, and the percentage of animals which fall within these limits.

Instar	Log. Values	Radii in cms.	% within Instar	%(±one Instar
1.	Instar spent in cocoon - no webs.			
2.	<.45	<2.8	89.5	94.7
3.	>.45 - .58	>2.8 - 3.8	43.7	93.9
4.	>.58 - .7	>3.8 - 5.0	25.0	100.0
5.	>.7 - .82	>5.0 - 6.6	63.6	95.5
6.	>.82 - .95	>6.6 - 8.9	66.6	100.0
7.	>.95	>8.9	70.6	88.4

Results.

M. merianae.

Each month, on days when there were many webs, all the webs were measured, and the pooled results for the 3 peat edges are laid out in Figure 15. These data are derived from the day in the month ~~which~~ with the maximum number of measured webs, and as it is webs, which form the basis of these counts, it must be remembered that the figures reflect not only the population level, but also the web spinning activity, and this latter effect is most noticeable at the very beginning and end of the season. 'Maximum Numbers' per month were used, as it was felt that these would give the best available estimate of the population, on the basis that a really favourable day would induce a large proportion of the population to spin.

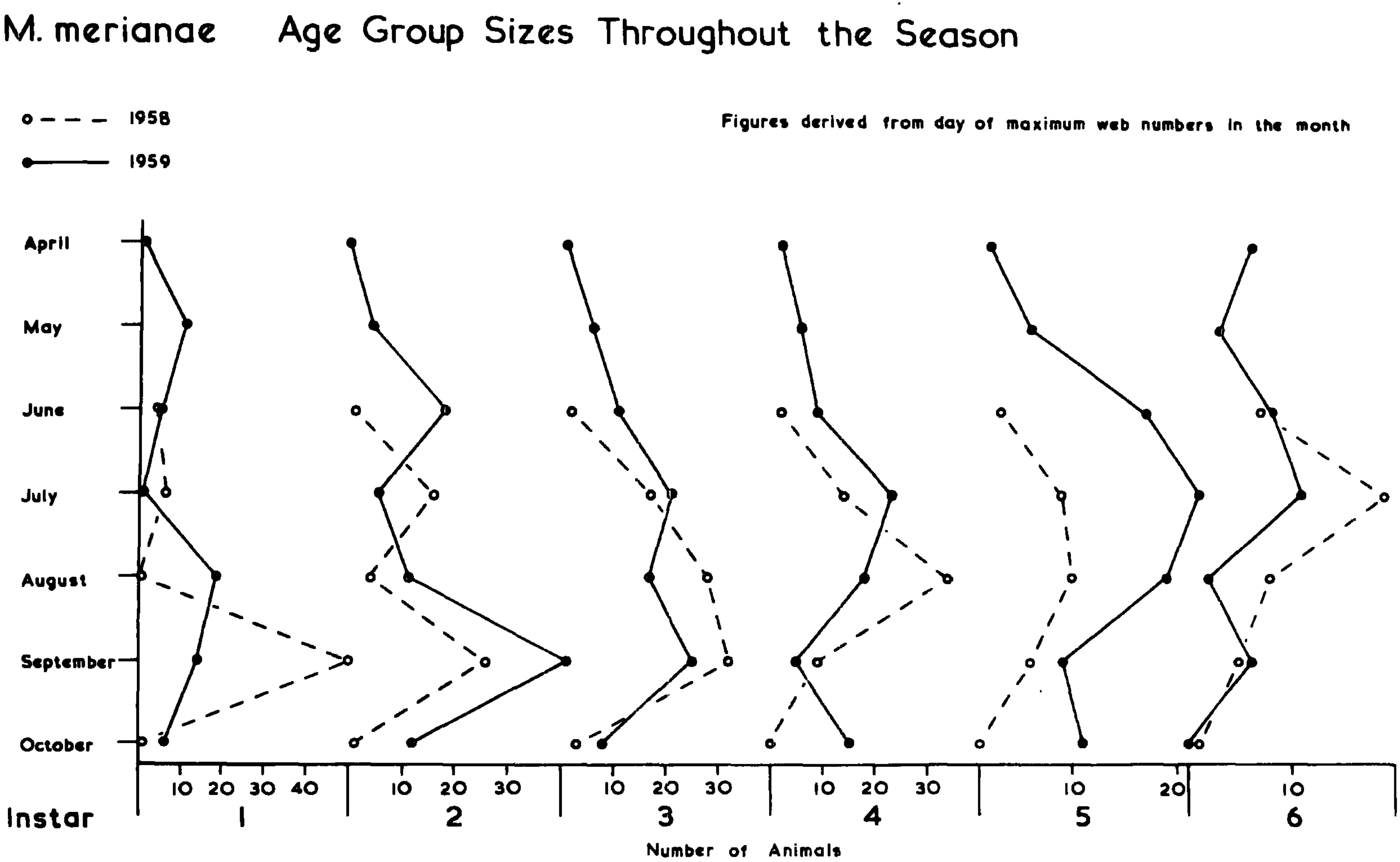

M. merianae Age Group Sizes Throughout the Season
1958
1959
Figures derived from day of maximum web numbers in the month
April
May
June
July
August
September
October
10 20 30 40
10 20 30
10 20 30
10 20 30
10 20
10
Instar
1
2
3
4
5
6
Number of Animals

Fig. 15.

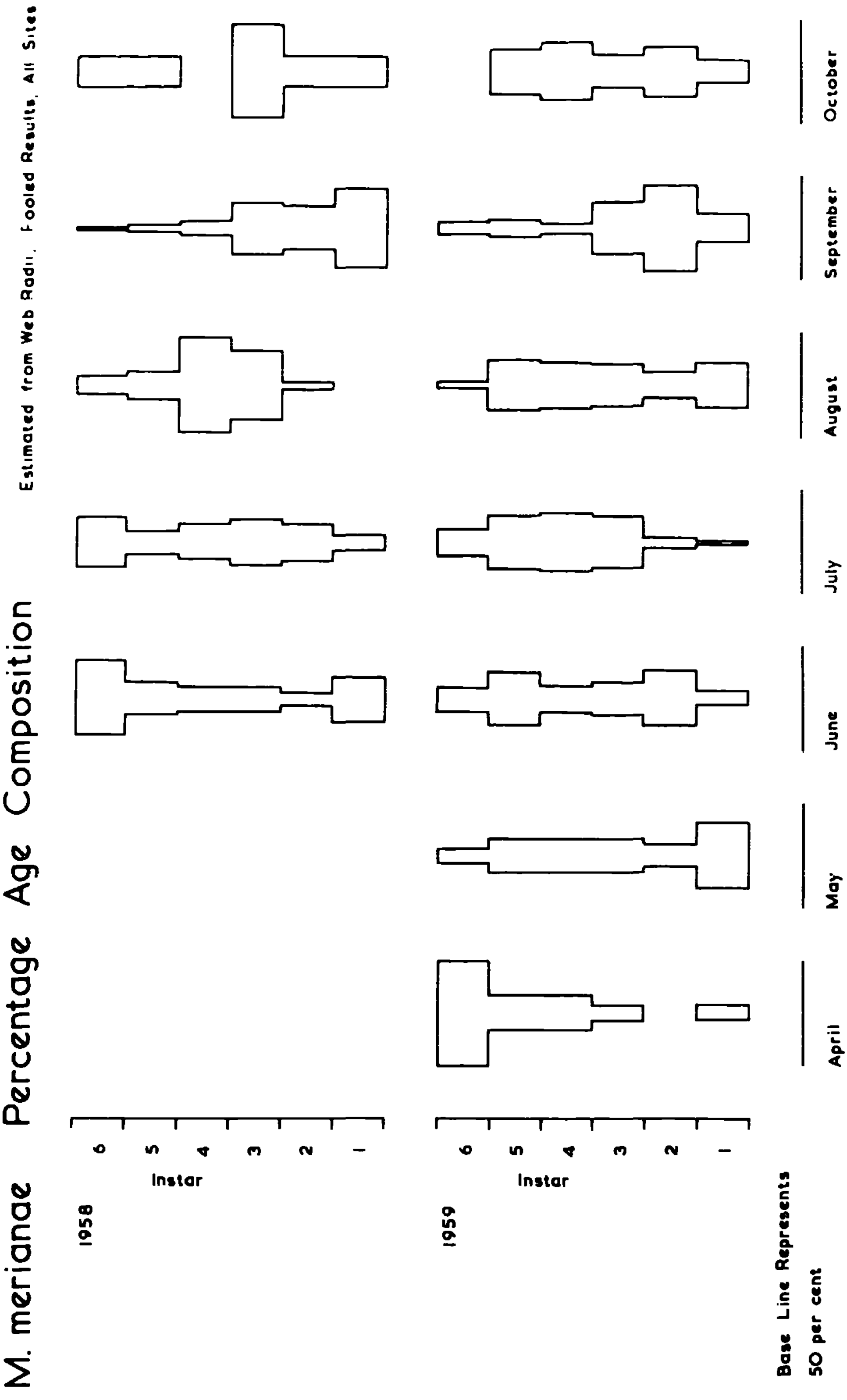
Two peaks occur in instar 1, the first in May immediately spinning is recommenced after the winter, which must represent animals which have overwintered after hatching the previous autumn, and a second, much larger peak in Autumn (in September 1958 which had had a rather cold, wet summer, and in late August 1959 after an extremely warm, dry summer.)

Taking the 1959 figures, the 1st. instar peak in May can be followed tentatively through the summer. Thus, a 2nd. instar peak appears in June, followed by 3rd. 4th. and 5th. instar peaks, all in July. In 1958, the whole trend is a little later. The mature animals show peaks in April and July, the first presumably due to overwintering, and the second to maturing animals.

It should be noted that while 76, 1st and 2nd instar spiders were counted in September 1958, the maximum count in April, May and June 1959 was 23, and this suggest that the young spiders suffer heavy mortality over the winter.

Figure 16 shows the same data expressed in the more familiar 'age pyramid' - see Odum (1959) p 171, used as an index to population trends. Thus, the September picture of a broad based polygon reveals a high proportion of young forms, in a regenerating population; whilst the 'top heavy' July polygon with its high proportion of

Fig. 16.


M. merianae Percentage Age Composition
Estimated from Web Radii, Pooled Results, All Sites
1958
1959
Instar
6
5
4
3
2
1
April
May
June
July
August
September
October
Base Line Represents
50 per cent

mature, and maturing forms would be characteristic of a population approaching senility. In this case, the technique more commonly used to assess the 'regenerative health' of a population at any given point in time, is being used in a different way, to study the annual changes in a population with marked annual life history fluctuations. The influence of web spinning activity on these results can be seen by comparing the April and May pyramids for 1959; these show a marked difference, at a time of the year when no major changes in the population would be expected, and can be accounted for on the assumption that the older animals commence web spinning earlier after the winter than do the young ones.

A. cornutus.

As only a small colony of this species lived in the peat edge study areas, the numbers here are particularly inadequate, and are simply listed in Table 27.

The activity season appears to be shorter in this species, than in M. merianae, and apart from re-affirming the suggestion of overwintering taking place in at least two age groups, these figures simply demonstrate how much more blurred, and difficult to disentangle are the life history patterns of animals with a two year life cycle, when compared with the striking patterns exhibited by animals with a single year life cycle.

TABLE 27.

A. cornutus - Number of each instar, on day of maximum web numbers each month.

	Instar.						
1958	2	3	4	5	6	7	Σ
June			1	1		2	4
July			2	1		2	5
August		1		3	3	2	9
September		1					1
October			N I L.				
1959							
April			N I L.				
May		2	2		2		6
June			3	2	2		7
July	1	2	4	1	2	1	11
August		6	5	1	1		13
September			N I L.				
October			N I L.				

6. Webs and Web Spinning.

(a). Methods.

As soon as daily counts of webs was begun, the wide fluctuations in numbers from day to day were noticed, and it was decided to investigate some of the factors affecting web spinning in the field. For studies of this kind, it was essential to know whether or not the web found at place A to-day was the same one which was there yesterday. Accordingly, it was decided to mark all webs whenever they were counted, and this was done by spraying a little Lycopodium powder on to one or two of the viscid spirals, so producing a noticeable white streak. This technique was suggested by Savory (1952) p 144, for making webs more visible for photographic purposes. The powder was dusted on to the web from a polythene bottle, and the marks were always kept small so that they would not influence the subsequent behaviour of the animal. N.B. Only 'large' webs were marked in this way.

(b) Web Numbers and Season.

Web counts show considerable variation from month to month, when the maximum counts are compared and these are presented graphically in Figure 17. These variations reflect two things, population levels, and the general suitability of the month for web-spinning. The former has already been studied in the analysis of the population age structure, and it is the seasonal effect on web-spinning which can best be seen in Figure 17. Virtually no webs were to be found for 5 months of the year and it seems probable that the majority of individuals did not spin for 6 months. This implies that the animals spend half the year without food, and this is the more remarkable in the early instars, where the food reserves must of necessity be small. It seems that *M. merianae* 'adults' have a slightly longer activity season than the young, and that both have a decidedly longer season than the 'adults' and young of *A. cornutus*.

Greatest Number of Webs Recorded on Any Day in the Month

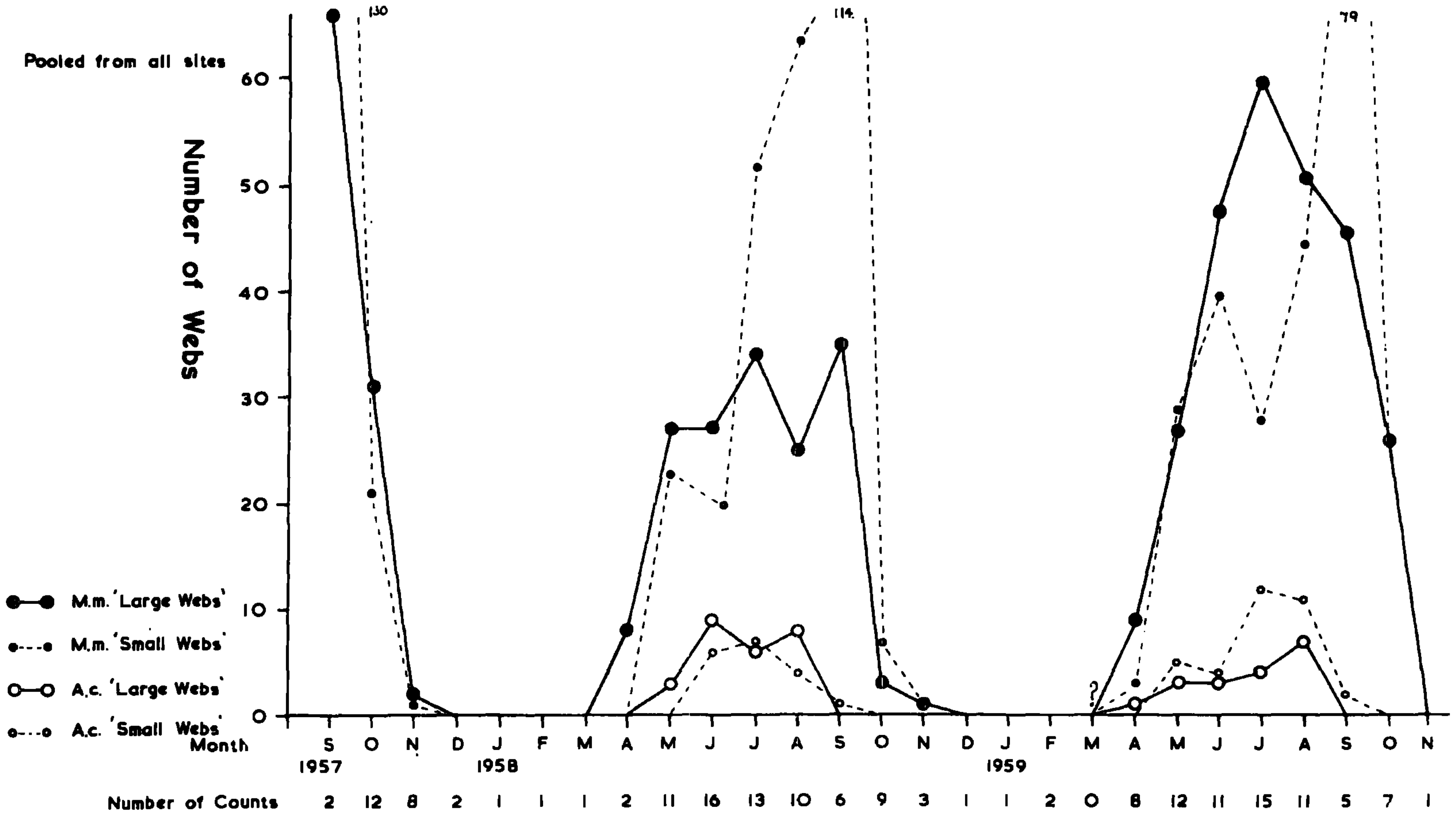


Fig. 17.

The population of M. merianae 'adults' was noticeably lower in 1958, which had a rather cold and wet summer, although A. cornutus did not seem to be affected. The autumn hatch of M. merianae spiderlings was a striking feature of all three years. As the accuracy of this method must depend largely on the number of counts made in each month, these have been recorded in the Figure.

(c) Frequency of Renewal.

As soon as web marking was begun, it was seen that in both species, the majority of 'large' webs found, had been spun since the previous day, and the relevant data have been collected together in Table 28. Here, the mean percentages of new webs in the daily counts are recorded for each month, together with an overall mean for each species, and two points worthy of note emerge.

First, the mean percentage of newly-spun webs on any day fluctuates from month to month, and is, as a rule, at its lowest at the beginning and end of each season. That is to say that at these periods, any webs seen are more likely to be old ones, an observation which fits in well with the suggestion that April, May, September and October lie at the limits of the web-spinning season.

TABLE 28.

Mean Percentage of New Webs in the Daily Counts.

'Large' webs only, counts under 15 rejected.

Month	Total No. of Webs counted.	Total No. of These New.	% New
M. merianae			
1957			
September	126	92	73
October	104	64	61.5
1958			
May	102	68	66.6
June	143	127	88.9
July	204	158	77.5
August	104	81	77.9
September	54	34	63
1959			
April	16	4	25
May	74	66	89.2
June	169	150	89
July	417	338	81.3
August	347	318	91.6
September	109	60	55
October	110	76	69

Overall = 79%

Month	Total No. of Webs counted.	Total No. of These New.	% New
A. cornutus			
1958			
June	47	44	93.6
July	16	13	81.4
August	36	26	72.2
1959			
July	16	12	75

Overall = 82%

Secondly, having said that the overall average percentage of new webs each day is 79 and 82 for M. merianae and A. cornutus, respectively, it appeared unlikely that such a large percentage of the webs had to be replaced because of damage, and it therefore seemed possible that the old webs were being actively destroyed by the animals. This was tested by taking two groups of M. merianae webs, and removing the owners in one group, whilst leaving the other group undisturbed. The webs were then examined as usual the following morning, and the results presented in Table 29.

TABLE 29.

M. merianae - The Persistence of Webs, and their Renewal.

Webs with Animals left in attendance.	Webs with Animals removed.
2 old webs survived out of 15 (9 new webs built)	12 old webs survived out of 16.

A 2 x 2 contingency test gave a χ^2 of 4.16, which, with 1 df has $p < .05$.

This shows that the mortality of attended webs was higher than that of unattended webs, i.e. the animals destroyed them. The term 'destroyed' has been used, but this needs further amplification. By the nature of the technique, it is only known that the section of the viscid spiral sprayed with powder was renewed, and experiments in which the main supporting threads of the web were coated with cellulose paint, indicated that these were usually used over and over again.

It was soon found that in both species, the process of 'taking in the old web' or 'web destruction' began soon after nightfall, and followed the pattern described by Nielsen (1932) p 166, and Fabre (1912), consisting essentially of the spider biting through several radii at the centre, and then moving outwards towards the frame, spinning a securing thread after it. One, two or three radii with their attached section of the viscid spiral were destroyed in this way at a time, the whole being rolled up into a tight ball, and pressed into the mouth region. Although this is an extremely important activity, and despite all the observations upon, and descriptions of, web spinning, only three other references to it have so far been found in the literature, Emerton (1883) p 67 describes the process in some detail, and McKeown (1952) p 27, and McCook (1889) mention it in passing.

Considerable confusion exists in the literature over these topics of web destruction, and the frequency of web renewal in orb-web spinning spiders.

The only references made to web destruction have already been noted, but there are considerable differences of opinion over the ultimate fate of the silk; in this case from the entire destruction of the old web, in the case of other authors from spare silk obtained during repairing, or in the removal of certain lines put into the web temporarily for construction purposes only.

Thus, Denis (1931), McCook (1889), Savory (1928, 1935), Fabre (1912), Gertsch (1949) and Westberg (as reported by Nielsen 1932) assert that after having rolled the silk into a ball the spider then eats it, whilst Newman (1871), Duncan (1949), McKeown (1952) Nielsen (1932), and Dahl, as reported by the latter, say that the ball of silk after being "mouthed over", is simply dropped. This is an intriguing problem, and it would be interesting to see if spiders possess enzymes capable of dissolving the silk, because in this way, a considerable amount of protein would be returned to the body. The present writer can only say that balls of silk of a very considerable size have been seen to be pushed between the maxillae, and no subsequent dropping has been observed, although it was noticeable that when the animal came to the silk which had been sprayed with lycopodium powder, it paused, and seemed to strip off the spores, dropping them to the ground.

This careful examination of objects on the silk which is being rolled up, is of course extended to small insects trapped on the sticky spiral. These are assembled together, carefully sucked, and then the remains discarded, and it seems that here is one of the clues to the whole process of web destruction. As McCook (1889) has said, many orb weavers do not trouble with insects of a minor sort, during the day, although great numbers, particularly of Nematocera, are often trapped there. This 'taking in' of the web at night, however, means that all these animals are utilized, when they must provide an important additional source of food. The other probable reason is given by Kirby and Spence (1815) when they write "... It is these gummed threads alone which retain the insects that fly into the net; and as they lose their viscid properties by the action of the air, it is necessary that they should be frequently renewed".

This introduces the other debated topic of the 'frequency of web renewal', to which the present investigation has paid some attention.

Here, McCook (1889) p 235 is at pains to refute any suggestion that web-spinning occurs nightly, as can be seen from the following quotation. "The assertion must be taken with much allowance, that nets of geometric spiders are renewed wholly, or at least their concentric circles are replaced every 24 hours, even when not apparently injured. In point of fact the renewal does not take place unless made necessary by the destruction of serious injury of the old snare. The reason assigned for this behaviour by the same authors, (Kirby and Spence 1815) viz. that the spirals rapidly lose their viscid properties by the action of the air, is not founded on fact, as is elsewhere shown. The viscid beads retain their adhesive qualities under ordinary circumstances for a considerable time. It is doubtful if any orb becomes thus disabled in so short a period as that assigned - 24 hours - except when exposed to rain". He is followed in this by Ellis (1912) p 36, although most other writers, Savory (1928, 1952), Bristowe (1941), Crompton (1950), Fabre (1912), and Nielsen (1932) talk of daily renewal as being the rule, and although Nielsen is the only one to give figures, when by counting the number of radii, he concluded that a web examined on 13 occasions had been renewed on 12 of them. It is Gertsch (1949) who points out that different species of orb weavers probably differ in the frequency with which they renew their webs, and it seems that what is required is not generalisations from a few observations on one species, to all orb-web spinning spiders, but a careful piece of comparative work on different species and genera, in the field, using standard techniques. The present work on the two species M. merianae and A. cornutus however, supports Kirby and Spence so far as these species are concerned, when they write, "The web of a house spider will, with occasional repairs, serve for a considerable period, but the nets of the geometric spiders are in favourable weather renewed either wholly, or at least their concentric circles every 24 hours, even when not apparently injured".

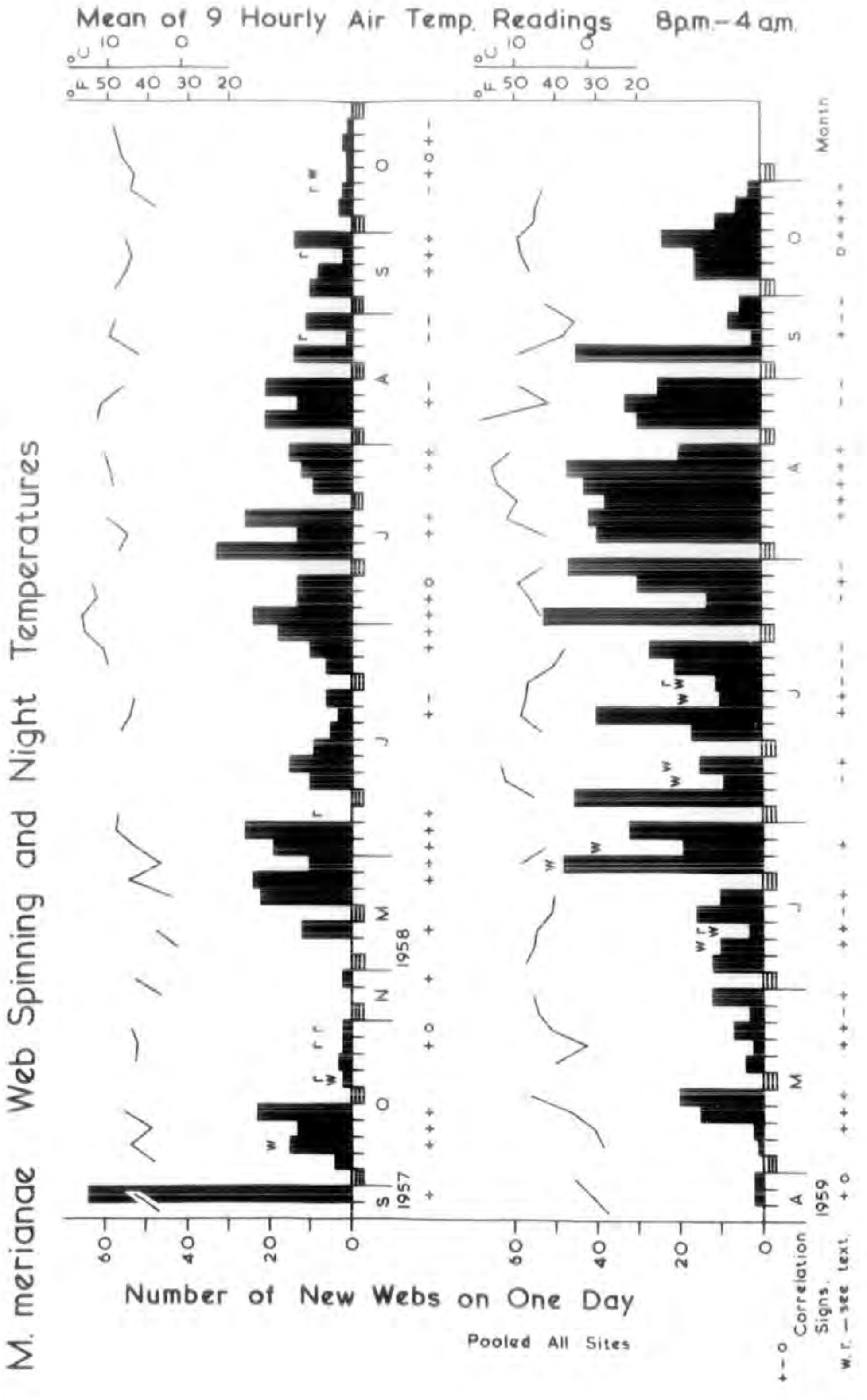
(d) Web Spinning Activity and Its Relation to Climate.

M. merianae.

Variations in web spinning activity can however be observed from day to day, as well as from month to month, and it must be assumed that this reflects day to day changes in the animals' behaviour.

In Figure 18, are recorded the data which have been collected for M. Merianae from September 1957 until October 1959. This is of necessity a fragmented record, as data could only be collected during a prolonged stay. In this analysis, only the number of new webs is used, and it is at once apparent that the number of animals indulging in web spinning varies considerably from day to day; thus in September 1957, on one day there were no webs on the peat edges, whilst on the next day there were 60.

Fig. 18.



M. merianae Web Spinning and Night Temperatures

If this were due simply to unrelated, isolated changes in the physiology of the individual animals, there would be no reason why the general level of web spinning activity in a colony of any size should be affected, and so external causative factors were sought.

The power of forecasting the weather has frequently been attributed to spiders, Nielsen (1932) p 49, Caraquel (1856), Fabre (1912), Deering (1942), Kirby and Spence (1815), Quatremere-Disjonval (1795), Pliny, and others mentioned in McCook (1894) p 77 and Bonnet (1945), and in a nocturnal species such as M. merianae, which only spins at night, it would be selectively advantageous for the animal to spin webs only on evenings preceding hot, insect-ridden days. Otherwise, the animal would simply waste energy and silk producing a web which might hang empty throughout a wet or windy day, free of insects. With this in mind, work was begun on correlating the observed web spinning activity with climatic conditions as recorded at the Moor House Meteorological Station, only a matter of 500 yards from the sampling sites.

The best way of correlating this sort of animal activity, with the multitude of varying climatic factors which could affect it, seems still to be a matter for statistical contention, and in this study, the following analysis was devised with two particular points in mind; first that it should be delicate enough to deal with the small figures which were available, and second that ease of computation, rather than a sophisticated treatment of the data was the more desirable, in this preliminary investigation, where only the one or two most highly correlated factors were required. The method eventually used, is illustrated for one climatic factor, (mean night air tempeature) in Figure 18. Here, a temperature graph has been superimposed on the web spinning histogram, the figures for which were obtained by adding the 9 hourly air temperature readings from 8 p.m. to 4 a.m. inclusive, a period which was chosen to cover most of the time during which the webs were actually being spun.

As can be seen from the figure, with a few exceptions, the fluctuations in web spinning activity follow fairly closely in direction the fluctuations in nightly temperature averages. An absolute quantitative relationship between the degrees of temperature fluctuation, and the numbers of animals spinning could hardly be expected, and with the unknown fluctuations in the population level, it would be impossible to measure, but it would be reasonable to expect that a warm night, following a colder night, might induce more animals to spin webs.

The function of the statistics, is to assess the reality of this apparent correlation of temperature and web spinning. If, when correlating two factors, the situation on two adjacent nights is taken, one of three situations can arise:-

1. As one factor increases, the other decreases and vice versa, = negative correlation.
2. As one factor increases, so does the other, and vice versa, = positive correlation.
3. As one factor fluctuates, the other remains the same, = no correlation.

In Figure 18, each correlation has been marked in, (+ - o) according to the above explanation, If there were no correlation between a pair of factors, i.e. if they fluctuated randomly with respect to one another, then the total number of + and - correlations should not differ significantly from a 1/1 relationship. For a significant + or - correlation to be established on the other hand, the number of + or - categories should be significantly greater than the other category together with the o's, as they support neither a + nor a - hypothesis.

i.e. For a significant Positive correlation.

$\Sigma (+)$ must be significantly greater than $\Sigma (-) + \Sigma (o)$.

In the particular instance under consideration, there were 52 (+); 18 (-); and 5 (o), and a χ^2 test showed that the ratio 52/23 differed highly significantly from a 1/1, χ^2 being 11.21 with 1 df, $p < .001$.

This suggests that if there is an increase in the mean air temperature from one night to the next, then it is significantly likely that there will also be an increase in the number of animals spinning webs that night.

The advantages of this method of analysis are its extreme simplicity, its ability to handle very small numbers which in fact may contain important biological information, and its relative independence of population changes, as the significance of each set of figures depends upon their relationship with those of the previous and succeeding day, a very short time span which must minimise other effects. However it is this last factor which introduces the main statistical drawback, namely that the data are linked, and do not represent independent events. Just what the importance of this is, in statistical terms is not at all clear, and Williams (1940) confronted with the same problem in a different analysis which will be presented later, simply halved his number of degrees of freedom.

One possible solution to this problem is to take every other pair of readings, but of course this involves losing half of the data which is ecologically most objectionable, but once this has been done, the student is then presented with two separate series of independent pairs, and given the small amount of data, and sampling error, it would be expected that these series would give differing degrees of significance. When this was carried out on the data in Figure 18, the results were as follows:-

Series A Readings. 30 (+) 7 (-) 1 (o) $\chi^2 = 12.7$ $p < .001$

Series B Readings. 22 (+) 11 (-) 4 (o) $\chi^2 = 1.32$ $p > .2$

and it can be seen that while both show positive correlations, one is highly significant but the other is not, and as the readings in both series were selected quite arbitrarily, this must represent sampling errors. If the two χ^2 together with their degrees of freedom are added, the resultant χ^2 of 14.06 with 2 df has a $p < .001$, although again the effect of adding together two χ^2 which are not completely independent is not fully understood.

Using this same data, attempts were made to compare the results obtained by this method, with those obtained by the more conventional correlation methods, as used by Williams (1940).

Initially, the untreated figures were used, the two factors to be correlated being:-

1. Difference (±) in the number of new webs from the previous morning.

2. Difference (±) in the mean night temperature (°F x 100) from the previous night.

The results were:-

$r = +.266$; Number of pairs = 75; d.f. = 45; $t = 1.81 = p > .05$

N.B. The calculation of the number of degrees of freedom was based on Williams' method of number of pairs/2, but allowance here was made for the discontinuous nature of the readings.

Again, following Williams, a logarithmic transformation was performed on the data, as in biological problems of this sort, it is often better to base conclusions on the consistency of the results, rather than on one or two wildly aberrant readings which influence all the rest disproportionately.

In this case, the two factors being correlated were treated:-

1. Log. (Difference (±) in the number of new webs from the previous morning, increased by 1)

2. Log. (Difference (±) in the mean night temperature (°F x 100) from the previous night, increased by 1)

N.B. The values of each factor were increased by 1, as Log. zero is minus infinity.

The results now were:-

$r = +.3995$; Number of pairs = 75; d.f. = 45; $t = 2.8575$

$p < .01$.

The log. transformed data gave a highly significant correlation, whilst the raw data did not, and this illustrates an increase in the sensitivity of the test, as a result of ' smoothing' the data. The first method illustrated, which was devised for this problem, gave an even higher degree of significance, and consequently greater sensitivity, and this is in effect, simply the result of further 'smoothing'; 'smoothing' the data indeed, until only the sign remained.

In view of all this statistical uncertainty, which the present writer is not competent to resolve, it was decided, with these qualifications, to analyse the factors, affecting web spinning by the first described 'sign method'. As this might conceivably tend towards over-sensitivity (i.e. too frequent rejection of the null hypothesis), significant correlations would then be analysed as two independent series, and their χ^2 added. In all these cases, it is a meaningful biological pattern which is being sought, and it is all too easy to become obsessed with the technicalities of statistical illustration, to the neglect of the biological results. Accordingly, a series of climatic factors, acting before, during, and after web spinning were analysed, and the results are presented in Table 30.

TABLE 30.

M. merianae, Summary of Web Spinning and Climate Analysis.

	No. of Cases			Corr.	χ^2	Significance
	+	-	o			
A. Results using consecutive data.						
1. Mean Night Temperature (9 hourly air temp. readings 8 p.m. - 4 a.m.)	52	18	5	+	11.21	p <.001
2. Mean Temperature Previous Day (13 hourly air temp. readings 6 a.m. - 6 p.m.)	39	25	5	+	1.17	p >.2
3. Mean Temperature Next Day (as above)	36	31	5	o	-	-
4. Mean Night Wind (9 hourly mean wind speed readings 8 p.m. - 4 a.m.)	22	31	4	-	.438	p >,5
5. Mean Wind Previous Day (12 hourly mean wind speed readings 8 a.m. - 7 p.m.)	28	35	5	-	.058	p >.8
6. Mean Wind Next Day (as above)	32	32	4	o	-	-
7. Mean Night Rain (Hours of rain >.004"/hr. for 9 hrs. - 8 p.m. - 4 a.m.)	15	21	40	o	-	-
8. Mean Rain Previous Day (Hours of rain >.004"/hr. for 12 hrs. - 8 a.m. - 7 p.m.)	17	22	34	o	-	-

	No. of Cases			Corr.	χ^2	Significance
	+	-	o			
9. Mean Rain Next Day (as above)						
	26	14	34	o	-	-
10. Sunshine Previous Day (Total Number of Hours)						
	39	32	7	o	-	-
11. Sunshine Next Day (as above)						
	32	41	5	-	.205	$p > .5$

B. Results using independent data.

Only the significant correlation (Mean Night Temperature) was reanalysed.

Mean Night Temperature.

Series A Readings	30	7	1	12.74***	
Series B Readings	22	11	4	1.32	
With 2 d.f. Sum				14.06	$p < .001$

From this it is apparent that web spinning was strongly correlated with the mean air temperature at the time, but with nothing else, and there is certainly no evidence of ability to forecast any of the climatic factors analysed. Despite this, there would appear to be a general connection between nights of exceptional rain and wind, and reduced web spinning activity, which is only, to be expected, and in Figure 18, r = 'Exceptional rain' i.e. > 4 hours of rain during the night, whilst w = 'Exceptional wind' i.e. a mean wind > 22 Knots. It is interesting that with these two factors, the depressing effect seems largely restricted to the extreme conditions.

As Williams has pointed out, of course, the climatic factors themselves are not independent of one another, and by similar analyses the relationships between climatic factors are listed in Table 31.

TABLE 31.

Summary of the Relationships between Climatic Factors over the Study Period.

No. of cases +	-	o	Corr.	χ^2	Significance
A. Results using consecutive data.					
1. Mean Night Temperature. /Mean Temp. Previous Day.					
50	22	1	+	9.99	p <.01
2. Mean Night Temperature. /Mean Temp. Next Day.					
41	33	2	+	.47	p >.3
3. Mean Night Temperature. /Mean Night Wind.					
31	27		+	.275	p >.5
4. Mean Night Temperature. /Mean Wind Previous Day.					
32	37		-	.36	p >.5
5. Mean Night Temperature. /Mean Wind Next Day.					
36	32		+	.23	p >.5

	No. of cases			Corr.	χ^2	Significance
	+	-	o			
6. Mean Night Temperature. /Mean Night Rain.	22	15	33	o	-	-
7. Mean Night Temperature. /Hours Sunshine Previous Day.	35	33	4	o	-	-
8. Mean Night Temperature. /Hours Sunshine Next Day.	29	42	5	-	.84	$p > .3$
9. Mean Day Temperature. /Mean Wind.	42	44	1	-	.0114	$p > .9$
10. Mean Day Temperature. /Mean Rain.	21	29	36	o	-	-
11. Mean Day Temperature. /Hours Sunshine.	54	30	8	+	2.78	$p > .05$

B. Results using independent data.

Only the significant correlation (Mean Night Temp. and Mean Temp. Previous Day) was reanalysed.

Series A Readings	27	10			7.81**	
Series B Readings	23	12	1		2.78	
			with 2 d.f.	Sum	10.59	$p < .01$

From this, the only clear correlation is between the mean night temperature, and the mean day temperature on the preceding day, and as it is fairly obvious that this must be the case, as the earth has to gain all its heat from radiant energy during the day before losing it again at night, it suggests that the analytical system is not over-sensitive in suggesting large numbers of spurious connections.

The data for A. cornutus was quite inadequate for this and related analyses.

(e) Web Destruction and Its Relation to Climate

Fluctuations in the number of new webs each morning have already been discussed, but likewise it was noticed that there were considerable fluctuations in the number of old webs, and the fact that fluctuations were also very apparent in the total numbers of webs, as is illustrated in Figure 20, meanf that, these were not simply the 'two sides of the same coin'. Large numbers of old webs were often found after particularly cold and unfavourable nights, and as it has already been shown that web destruction is an active process in this species, it was decided to investigate the connection between it and certain climatological data.

Web destruction was expressed as the % destruction, i.e. Σ Webs on day 1 - Σ Old webs on day 2 = Number destroyed.

$$\% \text{ destruction} = \frac{\text{No. Destroyed}}{\Sigma \text{ Webs on day I}} \times 100$$

and was found in practice to fluctuate between 20 and 100% over the study period. Table 32 expresses the results of these analyses.

TABLE 32.

M. merianae. Summary of the Analyses of the Relationships between Percentage Web Destruction and Climate.

	No. of Cases			Corr.	χ^2	Significance
	+	-	o			
A. Results using consecutive data.						
1. Mean Night Temperature.						
	50	24	2	+	7.58	$p < .01$
2. Mean Temperature Previous Day.						
	44	22	3	+	5.23	$p < .05$
3. Mean Temperature Next Day.						
	40	31	1	+	.88	$p > .3$
4. Mean Night Wind.						
	27	28	2	o	-	-
5. Mean Wind Previous Day.						
	41	25	2	+	2.88	$p > .05$
6. Mean Night Rain.						
	15	27	32	o	-	-
7. Mean Rain Previous Day.						
	17	24	32	o	-	-
8. Sunshine Previous Day.						
	40	33	3	+	.21	$p > .5$

B. Results using independent data.

Only the significant correlations were reanalysed.

1. Mean Night Temperature.

Series A Readings	22	14	2	.95	
Series B Readings	28	10		8.53**	
			With 2 d.f.	Sum 9.48	p <.01

2. Mean Temperature Previous Day.

Series A Readings	23	12		3.46	
Series B Readings	21	10	3	1.88	
			With 2 d.f.	Sum 5.34	p >.05

Again, there is a most significant correlation with the mean night air temperature, and some suggestion of a correlation with the mean temperature the previous day. If the latter correlation is indeed significant, two explanations can be offered;

1. that there is in any case a high degree of correlation between the mean night temperature, and the mean day temperature on the previous day.

2. that web destruction is the first activity to occur, beginning as it often does in the last stages of twilight, and therefore very nearly overlaps the day

temperature records, by which it must be strongly influenced.

As expected, Table 33 directs attention to the very close relationship between the percentage web destruction, and the incidence of web spinning, a situation brought about only in part by the fact that some of the animals which destroy their webs go on to build new ones, and in part also by the fact that many of the conditions which induce some animals to destroy their webs also induces others to spin them.

TABLE 33.

M. merianae. Relationship between the Percentage Web Destruction, and the Incidence of Web Spinning.

	No. of Cases			Corr.	χ^2	Significance
	+	-	o			
A. Result Using Consecutive Data.						
	57	18	6	+	13.44	p <.001***
B. Result Using Independent Data.						
Series A Readings	26	11	4	+	2.95	
Series B Readings	31	7	2	+	12.1***	
			With 2 d.f.	Sum	15.05	p <.001***

It should perhaps be pointed out here that whilst the mean wind speed the previous day is positively correlated with web destruction, it is not significantly so, and this suggests that with the obvious exception of some outstandingly windy days, wind is not a particularly important factor in destroying webs. This is also true of rain, where the mean number of hours of rain the previous day is in fact negatively correlated with the disappearance of old webs as seen the following morning.

It has been shown then, that both web destruction and web spinning are positively correlated with the mean night air temperature. If the temperature effects on both these processes were the same, then it would be expected that the total number of all webs would remain substantially the same from day to day, because a cold night, whilst depressing web spinning would also depress web destruction, and vice versa. This is to say that temperature would not affect the total number of webs, but only their rate of renewal.

In fact, as has been seen in Figure 20 this is not the case, the total number of webs fluctuating wildly, and so a correlation was attempted between the total number of webs, and the mean night temperature, as is shown in Table 34.

TABLE 34.

M. merianae. Relationship between the Total Number of Webs found the Following Morning, and the Mean Night Temperature.

	No. of Cases					
	+	-	o	Corr.	χ^2	Significance
A. Result Using Consecutive Data.						
	47	20	8	+	4.81	$p < .05$
B. Result Using Independent Data.						
Series A Readings	26	9	3	+	5.16*	
Series B Readings	21	11	5	+	.67	
	With 2 d.f.			Sum	5.83	$p > .05$

Because of this probably significant positive correlation between the total numbers of webs and the mean night temperature, only one explanation can be suggested.

As web destruction, web spinning, and the total number of webs, all fluctuate with temperature, it follows that the temperature effects on the first two activities must be different, and in particular, that web destruction can proceed at temperatures unsuitable for web spinning.

Thus, if the total number of webs goes down, it must mean that web destruction is exceeding web spinning, and we know this to be associated with a drop in the mean night temperature. If however, the total number of webs increases web spinning must be exceeding web destruction, but as it has already been suggested that web destruction can proceed at temperatures too low for web spinning, it can only be concluded that whilst destruction proceeds apace, the excess of web spinning is brought about by the activity of animals which had destroyed their webs previously, and had not spun new ones.

In conclusion, it would appear from these results, that variations in web spinning activity are associated with variations in the mean night air temperature, and depending upon the conditions, the spider has three courses of action open to it:-

1. On warm, favourable nights, it destroys its old web if it has one, and spins another.

2. On colder, less favourable nights, it destroys its old web but does not spin another.

3. On very cold unfavourable nights it remains completely inactive, neither destroying nor spinning.

Of course the 'operational levels' of these categories 'favourable' and 'unfavourable' are determined by the individual spider, and are presumably related to its individual physiology, and past history, and it is these individual variations which make this a problem for statistical analysis in the first place.

Further understanding of these field observations will only be possible after laboratory testing of the hypotheses.

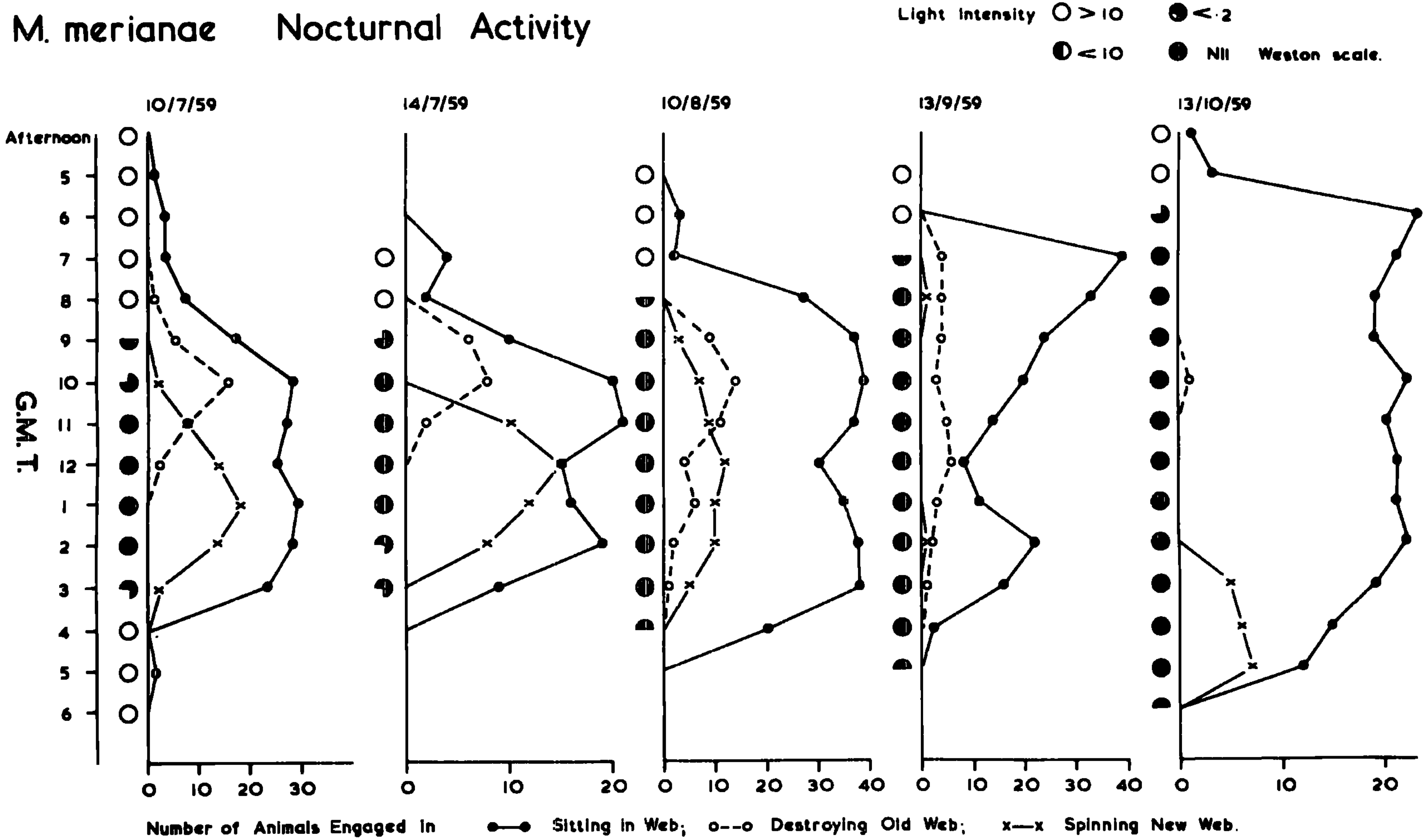
(f) An Examination of Web Spinning in the Fields.

Having made some inferences about web spinning and the effects of climate, it was decided to watch this process in the field. Accordingly 5 all-night observations were carried out from July until October 1959.

These results are presented in Figure 19, the data being collected by hourly examinations of up to 50 webs, using a weak torch to disturb the animals as little as possible. The activity of each animal was recorded under the heading of 1. 'Sitting in web', which meant the spider being engaged in any activity which brought it out of its retreat. 2. 'Taking in old web'. 3. Spinning new web.

The light intensity, as measured by a 'Weston' exposure meter, and the time in G.M.T. are recorded, and it can be seen that as the days get shorter, the spiders spend longer in their webs, indeed the emergence of M. merianae from its daytime retreat always coincides with nightfall, a fact also remarked on by Bristowe (1958) p 238 for Araneus umbraticus, and Park and Strohecker (1936) for a number of climax forest noturnal spiders.

In order to gain some idea of the importance of darkness, several lengths of peat edge were 'floodlit'



M. merianae Nocturnal Activity

Fig. 19.

by paraffin pressure lamps throughout the night, a light intensity of around 6.8 Weston being maintained. The lamps were kept some distance from the webs, in an attempt to eliminate heat effects, and in all, 20 webs were illuminated, whilst a control of 29 webs was not.

The results as set out in Table 35 suggest that whilst artificial light had little effect on the timing of the various activities, it did seem to inhibit general activity, and so 50% of the old webs remained at 3 a.m. (by which time it was getting light again), whilst only 27.6% of the controls had old webs. Also, by 3 a.m. 65.5% of the controls had spun new webs, as compared with 10% of the illuminated animals; it is however interesting to note that this latter figure had risen by 11 a.m. indicating that in the end some of the animals had spun after dawn.

Still seeking some explanation of the climatic effect, the 5 nights of observation were listed with their mean night air temperatures, and the mean length of time spent on each operation, so far as it could be assessed from hourly visits, was calculated, as recorded in Table 36, to see if the effect of the low temperatures was, seriously to slow down, the speed of the various activities. As can be seen, the results are wholly inconclusive, and when the 'best' of the 5 nights (in

TABLE 35.

M. merianae. The Effect of Artificial Lighting on Nocturnal Activity.

Results expressed as a percentage of the total number of webs observed.

Process	Treatment	Aftn.	7 p.m.	8 p.m.	9 p.m.	10 p.m.	11 p.m.	12 mid. ngt.	1 a.m.	2 a.m.	3 a.m.	Morng. 11 a.m.
Spider Present	C	0	13.8	6.9	34.5	69	72.5	51.7	55.2	65.5	31	0
	L	0	5	15	15	45	20	25	20	20	5	0
Destruction	C	0	0	0	20.7	27.6	6.9	0	0	0	0	0
	L	0	0	10	10	20	0	0	10	5	0	0
Spinning	C	0	0	0	0	0	34.5	51.7	41.4	27.6	0	0
	L	0	0	0	0	0	5	10	0	10	0	0
Old Webs	C	100	93	89.7	89.7	58.6	34.5	27.6	27.6	27.6	27.6	24.1
	L	100	100	95	90	80	55	55	55	55	50	35
New Webs	C	0	0	0	0	0	0	0	10.3	38	65.5	72.5
	L	0	0	0	0	0	0	0	5	5	10	45

C = Control.   L = Artifically lit webs.

which 76% spun new webs) was compared with the worst, (in which only 4.5% spun), the chief noticeable difference was, that on the latter night the animals simply appeared to 'decide' not to engage in certain activities at all. One important point which should be noted from all this, is that the activities connected with web spinning occupy most of the night, and the new webs are rarely finished until just before sunrise. This implies very little nocturnal feeding, as for most of the night, there is no suitable catching apparatus available, a suggestion which has been borne out by observation.

TABLE 36.

M. Merianae. Duration of Each Nocturnal Activity.

Date	10/7/59	14/7/59	10/8/59	13/9/59	13/10/59
Mean Temp.	47.6°F	37.2°F	54.0°F	38.33°F	45.08°F
Destruction Mean No. Hrs.	1.24	1.11	1.41	2.83	1.0
Spinning Mean No. Hrs.	2.22	2.21	1.77	1.0	2.09
Total Renewal Time Mean No. Hrs.	5.6	5.54	4.5	3.5	4.64

Finally, a brief comparison was made between the nocturnal activity of M. merianae, and a small artificially established colony of A. cornutus, which is demonstrated in Table 37.

It will be observed that on the whole, A. cornutus began its activities later, but completed them more quickly than M. merianae. It has also been observed that A. cornutus is less intensely nocturnal, and for example on the 25th August, 1958, a fine sunny day, 8 webs were found on Peat Edge C at 10-30 a.m. but by evening, there were 5 new webs. In this way, the animal can renew its web whenever conditions during the day are especially favourable.

(g) Population Inferences from Web Numbers, and a Comparison of the Three Sites.

M. merianae.

In the previous discussions, certain inferences about the number of spiders in an area have been drawn from an examination of the number of webs, although it has been shown in M. merianae that the number of animals present must often exceed the number of webs on a given day. As this seemed to be rather unsatisfactory, some attempts were made to enumerate the M. merianae population of Peat Edge A by methods which did not rely on web numbers.

Figure 20 is a series of nightly observations on the animals, coupled with the number of webs seen the following day. The first fact which emerges is that even with a continuous series of readings, the number of

TABLE 37.

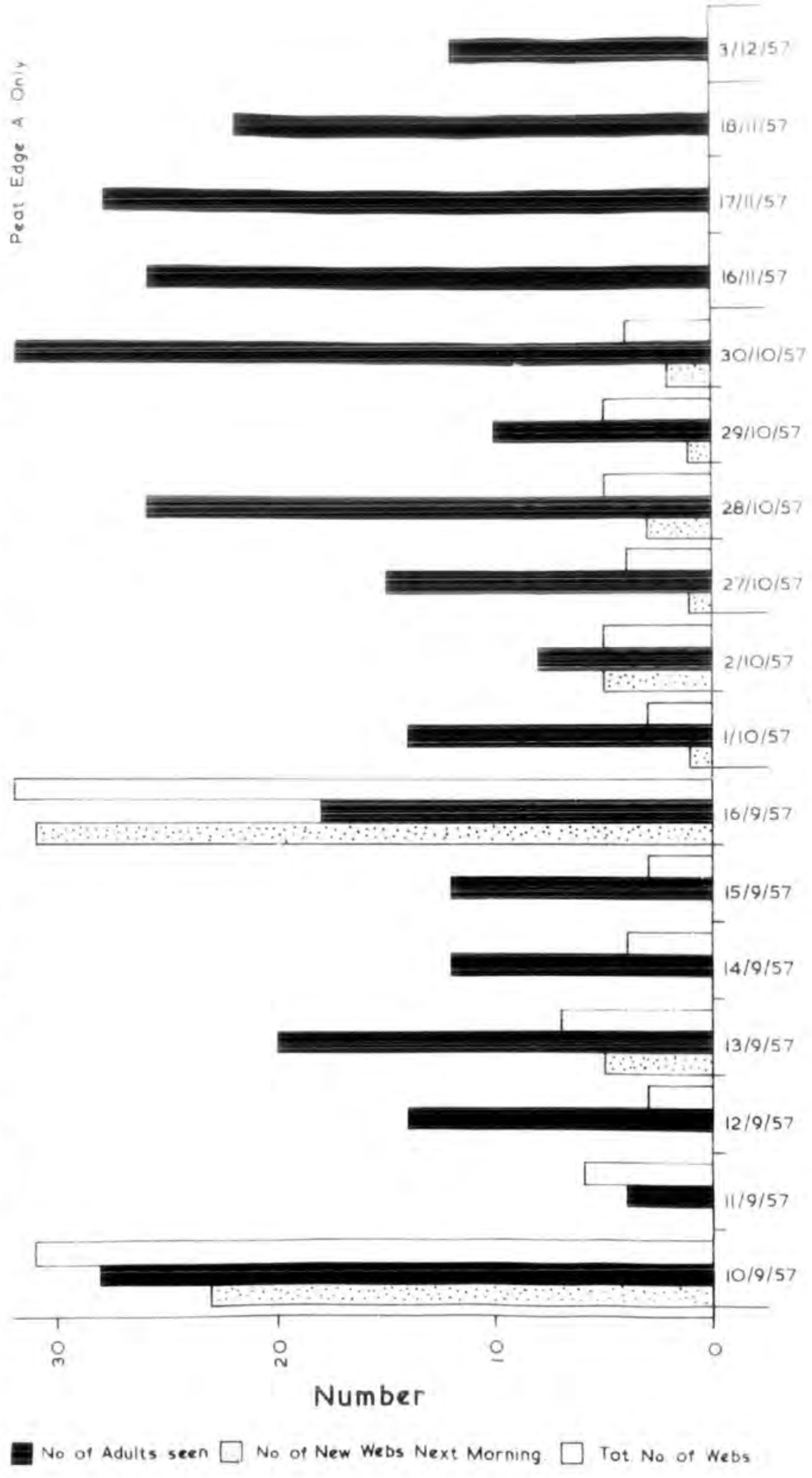
Nocturnal Activity, a Comparison Between M. merianae, and A. cornutus.

10/7/59 Hour G. M. T.

	Aftern.	5	6	7	8	9	10	11	12	1	2	3	4	5	6
Meta merianae.															
Spider Present	0	1	3	3	7	17	28	27	25	29	28	23	0	1	0
Destruction	0	0	0	0	1	5	16	8	2	0	0	0	0	0	0
Spinning	0	0	0	0	0	0	2	8	14	19	14	2	0	1	0
Old Webs	38	36	35	35	35	33	24	12	5	2	2	2	2	2	2
New Webs	0	0	0	0	0	0	0	0	0	4	12	24	26	26	27
Araneus cornutus.															
Spider Present	0	0	0	1	1	1	9	9	9	10	9	6	2	1	2
Destruction	0	0	0	0	0	0	3	4	1	1	0	0	0	0	0
Spinning	0	0	0	0	0	0	0	2	6	4	1	2	0	0	0
Old Webs	8	8	8	7	7	7	6	5	2	2	1	1	1	1	1
New Webs	0	0	0	0	0	0	0	0	1	2	6	6	7	7	7

Fig. 20.

M. merianae Relationship Between No. of Webs and Spiders Observed



animals seen varied enormously from night to night, ruling this out as a simple method of estimating the population. Secondly, it will be noted that there were indeed, generally many more spiders seen than there were webs spun, particularly late on in the season, but thirdly it will be observed that a good night for web spinning can often result in there being more webs the following morning than it was ever suspected there were adults to spin them.

Simple release/recapture techniques were also attempted, animals being caught, marked with a spot of cellulose paint and released, the numbers of marked and unmarked animals found in subsequent searches being noted. As population estimates ranging from 39 to 246, and on to infinity were obtained however, the technique was abandoned. The chief objections were that once an animal had been marked, it was much more conspicuous, and also that this method depended upon the marked, released animals, mixing randomly with the parent population, and as has been seen, this is most unlikely to happen in these spiders.

In view of these failures, it was eventually concluded that the maximum number of webs recorded in a reasonable length of time, such as a month, was still likely to give the best available population estimate, and accordingly the populations of the three peat edges were compared on this basis. See Figure 21.

Although it should be remembered that these 3 peat edges are not quite the same length, (A = 44ft. B = 34 ft, C = 44ft) it is apparent from these comparisons, that their spider populations vary considerably. Thus, taking the populations of the older instars as an example, the population of Peat Edge A has steadily decreased over the three study years. The population of Peat Edge C on the other hand has shown a definite increase. These changes can, to some extent, be related to the number of 'small' webs found at the end of the previous season, just after the main egg hatch. The ratio of small to large webs at this period, does give some measure of the 'reproductive success' of the colony, that is to say, the extent to which it has shown itself capable of regeneration.

This 'Reproductive Success' of the 3 sites for the 3 study years has been calculated, and is shown in Table 38.

TABLE 38.

M. merianae. 'Reproductive Success' of the Three Sites.

'Small'/'Large' web ratio for the greatest number of webs recorded in September.

Peat Edge	A.	B.	C.
1957	1.66	0	3.5
1958	1.29	1.11	5.1
1959	.54	5.9	.5

M. merianae Greatest No. of Webs on Any Day in the Month, for Each Site.

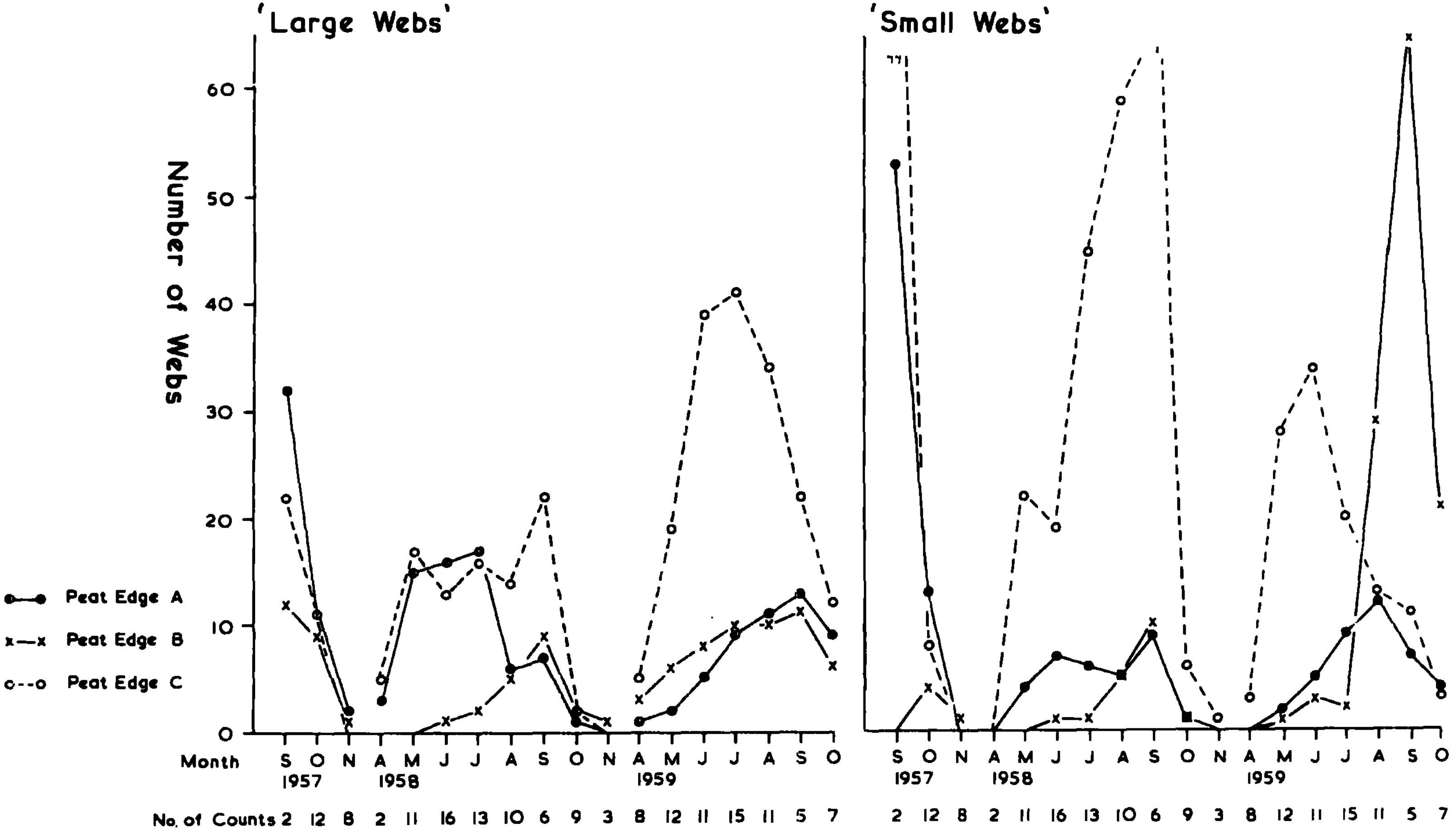


Fig. 21.

This shows equally, great variation in the success of a given site, and in the most successful regenerating site from year to year.

From these studies on both the population, and 'Reproductive Success' of 3 sites, one is left with the impression that in M. merianae at least, population balance is evident only when the broadest view is taken, and that detailed examinations of small groups of animals reveal rather violent fluctuations, a point which has also been demonstrated recently for Collembola by Wallace (1957).

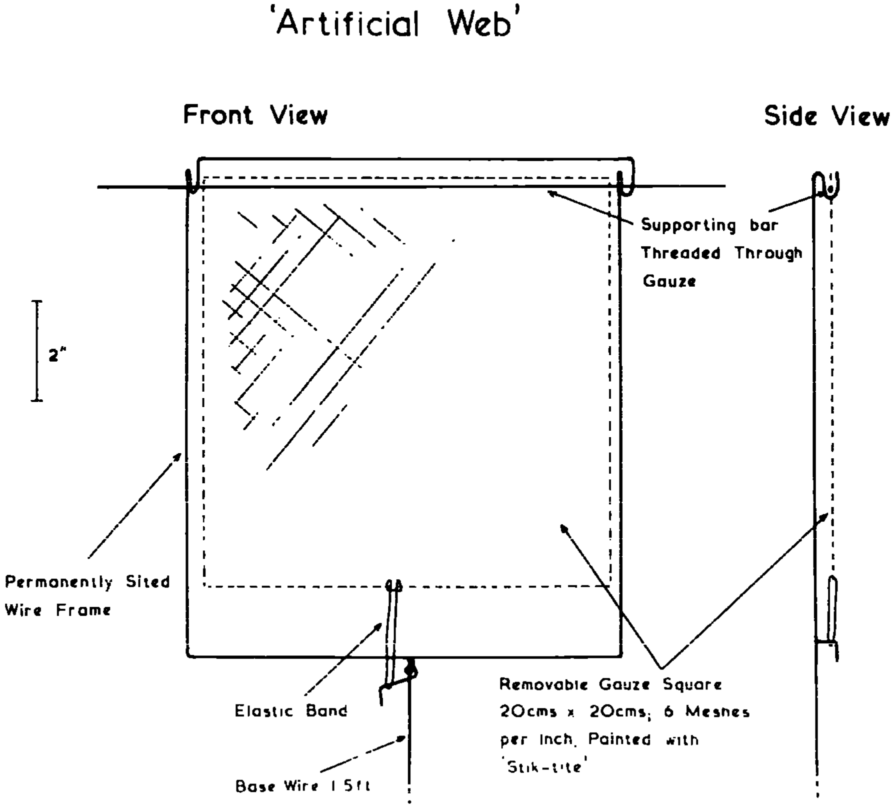
7. Feeding Relations.

(a) Positioning of Web and Availability of Food.

In discussing the habitats of M. merianae and A. cornutus, it was stated at the outset that both species were virtually confined to what might be termed "breaks in the blanket bog cover" i.e. erosion channels, stream edges, rocky outcrops, and old mine workings, but no reasons for this restriction were given. Now it has often been suggested that spiders site their webs, possibly by trial and error, in positions where their insect prey is particularly abundant. Thus Kirby and Spence (1815) p 398 write, they..."Suspend them with the nicest judgment in the place most abounding in the wished-for prey", although McCook (1889) seriously doubted this. In the present investigation therefore, it was thought that this might offer an explanation for the siting of orb-webs on the moor, namely, that the erosion channels acted as 'migration lanes' for insects moving about the moor, so making them particularly favourable sites for the insect-catching spiders.

To test this, a series of 'Artificial Webs', as illustrated in Figure 22 was devised. These consisted of a wire frame, which was left permanently sited in the ground, and into which fitted a square of metal gauze, 20 cms. X 20 cms. This had 6 meshes to the inch, which was the closest approximation to the mesh of the viscid spiral in the actual orb webs, which could be found, and was painted over both sides with 'Stik-tite', a commercial grease banding compound. It was not expected that these 'artificial webs' would simulate in any precise way the catching action of the real orb webs, but it was hoped that they would give a comparative measure of the 'availability of prey' in different sites, and in the same site on different days. In practice, the gauze squares were put out each day for 8 hours, and then brought in again at night, all the trapped insects being removed, counted, roughly classified, cleaned in benzene, weighed, dried at 100°C for 24 hours and reweighed. The gauzes themselves, were cleaned on each occasion, re-

Figure 22.



Details of the 'Artificial Web'.

painted with 'Stik-tite', and prepared for the following day's catching.

In order to compare the 'availability of prey' in both the 'gully' positions where orb-webs were to be found, and in the 'open moor' positions, where they were not, 6 'artificial webs' were sited in each area, and Plate 9 shows such a trap in a position frequently occupied by M. merianae.

It was in reference to its behaviour in air currents, and its general visibility to insects (whether attractive or repellent), that this device was used in preference to the large, light coloured, solid cylindrical traps which use a similar sticky material, described by Coulson (1959) and Broadbent (1948).

In Table 39, the total dry weight of insects caught in each of the two positions throughout the observation days in the 1959 season is recorded, and from this it is at once apparent that the gullies in which the spiders spin are not at all favourable places for catching prey.

TABLE 39.

Comparison of the 'Availability of Prey' by Weight in 2 Habitats.

	Gully	Moor
	.5223 gms.	1.959 gms.
Ratio	1/3.75	

Representing the total dry weight of insects taken in 47 days throughout the 1959 season.

In Table 40, a broad analysis of the insects caught in each situation has been attempted, and with the exception of an increase in the percentage of Tipulids in the Gully position, which appear to form an important part of the spiders' diet, from a 'prey-composition' standpoint, the Gully appears to be equally unattractive, there being a much higher percentage of small Nematocera there.

(b) Web Spinning and Availability of Food.

The 'availability of prey' varied of course from day to day, and month to month, and Table 41 shows the available prey by dry weight for the 7 months of the 1959 season. Owing to the small number of replicates in each month, and the great variability of the daily catches, attributable to climatic effects, little reliance can be placed on these figures, but they do at least show the large amount of available food in May, composed largely of *Empis borealis*, a Dipteran taken readily by both species, and it must be this food supply which is utilised to mature eggs for the cocoons found in June.

Day to day variations in insect activity have been observed by many workers, for example Williams (1940) on insects responding to a light trap, Kettle (1957) on the

TABLE 40.

Type of Prey Caught in the Two Positions.

Total Number of Animals Caught Throughout the Season.

Group.	Gully.			Moor.		
	Total No.	% of Total	% less Nemat.	Total No.	% of Total	% Less Nemat.
Small Nematocera	1403	79.67		2993	62.29	
Tipulids	51	2.90	14.25	32	.66	1.77
Empids	181	10.45	51.40	1456	30.30	80.35
Muscids	40	2.27	11.17	57	1.19	3.14
Other Diptera	21	1.19	5.87	57	1.19	3.14
Hymenoptera	16	.91	4.47	86	1.79	4.75
Plecoptera	10	.57	2.79	50	1.04	2.76
Hemiptera	33	1.87	9.22	37	.77	2.04
Ephemeroptera	1	.06	.28	3	.06	.16
Lepidoptera	2	.11	.56	30	.62	1.65
Neuroptera	0	0	0	1	.02	.05
Coleoptera	0	0	0	3	.06	.16
Σ Less Small Nemat.	358			1812		
Σ Plus Small Nemat.	1761			4805		

activity of biting flies, Johnson (1954) on Aphids, Hughes (1955) on the catches of Meromyza variegata in a sweepnet, whilst a more general summary is provided by Uvarov (1931) of the earlier work, and it seems generally agreed that air temperature, and wind speed are two factors which exercise a profound effect on insect flight. See Figure 23.

TABLE 41.

Availability of Prey by Weight, in Various Months.

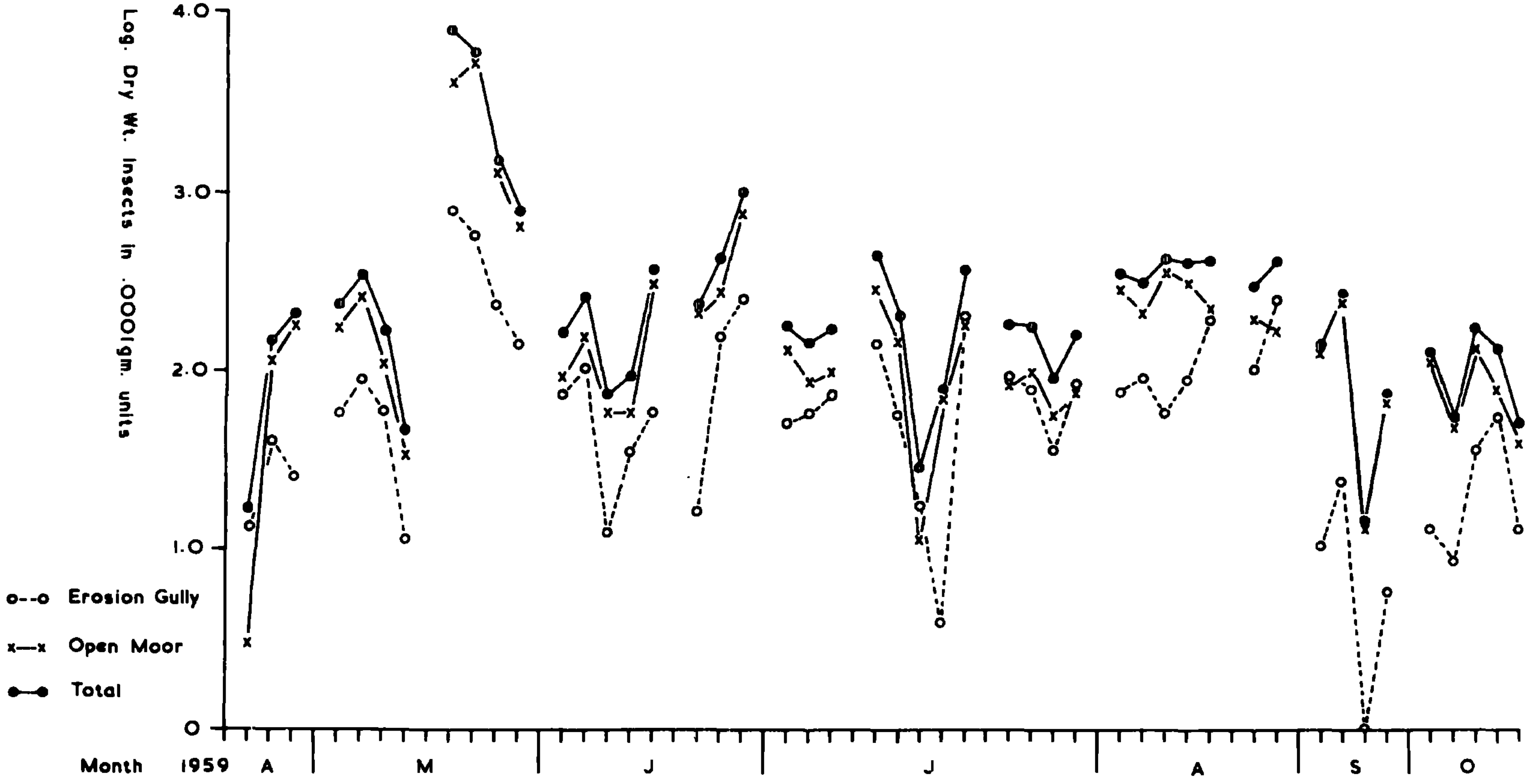
Month	Total Dry Wt. (6 Traps) gms.	No. Days	Daily Mean
April	.0384	3	.0128
May	1.4124	8	.1765
June	.2764	8	.0345
July	.2375	12	.0198
August	.2833	7	.0405
September	.0540	4	.0135
October	.0589	5	.0118

In the present work, some attempt was made to correlate the 'availability of prey' with climatic conditions, and these results are summarised in Table 42, although it must be emphasised that the correlations, which were performed using the total dry weight of prey caught per day in both positions, are not very sensitive, as the work was only carried out for one season.

Fig. 23.

Fluctuations in the 'Availability of Prey'

Daily Totals, Pooled from All Sites.



The expected significant positive correlation between the dry weight of insects caught, and the mean air temperature for the day, was established, but although a negative correlation with wind speed was found, it was not significant on the basis of the meagre data available.

When the effects of climate upon web spinning were being discussed, it was said that "It would be selectively advantageous for the animal to spin webs only on evenings preceding hot, insect-ridden days". Whilst it appeared that there was no connection between web spinning and the next day's temperature, there yet remains the possibility that the fluctuations in web spinning were correlated with the fluctuations in the 'availability of prey', and this possibility has been investigated in Table 43.

Whilst the sampling method seems tolerably reliable, in that fluctuations recorded in the 'Gully' and 'Moor' positions show a significant correlation, as seen in Figure 23, the present data show no evidence of any correlation between web spinning, and the amount of prey available the following day; no evidence that is, that _M. merianae_ can forecast the availability of insects the next day, and adjust its web spinning activities accordingly. Neither was there any evidence

TABLE 42.

Availability of Prey and Climate.

A. Results using consecutive data. Dry wt. of potential prey caught with:-

	No. of Cases			Corr.	χ^2	Significance
	+	-	o			
1. Mean day Temperature (13 hourly air temp. readings 6 a.m. - 6 p.m.)	23	9		+	6.12	p <.02
2. Mean day Wind (12 hourly means in knots 8 a.m. - 7 p.m.)	13	19		-	1.12	p >.2
3. Hours Sunshine.	22	13		+	2.31	p >.1
4. Day Rain (Hours with rate >.004"/hr. 8 a.m. - 7 p.m.)	6	8	18	o	-	-
5. Mean Temperature - previous night. (9 hourly air temp. readings 8 p.m. - 4 a.m.)	12	22		-	2.9	p >.05

B. Results using independent data.

Only the significant correlation, (Mean day Temperature) was reanalysed.

	+	-	o	Corr.	χ^2	Significance
Series A Readings	14	2		+	9.0**	
Series B Readings	9	7		+	.25	
With 2 d.f.					Sum χ^2 9.25	p <.01

TABLE 43. Readings for one season only.

M. merianae. Web Spinning and the Availability of Food.

	No. of cases			Corr.	χ^2	Significance
	+	-	o			
A. Results using consecutive data.						
Correlation between dry wt. of prey caught daily in the 'Gully' and 'Moor' positions.						
	24	11		+	4.82	$p < .05$*
Correlations between web spinning activity the previous night, and the dry weight of potential prey caught on 'artificial webs' the following day.						
1. With Gully Traps	18	15	1	+	.117	$p > .7$
2. With Moor Traps	15	18	1	-	.117	$p > .7$
3. With Pooled Traps	19	14	1	+	.47	$p > .3$
Correlations between web spinning activity, and the dry weight of potential prey caught on 'artificial webs' the previous day.						
1. With Gully Traps	11	17	1	-	.86	$p > .3$
2. With Moor Traps	17	11	1	+	.86	$p > .3$
3. With Pooled Traps	13	15	1	-	.034	$p > .8$
B. Results using Independent data.						
Dry weight of prey caught in 'Gully' and 'Moor' positions.						
Series A Readings	13	5		+	3.56	
Series B Readings	11	6		+	1.47	
	With 2 d.f.			Sum	5.03	$p > .05$

of Web spinning being influenced by the amount of food which the animal had just caught.

(c) Qualitative and Quantitative Estimates of the Food Taken.

Throughout the study, records were made of the prey of M. merianae and A. cornutus. Animals found dead in the webs, and being eaten in the field were noted, as was the result when certain insects captured in the area were thrown into the webs. In this way, the prey catalogue in Table 44 was allowed to grow, and it makes no claim to be exhaustive. Quantitative studies were much more difficult, and as M. merianae removed its prey from the web, sucked, and then dropped the remains, no methods for this species were devised. A. cornutus however, tended to suck the prey in its retreat, and then build the remains into the structure. Accordingly, a series of nests were examined, and the insect remains were classified as accurately as possible, by comparing them with prepared, mounted remains from known animals, whilst a highly subjective guess was made at the number of animals involved. The results for 21 such nests are shown in Table 45, and 2 points should be made.

First, the type of prey caught is greatly dependent upon the position of the web, as can be seen by the fact that several animals appear to have lived exclusively on

TABLE 44.

Catalogue of Spider Prey-after Kloet and Hincks (1945).

O. Plecoptera			
	Unidentified		A_2
O. Ephemeroptera			
Ecdyonuridae			
	Rhithrogena semicolorata	M_{23}	A_{12}
O. Neuroptera			
	Unidentified		A_2
O. Trichoptera			
Limnophilidae			
	Unidentified		A_2
O. Lepidoptera			
Satyridae			
	Coenonympha pamphilus		A_{12}
O. Coleoptera			
Elateridae			
	Corymbites sp		A_2
O. Hymenoptera			
Tenthredinidae			
	Unidentified		A_2
Braconidae			
	Unidentified		A_{12}
O. Diptera			
Tipulidae			
	Tipula marmorata	M_2	A_2
	T. alpium	M_{23}	A_{13}
	T. vafra	M_2	
	T. staegeri	M_2	
	T. oleracea		A_3
	T. paludosa	M_3	A_3
	T. subnodicornis	M_{23}	A_{123}
	T. coerulescens	M_2	
	T. montium	M_2	

TABLE 44 continued

	T. pagana	M_{3}	
	Dolichopeza albipes	M_{2}	
	Pedicia rivosa	M_{2}	
	Trichyphona immaculata		A_{1}
	Dicranota subtilis	M_{2}	
	Limnophila nemoralis	M_{2}	
Trichoceridae	*Trichocera sp*	M_{1}	
Chironomidae	Unidentified	M_{12}	A_{12}
Ceratopogonidae	*Culicoides pulicaris v. punctatus*	M_{12}	
Rhagionidae	*Rhagio scolopacea*	M_{3}	A_{3}
Tabanidae	*Haematopota crassicornis*		A_{2}
Empididae	*Hilara sp*		A_{1}
	Empis borealis	M_{23}	A_{23}
Cordiluridae	*Scopeuma stercorarium*		A_{2}
Calliphoridae	*Calliphora vomitoria*		A_{2}

M = *Meta merianae*

A = *Araneus cornutus*

1. = Found dead in web.

2. = Eaten by the spider in the field.

3. = Accepted in the field, during a feeding experiment.

Tipulidae, others on Trichoptera, whilst others have an extremely high proportion of Empididae. This point has also been stressed by Bilsing (1920) after some quantitative studies in America.

Secondly, as Turnbull (1957) has shown, seasonal changes in the insect fauna mean that the spiders are exploiting different prey at different times of the season, something which does not emerge from Table 45 as the prey remains are cumulative. Thus, for example, the main period of Empid activity lasts for only a very few weeks.

The general picture of the feeding habits of A. cornutus which emerges, is that Tipulidae form the main bulk of the food, a picture which is corroborated by observations on M. merianae by Cuthbertson (1926) with Empididae next, and surprisingly, Trichoptera third, whilst Moths, and some Butterflies are taken in appreciable numbers. The smaller Diptera do not, of course, figure in this list, as they would not be carried back to the retreat.

It is interesting to compare Table 45, with Table 40, which describes the animals caught on the 'Artificial Webs', when the results for the 'Gully Position, less Small

TABLE 45.

Analysis of Remains from Cocoons of A. cornutus. Prey, and Subjective Estimate of Numbers.

Date Taken	Trichoptera	Tipulids	Lepidoptera	Other Dipt.	Neuroptera	Coleoptera	Hymenopt.	Empids.	Σ
1958									
15/6	8								8
13/8	3	2							5
13/8	3	3	3	2	1	1			13
13/8		10				2	2		14
13/8		5	1					11	17
13/8		2	1						3
25/8		2	3						5
25/8	2		1						3
20/9		12	2						14
20/9		4	3		1		1	21	30
22/9	2	1							3
22/9	3	3	2						8
1959									
3/7		3			1	2	1	2	9
3/7		4							4
12/7	2	5		1		1	1	2	12
12/7		5	1			1			7
28/7		4				1			5
?	2	4	1					1	8
?	2	3	2						7
?		15							15
?		10							10
Σ	27	97	20	3	3	8	5	37	200
%	13.5	48.5	10	1.5	1.5	4	2.5	18.5	

Nematocera' are examined. While the Tipulidae are of great importance in both, the Empididae are of greatest importance in the artificial traps, and this is possibly due to 2 factors, the animals tending to alight on the traps as a resting place, and the shortness of time in which they are available, which would mean satiation of the spiders. The absence of Trichoptera from the 'artificial webs' is interesting, and may indicate that as these animals are largely nocturnal, A. cornutus which starts its web later, and finishes it more quickly may indulge in a certain amount of night feeding. The apparent shortage of Muscids, here classified as 'Other Diptera' in the A. cornutus prey remains is inexplicable.

8. Discussion.

In a general review of this sort, which is in contradistinction to the specialised study of a particular phenomenon, problems of wide importance tend to be examined only in so far as they impinge upon the animal or group of animals under consideration and as it is the narrower, rather than the wider implications which are of interest, a subsequent general discussion is not as a rule merited.

In this discussion therefore, only two of the topics, which have a rather broader interest, will be examined.

1. The Distribution of *M. merianae* and *A. cornutus*. Whilst it is obvious that these two species occupy different habitats, which are nevertheless in the same parts of the area, the reasons for these differences, and the ways by which the animals select them, are much less obvious.

Cloudsley - Thompson (1957) has pointed out that a number of authors have stressed the importance of atmospheric humidity on the ecology and distribution of spiders. Savory (1930) accounts for the differences in the distribution of *Zygiella atrica*, which builds its web in the more moist shrubs and bushes and *Z. x - notata* which builds on drier walls, window frames etc., in this way, whilst Lowrie (1948) wrote "Moisture in all its aspects is of prime importance to spiders". Cloudsley - Thompson himself was able to correlate the resistance to desiccation, and the reactions to humidity and light with the dryness of the habitat selected, in 3 species of *Ciniflo*. Thus, *C. similis* which inhabited drier areas was more resistant to desiccation, less photonegative, and selected a lower R. H. in the choice chamber. Nørgaard (1951) investigating the ecology of *Pirata piraticus* and *Lycosa pullata* found that survival depended upon both temperature and relative humidity, although it is interesting that here no preference was shown when a choice of different humidities was offered.

Whilst in the present investigation, it has been shown that the two species differ in their ability to withstand desiccation, and the habitats which they select in the field reflects this, the selection of sites appears to be based on optimal conditions, rather than the inability of one species to survive in the other's habitat. However, once the mechanism of this selection is examined, the picture is less clear. *A. cornutus* does seem to react positively to dry conditions, and it could be argued that this preference might establish the animal in its 'heather tip' habitat.

M. merianae on the other hand showed no clear response to humidity, and in this a parallel can be found in the work of Nørgaard already mentioned. This could be due to the failure of the animal to react normally in the choice chamber, but Cloudsley - Thompson's criticism of Nørgaard's work, that the animals were not given long enough to settle down, could hardly apply to the present investigations, where they were left in the apparatus for at least 15 hours. Indeed, this very point that Cloudsley -

Thompson makes that "... it was found convenient to test the responses of the spiders to humidity over periods of 24 hours because they did not react quickly to this stimulus", suggests that this sense would not provide a very efficient habitat-orientating mechanism in the field, especially when it is remembered that on a wet or even damp day, the humidity gradients would disappear, and the animal would be in danger of getting lost. Cloudsley - Thompson (1958) suggests a possible answer to this dilemma, as a result of work on the water relations and diurnal rhythms in woodlice. He writes (p 117) "It was found that the woodlouse has a composite diurnal rhythm of movement correlated primarily with alternating light and darkness and not with fluctuating temperature and humidity. (Although the latter may be of greater ecological significance, diurnal changes in light intensity often act as a TOKEN STIMULUS which leads to places where other environmental conditions are favourable.)" - my capitals. This term 'Token Stimulus' was first used by Fraenkel and Gunn (1940) p 190, when referring to light, which they suggested often indicated circumstances which were, for other reasons, favourable or unfavourable, and it seems probable that in the present case, light is a 'token stimulus', as it appears to be in woodlice, Cloudsley - Thompson (1956) where

"The species.......show a gradation in the intensity of their responses to light, which parallels that of their rates of water loss by evaporation in dry air", and it is interesting that the different habitat preference shown by the young is paralleled in M. merianae by a different light reaction. In Nørgaard's work there is some suggestion that temperature preference may provide the 'token stimulus', and it would be interesting to review work on this topic to see how often humidity responses are the prime orientating mechanism ecologically, and how often they are replaced by another, less equivocal, token stimulus, in the field.

An illustration of this is provided by Waloff (1941) who placed Oniscus in a choice chamber, where the choice was between dark dry conditions, and moist light ones. The animals at first moved away from the light towards the drier end, thus reversing their normal response to moisture, i.e. their initial reaction was to the token stimulus, but after staying awhile at the dark end, they overcame their negative light reaction, and moved to the light moist end. Finally, this problem is emphasised by Andrewartha and Birch (1954) p 221 "But there are some puzzling examples of animals which, when tested in laboratory experiments, moved toward the dry end of a moisture gradient, although in nature they seem to survive and multiply better in moister situations...... It is possible that in nature these animals are preserved from moving into places where the moisture is unfavourable by response to some stimulus other than humidity.".

It may be signifiant that *A. cornutus* which occupies the more exposed habitat lives in a silken retreat, whilst the more retiring *M. merianae* does not, and this might suggest that at some stage protection from predators had a high selective value, although no predator was ever observed during the present study.

Details of the differences between the habitat requirements of these two species do not, however, explain their mutual restriction to "breaks in the blanket bog cover", or shed any light on their distribution within the favoured habitat.

As it appears that the gully position occupied by *M. merianae* provides a rather low potential food supply, whilst the *A. cornutus* habitat is probably only a little better, the reasons for this particular pattern of distributions must be sufficient to outweigh the lower food supply. A possible clue to this is the occasional aberrant sites selected by both species, thus *A. cornutus* is often found amongst *Juncus effusus*, and sometimes amongst grass overhanging stream banks, whilst *M. merianae* is also found in the cracks of damp walls, in drainage gutters as in Plate 1, and in the mouths of old mine shafts. The one common factor in all cases seems to be adequate vertical space in which to sling the web and it may be that simple mechanical considerations of this sort are of paramount importance, the animal being unwilling to attempt web building on the open moor where supports would be restricted to rather low growing *Calluna* shoots and the litter substratum.

Given the favoured habitat, the distribution of each species within it is a matter of general interest, and it was with this in mind that attempts to study the distribution of *M. merianae* along the peat edges were made.

'Aggregation' is a term often used to describe the pattern of distribution of individual animals, but without qualification, it has no meaning. At its most vague, it could mean nothing more than the concentration of individuals within the geographic boundaries of the species, and even within this range the 'patchiness' of suitable habitats imposes a fundamental 'patchiness' on the distribution of the animals. Thus, the distribution of freshwater fishes in an area would show extreme aggregation, which incidently would coincide with the distribution of freshwater bodies! Although these qualifications are obvious enough on this scale, they must also apply in the more usual problems to which this method is applied, when the distribution of animals in small, apparently homogeneous areas is examined. So, it would be quite misleading to make any automatic inference from aggregation even at this level to any sort of social interaction or family grouping. Aggregation describes a phenomenon in animal distribution, not the reasons for it.

The most usual method of discovering the nature of distribution patterns, is the comparison of the frequency occurrence of individuals insamples, with that expected from a Poisson distribution, and this has been fully described by MacFadyen (1957) p 80, Allee et al (1949) p 364, and others, although another method has been suggested by Dice (1952) involving measurement of the actual distance between individuals.

In the present work, such calculations suggested that in practically all cases when the distribution of webs at a given point in time was studied, a random distribution was found, and a similar instance of such a distribution is described for spiders under boards by

Cole (1946). Two possible explanations for a random distribution can be advanced, first that it is the animals which are distributed randomly in an otherwise uniform habitat, an explanation which it would seem applies to the random distribution of the flour beetle Tribolium in a volume of flour as described by Park (1933), or secondly, suitable individual habitation sites may be distributed at random in the area. To distinguish between these alternatives, the time factor must be considered, and if subsequent examinations show the animals still randomly distributed, but in the same places, this can only be accounted for by the random distribution of suitable sites. In the present case where definite mechanical requirements for web building are required, this seems to be the explanation; as extreme aggregation was found when the number of webs per foot interval over a long period of time was examined, and although in these rather sedentary animals 'site tenacity' is of great importance, the occurrence of 'multiple web occupation', and the ability to distinguish differences in the field between 'good' and 'bad' areas suggests that this latter phenomenon is still significant.

Biologically, the most interesting feature, is the apparent failure of the animals to establish any territorial system, which would ensure the more efficient functioning of their traps, which, as Elton (1927) p 13 has pointed out enable web-spinning spiders, like sedentary marine filter feeding animals, to sit still, and have their food brought to them.

2. Factors affecting spider activity.

In Table 46, the factors affecting activity have been summarised for convenient reference, for as Wellington (1957) has said, behaviour studies are a necessary part of any ecological investigation, and of such studies the effects of weather are particularly important.

For an orb-web spinning spider, feeding depends upon the presence of a web, and in this study it has been suggested that web-destruction is connected with the utilization of the final remains of food already caught, whilst web-spinning is performed in 'anticipation' of future needs. Both activities, it would appear, are affected by temperature, but it is web-destruction, the utilization of food already caught, and possibly the salvaging of the protein in the web already spun, which appears to be the more 'compulsive' act, in that it will continue to take place in conditions not suitable for web spinning. Birch (1957) has said that food supply is often dependent, not upon the

Table 46.

Meta merianae. Summary of the Analysed Factors Affecting Activity.

- Results using consecutive data.

* Only one season's data available.

	Web Spinning	Web Destruction	Availability of Prey *	Mean Night Temperature	Mean Day Temperature
Web Destruction	+ P <.001				
Availability of Prey * Next Day	+ P >.7	+ P >.5			
Previous Day	- P >.3	- P >.1			
Mean Night Temperature	+ P <.001	+ P <.01	- P >.05		
Mean Day Temperature Next Day	0	+ P >.3	+ P <.02	+ P >.3	
Previous Day	+ P >.2	+ P <.05		+ P <.01	
Mean Night Wind	- P >.5	0		+ P >.5	
Mean Day Wind Next Day	0		- P >.2	+ P >.5	- P >.9
Previous Day	- P >.8	+ P >.05		- P >.5	
Mean Night Rain	0	0		0	
Mean Day Rain Next Day	0		0		0
Previous Day	0	0			
Hours Sunshine Next Day	- P >.5		+ P >.1	- P >.3	+ P >.05
Previous Day	0	+ P >.5		0	

number of animals feeding on it, but upon the weather, and this would seem particularly true in this case, where, 1. a cold night followed by a warm day would produce ample potential prey, although the spiders would not have webs out to catch it, - and where, 2. a warm night followed by a cold day, would result in very little potential prey, despite the spiders having plenty of webs to take it.

It is perhaps a little surprising, that *M. merianae* far from being able to forecast the weather, as has often been suggested, is apparently unable even to forecast the availability of its food, an ability, it might be thought which would have great selective advantage. Faced with this problem, spiders appear instead to have evolved the ability to go for long periods without food, so being able to wait until a suitable combination of climatic factors both during the night, and the subsequent day, once again make food available.

It must be assumed, that this latter adaptation was the easier to evolve.

VI. THE WOLF SPIDERS.

1. General Habits.

The members of this group do not spin a web, but lead a wandering life, and are reputed to run about in search of their prey, which, it is supposed, they run down and pounce upon when the opportunity presents itself. To this end, the eyes are well developed, as can be seen in Plate 10, which shows a female *Tarentula pulverulenta*. In Britain, they are represented by the families Lycosidae and Pisauridae.

2. Notes on the Wolf Spider Species Recorded.

Only 7 species have been recorded from the Reserve, and they all belong to the family Lycosidae.

Family Lycosidae.

Lycosa tarsalis Thorell

This species was taken, as a result of hand collecting, and pit fall trapping, from closely grazed limestone grassland, and from short alluvial grassland, where it was not uncommon.

Lycosa pullata (Clerck)

One of the most common Lycosids at Moor House, it was taken as a rule in *Juncus squarrosus* 'Moor Edge' habitats.

Lycosa amentata (Clerck)

This spider was only encountered infrequently during

Plate 10.

Female Lycosid, - Tarentula pulverulenta.

Plate 9.

'Artificial Web' in position, Peat Edge B.

Plate 11.

Lycosid Microdistribution Site on Rough Sike.

hand collecting, when it seemed to be associated with broken ground, and eroding peat.

Lycosa nigriceps Thorell

Only one or two specimens were recorded by hand collecting, when they were found in the rough grassland over redeposited peat.

Tarentula pulverulenta (Clerck)

A most striking, and frequently occurring animal, it was collected and trapped in a large variety of habitats in the area.

Trochosa terricola Thorell

Not uncommonly trapped in the Calluna/Eriophorum blanket bog areas, the only other record is of one specimen found on alluvial grassland.

Pirata piraticus (Clerck)

An extremely common inhabitant of the wettest parts of the moor, where it was collected and trapped in large numbers.

3. Some Habitats Occupied by Members of this Group, and the Significance of their Distribution.

Bristowe (1958) discussing the distribution of Wolf Spiders writes (p 166) "....the fact is that the micro-climate required by each species varies slightly although there is considerable over-lapping. Clues to their differing requirements can be gained by noticing where they are or are not found". and again (p 167) "The conclusion to be reached from this survey of facts and speculations is that climatic and microclimatic factors see to it that territories are roughly rationed so that only a few species are likely to be in direct competition on the same plot of land. It must be realised, however, that there are often damp and dry, exposed and sheltered patches within even a small area". In the present studies, attempts have been made to illustrate this general thesis, by reference to the Lycosids of the Moor House area.

A transect was made across the valley of Moss Burn, just below Nether Hearth, and is marked as sample site 4 in Figure 1. Within this transect, four broadly different habitats, as indicated by the vegetation, were recognised:-

1. _Juncus squarrous_ moor edge.

An area of disturbed peat, fairly damp, and dominated by the moor rush.

2. _Eriophorum vaginatum_ moor edge.

A very waterlogged area of disturbed peat, consisting almost exclusively of cotton grass, and situated, like the last site, on 'moor edge', a term used by Svendsen (1957) to describe "a predominantly peat habitat,.....

between the deep peat of moor and bog and the mineral soils".

3. Alluvial grassland.

A very well-drained alluvial terrace on the side of Moss Burn, covered with heavily grazed grassland the herbage depth of which was only 2 - 3 cms.

4. *Calluna* moor.

A *Calluna vulgaris* dominated site, which was not nearly so wet as the *Calluna/Eriophorum* mixed moor, due to some degree of artificial drainage.

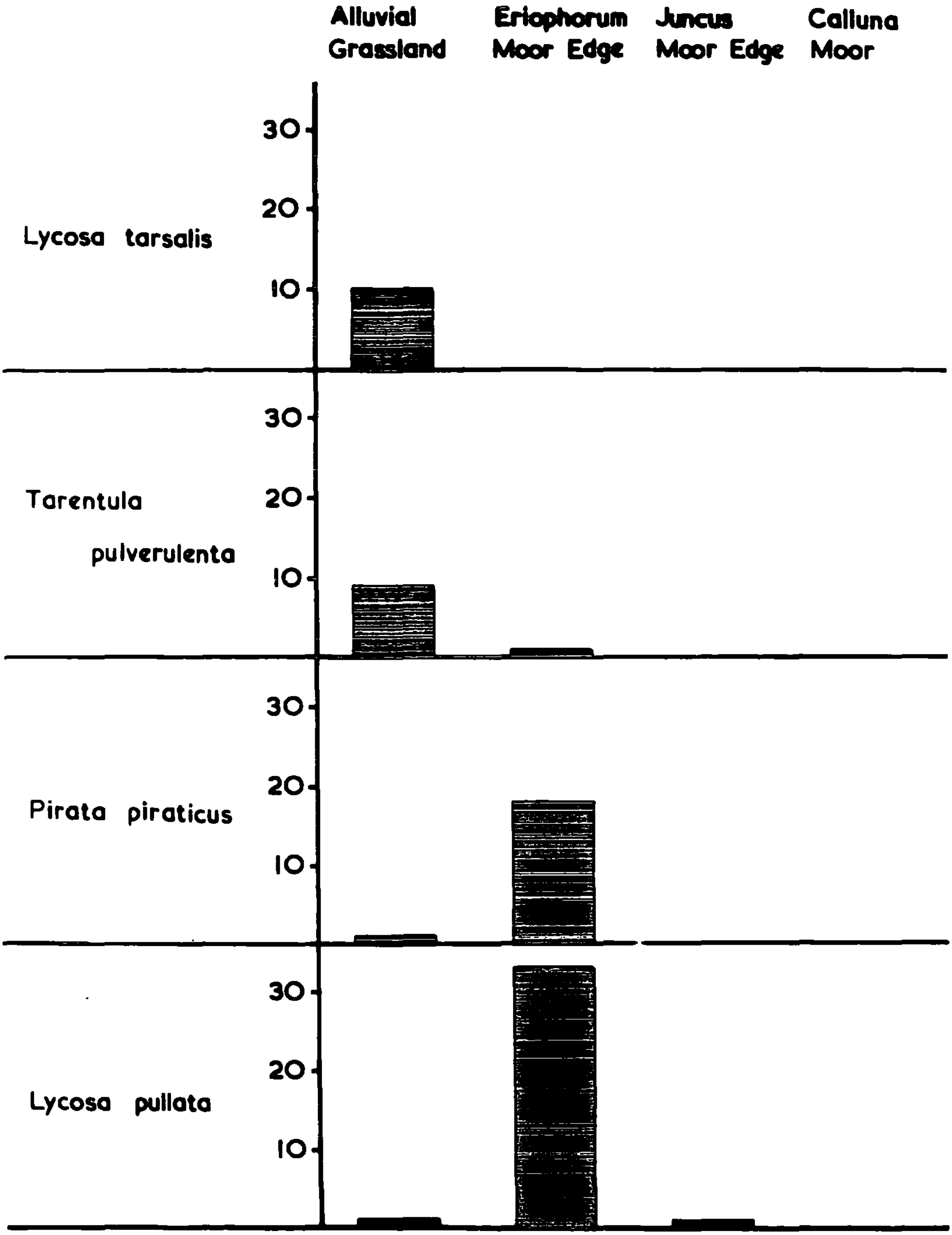
Six pitfall traps consisting of jam jars dug into the ground, their necks level with the surface, were placed in each of the 4 habitats, and emptied regularly throughout the months of July, August and September 1959. The results are tabulated in Figure 24, where it can be seen that it is only the Alluvial Grassland, and *Eriophorum* Moor Edge sites which give appreciable catches. There is, however, a sharp division in the faunas of these two sites, *L. tarsalis* and *T. pulverulenta* being virtually restricted to the dry Alluvial site, while *P. piraticus* and *L. pullata* were, by and large, found only on the water logged *Eriophorum* area.

Further information on the distribution of Lycosids in the area, has been obtained as a result of sampling, and pitfall trapping in other areas, for

Fig. 24.

Distribution of Lycosidae in 4 Moorland Habitats

Tot. Nos. trapped in July and Aug. 1959



other purposes, and a summary of this data can be found in Table 47, whilst a description of the sites mentioned can be found under the appropriate sections (VII 4a, b, c, d, e.)

TABLE 47.

A Summary of Further Lycosid Records.

Habitat	Method	Species	Number
Valley Bog.	10 x .0625 m^2 samples	Immature	9
Calluna Eriophorum	10 Pitfall traps for 6 months	*T. pulverulenta* *T. terricola* *P. piraticus* Immature	6 5 4 1
	178 x .0625 m^2 samples	Immature	4
Juncus squarrous	45 x .0625 m^2 samples	*L. pullata* *P. piraticus* Immature	1 1 6
Limestone Grassland	6 Pitfall traps for 1 yr.	*T. pulverulenta* *L. tarsalis* *P. piraticus* Immature	2 1 1 2
	53 x .0625 m^2 samples		0
Festuca/Nardus	40 x .0625 m^2 samples	Immature	5

These sites have been arranged in their probable order of dampness, the Valley Bog site being the wettest, and the *Festuca/Nardus* the driest.

From all this, it would appear that there is indeed some measure of separation amongst the Lycosid fauna, on the basis of habitat type, and that *P. piraticus* is restricted to the wettest area, whilst *L. tarsalis* is found only in the driest. *T. pulverulenta* seems to be ubiquitous, while *L. pullata* is most frequently associated with the *Juncus/Eriophorum* Moor Edge areas.

The restriction of *P. piraticus* to very wet conditions has been noted by several authors - Nørgaard (1945, 1951, 1952), Williamson (1949), Savory (1935), Mackie (1959), and Bristowe (1958). Nørgaard says *L. pullata* is normally found on moist acid soil, Bristowe and Savory talk of it as ubiquitous, whilst Williamson working on Skokholm classed it with *T. pulverulenta* as a species found in long grass, bracken, and heather clumps. Throughout this discussion, emphasis has been put upon the dampness of the various sites, and in this, the present writer has followed the example of Nørgaard (1951) and Bristowe (1958) p 167. Davies and Edney (1952) and Cloudsley-Thompson (1957) have shown that the rate of water loss varies for different species, whilst Parry (1954) has found a varying ability to drink capillary soil water, and in view of the site preferences found, a parallel gradation of ability to withstand desiccation was sought.

Accordingly, desiccation experiments were performed on adults of P. piraticus, L. pullata, and T. Pulverulenta by the method already described in Section V 3, and the results are shown in Table 48.

TABLE 48.

Lycosid Desiccation Experiments.

Species	Pirata piraticus		Lycosa pullata		Tarentula pulverulenta	
Treatment	Wet	Dry	Wet	Dry	Wet	Dry
No. of animals involved	6	35	4	23	1	5
Mean Survival in days	19.2	1.17	15.5	2.9	15	9.6

Thus, on the average, subjecting the members of a species to moderately desiccating conditions, reduced the survival time in days, over controls kept moist, by the following factors.

P. piraticus	16.4
L. pullata	5.4
T. pulverulenta	1.6

This confirms Nørgaard's (1951) results for P. piraticus and L. pullata, and shows that T. pulverulenta is still more resistant to desiccation, a pattern which fits in well with the field data. In this case, unlike the situation previously discussed for the two orb weavers M. merianae and A. cornutus, there are no data availabl to show what it is, that guides the animal into a favourable environment.

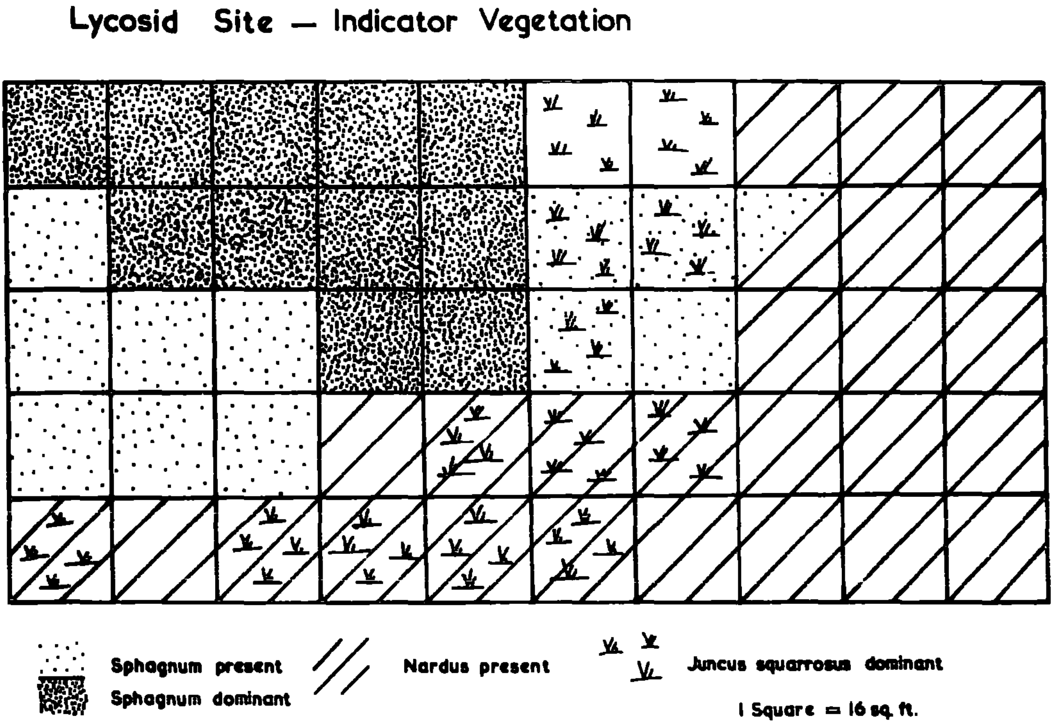
In view of these differences in distribution, a small study area was selected which included both wet and drier conditions, so that the microdistribution of the Lycosids could be investigated.

4. Microdistribution of 3 Species.

(a) The Study Area.

The site, situated on the bank of Rough Sike (Sample Site 5 on Figure 1) was on Moor Edge, and is illustrated in Plate 11. It consisted of a grid, 40 ft. by 20 ft. divided into 50 squares, each 4 ft. by 4 ft. Part of the area was a *Sphagnum* flush, below which the water seeped away into the peat, producing an area dominated by *Juncus squarrosus*. The driest areas on the more mineral alluvial soils were colonised by *Deschampsia flexuosa*, *Nardus stricta* and *Festuca ovina*, where the drainage effect of the nearby stream was most pronounced. This succession of plant communities is best illustrated in Figure 25, where the 'Indicator Vegetation' for each square has been plotted, using percentage cover abundance as the unit of measurement, and it is assumed that this is indicative of the moisture content of the substrate.

Figure 25.



Lycosid Site, - Indicator Vegetation.

(b) Methods Employed.

As the spiders are reputed to hunt actively, and extensively for their prey, it was decided that pitfall traps would be the best means of catching them. Pitfall traps have been used by many ecological workers, and vary from the sophisticated designs of Fichter (1941) and Williams (1958), the latter incorporating a time sorting mechanism, to the simple jam jars of Duffey (1956) and drinking glasses of Tretzel (1955 b) who gives a summary of other work and techniques in this field. For this study of population levels and longevity, the animals were required alive, and as they tend to be cannibalistic, a large number of very small pitfall traps was used, so that few animals would be expected in any given trap. Consequently, 2 x 1" glass specimen tubes were sunk into the ground, until their open tops were level with the surface. They were left quite empty, but the glass sides were kept polished, to make it difficult for the animals to climb out. 50 such tubes were placed in the grid, and for the purposes of analysis, the whole could be imagined as a 50 square grid, with a pitfall trap in the centre of each square.

During the 1958 season, the traps were allowed to catch 24 hours per day, and were examined morning and evening, whilst in the 1959 season, trapping was for

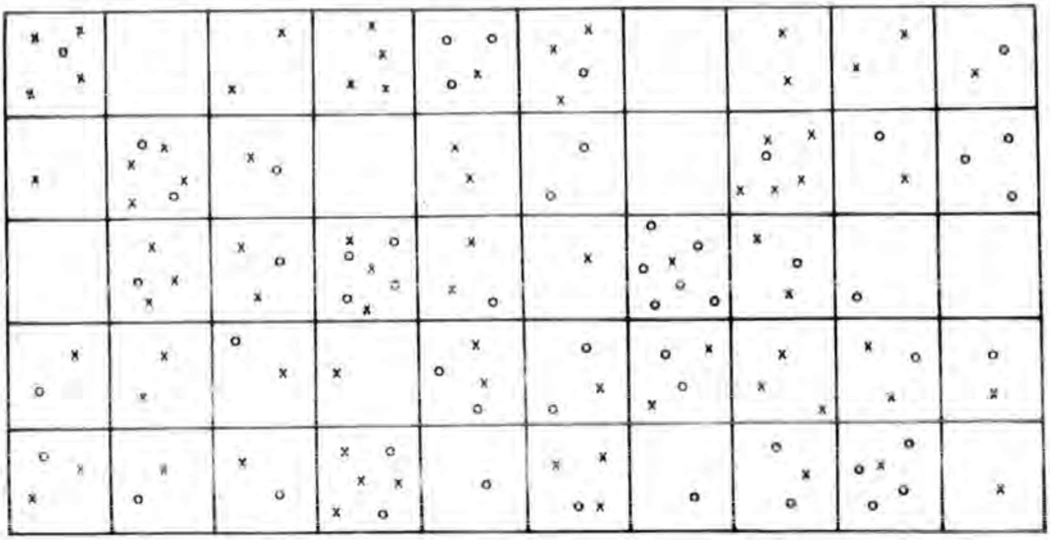
8 hours per day only. When not in use, the tubes were inverted so that no animals would be caught, whilst for marking, a spot of coloured cellulose paint was put on the abdomen, while the animal was still in the tube.

(c) Results for Moor Edge Site.

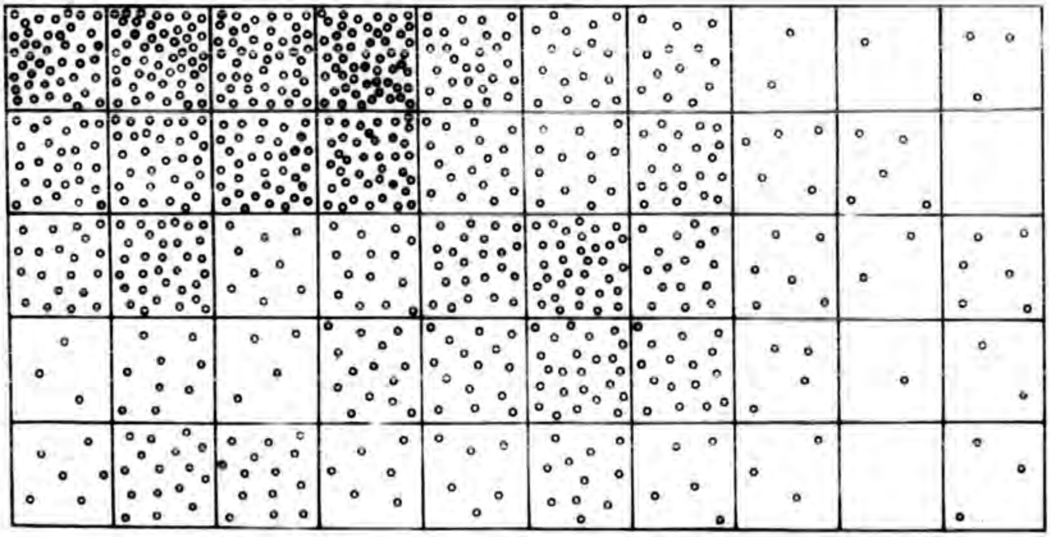
Once trapping was begun, it was noticed that the catch of P. piraticus varied greatly from trap to trap, and to discover something of the pattern of this variability, the total catch during each season for each trap was calculated, as it was for the other two species taken here, T. pulverulenta and Lycosa sp. (Animals referred to Lycosa sp. were not identified further, as this can only be done with a microscope and dead specimens, but subsequent examination of dead and accidentally killed animals, showed the overwhelming majority to be L. pullata). Figure 26 shows these distributions presented in graphical form, and the aggregation of P. piraticus captures in the top left hand region of the grid is most striking. Reference back to Figure 25 will show that this largely coincides with the Sphagnum flush seeping in from a partially recolonised erosion channel leading from the Calluna/Eriophorum bog above. The distribution picture for this species is markedly different from those for T. pulverulenta, and Lycosa sp., mainly in that the captures of these last two appear to be randomly distri-

Fig. 26.

Distribution of Tarentula pulverulenta (○) & Lycosa sp. (×)



Distribution of Pirata piraticus



○ = 1 Spider trapped in square. Pooled results for period June 1958 to Aug. 1959.

buted over the whole area. As Table 49 shows, this whole picture is simply confirmed by a statistical examination of the data. Here, the numbers of captures for each species are classified in two ways.

1. Very wet (Sphagnum dominated) grid squares versus the remainder. and

2. Wet (Sphagnum present) grid squares versus the remainder.

In accordance with this classification, the figures for the two seasons were compared, in each case, to see if they were consistent i.e. homogeneous, and in all instances this was so. Having established that none of the patterns of distribution differed significantly from each other in the two seasons, it was permissible to add them, and compare the total catch distributions in the various categories with those expected from a random distribution, knowing the number of pitfall traps in each category. As can be seen P. piraticus shows a very high degree of aggregation in both the 'Very Wet' and 'Wet' regions, although this is most noticeable when the squares in which Sphagnum is present are compared with those where it is not. The other two species, however, exhibit no significant variation from random distribution in respect of numbers of captures in these partic-

TABLE 49.

The Distribution of Lycosids and Sphagnum.

Species	Year	Very Wet (Sphagnum Dom.)				Wet (Sphagnum Present)			
		No. in Sph	Rest	χ^2	Prob.	No. in Sph	Rest	χ^2	Prob.
No. of Grid Squares		11	39			23	27		
Pirata piraticus	1958	259	242	3.83	>.05	376	125	.94	>.3
	1959	118	149			191	76		
	Σ	377	391	12.75	<.001***	567	201	16.72	<.001***
Lycosa sp.	1958	17	29	1.95	>.1	28	18	2.8	>.05
	1959	6	25			12	19		
	Σ	23	54	.6	>.3	40	37	.22	>.5
Tarentula pulverulenta	1958	7	26	.04	>.8	14	19	.07	>.7
	1959	5	17			11	11		
	Σ	12	43	.05	>.8	25	30	.02	>.8
No. of P.T's		11	39			23	27		

TABLE 49 (cont.)

	No. in Sph	Rest	χ^2	Prob.	No. in Sph	Rest	χ^2	Prob.
Heterogeneity between Lycosa sp. and Tarentula pulverulenta from totals.								
Lycosa sp.	23	54	.69	>.3	40	37	.31	>.5
T. pulverulenta	12	43			25	30		
Heterogeneity between Pirata piraticus, and the other two species combined.								
Pirata piraticus	377	391	22.2	<.001	376	125	31.7	<.001
Lycosa/Tarentula	35	97			65	67		

ular 'Wet' and 'Drier' categories. It has also been shown that in this context, the distributions of *Lycosa sp.* and *T. pulverulenta* are similar, whilst they both differ highly significantly from that of *P. piraticus*. It would appear, therefore, that *P. piraticus* shows a very strong preference for wet, *Sphagnum* covered areas, and that this could readily be detected in an area only 800 sq. ft. in extent, which it would be possible for the animals to traverse in 2 or 3 minutes.

(d). Notes on Alluvial Microdistribution Site.

In connection with work on the hammock-web building spiders, a tussocky area of alluvial grassland was divided up and extracted, and both the area and technique are fully described in Section VII. 6. During the course of the work, 13 immature Lycosids were extracted, which were distributed in the area:-

See Figure 35.

9/1; 10/1; 11/5; 12/1; 13/4; 18/1

(The first figure refers to the grid sample, and the second to the number of Lycosids extracted from it).

From this it can be seen, that in a heterogeneous habitat, consisting of closely grazed alluvial turf, interspersed with tussocks of *Nardus stricta*, and

Juncus effusus, the Lycosids, at any rate during the day, are to be found commonly sheltering in these tussocks.

5. Seasonal Activity, and its Feeding Implications.

In Figure 27, the patterns of seasonal activity as indicated by the maximum day's catch for each month, are shown for each of the 3 species, from which an activity peak in all species in May and June can be seen.

Only small numbers of T. pulverulenta were caught, and they suggest a shorter activity season, animals having been taken in May, June and July only. In P. piraticus and Lycosa sp. the number of male captures fell steadily until August, whilst the female captures after a sudden drop in numbers in June and July, showed a tendency to increase again, at least in the case of P. piraticus, in August.

The meaning of these activity patterns is made clear, when the animals caught, are sexed and aged. Thus, out of 751 P. piraticus captures, 549 were of males, 182 females, and only 20 were of immature animals. For Lycosa sp. the figures were - total 80; 51 males, 28 females and 1 immature, while the T. pulverulenta records were - total 52; 38 males, 12 females, and 2 immature. This confirms the impression

Pattern of Seasonal Activity in 3 Species of Lycosids

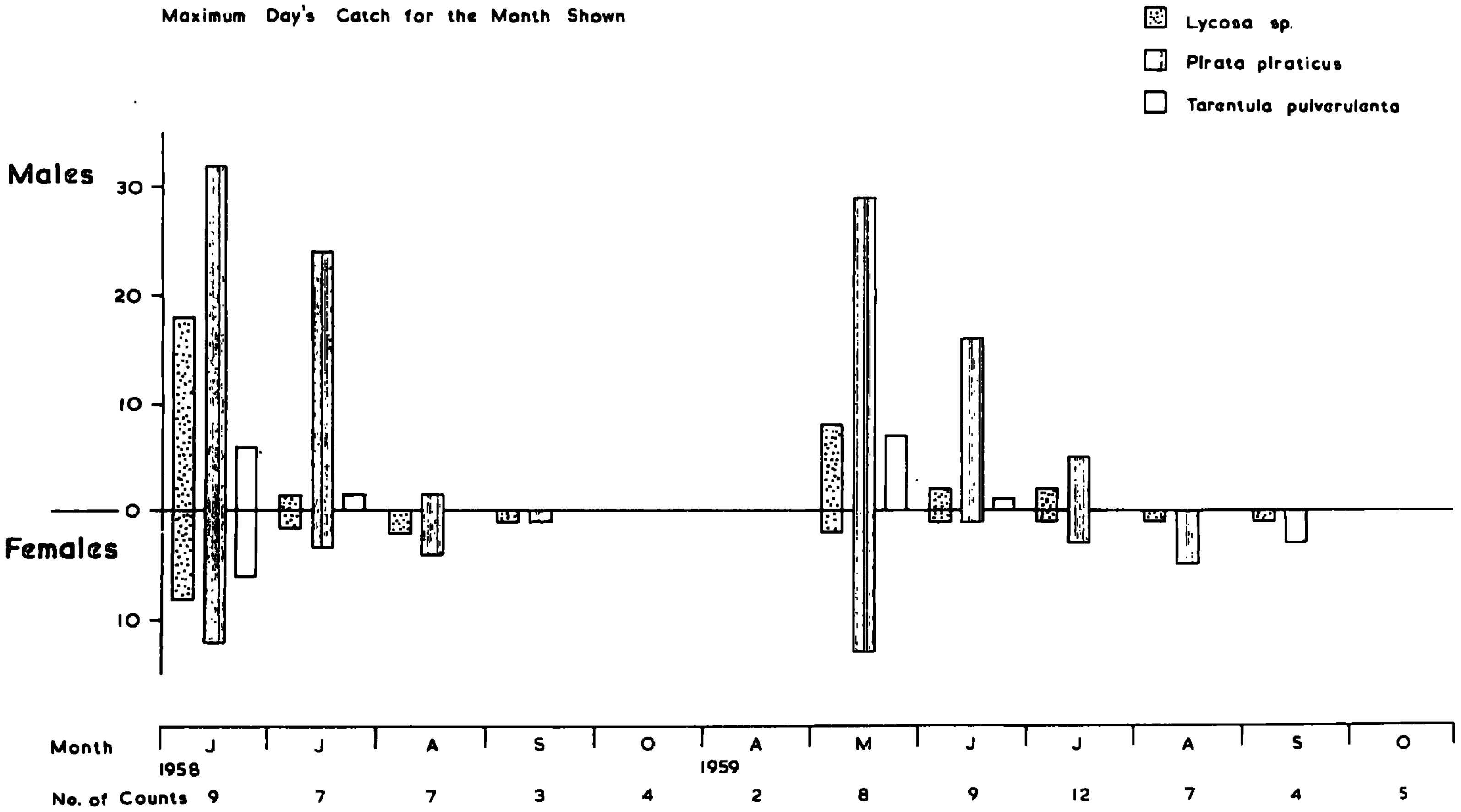


Fig. 27.

of many workers in this field, that the activity peaks recorded by pitfall traps represent the periods of mating activity, and that the predominance of males is in part a reflection of their active searching for females.

It seems to the present writer, however, that this explanation carries definite implications about the hunting methods of this group. Pitfall traps catch animals which are active on the ground surface, and if, as has always been suggested, these Lycosids hunt their prey actively over the surface, relying upon their eyesight, to see, ~~the~~ and fleetness of foot, to run down, suitable prey, it is difficult to understand first, why so very few immature animals are taken in pitfall traps, and secondly, why the records for adults reflect their mating activities so faithfully, and apparently exclusively. It does seem possible, that hunting in many species of Lycosids may be a much more passive activity, the animal tending to wait until prey comes into its immediate vicinity, and it is interesting to note that a similar conclusion has been reached in the case of the Harvest-spiders by Phillipson (1960). So, much of the apparently ceaseless searching which is a familiar characteristic of these animals in Spring, may in fact be the result of mating, and not hunting behaviour. Indeed Savory (1935), p 34, after watching the behaviour of *P. piraticus* in the laboratory has said that it tended to remain at the mouth of its silk tube, with its fore-legs resting on the water film, through which, he suggests, it can detect vibrations, as it always ran out to attack a vibrating tuning fork.

To test the period of greater activity, the pitfall traps were allowed to catch through the night, as well as during the next day, and Table 50 shows the figures obtained for 50 traps, when corrected for 10 hours catching, on 6 occasions.

TABLE 50.

Catches of *P. piraticus* in Pitfall Traps - Numbers Corrected for 10 hours catching.

	Day	Night
	40	14.1
	35	9.6
	33	17.1
	46	26.4
	48	23.8
	6	2.4
Σ	208	93.4

A paired 't' test on this data showed that the daylight catches were significantly larger, with a probability of <.001 confirming that the animals were diurnal.

It will be appreciated that the difference may well have been more marked still, if it had been practicable to empty the traps at dusk, and again at sunrise. This was not done, and so at least some of the animals found in the 'night' trap collections would consists of animals active in the late evening and early morning.

6. Activity and its Relation to Climate.

The pitfall trap catches varied considerably from day to day, and such variations in Lycosid activity are well understood by the collector. To investigate this further, trapping was standardised from 10-30 a.m. to 6-30 p.m. during the 1959 season, and attempts to correlate the catch fluctuations with climate, by the previously described 'sign' method, were attempted. The results can be seen in Table 51, where a positive, but not significant correlation was found with the mean air temperature during the catching period, the impression often received when collecting in the field, that the surface activity of the animals is related to sunshine was not corraborated. Kuenzler (1958), in a paper published after the present work had been begun, found no clear cut correlations between the activity of three *Lycosa sp*. and barometric pressure, wind velocity, cloud cover, or the amount of moonlight, but did find a positive relationship with temperature and relative humidity.

In the present studies, it may well be that the non-significant nature of the activity and temperature correlation is due chiefly to the small number of results obtained.

TABLE 51.

P. piraticus. Activity and Climate.

Correlation between daily pitfall trap catches of P. piraticus and

1. Mean Air Temperature over catching period from hourly records.

20 positive, 8 negative, and 3 no correlations.

$$\chi^2 = 2.6 \quad p > .1$$

2. Hours Sunshine over catching period.

12 positive, 12 negative, and 4 no correlations.

- No Correlation.

7. Notes on Life Histories and Populations.

Life history information was collected throughout the study, and the appropriate data are to be found in Table 52. If the ratio of egg and young - carrying females to the total number of females trapped in P. piraticus and Lycosa sp. is examined, the picture seems to be one of mating activity in June 1958 (with everything apparently a month earlier in the very warm year of 1959), followed by a sharp fall off in female activity during July, when most of the animals caught, were carrying cocoons, whilst in August and September, occasional animals with young clinging to them were taken, It would seem, that the production of a cocoon renders the animals less likely to be caught in pitfall traps i.e. they become more sedentary, probably as a result of the abatement of the mating drive. This is supported by Nørgaard (1951), who observed that P. piraticus females remained in silken retreat tubes spun amongst Sphagnum shoots, exposing their egg cocoons to the sun to incubate.

Once the eggs have hatched, and the young dispersed, however there is some evidence of renewed mating activity although by this time, there are probably very few males and the capture of a female Lycosa sp. with cocoon in September might indicate a few second broods. No females of T. pulverulenta with either egg cocoons or young were taken, but the high proportion of obviously gravid females in June 1958, suggests that this species has a similar life history to the other two. The timing of these activities at Moor House fit in well with the work done on these species by Duffey (1955), Tretzel (1955 a) and Turnbull (1957).

TABLE 52.

Lycosid Life Histories - Results from Pitfall Trapping.

	Lycosa sp.					*Pirata piraticus*					*Tarentula pulverulenta*			
	Tot. No.	M♂	M♀	♀+Eggs ♀+Young*	Imm.	Tot. No.	M♂	M♀	♀+Eggs ♀+Young*	Imm.	Tot. No.	M♂	♀Gravid* M♀	Imm
1958														
June	35	25	7	3		403	310	92	1		28	17	4+7*	
July	8	4	1	3		83	76	1	5	1	2	1	1*	
August	4		2	1+1*		24	6	14	2+1*	1				
September	1			1		1		1						
October														
1959														
April														
May	20	16	2	1	1	128	93	31		4	20	18		2
June	5	3	1	1		47	44	2	1		2	2		
July	5	3	1	1*		37	20	13	1	3				
August	1		1			20		13	1	6				
September	1			1		5		2	1*	2				
October						3				3				

N. B. Max Longevity recorded ♂ 51 days, ♀ 76 days.(*P. piraticus*)

These life histories imply that it is the immature animals which overwinter, and this is supported by the work of Holmquist (1926) on *Pirata sp.* In America, and of others.

During the whole of the study period, release/recapture population estimates, were attempted on the males of *P. piraticus*, as only these animals were trapped in sufficiently large numbers.

Trapped animals were marked a particular colour, which was changed with date, and this continued throughout the study period, all marked and recaptured animals being noted. In analysing the results, the total number of recaptures from any marking period was used, provided that they numbered more than 5, recaptured within 14 days of marking. Using these criteria, one population estimate was possible in 1958, and two in 1959, and these are set out in Table 53, using an analytical method for determining a population estimate, with its 95% confidence limits which follows Coulson (1956), and Bailey (1951).

Two points seem worthy of note, that in the drier 1959 season, the area carried a lower *P. piraticus* population, than in the wetter 1958 season, a trend which is opposed to that found in the two species of orb-web spinning spiders. During the 1959 season, a

TABLE 53.

P. piraticus. Population Estimates of Males in an 800 sq. ft. Grid.

Marking			Recapturing.			
Date	Colour	No.	Date	Tot. No. Caught.	No. Recaptures	Pop. Est. ± 95% C.L.
17/6/58	Red	21	19/6/58	11	3	
18/6/58	Yellow	13	28/6/58	29	4	
		Σ 34	29/6/58	25	4	
			"	39	3	
			30/6/58	26	4	
			"	42	8	212
			1/7/58	32	8	± 4.38
			2/7/58	26	2	
				Σ 230	36	
23/5/59	Green	17	24/5/59	29	6	
			25/5/59	20	0	127
			26/5/59	25	3	± 8.21
				Σ 74	9	
16/6/59	Yellow	15	19/6/59	12	7	
17/6/59	"	11				
18/6/59	"	12				62
		Σ 38				± 9.17

considerable part of the *Sphagnum* flush dried out, and this was presumably responsible for the lower population, but it is interesting that the 'favourability' of the year depends upon the spiders in question. Second in the 1959 season, there was a marked fall in the male *P. piraticus* population from May to June, and it would therefore appear that this fall, also noted in Figure 27 when the maximum day catch in the month was examined was indeed caused by a population decrease, and not simply by the general activity decrease suspected in the females.

As it has already been shown that P. piraticus is concentrated within certain parts of the study grid, no attempt has been made to express these population estimates in terms of the number of animals per square metre.

VII. THE HAMMOCK-WEB BUILDING SPIDERS.

1. General Habits.

A wealth of very small spiders, often called Money Spiders belonging to the family Linyphiidae, are to be found in almost all types of herbage in temperate countries. The majority of these build small hammock-shaped webs amongst the foliage, and the web of one of the larger genera found at Moor House, *Lepthyphantes*, is shown in Plate 12.

Here the web consists of a horizontal sheet of criss-crossed, non-sticky threads, surmounted by a tangle of 'stop threads'. The spider runs upside down on the underside of the sheet, biting through it to kill any prey which fall down, as described by Nørgaard (1943). Very little appears to be known of the food taken by the smaller, herb-layer Linyphiids in the field, although work on the feeding of one of the largest species *Linyphia triangularis*, common in hedges and bushes has been done by Nørgaard and Turnbull (1957).

To discover something more of the potential prey of animals with this type of web, an artificial Linyphiid web was designed. This consisted of a square of stiff celluloid, 5 cms x 5 cms impaled upon a metal spike some 9 inches long, which could be pushed into the ground, so adjusting the celluloid platform to any desired height.

Linyphiid Hammock-Web, - Top View.

Linyphiid Hammock-Web, - Side View.

The upper surface of this platform was spread with 'stik-tite'. A number of these traps were placed in the upper foliage layer of Calluna/Eriophorum mixed moor, and Juncus squarrosus, vegetations, in positions where the webs of Lepthyphantes sp. were frequently found. Whilst it cannot be imagined that they imitate the catching power of the real webs in any detailed way, as these also possess stop threads and depend not so much on the physical properties of the webs for their catching success, as upon the activity of the spider, it was hoped that some idea of the 'available prey' could be gained.

The results obtained from two separate periods of investigation are shown in Table 54, and it does seem that this method might be used to give some comparative measure of the activity of a variety of small herb layer arthropods, in particular the Collembola, Diptera and Hemiptera.

Collembola appear to be the most plentiful food source in this position, and the importance of this group as food for Linyphiid spiders has been stressed by MacLagan (1932) and Bristowe (1941) p 292. Diptera, in particular small Nematocera were exceedingly common on the traps in summer, and their habit of rising out of, and sinking back into the vegetation at various

TABLE 54.

The Potential Prey Composition of Linyphiid Spiders.

A. Animals taken during 347 trap days in the *Calluna/Eriophorum*, and *Juncus squarrosus* sites from 6/11/57 until 13/12/57.

B. Animals taken during 483 trap days in the *Calluna/Eriophorum* site from 1/7/58 until 7/10/58.

Group	Series A		Series B	
	No.	% of Total	No.	% of Total
Collembola	351	94.7	253	34.9
Diptera	6	1.62	204	28.1
Hemiptera	2	.54	139	19.25
Acarina	10	2.7	103	14.2
Hymenoptera	1	.27	24	3.31
Coleoptera	1	.27	1	.14
Opiliones	0	0	1	.14
Σ	371		725	
No. Animals/Trap Day	1.07		1.5	

N.B. 'Trap Day' means 'one trap catching for one day'.

times during the day must often have been responsible for their capture. In summer also, the jumping Hemiptera were particularly susceptible to any hammock-shaped trap, and Bristowe (1941) states that many members of both of these last two groups are readily taken by spiders. The only other group taken in large numbers was the mites, and their significance as a food for spiders seems to be in question, as Bristowe (1941) p 325, says that "It is rare for spiders to eat or kill mites", while Chant (1956) found that spiders in orchards readily fed on them.

In any case, it seems that with the exception of the small Nematocera, the Linyphiid spiders exploit a different food supply from the Orb-web spinning spiders.

2. Notes on the Hammock-Web Building Species Recorded.

(a). Species Notes.

The Linyphiidae is by far the commonest family on the Reserve, and 52 species have been recorded, of which the 17 marked by a * appear to be new County Records for Westmorland. Bristowe (1939) gives a comprehensive list of County Records up to that year, and where species, not in this list have been recorded, notes on any subsequent records for the County have been included. N.B. Unless there is a statement to the contrary, both sexes were recorded.

* Ceratinella brevipes (Westring)

Collected in a variety of habitats although most commonly in Juncus squarrosus, Miller (1951) records it from peat bogs in 'South-Bohemia', as a species particularly worthy of note there.

Ceratinella brevis (Wider)

One female was caught in a pitfall trap on the Limestone Grassland, the only previous record for Westmorland being by Murgatroyd (1955) from Stakes Moss.

Walckenaera acuminata Blackwall

Although uncommon, it was recorded from the *Festuca/Nardus*, and Limestone grasslands, and Forman (1951) associates it with the 'Moorland Habitat'. Murgatroyd (1955) found it at Stakes Moss, in the County.

Wideria antica (Wider)

Several specimens were captured in the *Festuca/Nardus* grassland.

Trachynella nudipalpis (Westring)

An uncommon species, only taken in the *Calluna/Eriophorum* mixed moor, there is one record for the County, from Meathop moss by Murgatroyd (1955).

Cornicularia karpinskii (O.P. - Cambridge)

This rare spider, normally associated with mountains over 3,000 feet was taken in the *Calluna/Eriophorum* mixed moor site, and in a pitfall trap on Limestone Grassland. As these two sites are at about 1,800 feet, these must be amongst the lowest records for this species. Locket et al (1958) provide the only other record for Westmorland, of a female caught under stones in High Street.

**Cornicularia cuspidata* (Blackwall)

This species, was taken rarely in *Juncus squarrosus*, and *Calluna/Eriophorum* vegetation, although Miller (1951) records it as common to the Rejviz and N.W. German peat-bogs. Bristowe (1939) records it as 'common on mountains'.

*Dicymbium tibiale (Blackwall)

This species was very abundant and widely distributed on the Reserve, being perhaps most common on the grassland sites.

Gonatium rubens (Blackwall)

A not infrequently occurring species in the Calluna/ Eriophorum mixed moor, Forman (1951) speaks of it as a species found on Moorlands.

Pepononocranium ludicrum (O.P.-Cambridge)

One female only was recorded, from the Festuca/Nardus site.

* Hypselistes jacksoni (O.P.-Cambridge)

A rare species, two females only were obtained from the Calluna/Eriophorum Blanket Bog site.

Oedothorax gibbosus/tuberosus

One female, found in the Festuca/Nardus grassland site was examined, but in the absence of the male, these two species cannot be distinguished.

Oedothorax fuscus (Blackwall)

Two specimens were taken, one from alluvial, and the other from limestone grassland. Recorded from a Moorland habitat in Aberdeenshire by Forman (1951), Miller (1951) confirms that it is common in peat bogs in N.W. Germany.

Trichoptera mengei (Simon)

One female was collected in the Calluna/Eriophorum site.

Silometopus elegans (O.P.-Cambridge)

A widely distributed, frequently encountered species on the Reserve, there appear to be two published records for Westmorland, one from Fairfield mountain by Jackson - see Britten (1912), which must have been missed by Bristowe, and the other from Martindale by Millidge and Locket (1955).

*Tiso vagans (Blackwall)

This species was very common and widespread in the area, being the dominant form in the Limestone Grassland site.

*Monocephalus fuscipes (Blackwall)

Almost entirely restricted to the Festuca/Nardus grassland site, where it was the dominant species, it is recorded by Forman (1951) as associated with Moorlands.

*Jacksonella falconeri (Jackson)

Males alone of this very small, and infrequently recorded species were taken in the Juncus squarrosus and Limestone Grassland sites. Though a County Record for Westmorland, it was found in nearby Upper Teasdale by Falconer (1925). Blest (1956) considers it to be a soil, rather than a litter living species.

*Gongylidiellum vivum (O.P.-Cambridge)

Occurring abundantly in the Festuca/Nardus site, it was taken in other habitats on occasions.

*Gongylidiellum latebricola (O.P.-Cambridge)

The 5 specimens collected were all caught in the Juncus squarrosus site.

Micrargus herbigradus (Blackwall)

The dominant Linyphiid of the Juncus squarrosus site, this widely distributed species was one of the most common in the area.

Erigonella hiemalis (Blackwall)

This spider was virtually restricted to the Festuca/Nardus habitat, where it was abundant, the only other record for Westmorland being from Stakes Moss by Murgatroyd (1955).

Savignia frontata (Blackwall)

Uncommon, material having been collected only from the Alluvial Terrace, and the Limestone Grassland sites, the species was recorded from Stakes Moss by Murgatroyd (1955), and from Windermere by Parker (private communication).

Diplocephalus permixtus (O.P.-Cambridge)

Again an uncommon animal, only 3 specimens were recorded from the Reserve, all from the Alluvial microdistribution plot. The previous Westmorland records are by Millidge et al (1955), from Moor Divock, and Parker (private communication) from Sunbiggin Tarn. Falconer (1925) recorded it nearby from Teasdale, and Miller (1951) from the peat bogs in South Bohemia.

Erigone dentipalpis (Wider)

This species was taken frequently on the Limestone and Alluvial grasslands.

*Erigone atra (Blackwall)

Only the occasional female of this species was taken from the cultivated meadow, and one from the slopes of Knock Fell. Although there are no published records of this species from Westmorland, Parker (private communication) has taken it at Windermere.

Eboria fausta (O.P.-Cambridge)

The two specimens captured were from the Calluna/Eriophorum and Alluvial microdistribution sites. Previously recorded in the County from moss near Angle Tarn, above Patterdale by Locket et al (1958), this rather rare spider is thought by Miller (1951) to be a relict species in the Rejviz peat-bogs, and to have originated in North Europe.

Drepanotylus uncatus (O.P.-Cambridge)

Again only two individuals, but this time from the very wet Valley Bog site, this species was first found in Westmorland by Locket et al (1958) in moss at Bannerdale, while Miller (1951) also records it from peat bogs.

Phaulothrix hardyi (Blackwall)

The few specimens captured, were all taken from pitfall traps on the Limestone grassland site, and Bristowe (1939) associates it with mountains.

Porrhomma montanum Jackson.

This species was uncommon, and the females which were taken, were all found in the *Calluna/Eriophorum*, and *Juncus squarrosus* sites. Millidge and Locket (1955) found it in High Street, Westmorland, and Bristowe (1939) says that it is commonly associated with mountains.

***Agyneta decora* (O.P.-Cambridge)

Two specimens only were taken, from *Juncus squarrosus*.

**Meioneta rurestris* (C.L. Koch)

One male of this species was collected from *Calluna/Eriophorum* mixed moor, and represents an addition to the published County Records, although Parker (private communication) has taken it at Windermere.

Meioneta saxatilis (Blackwall)

A frequently encountered spider in the wetter peaty habitats, it was first collected in Westmorland by Locket et al (1958) from moss near Hayes Water.

Meioneta beata (O.P.-Cambridge)

One male of this species which Locket and Millidge (1953) describe as 'rare', was found in the *Festuca/Nardus* grassland site.

*_Maro minutus_ O.P.-Cambridge

Two specimens were encountered in the ungrazed limestone grassland, and Blest (1956) has classed this as a 'soil species', having found it to be particularly associated with loose, fine, mixed chalk-and-soil detritus on the South Downs. Miller (1951) writes of it as a relict species of the South-Bohemian peat-bogs, with its native country in N.W. Europe (England and Scotland).

Centromerus prudens (O.P.-Cambridge)

The only specimen, a male, was taken from the slopes of Knock Fell, the previous record for the County being by Parker (1959) from the summit of Great Rigg at 2,500 feet which agrees with Bristowe (1939) who says it is common on mountains.

*_Centromerus arcanus_ (O.P.-Cambridge)

Confined to the _Calluna/Eriophorum_ mixed moor site, where it was one of the dominant species, it is again associated by Bristowe (1939) with mountains.

Centromerita bicolor (Blackwall)

Centromerita concinna (Thorell)

One of the most frequently occurring genera in the study area, considerable difficulty was experienced in separating the species, although it is known that both occur, the former having been confirmed from _Calluna_, and the latter from Juncus. In view of this difficulty, these animals have only been identified to the Genus, in the subsequent ecological work, but it is hoped that a further, more critical examination of the material will enable a more detailed classification of the results to be made. Mackie (1958) working in a Lancashire clough says that both species were found to frequent high ground regularly, and in this agrees with Bristowe (1939).

Oreonetides abnormis (Blackwall)

While apparently restricted to the Calluna/Eriophorum mixed moor, it was not uncommon there, and Bristowe (1939) classes it as 'common on mountains'. Millidge and Locket (1955) also record it from Moor Divock in Westmorland.

Oreonetides vaginatus (Thorell)

The one female which was taken, came from the slopes of Little Dun Fell, Stated by Locket and Millidge (1953) and Bristowe (1939) to be rare and virtually restricted to high altitudes, it has also been recorded recently by Locket et al (1958) from High Street, and in a scree at the head of Martindale in the County.

*Bathyphantes gracilis (Blackwall)

One of the dominant species in the Calluna/Eriophorum site and quite widely spread over the Reserve.

Tapinopa longidens (Wider)

Encountered in a variety of habitats, this animal spun a characteristic, very fine sheet web, deep in the herbage, and is described as a form frequent on mountains by Bristowe (1939).

**Stemonyphantes lineatus* (Linnaeus)

The single female was caught in a pitfall trap in the *Calluna/ Eriophorum* site.

Bolyphantes luteolus (Blackwall)

This spider was taken in number from a variety of habitats where it spun an open web high up in the herbage. Forman (1951), Bristowe (1939) and Mackie (1958) record it as a species inhabiting mountains and moorlands.

Lepthyphantes tenius (Blackwall)

Only one female was taken, in *Calluna*.

Lepthyphantes zimmermanni Bertkau

Frequently encountered in heather, the only other record was for ungrazed Limestone grassland, although Bristowe (1939) associates it generally with mountains.

**Lepthyphantes cristatus* (Menge)

Females, were occasionally taken from the *Calluna/ Eriophorum* site.

Lepthyphantes mengei Kulczynski

Obtained from a wide variety of habitats, this fairly common species was first recorded in Westmorland by Parker (1959) from Boltons Yarm, Crook, and Neathop Moss.

Lepthyphantes ericaeus (Blackwall)

This species was both common, and widely distributed.

Lepthyphantes angulatus (O.P.-Cambridge)

Although occurring frequently in the *Calluna/Eriophorum* blanket bog habitat, the only other record was for the *Festuca/Nardus* grassland. Described as 'local' by Locket and Millidge (1953), and 'virtually restricted to high altitudes' by Bristowe (1939), it was first found in Westmorland by Locket et al (1955) under stones at High Street. Miller (1951) suggests that it penetrated the South-Bohemian peat-bogs from here, in N.W. Europe.

Mengea scopigera (Grube)

The only female to be caught was taken from the *Festuca/Nardus* grassland.

(b) Geographical Distribution of the Moor House Linyphiids.

The status of the Moor House Linyphiid fauna is recorded in Table 55, compiled from Bristowe (1939) where a synopsis of the world distribution of each species together with any known associations it may have with British mountains it given. From this table no close correspondences with the faunas of any particular region can be detected.

Table 55.

Status of the Moor House Linyphiid Fauna - After Bristowe.

Species.	Greenland	Iceland	Scandinavia	Switzerland	Central Europe	Mediterranean	Species virtually restricted to high altitudes.	Common on Mountains	Typical of low altitudes, but also found on mountains.
Ceratinella brevipes			X	X	X	X			X
C. brevis		X	X	X	X	X			
Walckenaera acuminata			X	X	X				X
Wideria antica			X	X	X				
Trachynella nudipalpis		X	X	X	X			X	
Cornicularia karpinskii	X		X	X			X		
C. cuspidata		X	X	X	X			X	
Dicymbium tibiale			X		X				
Gonatium rubens		X	X		X				X
Peponocranium ludicrum			X		X				
Hypselistes jacksoni			X	X	X				
Oedothorax fuscus			X		X	X			X
Trichopterna mengei					X				
Silometopus elegans				X	X				X
Tiso vagans			X	X	X				X
Monocephalus fuscipes				X	X				
Jacksonella falconeri									X
Gongylidiellum vivum				X	X	X			
G. latebricola				X	X				
Micrargus herbigradus			X	X	X	X			X
Erigonella hiemalis			X		X				
Savignia frontata		X	X		X				X
Diplocephalus permixtus		X			X				X
Erigone dentipalpis			X	X	X	X			X
E. atra		X	X	X	X	X			
Eboria fausta					X				X
Drepanotylus uncatus			X		X				
Phaulothrix hardyi		X			X			X	
Porrhomma montanum		X						X	
Agyneta decora			X						
Meioneta rurestris		X	X	X	X	X			
M. saxatilis					X				
M. beata									
Maro minutus					X				
Centromerus prudens					X	X		X	
C. arcanus			X	X	X			X	
Centromerita bicolor			X	X	X	X		X	
C. concinna					X			X	
Oreonetides abnormis		X	X	X	X	X		X	
O. vaginatus	X		X	X	X		X		
Bathyphantes gracilis			X	X	X	X			X
Tapinopa longidens			X	X	X	X		X	
Stemonyphantes lineatus			X	X	X	X			X
Bolyphantes luteolus			X	X	X	X		X	
Lepthyphantes tenuis			X	X	X	X			X
L. zimmermanni		X	X	X	X	X		X	
L. cristatus		X	X	X	X	X			
L. mengei		X	X	X	X				
L. ericaeus					X				X
L. angulatus			X		X		X		
Mengea scopigera		X	X		X				

Thus, 29% of the species occur in Iceland; national figure 17.5%

$\chi^2 = 1.89 \quad p > .1$

69% " " Scandinavia " " 59%

$\chi^2 = .28 \quad p > .5$

90% " " Central Europe " " 83%

$\chi^2 = .67 \quad p > .3$

(c) The Moor House and British Linyphiid Faunas Compared.

Of the 241 species of British Linyphiids then known, Bristowe (1939) mentions 61 (25%) as associated with mountainous regions i.e. over 2000 ft. Of the 51, fully identified, species found at Moor House, however, 31 (61%) fall into Bristowe's 'mountainous' category, and a χ^2 test showed this difference to be significant at the .01 level. See Table 55. As would be expected, the parts of the Reserve investigated which lie at about 1850 ft. contained a higher than normal proportion of species associated with mountains, and although the fauna is typical of high exposed ground, it is relatively unspecialised, having but a few of the species associated with the extreme exposure of the highest British mountains, the only three important examples being Cornicularia karpinskii, Oreonetides vaginatus, and Lepthyphantes angulatus.

3. Methods Employed.

(a) Introduction.

As stated, Linyphiid spiders exist in large numbers in most types of herbage, and methods of studying these had to be devised. In the past, ecological work on this group has been largely concerned with the semi-quantitative comparison of the faunas of different areas and vegetation types, and it is the nature of these, which has largely determined the methods used. For spiders in the vegetation, sweeping, and beating have been the most commonly used techniques - Barnes (1953), Barnes and Barnes (1954, 1955), Chant (1956), Elliott (1930), Muma and Muma (1949), Shelford (1951) and Turnbull (1957), but for the animals in the litter, pitfall traps, standard collection times, handsorting and Berlese funnels have been used, particularly by Tretzel (1954, 1955 b), Barnes (1953), Barnes and Barnes (1954), Elliott (1930), Muma and Muma (1949) and Turnbull (1957). Of the workers specifically concerned with spiders however, Duffey (1955) and Gabbutt (1956) are amongst the fewwho have examined the detailed problems of extracting them from litter.

In the present study, a variety of techniques were considered and rejected; the vegetation was too short, and in the case of *Calluna* too woody for successful beating or sweeping, which, as Carpenter (1936) has pointed out give only a measure of the animals active in the vegetation stratum. Direct searching also had this latter disadvantage, especially in winter when the ground was frozen, and the whole population became immobile and therefore almost impossible to see; thus, during February 1959 when the population was about $230/M^2$, searching in the field failed to produce a single animal. As the substrate was frequently very wet peat, bound together with tough Calluna roots, any sort of sieving was impracticable, whilst handsorting was laborious in the extreme. Examination of webs was not satisfactory in this group, because at the slightest disturbance, the spiders drop by a thread from the underside of their webs, and lie hidden in the vegetation. It is also very difficult to see these webs, except under certain atmospheric conditions such as mist or dew, when they are covered with water droplets, and in any case, it is probable that only the webs of the largest, and least secretive species would be found. Pitfall trapping, being a highly selective 'activity' measurement, the only technique left was the removal of sample pieces of the habitat for subsequent extraction of the animals in the laboratory. N.B. Johnson et al (1955, 1957) have described a method of extracting Arthropods from herbage in the field by a suction system, but the spider yield from rough grassland of $76/M^2$ appears at first sight to be remarkably low, despite an estimate of efficienty of 97.4% when checked by hand sorting. (Rough grassland at Moor House gave yields in the region of $300/M^2$.)

Methods of extracting arthropods from litter in the laboratory are legion, and are summarised by Macfadyen (1953, 1955), who writes, (1955 p 316) "As things stand to-day, the only hope of obtaining valid quantitative information about the ecology of the soil fauna is to select carefully both material and extraction method so that they are complementary to one another and strictly relevant to the problem which is being studied". In this respect, the two most important features of spiders are their relatively large size, and small numbers, both of which indicates the need for a large sample size. Floatation methods are capable of dealing with large samples, but as Raw (1958) and Macfadyen (1955) have pointed out, this is unsatisfactory when there is a large amount of organic matter. Accordingly 'repellant' extraction systems, capable of taking a large sample were the only alternative. Both Macfadyen (1958) and Duffey (1955) have described suitable pieces of apparatus, which, appear to be equally efficient according to Duffey, the former being an elaboration of the traditional Berlese funnel pattern, whilst the latter was a lateral extraction system. In the present study, the Duffey lateral extraction apparatus with modifications was used, principally because of its lower cost, smaller size, and greater ease of manufacture, and also because less debris finds its way into the collecting trough, so making the final sorting and counting of animals much easier.

(b) Sample Size and Sampling Procedure.

By dividing samples up horizontally into three layers, vegetation above 5 cms; surface and litter layer down to about 3 cms. below the ground; and the bottom 10-12 cms. of raw peat, it was found that all the spiders came from the surface and litter layer region. Remembering that when disturbed, they always dropped to the ground from their webs, this is not surprising, but it does mean when sampling that so long as a constant surface area of ground is taken the depth to which the sample is cut is immaterial, and simply a matter of convenience.

The size of the samples was decided, as it must so frequently be in field ecology, not so much by statistical desirability as by practical necessities, in the hope that subsequently, the best possible use could be made of the data which they contained. Statistically, a fairly large number of small samples would have been most desirable, but the structure of the vegetation, particularly on the Calluna/Eriophorum site was such that below a certain size, it was not possible to cut accurate samples to include vegetation. The size finally chosen was 21 cms. by 30 cms. (1/16th M^2), and as 5 samples of waterlogged peat filled a sack and weighed about ½ cwt. It was only considered practicable to take 10 such samples on each occasion.

In practice, a wire quadrat was used, which was thrown at random within the sample area in all the sites except the Calluna/Eriophorum site, where it was thrown randomly only within the appropriate square of the grid. A turfing iron was then used to cut cleanly around the edge of the quadrat, which was undercut at a convenient depth, usually of about 8-10 cms. In winter however, when the ground was frozen solid, a pick had to be used! Finally, each turf was transported in a polythene bag to the laboratory, where it was extracted as soon as possible. Overnight storage, if necessary, was in a cold room at 4^oC.

It should be noted that whilst overhanging vegetation is always a difficulty when cutting samples on the basis of ground area, this error is less likely to be important when, as in this case, the animals fall to the ground at the first signs of disturbance.

(c) Extraction Apparatus.

(i) Description and Mode of Action.

Figure 28 shows a side view of the apparatus, as modified after Duffey (1955), the right wall of the heating unit being cut away in the sketch to show the metal box containing the sample. The extraction box is made from sheet tin, with metal floor and sides, a fine mesh phosphobronze gauze back, and at the other end, a trough with tap to run off animals. On a ½ inch metal ledge just inside the box, shown by a dotted line in Figure 28, and more clearly seen in Plate 14, rests the asbestos lid, on the lower end of which is another phosphobronze gauze strip, which bolts over the trough to allow a draught to pass into the apparatus. In use, the whole lid can be bolted down, all joints being sealed with felt to prevent the escape of animals. Inside the box is a wire basket, 21 cms. by 30 cms. and 12 cms. deep, in which the inverted sample is placed, as can be seen in the left hand unit on Plate 14. The trough is then filled with a fungicidal solution of 1/10,000 Phenyl mercuric acetate in water, with commercial detergent added to reduce the surface tension.

This box containing the sample, fits into the heating unit shown in Figure 28, and the right hand unit of

Lateral Extraction Apparatus   Modified after Duffey.

Side view of one unit

N.B. On the right, the sides of the heating unit have been cut away to show the contained, removable extraction box.

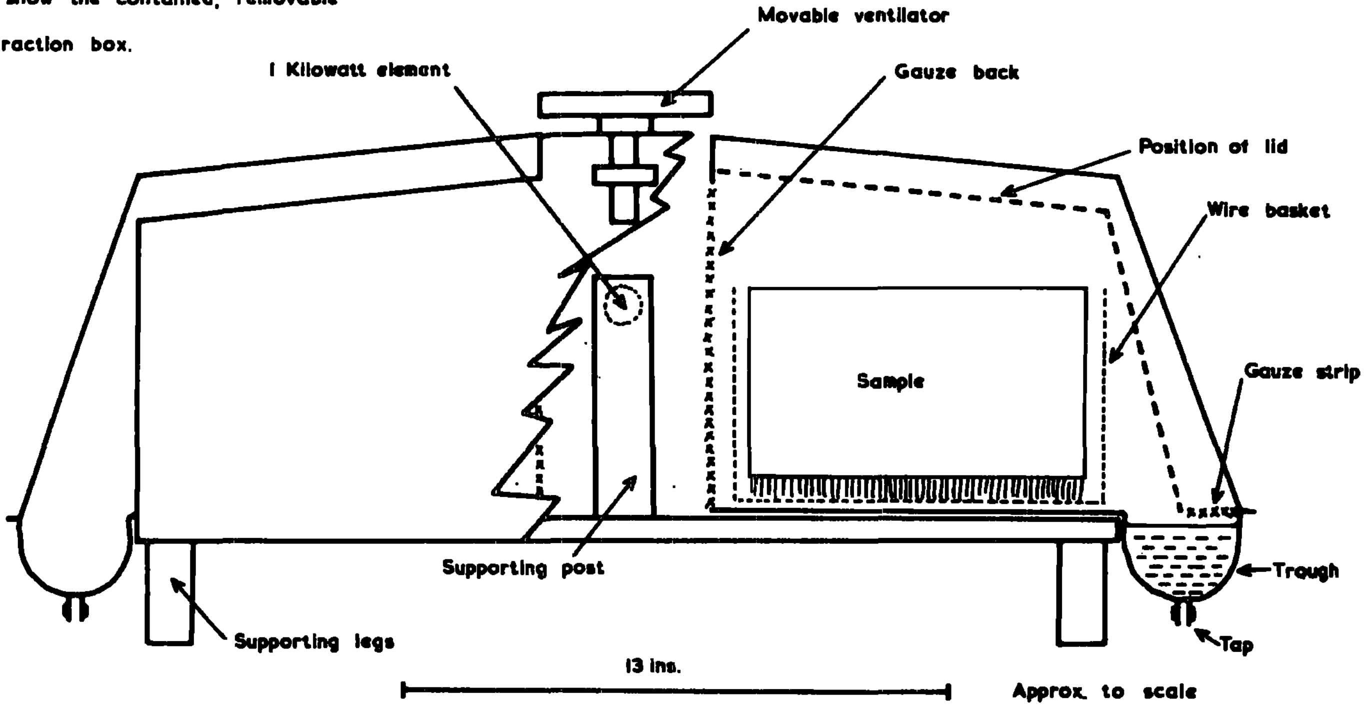


Fig. 28.

Plate 13.

Extraction Apparatus, - Complete assembly.

Plate 14.

Extraction Apparatus, dismantled to show parts.

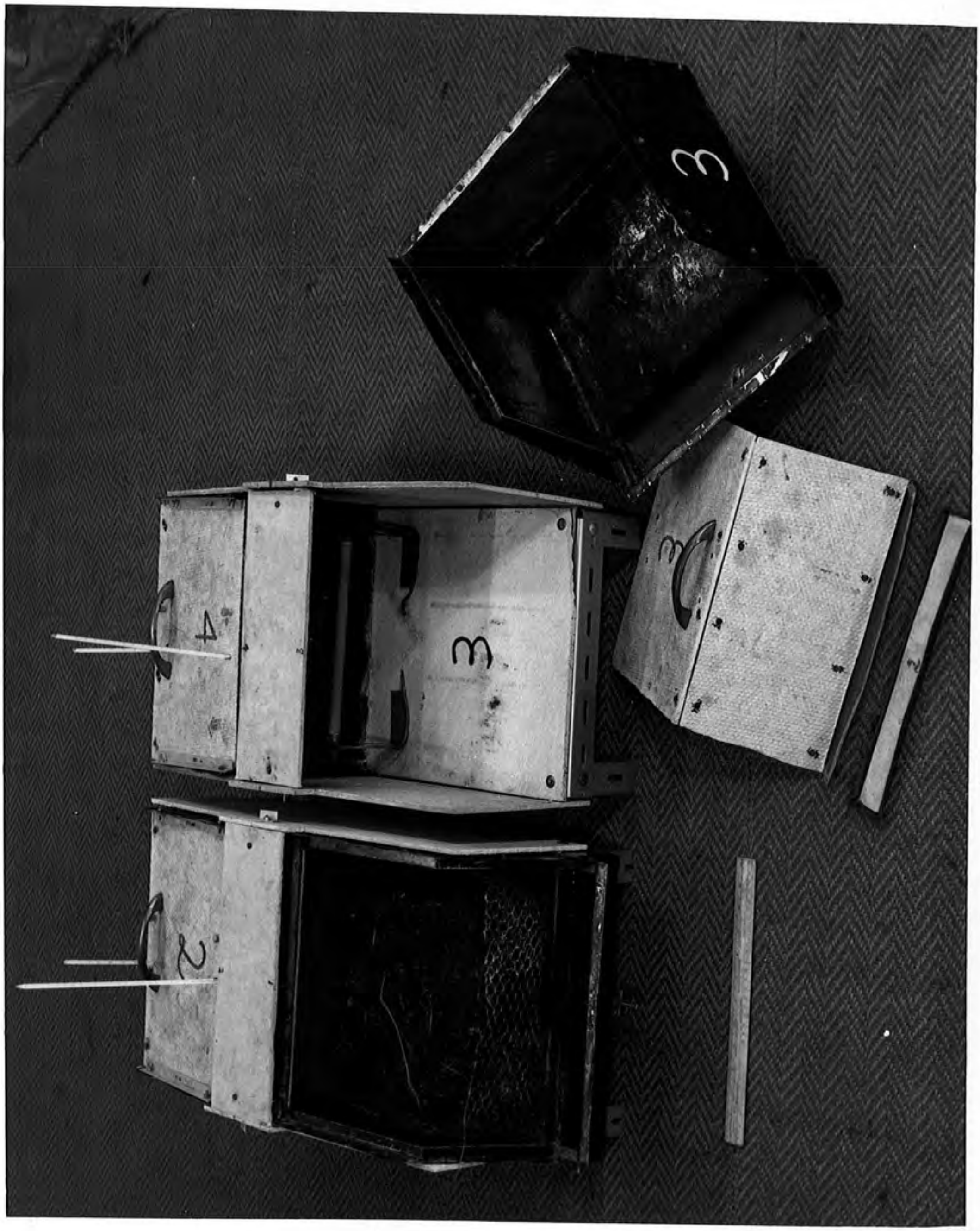

3
4
3
3
2

Plate 14, consisting of an asbestos floor and side walls, with a one kilowatt pencil type electric element in the middle suported on posts. In this way, two sample boxes, back to back, can be put into one heating unit. Above the element, and making contact with the lids of the two sample boxes is an asbestos sheet, which, as it can be raised and lowered, acts as a ventilator.

Five such heating units, with 10 sample boxes were made and mounted side by side in an extraction room, see Plate 13, where the temperature was kept as constant as possible, by means of a thermostatically controlled circulation fan. The heating elements were all controlled via relays by means of a 'simmerstat' energy regulator, so that the degree of heating could be controlled.

The mode of action is simply that the heat from the element sets up lateral temperature and humidity gradients which drive the animals into the trough of water.

(ii) Relative Efficiency of Heating Regimes.

Provided that the temperature of the sample nearest the trough was eventually raised to at least 40°C, animals were found in the trough in quite large numbers. It was therefore decided to conduct two experiments on randomised samples, in which the final temperatures were achieved in a day and a week respectively.

The first experiment was performed on relatively dry lowland pasture grassland, and the second on very wet Calluna/Eriophorum blanket bog vegetation, and the two are summarised in Table 56.

TABLE 56.

Comparison of Two Heating Regimes on Heather and Grass Samples.

Computed from 8 samples, only groups with more than 30 individuals on each occasion considered.

Group	1 Day Extrac.		1 Week Extrac.		Factor of Increase	P from Random't'tes
	Σ	$\bar{X}$	Σ	$\bar{X}$		
Lowland Pasture Grassland.						
Araneae	179	22.37	212	26.5	1.18	$>.4$
Acari	70	8.75	83	10.37	1.18	$>.3$
Large Collembola	45	5.62	58	7.25	1.29	$>.4$
Coleoptera -						
Adults	497	62.12	678	84.75	1.36	$>.1$
Larvae	31	3.87	70	8.75	2.26	$<.01$
Diptera -						
Adults	24	3.0	55	6.87	2.29	$>.1$
Myriapoda	28	3.5	53	6.62	1.89	$<.05$
Calluna/Eriophorum Blanket Bog Vegetation.						
Araneae	29	3.62	64	8.0	2.21	$>.05$
Acari	131	16.37	565	70.62	4.31	$<.001$
Large Collembola	243	30.37	421	52.62	1.73	$>.05$
Coleoptera -						
Adults	36	4.5	36	4.5	0	
Hemiptera	95	11.87	406	50.75	4.27	$<.01$
Opiliones	0	0	34	4.25	∞	$>.05$

In each case, more spiders were extracted when the process was extended over a week, than when it was completed in a day, and this was true of all the other arthropod groups from both habitats, except in the case of the adult Coleoptera from the *Calluna/Eriophorum* habitat. In only a few cases, which did not include spiders, were these differences significant.

As the final temperature was about the same in all cases, a possible explanation is the importance of desiccation, which is supported by the fact that the advantages of a week's extraction are, by and large, much more clearly shown in the *Calluna/Eriophorum* experiment, where it was noted, the samples were very wet.

The importance of the time factor in heat extraction, is re-emphasised in Table 57, which points to the same conclusion, though less critically than the last experiment, as the samples were neither randomised, nor taken at exactly the same time.

TABLE 57.

The Number of Animals Extracted, Compared with the Duration of the Process.

Total number of animals extracted from 8 samples, from the *Calluna/Eriophorum* site. * = figures corrected from 10 samples.

Date	Hours of Extractn.	Araneae	Acari	Large Collembola	Hemiptera	Coleopter adults.
7/3/60*	10	11.2	39.2	41.6	18.4	4
21/4/58	27	29	131	243	95	36
21/5/58	120	41	559	237	231	38
30/4/58	168	64	565	421	406	36

During these experiments, the troughs were emptied daily, and after studying the patterns of extraction for the different groups, a standard heating regime was devised. It was decided to take 5 days over the extraction, producing the following temperatures in the top of the sample nearest to the heat source.

At the end of Day 1	36-40°C
" " " " " 2	50-60°C
" " " " " 3	80-90°C
" " " " " 4	100°C +
" " " " " 5	150°C +

To achieve this, the ventilator was closed on Day 4, to cut down the draught, and on Day 5, asbestos shutters were placed over the gauze draught opening above the trough.

(iii) Physical Conditions Produced During Extraction.

Temperature Gradients.

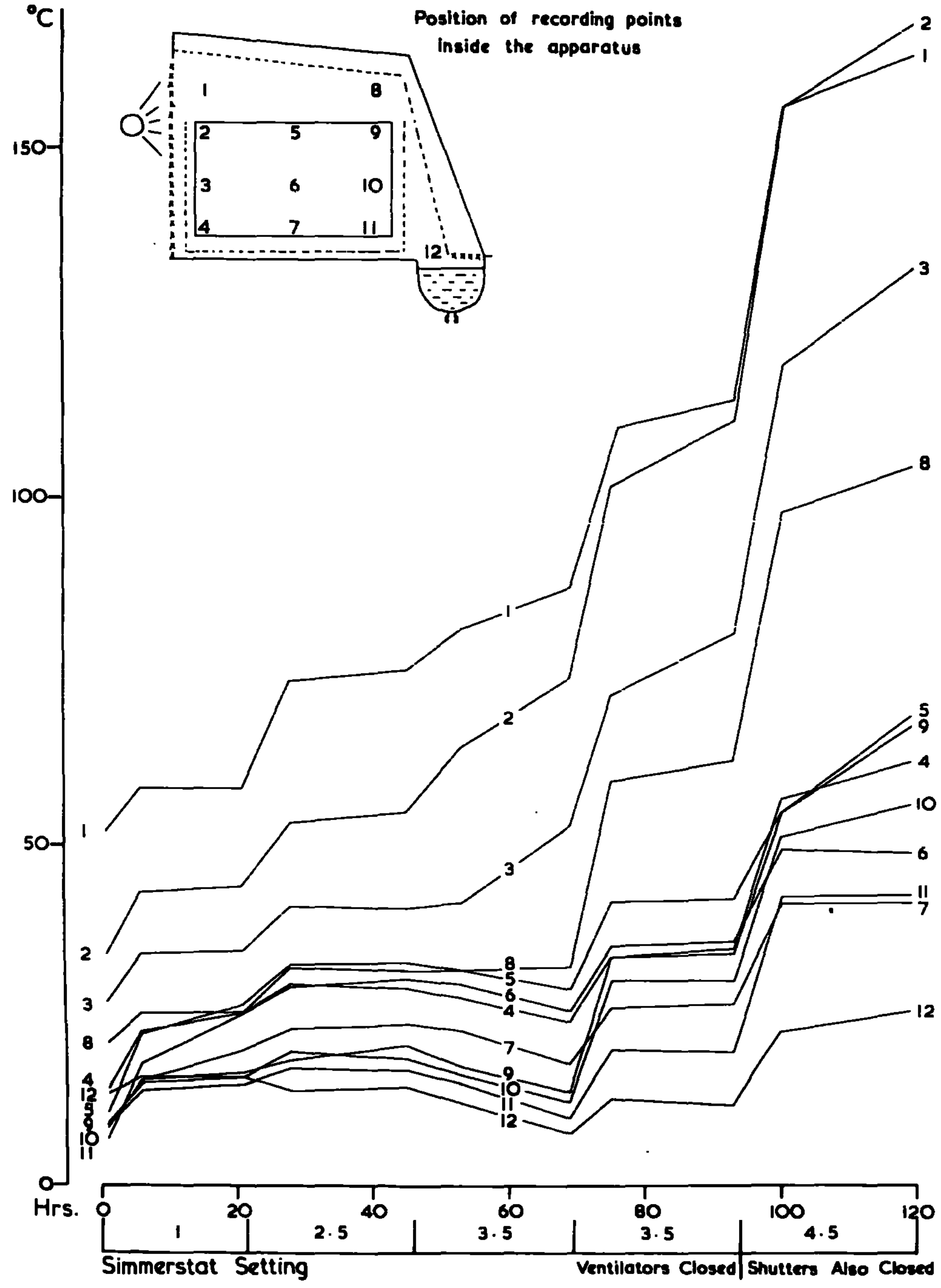
Temperature checks on various parts of the samples were carried out during every extraction, while in Figure 29 the temperature gradients within a *Calluna/ Eriophorum* sample throughout a standard extraction are presented.

For this investigation, a series of thermometers and thermistors were sited in the sample, and apparatus as shown by the numbers 1 - 12 in the inset diagram, and

Fig. 29.

Temperature Gradients within the Extraction Apparatus

Measurements made on the standard extraction regime — Heather



read at regular intervals throughout the 5 days extraction.

A large temperature gradient was soon established from the hottest to the coolest parts of the turf, which reached 120°C by the final day, and, as seen in the diagram, the increasing temperatures advanced through the inverted sample from the top left hand corner near the element, to the bottom right hand area nearest the trough. This had the effect of driving the animals from all parts of the sample box into the water trough.

Heat from the element caused a draught to enter the apparatus through the gauze strip over the trough, and pass over the sample, through the gauze back to the sample box, and out through the ventilator above the element. The importance of draught control has been recognised recently by Macfadyen (1958) and Murphy (1955 b 1958 a and b) and is further emphasised in Figure 29, where it can be seen that the closure of the ventilator produced a considerable temperature increase, without there being any increase in the energy input. This, and the subsequent placing of the shutter in position, also altered the pattern of the temperature gradients, by producing an enveloping layer of hot air, which in turn heated the top right hand section of the sample. Finally, the dependence of the temperature gradients upon room temperature is demonstrated by the fall in temperature during days 2 and 3 of positions 4, 5, 6, 7, 9, 10, 11, 12, which simply mirror temperature changes in the extraction room. See Macfadyen (1955).

Humidity Gradients.

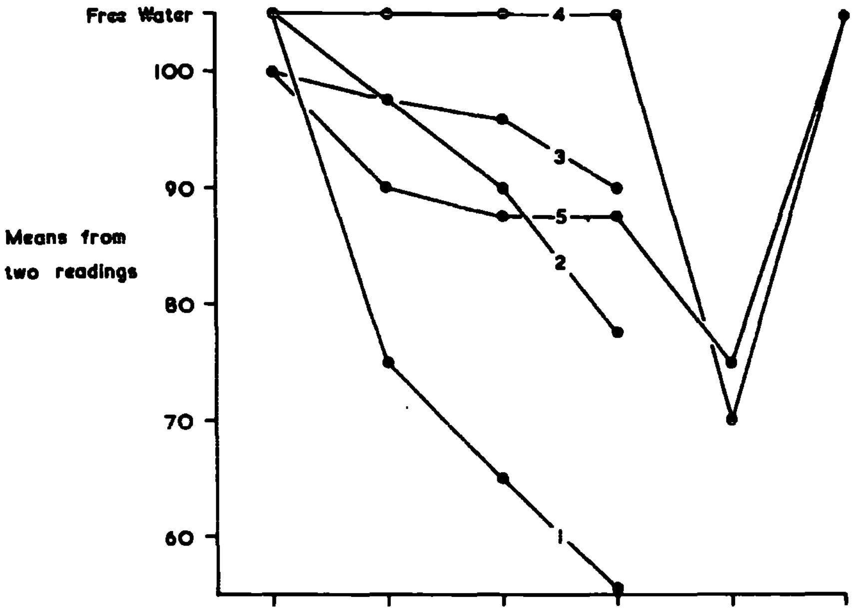
Humidity gradients in the apparatus during an extraction were also investigated, by the use of cobalt chloride, and cobalt thiocyanate papers, as described by Solomon (1945, 1951, 1957), and the first graph in Figure 30 shows the estimated gradients, from the mean readings of two samples. Readings for positions 1, 2 and 3 stopped when the temperature became too high for the method to work properly.

The R.H. of the air just above position 1 dropped rapidly, presumably caused by the rapid drying out of the sample near the heat source, whilst the accompanying early drop in R.H. at position 5, must have been a result of the incoming draught of dry air from the outside, a phenomenon noted by Macfadyen (1955). Positions 2 and 3 dried out in a like manner to position 1, though less rapidly, owing to their distance from the heating element, and in position 2, to the fact that air trapped beneath a wet sample would be less affected by draughts.

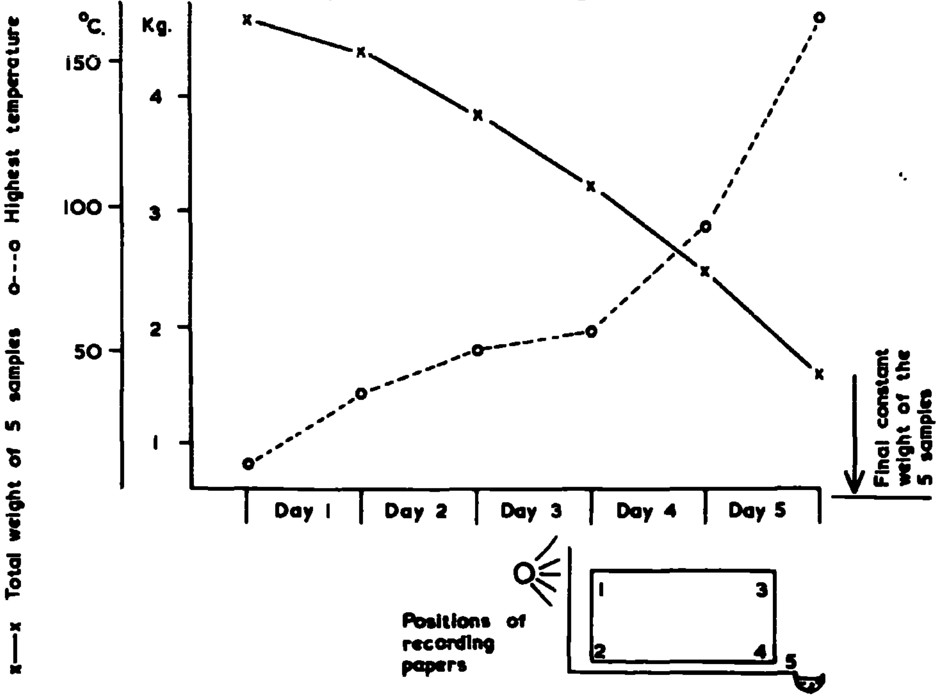
Fig. 30.

Desiccation Within the Extraction Apparatus

Humidity Gradients



Water Loss from Sample with Heating



There was little or no drying out at position 4 until the fourth day, and here the animals must have been safe from desiccation. By the end of the fourth day however, the effects of the rapidly drying sample began to be felt even here, until the shutters were put into position. These cut out the draught entirely, and condensation, particularly on the cold asbestos lid, at once produced free water in positions 4 and 5.

All this indicates humidity gradients across the sample, closely allied to the temperature gradients, with no obvious humidity barriers to the animals as they crawl out, with the possible exception of the rather dry air over the trough at position 5. The closing of the shutters is important, as it produces a big rise in the R. H. of the apparatus at the end of the extraction, and as will be seen later, this may be responsible for trapping some animals in the condensation water.

As in the Controlled - Draught Funnel Extractor of Macfadyen (1958), the moisture came from the sample itself, as can be seen in the second graph on Figure 30, where the loss in weight of the sample, with increasing temperature throughout the extraction is shown. In 5 days of extraction, the *Calluna/Eriophorum* samples lost 3,200 gms, or 66.6% of their weight, although when dried to constant weight, the samples had a mean weight of 510 gms, indicating that about 90% of the original samples consisted of available water.

(iv) Reaction of the Animal Groups.

The reactions of the more important animal groups to the extraction apparatus were investigated in an attempt to clarify some of the problems which attend the interpretation of this type of extraction data. Accordingly, the collecting trough of the apparatus was emptied and washed out on each of the 5 extraction days, and the animals were counted and identified separately. This was done on all 13 of the routine monthly *Calluna/Eriophorum* samples, taken from the habitat described in Section VII. 4 a.

The total number of spiders emerging from the 10 samples on each of the 5 extraction days, for all 13 monthly replicates, is set out in Appendix I. Here, a homogeneity χ^2 test has been performed on the data, to see if the totals for each day throughout the 13 months give an 'emergence pattern' which is itself reasonably consistent with the individual patterns observed on each of the previous 13 sampling occasions.

With 48 degrees of freedom, a χ^2 of 168.135, and a probability <.001, this is obviously not the case; that is to say, that within limits, the emergence patterns of spiders from sampling occasion to sampling occasion were not consistent. The total χ^2 for each sampling date gives some measure of the extent to which the 'emergence pattern' in that month differs from the total or average 'emergence pattern' computed from the day totals. An examination of the total χ^2 for each extraction day, shows that this variability is indeed brought about by the action of the extraction device, as the variability increases with the length of time the sample is in the apparatus. Thus, a relatively constant proportion of the total number of spiders emerge on Day 1, a highly variable proportion on Day 5.

It was decided to test the effect of season on this spider 'emergence pattern', and this has been done in Table 58. Here, the number of animals emerging each day has been expressed as a percentage of the total number finally found in the trough, and for each season, the mean daily percentage, together with its standard error has been calculated. This was necessary, as it is the proportion of animals emerging each day which is of interest, and although statistically it gives a crude measure, no better technique could be found. Inaccuracies are introduced by the varying reliability of percentages when estimated from different totals, although in this instance, they differ by a maximum factor of less than 4.

TABLE 58.

A Comparison Between the Spider 'Emergence Patterns' during 'Summer' and 'Winter'

	(M.J.J.A.S.O.)			(N.D.J.F.M.A.)		
	'Summer'			'Winter'		
Day	Mean %	S.E.	2 x S.E. C.L.	Mean %	S.E.	2 x S.E. C.L.
1.	26.57	1.8	22.97 30.17	17.5	3.22	11.06 23.94
2.	13.0	2.25	8.5 17.5	9.0	2.29	4.42 13.58
3.	10.14	2.51	5.12 15.16	6.33	.84	4.65 8.01
4.	21.29	3.74	13.81 28.77	15.0	3.01	8.98 21.02
5.	28.57	4.84	18.89 38.25	51.83	2.44	46.95 56.71

May to October inclusive were classed as 'Summer' November to April as 'Winter', and it does appear that the 'emergence patterns' of these two seasons differ. As shown in Figure 31, which will be discussed later, spiders show a bimodal 'emergence pattern' and whereas in 'summer', the first and last peaks are almost the same, in 'winter', the first peak is very small, and the last peak very large. In the case of the last peak, these differences are significant. Three explanations of this can be suggested:-

1. In 'Winter', the lower temperatures in the extraction room make the initial heating of the sample less successful.

2. The spiders when brought in from the field in Winter when the ground is often frozen hard, are in a much less active condition, and do not respond to the apparatus for several days.

3. A different type of animal, with a different physiology is present in the Winter.

Because of the difficulties encountered in controlling the room temperature of the extraction house, which being a converted glass-house was very susceptible to climatic changes, it has not been possible to distinguish between 1 and 2, although on general field observations, considerable change in the activity of the animals is known.

As the life cycle of these animals takes at least a year, the third explanation could only refer to differences in the maturity of the spiders, and in Table 59, the 'emergence patterns' of mature and immature animals have been compared.

TABLE 59.

A Comparison Between the 'Emergence Patterns' of Mature and Immature Spiders.

	Mature			Immature		
Day	Mean %	S.E.	2 x S.E. C.L.	Mean %	S.E.	2 x S.E. C.L.
1.	28.3	4.44	19.42 37.18	20.38	1.84	16.7 24.06
2.	10.0	2.04	5.92 14.08	11.15	2.05	7.05 15.25
3.	9.85	2.64	7.21 12.49	8.38	1.48	5.24 11.34
4.	20.61	3.77	13.07 28.15	18.38	2.76	12.86 23.9
5.	31.15	4.55	22.05 40.25	41.23	5.05	31.13 51.33

A slight but not significant difference is revealed, immature spiders tending to exhibit a smaller initial peak, and a larger final peak than mature animals. As Figure 37 shows, however, the life history trends cut across the 'Summer/Winter' categories of Table 58, and are therefore unlikely to be the cause of the phenomena noted there.

Even with all these variations in the 'emergence pattern' of spiders, it may yet be the case that the generalised 'emergence pattern' for this group is distinctive, when compared with the patterns for other arthropod groups. This problem was investigated, and in

Figure 31, the mean percentages of animals emerging on each extraction day, together with twice their standard errors are plotted, for the 5 most abundant groups.

Three distinct 'emergence patterns' appear:-

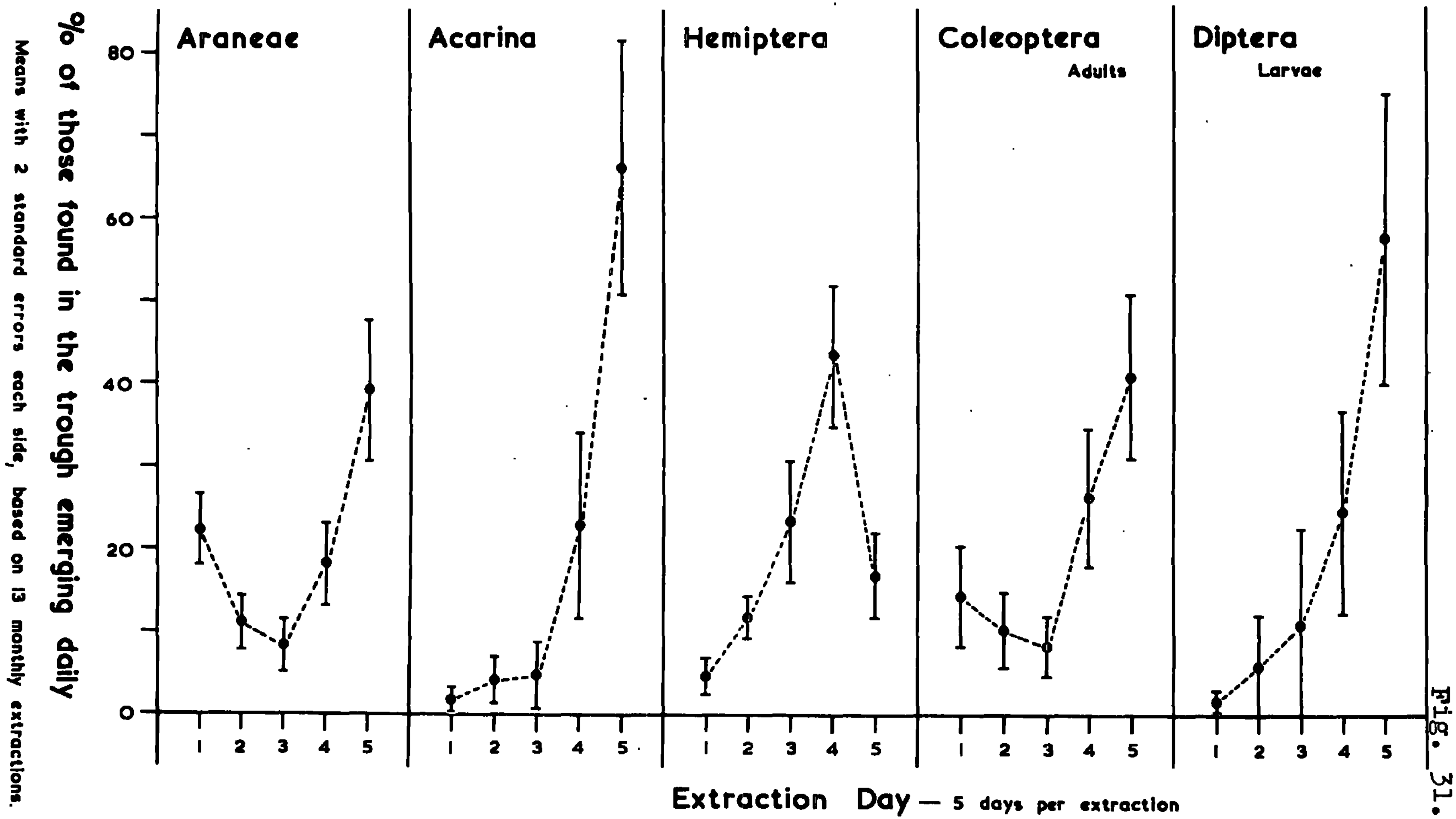
1. A biomodal emergence, as seen in the Araneae and adult Coleoptera, with peaks on the first and last day of extraction.

2. An 'emergence pattern' which builds up steadily to a single peak on the last day, as in the Acarina and larval Diptera.

3. A simple peak of emergence occurring before the end of the extraction, demonstrated here by the Hemiptera with a peak on Day 4.

Other workers mention similar observations, thus Macfadyen (1955 and private communication) in a small pilot experiment found a bimodal spider 'emergence pattern' with both wet and dry extraction regimes although the adult Coleoptera showed an early emergence peak only. Haarløv (1947) and Murphy (1958 b) both mention the late egress of Acari, which they associate with the drying out of the sample, although Macfadyen cites <u>Belba sp</u>. as emerging early. N.B. In the present work, no such specific differences would be detected.

Extraction Apparatus — Emergence Patterns for 5 Animal Groups



Means with 2 standard errors each side, based on 13 monthly extractions.

Fig. 31.

In Haarløv's pioneer study, the Collembola and Acari, showed different 'emergence patterns', and he interpreted these as being primarily responses to temperature and desiccation respectively. Macfadyen largely agreed with this, suggesting that the dry atmosphere of the laboratory was repellant to the late exodus forms, which postponed their emergence, until the sample was drier than the air, or until the rising temperature drove them out regardless, and he noted that these forms emerged earlier if the draught was damper.

In the present work, no exclusively early exodus groups have been found and they seem to have been replaced by the bimodal patterns of the Araneae and Coleoptera. This could be caused by the differential emergence of species, a question which has been examined for the spiders only in Table 60. Unfortunately, the numbers involved are too small for firm conclusions to be reached, and whilst _Centromerus arcanus_ and _Bathyphantes gracilis_ do appear to be respectively early and late exodus species, it can equally well besaid that _Centromerita sp._ and _Lepthyphantes zimmermanni_ are bimodal.

Although early peaks have usually been attributed to an egress of animals in response to quickly established heat gradients, it is difficult to see how this

TABLE 60.

The Species 'Emergence Patterns' of Spiders.

Computed from the results of all 13 sampling occasions.

Species	Extraction Day.					
	1.	2.	3.	4.	5.	Σ
Centromerus arcanus	14	6	3	8	4	35
Centromerita sp.	8	2	2	1	7	20
Micrargus herbigradus	3	1	3	1	1	9
Lepthyphantes zimmermanni	8	5	1	2	9	25
Robertus lividus (Theridiidae)	3	0	1	5	8	17
Bathyphantes gracilis	1	3	2	11	17	34
Lepthyphantes angulatus	1	3	0	1	6	11

can account for the initial peaks in the present work, as the temperatures produced on Day 1 are very low, and effect only a small part of the sample. This is evidenced, by the large number of hammock webs frequently found in the apparatus, where conditions have been such that the spiders have spun webs and presumably fed well off animals driven from less favourable parts of the sample, and by Macfadyen (1955) where first day peaks were observed in both adult beetles and spiders, although it appears that the heating was not switched on until the end of the first day. An investigation of this last point in the present apparatus would be well work under-taking in future work.

Both the groups with bimodal 'emergence patterns' consist of active animals capable of extensive wanderings, and an alternative explanation is that these animals tend to get disturbed when the sample is inverted and put into the apparatus, thus producing a large initial emergence due to their excited random movements, but that those which do not happen to fall into the trough then settle down, until they are driven out by the heat and humidity gradients. This would also account for the smaller initial peak, in Winter, when the animals are more torpid, and possibly in the immature forms, which are small, and less free ranging.

For the rest, it is difficult to disentangle the roles of temperature and humidity gradients, because here, as in most cases, increasing temperatures and decreasing relative humidities occur together. Thus, the decrease in Hemiptera on Day 5 could be due to lethal temperatures, or lethal humidities (too low in the sample, or too high in the surrounding apparatus owing to condensation). It is interesting to observe that of the groups showing the biggest 'last minute' exodus, the acari, which was the only one of these to be examined (Table 56) showed the greatest increment when extraction was extended to a week, and desiccation was allowed to play its full part. It is interesting that Kuhnelt (1955) recommends an initial period of gentle heating for this group. The two bimodal groups, the Araneae and adult Coleoptera, were least affected by the extended extraction time.

In the light of this, it is a little surprising that Macfadyen (1958) has classed Coleoptera adults as requiring a 'Dry' extraction regime (rapid heating, and more draught for rapid drying), spiders as requiring a 'Wet' regime (slow extraction with little draught, and high humidities), and the Acarina (Belba) as being indifferent.

The whole question of the reaction of Arthropods to heating regimes in a standard extraction apparatus, is one which requires a good deal of further research, directed specifically at this problem.

(v) Estimates of Efficiency.

Several attempts were made to estimate the efficiency with which the apparatus extracted spiders, usually by comparing the results with those obtained by other methods.

With Hand Sorting

As has already been metioned, when compared with hand sorting in the field, especially under difficult weather conditions, the method appears highly efficient, but in the laboratory, the difference is not so great. Five Calluna/Eriophorum samples, were pulled apart and carefully hand sorted in the laboratory (an extremely laborious process), whilst 10 samples taken on the same occasion were extracted by the usual method. Table 61, shows no significant difference between the methods, a random 't' test giving a probability >.6.

TABLE 61.

Comparison Between Extracting and Hand Sorting Heather Samples.

	Hand Sorting.	Extraction.
1.	15	9
2.	1	14
3.	32	11
4.	11	5
5.	2	13
6.		24
7.		20
8.		18
9.		8
10.		22
Σ	61	144
Mean	12.2	14.4

This suggests that the extraction technique was at least comparable in efficiency with careful hand sorting.

Subsequent extraction of the 4 hand sorted samples produced 3 spiders, whilst the hand sorting of 3 of the extracted samples gave only one spider (still alive).

With a Floatation Technique.

A single sample was extracted by a floatation technique, approximately similar to that used by Milne et al (1958), where the sample is heated from below, and the hot water level gradually raised, animals being picked off as they emerge. This proved much less efficient that the extraction apparatus, as animals were easily lost in thefloating debris, whilst the smallest were probably never seen.

By Introduction of Animals into a Sterilized Medium

Attempts were made to introduce into, and subsequently extract spiders from, heat sterilized samples. Table 62 contains the results of 3 such experiments.

TABLE 62.

Introduction of Spiders into Sterilized Media, with Subsequent Extraction.

	No. put in.	No. extracted.
1.	10	9
2.	30	5
3.	13	3

These results are so variable, and so different from all the other indications, that they cannot be considered to have any significant bearing on the true situation. Indeed it would appear, as Macfadyen (1953) has pointed out that results from this type of experiment are always highly suspect.

Under present circumstances, the determination of the absolute numbers of any small arthropods in soil and litter samples is impracticable, and hence it must follow that the absolute efficiency of any piece of extraction apparatus cannot be determined. This has been illustrated by the way that the maximum estimates of soil animals in a given area have risen steadily over the last 40 years - see Murphy (1955 a) and for Spiders, Gabbutt (1956). For the present apparatus then, it can only be said that the alternative methods indicated a fairly high degree of efficiency, in so far as they proved less efficient, and the number of animals extracted compared very favourably with results obtained for this group by other workers, a matter which will be referred to later.

(vi). Examination of the Systematic Nature of a Known Error.

When using heat and desiccation for extraction, several authors, Haarløv (1947, 1955), and Macfadyen (1953) have noted that water condensing on the funnel sides trapped some "weaker" animals, and was an important source of error, whilst Murphy (1958 b) realising this, and attempting to counteract it, still found up to

20% of the animals trapped in this way. After the present apparatus had been in use for a short time, a similar serious source of error was discovered. When the apparatus was dismantled, large numbers of animals were found dead on the floor of the extraction box which was often wet, a situation analogous with the Tulgren funnel example, and instead of modifying the apparatus, it was decided to examine this error separately, to see if its behaviour might clarify some general, theoretical points about errors in extraction systems. It is interesting that this source of error was not observed by Duffey (1955), but, as will be shown later, it is particularly serious with the wettest peaty samples. In practice, the floor and walls of the extraction box were carefully washed down after each extraction, all washings being counted and classified separately.

The magnitude and consistency of this error was examined in relation to a wide variety of animals and conditions, and the results are summarised below.

Error and Animal Groups.

The proportion of animals trapped on the floor from Calluna/Eriophorum samples varied considerably from group to group, and it was thought desirable to begin by examining the spider error in the context of the error, as it affected other animals. In Figure 32, Section 2, the mean percentages with two standard errors, of animals belonging to the 5 most important groups are graphed, figures having been obtained from 15, 10-sample replicates. The results indicate that the efficiency of the extraction apparatus varies with the group of animals extracted, a point which has been realised by several workers, Kuhnelt (1955), Satchell and Nelson (1958), Macfadyen (1955) and Tragardh and Forsslund (1932). Within each group however, the proportion of animals involved in the error was heterogeneous. For each group, the relationship between the number of animals in the trough, and the number trapped on the floor was tested for consistency by a heterogeneity χ^2, the results being listed in Table 63.

TABLE 63.

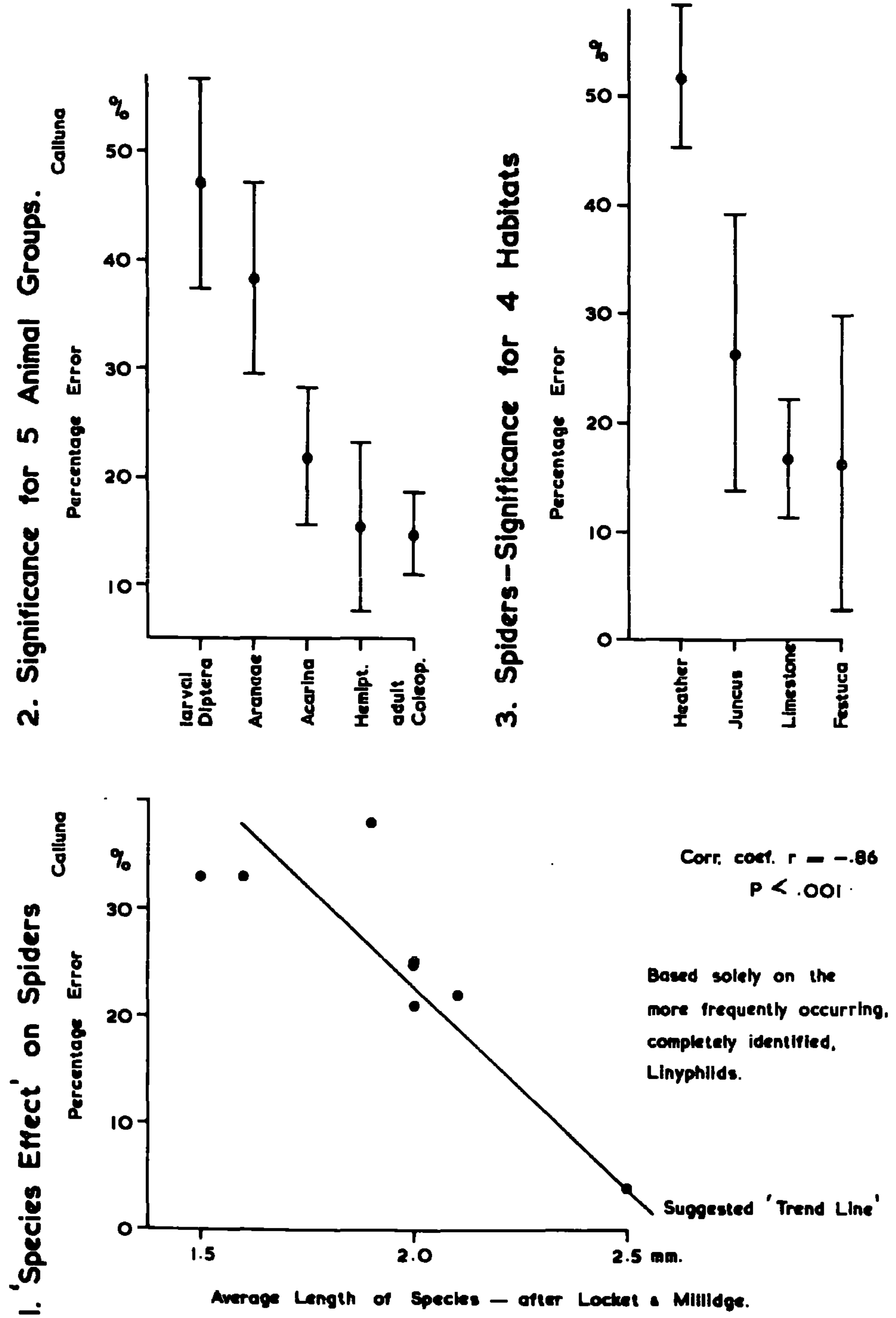
Homogeneity of Error in 5 Animal Groups.

Group	χ^2 from 2 x J Contingency Table	df	P
Araneae	177	14	<.001
Acari	919	12	<.001
Hemiptera	670	12	<.001
Coleoptera - adults	26	12	<.01
Diptera - larvae*	134	9	<.001

* Totals below 30 were not considered.

Fig. 32.

Extraction Apparatus — Behaviour of a Known Error



The wild inconsistency of the error is important, because it means that although sampling technique, conditions, and routine, were kept constant within the normally acceptable limits, throughout the 13 months of the investigation, this error at least, did not remain constant. Accordingly, other factors which could possibly affect this error in the spiders were examined.

Error and Season in the Spiders.

The importance and consistency of the error were estimated separately for the 'Summer' and 'Winter' categories previously used (See Section VII. 3c iv), as set out in Table 64.

TABLE 64.

Spider Error and Season.

	Mean % Error	S.E.	2 x S.E. C.L.
'Winter'	48.67	3.09	42.49 54.85
'Summer'	29.29	6.08	17.13 41.45

't' test on % errors gave t = 2.67 with 11 df p <.05

	χ^2 from 2 x J Contingency Table	df	P.
'Winter'	12.99	6	<.05
'Summer'	78.57	6	<.001

From this it appears that the error was significantly larger in 'Winter' than in 'Summer' - possibly due to the increased wetness of the samples, although the winter error seemed to be a more consistent one.

Error and Maturity in the Spiders.

The relative importance of the error in mature and immature animals is shown in Table 65.

TABLE 65.

Spider Error and Maturity.

	Mean % error	S.E.	2 x S.E. C.L.
Mature	23.36	3.64	16.08 30.64
Immature	41.5	4.96	31.58 51.42

't' test on % errors gave t = 5.48 with 12 df $p < .001$

	χ^2 from 2 x J Contingency Table	df	P.
Mature	19.57	12	$>.05$
Immature	138.69	12	$<.001$

From this, it can be concluded that immature spiders are much more likely to be trapped in the condensation water than mature spiders, and that whilst this source of error is reasonably consistent in its effect on the mature animals (homogeneous), it is highly inconsistent in the immature forms.

A possible reason for this relatively great effect on the immature animals, is that being small they are more fragile, and less able to escape from the condensation droplets as they begin to form. If this were so, then a differential 'species effect' on mature spiders would be expected, related to their size, as indeed Haarløv (1958) suggested when he wrote "the relatively bigger micro-arthropods are extracted in almost natural numbers, while the smaller ones may suffer even severe losses".

Error and the Size of Spider Species.

In Figure 32, Section 1 the percentages of 8 species of the more frequently occurring fully identified Linyphiids trapped on the floor, are plotted against the average length of that species as given by Locket and Millidge (1953), and a highly significant negative correlation is shown. This tends to confirm the previous suggestion, small species being trapped more easily than larger ones.

Error and Habitat in the Spiders.

In the foregoing analyses, a connection between sample wetness and error has been referred to, and in Figure 32, Section 3, the magnitude of the error in 4 different habitats has been computed. This differs markedly from one habitat to another, and when compared with Table 66 where the water content of samples from each site has been estimated, it will be seen that they correspond.

TABLE 66

Water Content Analysis of the 4 Sampling Areas.

Habitat	Calluna		Juncus		Limestone		Festuca	
Sample	1	2	1	2	1	2	1	2
% Water Content	87.2	93.6	84.0	83.8	47.5	55.4	54.0	36.3
Mean	90.4		83.9		51.45		45.15	

Soil cores dried at 100°C for 2 days.

Thus, the *Calluna/Eriophorum* site involved the greatest error, and was the wettest, whilst the *Festuca/Nardus* site had the least error and was the driest, and this implies that the efficiency of this type of extraction apparatus varies with the habitat from which the animals are extracted, a point previously made by Macfadyen (1955).

Finally, lest it be thought that most of the causes of error heterogeneity had been accounted for, the consistency of the error within the 10 individual samples taken from a single habitat on a single occasion was examined.

Error and Individual Samples Taken at the Same Time and Place.

For this investigation, three sampling occasions in each of the 4 habitats were selected for study, the error for each of the 10 samples being tested for consistency.

The results are set out in Table 67.

TABLE 67.
Homogeneity of Error Amongst Individual Samples Taken at the same Time and Place.

Habitat	Date	χ^2 from 2 x J Contingency Table	P (with 9 df)
Calluna/Eriophorum	22/10/58	18.97	<.05
	21/1/59	8.704	>.3
	29/4/59	18.24	<.05
Juncus squarrosus	3/11/58	14.87	>.05
	4/2/59	23.0	<.01
	13/5/59	30.93	<.001
Festuca/Nardus	28/10/58	57.1	<.001
	28/1/59	31.9	<.001
	6/5/59	8.89	>.3
Limestone Grassland	13/10/58	9.79	>.3
	13/2/59	12.0	>.2
	19/5/59	5.31	>.8

The fact that great inconsistency in the percentage error still remains when individual samples have been cut at the same time, and from the same place, shows that there must be many influencing factors, perhaps the degree of compaction, details of the vegatation structure, and previous handling, at which we can only guess.

(d) Counting Procedure.

The extracted material was run off into light - coloured enamel pans, and the animals counted directly by inspection with the naked eye. Attention was primarily focussed on the spiders, all specimens being removed and pickled in 70% alcohol for subsequent identification. Other animals were also counted, and broadly classified into groups, although only the "large" species of Collembola were noted, a rather arbitrary category, on which very little reliance can be placed.

Several attempts were made to check the efficiency of the counting procedure so far as spiders were concerned, by having the material re-examined by an independent observer, and from 10 samples, never more than 5 spiders were discovered. As would be expected, these were always the smallest, immature animals, often 1st instar Linyphiids, and so as a source of error, this affected only the estimates of immature animals; apparently to a negligible extent.

(e) Discussion.

In so far as it is possible to generalise from a particular extraction apparatus to other types of heat extraction techniques, and from one particular error, the behaviour of which is known, to the whole host of errors, about which nothing is known, the picture is extremely depressing.

That many different animal groups require different extraction techniques, needs no stressing, but it is also obvious from the data on 'emergence patterns' that a given apparatus designed to cover a small range of organisms, such as the larger litter-living Arthropods, has to be used with different heating and drying regimes for most of the smaller groupings if even a reasonable proportion of these animals are to be extracted.

Many an ecologist however, would be content to study one group of animals only, and adjust the apparatus to get the maximum number of these animals out of the samples, as has been attempted in this case. He may even be prepared to renounce his interest in absolute numbers, and accept a simple comparative basis for his work, and yet, the present results give little ground for confidence.

The efficiency of the apparatus seems to vary with the age of the animals, their species, and the time of year when the samples were taken. The fact that efficiency also varies with the sample habitat makes the comparison of vegetation types and areas a hazardous procedure, and worst of all, even when all these have apparently been eliminated by taking replicate samples at the same time and place, for no apparent reason, marked variations in efficiency from sample to sample are still found.

It has always been customary to assume, or at least argue as if it were assumed, that standardisation of sampling and extraction technique led to a standardisation of errors. Attempts to do this have been made in the present study, with no success, and two points should be realised

1. These methods depend upon the responses and activity of the animals, themselves highly variable and uncontrollable factors.

2. The number of factors which the investigator is able to standardise (temperature regime, sample cutting, transportation etc.) in the usual extraction systems, pales in comparison with the variable factors over which he has no control (water content of sample, compaction, detailed structure of its vegetation, recent occurrences, such as trampling, grazing etc.).

Having said all this, it must be recognised that the extraction of a group such as the spiders from a habitat such as peat bog vegetation presents singularly difficult extraction problems, and there is no reason to suppose that all, or any of these strictures necessarily apply to simpler situations, like the heat extraction of wireworm larvae from mineral soil turfs, as described by Milne et al (1958).

At the present time, heat extraction techniques for soil and litter Arthropods are widely used because no alternative better techniques are available. The floatation methods of Salt et al (1948), and Raw (1958) are probably no more efficient, judging by the numbers of spiders extracted, even though they do not rely on the activity of the animals, although it must be admitted that the apparatus was not deisgned with spiders in mind. Extraction apparatuses are not an enigma, which give a simple insight into the affairs of an animal community, they are more often a highly variable, sometimes highly biased index of the actual situations and trends. The only real measure of their success, is that the results should fit commonsense criteria of the kind which Shelford (1951) has devised for sweep netting and give a reasonably comprehensive biological picture. Thus in a species with overwintering adults, theye should be fewer in number by the Spring, than they were in the Autumn, and the population should fall from one breeding season to the next. Macfadyen (1955) has written "We might as well face up to the facts that the methods are empirical..." "What matters is whether it works..."

4. The Vegetation Types Studied.

Six broadly different vegetation types were studied in varying degrees of detail and a description of these areas follows:

(a) Calluna/Eriophorum Blanket Bog.

An area of actively growing Blanket Bog near Troutbeck Bridge (Site 11 in Figure 1) was selected for study, and to the human eye, its plant cover appeared uniform. Three Braun Blanquet Analyses of the vegetation were made, and the results and explanatory notes can be found in Appendix II 2 a, b and c, whilst a photograph of the vegetation appears in Plate 15. It is apparent from these analyses, that *Calluna vulgaris* and *Eriophorum vaginatum* were co-dominant, overlying a general carpet of *Sphagnum cuspidatum* ag., although the distribution of these co-dominants was patchy. For a description of the uniformity of the plant cover within the grid sampling system used, see Section VII 8 a and b. The mean height of the vegetation cover from 20 measurements was 16.4 cms. ± 1.6 cms. S.E., and as the site appeared to be on deep peat the ground was very wet at all times throughout the sampling period. See Table 66.

(b) Juncus squarrosus Moor Edge.

A 'Moor Edge' site was selected near the Tees Bridge (Figure 1, sampling site 12), where the vegetation again had a peat base, which, whilst always moist, was not so wet as that found on the *Calluna/Eriophorum* site. See Table 66. A Braun Blanquet Analysis appears in Appendix II 3, from which it can be seen that *Juncus squarrosus* was dominant, intermixed with *Festuca ovina*,

Plate 15.

Calluna/Eriophorum Vegetation.

Plate 16.

Juncus squarrosus Vegetation.

and Galium hercynicum, see Plate 16. The mean vegetation height was 14.2 cms. ± 1.2 for 20 measurements.

(c) Festuca/Nardus Grassland.

This was a very dry site, on a more mineral clay soil - see Table 66, situated on a bank sloping into a drainage gutter near the Tees at Tees Bridge - see Figure 1 Site 13. There was little raw humus in the soil, which was only a few inches in depth. The plant analysis in Appendix II 4 shows that Nardus stricta was dominant, with Festuca ovina and Agrostis tenuis present, and the mean depth of sward from 20 measurements was found to be 11.5 cms. ± .9 cms. See Plate 17.

(d) Festuca /Agrostis Limestone Grassland.

The next three vegetation types were all situated on a single outcropping band of limestone, and differed only in the treatment they received.

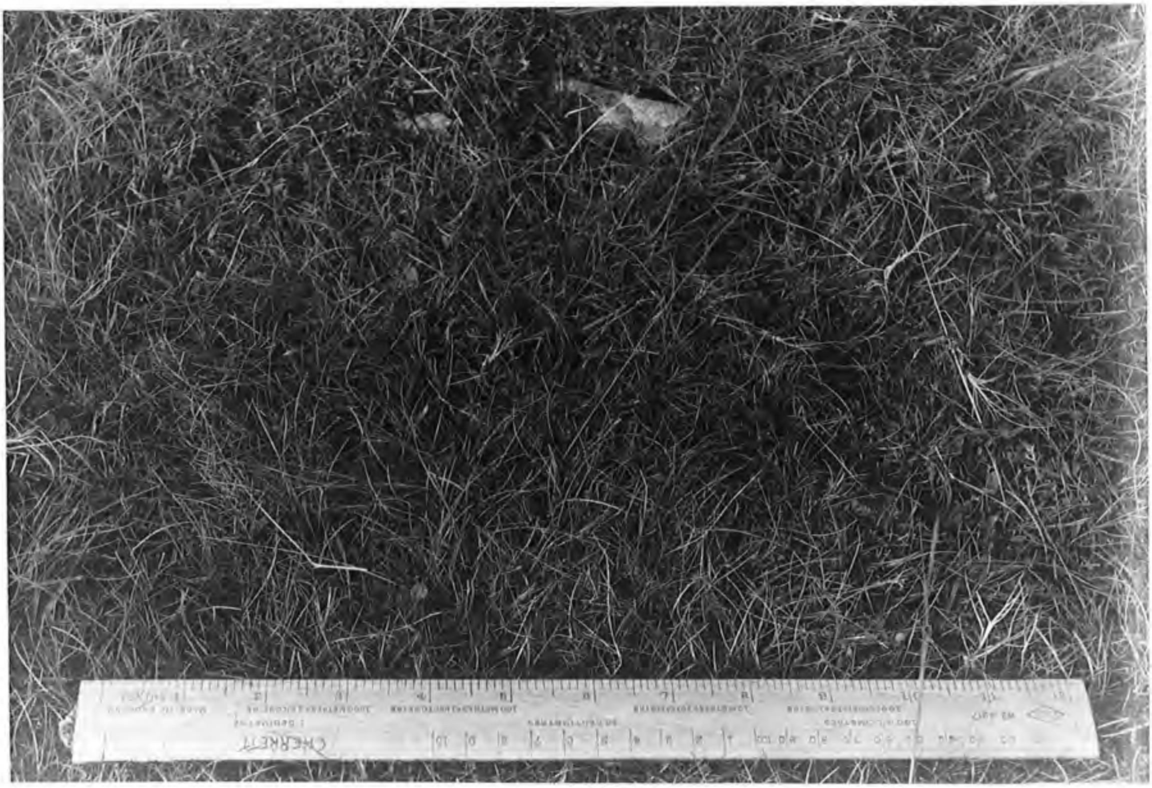
(i). Grazed.

A relatively dry site - see Table 66, near Rough Sike - Area 9, Figure 1, the vegetation grew upon a shallow soil often only 4 cms. deep overlying the limestone, which outcropped at intervals. Intense grazing by sheep had produced a fine, close cropped turf, the mean depth of which, 20 measurements showed to be 2.2 cms. ± .2 cms. The vegetation analysis in Appendix II 5, shows Festuca ovina to be dominant, with

Plate 17.

Festuca/Nardus Vegetation.

Plate 18.



Festuca/Agrostis limestone Vegetation, - Grazed.

Agrostis tenuis and Thymus drucei as important elements in a relatively rich flora. see Plate 18.

(ii). Ungrazed.

Whilst the previous 4 sites were sampled regularly, the following 4 were only sampled once, and the foregoing, more elaborate vegetation analyses were not performed.

This site, which was continguous with the last, had been enclosed for about 5 years, prior to the present investigations, and consequently there was no grazing. As a result, the sward was thicker, and some of the flowering plants shown on the grazed area had disappeared. For a comparative view see Plate 19. The mean sward depth for 20 measurements was 14.6 cms. See Figure 1, Site 8.

(iii). Cultivated.

On the same limestone outcrop, a paddock in front of the Station had been enclosed, and fertilized for many years, and from it was taken a regular hay crop, See Figure 1, Number 7. This prolonged treatment had resulted in a quite different 'sward type' of meadow, dominated by the meadow foxtail, Alopecurus pratensis, and with relatively few flowering plants. Other grasses of importance included Helictotrichon pubescens,

Plate 19.

Limestone, - Grazed and Ungrazed.

Plate 20.

Limestone, - Cultivated.

Agrostis tenuis, *Dactylis glomerata*, *Anthoxanthum odoratum*, *Festuca rubra* and *Holcus lanatus*. Whilst the mean height of the sward proper was about 25 cms. the flowering heads averaged 70 cms. and Plate 20 shows the meadow being cut for hay.

(e) *Sphagnum/Calluna/Eriophorum* Valley Bog.

This area, marked on Figure 1, as number 10 differed from the Blanket Bog site by being much wetter, with frequent pools of water. It was patchy, as described by Murphy D.H. (1955), and the area selected for sampling was one in which the water table was just below the surface, and which was dominated by *Sphagnum sp.*, with *Eriophorum angustifolium* and *E. vaginatum* co-dominants amongst the higher plants, with some *Calluna vulgaris* present. The mean depth of vegetation was 10 cms. and the whole is shown in Plate 21.

(f) Fell Top *Rhacomitrium* Heath.

Although not a *Rhacomitrium* Heath in the true sense of the word, patches of *Rhacomitrium lanuginosum* occurred on the summit of Knock Fell. These consisted almost entirely of *Rhacomitrium*, with a little *Festuca ovina*, and an occasional plant of *Agrostis tenius*. The habitat was a dry exposed one, being situated on mountain top detritus, and is illustrated in Plate 22.

Sphagnum/Calluna/Eriophorum, Valley Bog Vegetation.

Plate 22.

Fell Top Rhacomitrium Heath.

5. Habitat Comparisons of the Spider Faunas.

(a) Qualitative.

During the course of the investigations, collections were made from 9 different habitats, and in Table 68, the distribution of Linyphiid species in these habitats is shown. Despite the fact that the number of samples, and hence the chance of finding one of the rarer species in any given habitat, varied greatly, there was ample evidence of 'habitat specificity' amongst this group, almost every habitat having its indigenous species, often in large numbers. Barnes (1953) noted this from maritime communities in the U.S.A., and wrote that spiders constitute one of the best indexes for the investigation of community structure, stratification and succession, as the great degree of adaptation has resulted in them filling every available ecological niche.

The reasons for this habitat specificity are not clear, although moisture, and, as will be shown later, the detailed structure of the vegetation, are probably important.

N.B.

The Calluna, Juncus, Festuca/Nardus and Grazed Limestone sites were sampled on 4 successive weeks, on 4 occasions during the year, and this it was hoped would

The Spider Faunas of 8 Habitats at Moor House.

Species.	Valley Bog.	Calluna / Eriophorum.	Juncus squarrosus.	Festuca / Nardus.	Limestone - cultivated.	Limestone - enclosed.	Limestone - grazed.	Juncus / Alluvial - grazed.
Drepanotylus uncatus	x							
Meioneta saxatilis	x	X	x					
Bathyphantes gracilis	x	X		x		x		
Centromerita spp.	x	X	X	X		X	X	X
Dicymbium tibiale	x		X	x	X	X	X	X
Centromerus arcanus		X						
Cornicularia karpinskii		X						
Lepthyphantes cristatus		X						
Oreonetides abnormis		X						
Hypselistes jacksoni		x						
Meioneta rurestris		x						
Trichopterna mengei		x						
Porrhomma montanum		x	X					
Ceratinella brevipes		x	X	x		x		
Gongylidiellum vivum		x	x	X				
Lepthyphantes ericaeus		X	X	X		X		
Micrargus herbigradus		X	X	X			x	
Lepthyphantes mengei		X	x	X	x	x		
Silometopus elegans		X	x	X			X	x
Tiso vagans		x	x	X		x	X	X
Bolyphantes luteolus		X		X		X		
Lepthyphantes angulatus		X		x				
Gonatium rubens		X				x		
Lepthyphantes zimmermanni		X				x		
Tapinopa longidens		x		x				
Eboria fausta		x						x
Agyneta decora			x					
Cornicularia cuspidata			x					
Gongylidiellum latebricola			X					
Jacksonella falconeri			x				x	
Meioneta beata				x				
Mengea scopigera				x				
Oreonetides gibbosus/tuberosus				x				
Peponocranium ludicrum				x				
Walckenaera acuminata				x				
Wideria antica				X				
Erigonella hiemalis				X		x		
Monocephalus fuscipes				X		x		
Erigone atra					x			
Maro minutus						x		
Erigone dentipalpis						X	X	X
Diplocephalus permixtus								X
Oedothorax fuscus								X
Savignia frontata								X
Σ	5	24	15	21	3	14	7	9

x = < 3 specimens recorded;   X = > 2 specimens recorded.

Area Extracted in M^2	0.6	11.1	2.8	2.5	0.6	0.9	3.3	1.3

off-set the effects of seasonal succession and so make the fauna lists more comparable.

(b) Quantitative.

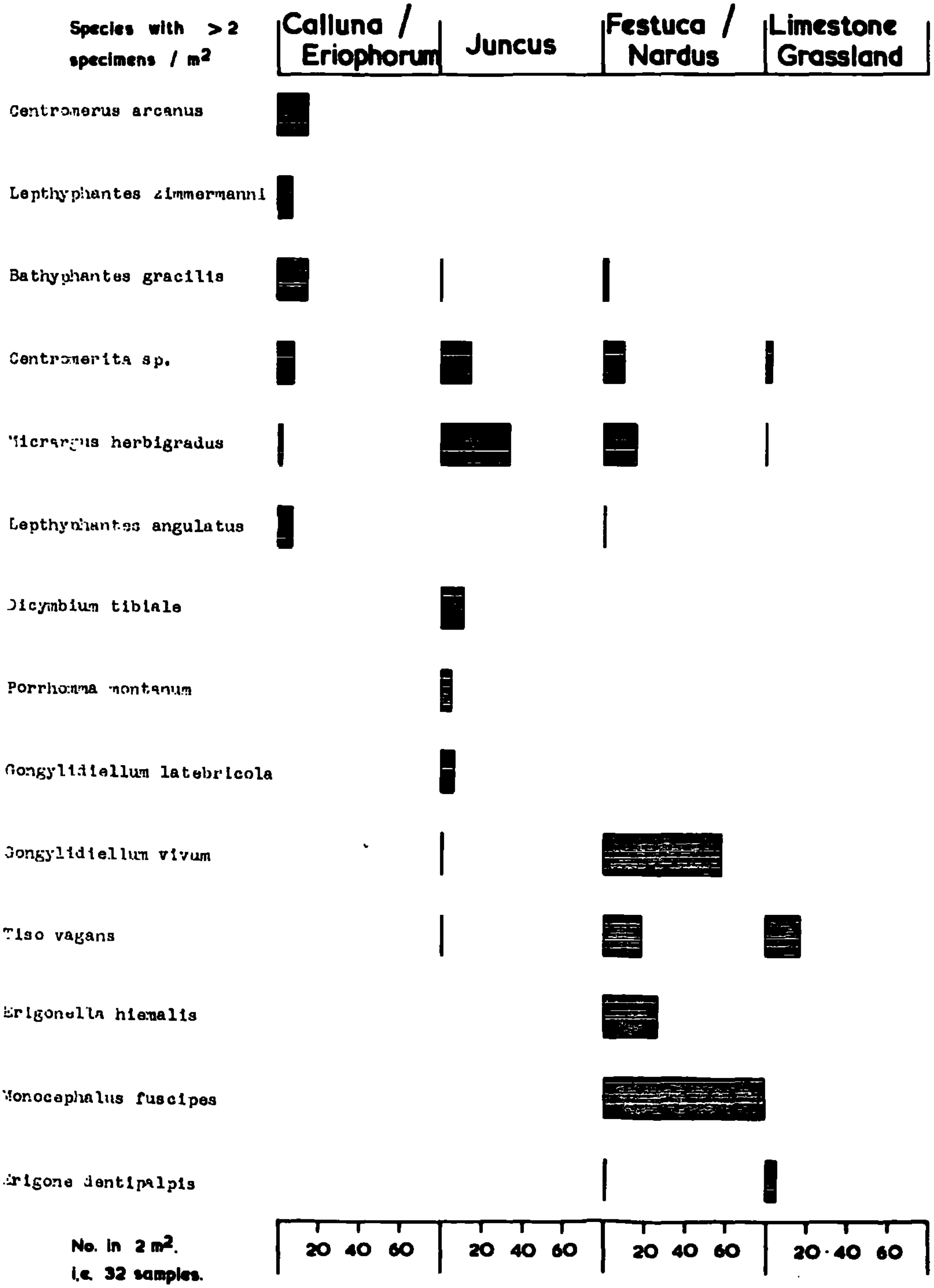
Despite the warning given, that theoretically there are no real grounds for comparing the fauna of one vegetation type with that of another numerically, the differences obtained were so marked, that they are presented, while theoretical uncertainties about the basis of the work, are yet borne in mind.

In Figure 33, all species which occurred in numbers greater than 2 per square metre, are listed, together with the actual numbers found in each habitat in 32 samples i.e. 2 square metres. Plotted in this way, habitat specificity becomes clearer, and for example Monocephalus fuscipes was found at a density of $35/M^2$ in Festuca/Nardus, and nowhere else. From this it can also be seen that the Festuca/Nardus site was the richest in numbers of spiders and species, whilst the Grazed Limestone Grassland was easily the poorest. Only one species, Micrargus herbigradus was found in all 4 habitats, although it was not evenly spread throughout them; the two species of Centromerita were not separated.

As these figures only refer to the mature, identified animals, in Figure 34, Section 1, estimated populations

Fig. 33.

A Quantitative Comparison of 4 Faunas



Based on 4 sampling periods each, throughout the year.

of all the spiders of the 4 habitats as mean numbers ± 2 standard errors per square metre have been graphed.

It is of interest, to compare these population estimates, with those obtained by other workers, amongst whom it has apparently been the custom to express densities per acre, - See Table 69. The *Juncus*, and *Festuca/Nardus* populations, calculated from yearly means,

TABLE 69.

Estimates of Spider Density per Acre.
- Partly after Gabbutt (1956)

Author	Habitat	Exn. Method	Density	Notes
Morris (1922)	Arable land Rothamsted, no vegetation.	Hand Sorting	22,000	
Ford (1935)	Clay meadows Oxford	Berlese and Floatation	406,500	
Baweja (1939)	Grass plots Rothamsted	Floatation	159,000	Soil only
Bristowe (1939)	Field of *Dactylis glomerata* Bexhill	Hand Sorting	691,000 min. to 2,265,000 max.	
Salt et al (1948)	Pasture Cambridge	Floatation	575,000	
Van der Drift (1953)	Beech Litter	Tullgren	934,857	
Gabbutt (1956)	Oak/Beech Litter	Tullgren	40,500 min. to 445,200 max.	
Duffey (1956)	Turf, Wytham Oxford	Lateral Heat Extraction	1,447,100 min. to 6,621,929 max.	

Table 69 (cont.)

Cherrett (1960)	Moor House Calluna/ Eriophorum	Lateral Heat Extraction	538,251 min. to 627,285 max.
	Juncus squarrosus	"	862,011 min. to 1,902,090 max.
	Festuca/ Nardus	"	1,145,301 min. to 1,950,654 max.
	Grazed Limestone	"	117,363 min. to 311,619 max.

are surprisingly large for such a high and exposed area, comparing favourably with Duffey's results, which show the highest spider concentrations ever recorded, and indicate that the apparatus was giving reasonably satisfactory yields.

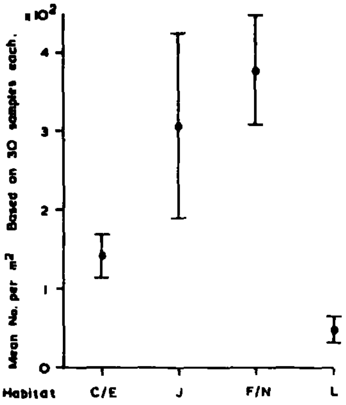
These results were also expressed in terms of Biomass, the extracted animals being first weighed 'wet', straight from the alcohol in which they were pickled, and then weighed 'dry', after being kept for 24 hours at 100°C, and the results appear in Figure 34, Sections 3 and 4. The Biomass picture is identical with the population picture, the maximum 'wet weight' of spiders being .195 gms. ± .0666 (2 x Standard Error) per square metre - for the Festuca/Nardus site.

As all spiders are predators, in an attempt to explain these differing population levels, all the

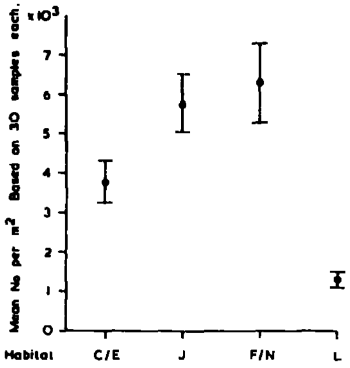
Fig. 34.

Spiders and Potential Prey — Their Numbers and Biomass in Various Habitats.

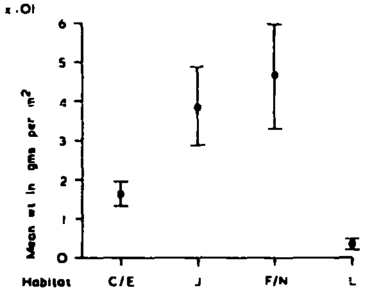
1. Spider Population of 4 Habitats



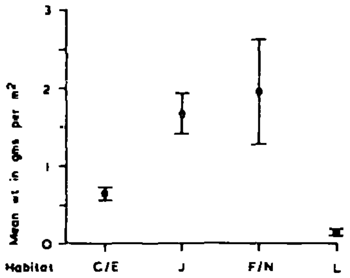
2. Extracted Arthropod Population of 4 Habitats



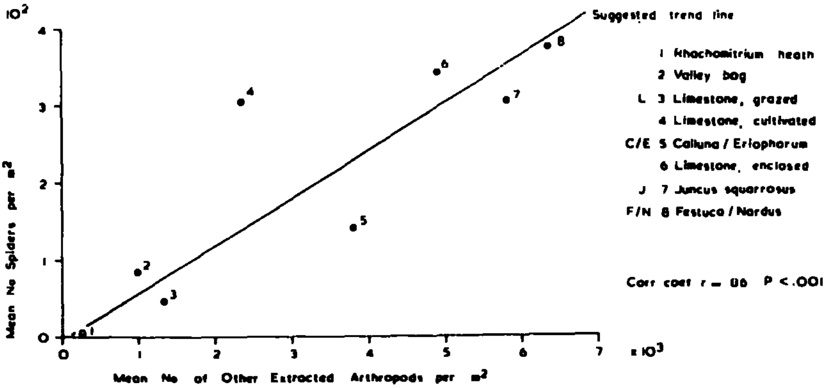
3. Dry Wt. of Spiders from 4 Habitats



4. Wet Wt. of Spiders from 4 Habitats



5. The Relation of Spiders to Other Extracted Arthropods in 8 Habitats



other Arthropods extracted from these samples were also counted, and graphed in Figure 34, Section 2.

Before examining further, any relationships between the numbers of spiders, and their 'potential prey', certain important reservations should be made about the 'Total Arthropod Population' figures. Much has been said about the varying extraction efficiency of any apparatus, with different groups of animals, and in the present case, the apparatus was specifically designed for spiders. No particular precautions were taken when counting the other groups, and as previously stated, in the case of the Collembola, only the 'large' animals were counted. Finally, with samples of this size, and using a lateral extraction system, the efficiency for small Arthropods is known to be extremely low; - See Table 70.

Having made these reservations, the present work must be considered as exploratory, and it is hoped that other workers in the same area might be able to fit their more detailed sampling of a particular group, into the general picture. It would however appear from Figure 34, Section 2, that the spider populations in the four areas, simply mirror the general Arthropod picture, as might be expected of a group which is a general predator of Arthropods. As Bristowe (1941) p. 269 notes "In situa-

TABLE 70.

Total Populations of Soil Arthropods in some British Habitats.

After Murphy (1955 a)

Author	Habitat	Numbers per M^2 (Thousands)	Notes
Murphy (1953)	Natural Heathland (maximum)	569.7	
	Cultivated do. With Trees (maximum)	834.5	
Evans (1950)	Spruce Plantation	154.6	
Macfadyen (1952)	Fenland	159.4	Acarina and Collembola only
Salt et al (1948)	Grassland	340.5	
Baweja (1939)	Arable Land	25.9	
Cherrett (1960)	*Calluna/Eriophorum*	3.9	
	Juncus squarrosus	6.1	
	Festuca/Nardus	6.7	
	Grazed Limestone	1.4	

tions which harbour a large Collembolan or Nematocerous population the numbers of spiders are almost invariably high. Elsewhere, where these insects are scarce the spider population is smaller".

To investigate this relationship further, the mean numbers of spiders, were plotted against the mean number of other Arthropods per square metre, as illustrated in Figure 32, Section 5, for the 8 habitats from which samples were taken. A correlation coefficient of + .86 gave a probability <.001, so establishing this connection, which could mean that the spiders, an easily extracted group, might be used as an index of faunistic productivity, so far as general litter-living Arthropods are concerned.

It is perhaps worthy of note, that the one really bad fit, in this relationship, point 4, is the cultivated hay meadow, and it is just possible that the regular cropping system in some way disrupts the predator-prey relationships established in more stable habitats.

As a mean figure, the spiders formed 5.9% of all Arthropods extracted from the 8 habitats, and this can be compared with the results of other workers, cited by Muma and Muma (1949):-

Lowrie (1948)	High Prairie	6.6%
	Post Climax Grass	7.8%
	Deciduous Shrubs	5.5%
Smith - Davidson (1932)	Stripped Areas	17.6%
	Clover covered ridge	10.7%
	Forest edge	11.3%
	Flood plain forest	20.6%
	Maple - Red oak Climax	13.3%
McAtee (1907)	Meadow	17.1%
Walcott (1918)		6.45%
Rice (1946)	Herb Layer in Elm-Maple	10.2%
Whelan (1927)	Bluestem, wintering fauna	14% = Spiders Mites

However, it was previously suggested that the total Arthropod estimate was extremely low, and in the light of the results of other workers a factor of 100 x might well represent a conservative increase. This would give a spider percentage in the .05% region, and would bring it much more in line with figures calculated from Baweja (1939) of .1% and Salt et al (1948) of .041%.

With the data available in the present investigation, the fact of a fairly constant relationship, is considered of more importance than its magnitude.

A particular study of the effect of grazing upon the fauna of limestone grassland was made, in which two parallel rows of 15 samples, each less than 2 metres apart, were taken on either side of the sheep-proof fence illustrated in Plate 19. The sites were those described in Section VII 4 d, (i) and (ii), and the results appear in Table 71.

It is tempting to suggest that this marked reduction in the fauna brought about by sheep grazing, is simply a result of replacing the phytophagous insects by sheep in the food chain. Such a simple explanation is unlikely, in view of some work by Weese, quoted by Carpenter (1936), who found that the population of insects in heavily grazed mixed prairie in South-West Oklahoma had more than four times as many individuals

TABLE 71.

A Comparison between Grazed and Enclosed Limestone.

Samples taken within 2 m. of each other, on either side of the enclosure fence.

	No. of Spiders		Total Arthropods	
	Grazed	Not Grazed	Grazed	Not Grazed
	28	19	106	86
	4	18	37	258
	7	38	90	378
	3	18	46	239
	10	18	77	74
	26	21	54	380
	8	14	51	267
	10	14	132	389
	12	10	82	183
	19	16	40	266
	6	41	56	431
	19	26	141	480
	10	26	151	387
	13	21	101	425
	4	20	100	345
Σ	179	320	1264	4588
$\bar{x}$	11.93	21.33	84.27	305.87

$t = 3.16$ df 28 $p < .01$ $t = 6.66$ df 28 $p < .001$

Biomass - Spiders in gms.

	Grazed	Not Grazed
Dry wt.	.0088	.0419
Wet wt.	.0411	.1843

as did the normally grazed grassland adjoining. It is interesting that in the same paper Carpenter writes

"Generally speaking, the population may be said to be greatest in areas having the greatest amount of exposed leaf surface".

In the present case, whatever the direct affect of the reduction in the feeding surface available for phytophagous insects, the indirect effects of loss of shelter and protection, and the large changes produced in the microclimate, must be of overwhelming importance.

6. Microdistribution in a Heterogeneous Habitat.

In order to throw more light upon spider populations and the structure of the vegetation cover, a detailed examination of the linyphiid fauna of a small, but very 'patchy' area was undertaken. The area, site 6 on Figure 1, was situated on a closely grazed alluvial terrace, by the side of the River Tees, interspersed at intervals with tussocks of Nardus stricta and Juncus effusus, as shown in Plate 23. A grid, also shown, 2.1 m. x 0.6 m. was laid down, and divided into 2 rows of 10 samples each.

The vegetation depth was mapped within the grid, as shown in Figure 35, and the number of Linyphiid webs, as seen at 5-0 a.m. on a suitable dewy morning were recorded for each sample. The whole area was then cut up, and extracted, and the number of spiders obtained from each sample is also given. It is apparent, that

Plate 23.

Alluvial Grassland, Microdistribution Site.

Micro Distribution of Linyphiidae

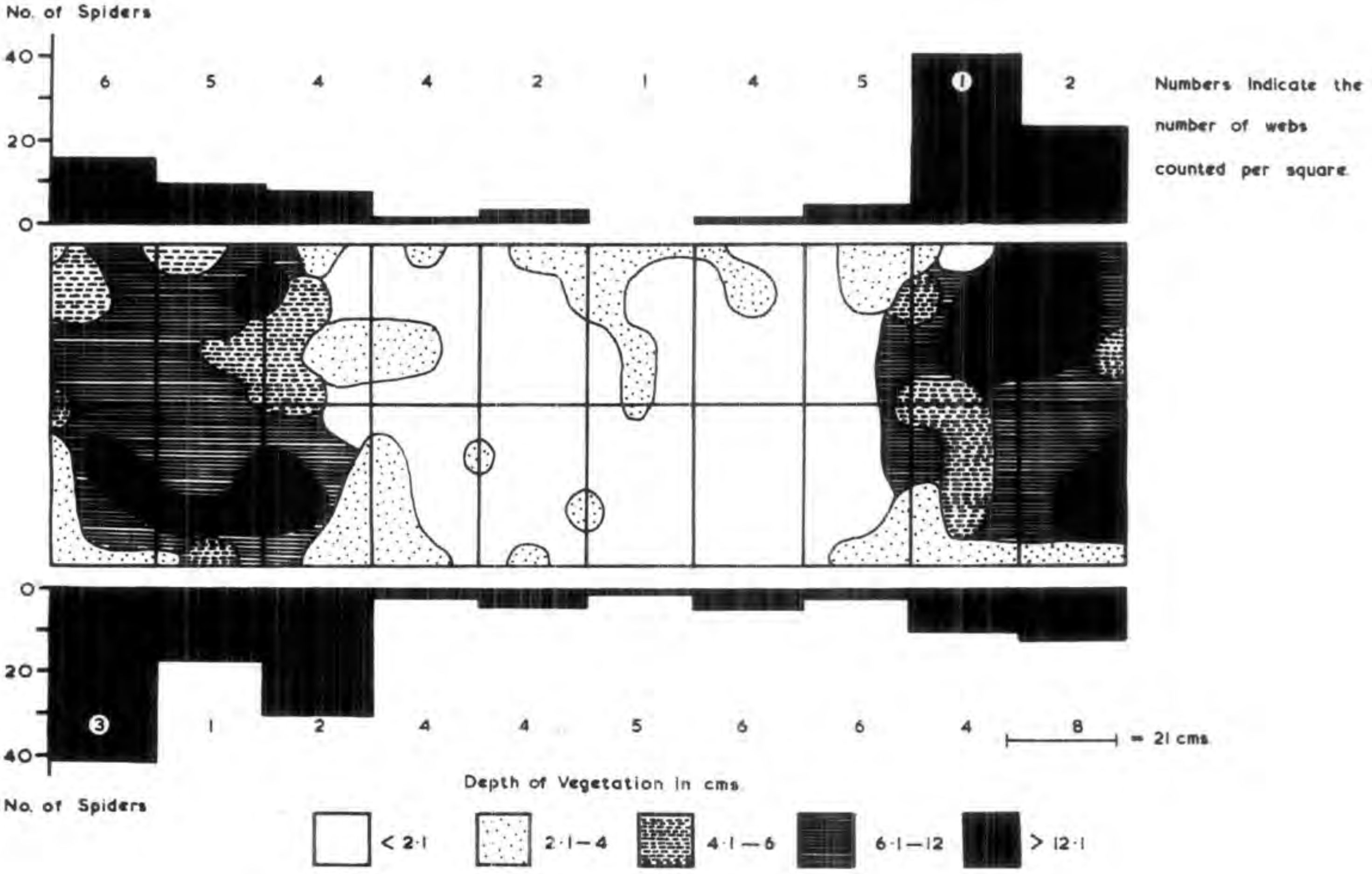


Fig. 35.

the spiders are largely restricted to the tussocks of denser foliage, so forming 'islands' of high density within the sparsely populated, close-cropped alluvial grassland. It is also clear, that counts of hammock webs, even under the most suitable conditions give a very inadequate picture of the numbers of Linyphiids present.

The restriction of many species of spiders to these dense tussocks is further illustrated in Table 72, where the mature spider faunas of each sample have been analysed on a species basis.

TABLE 72.

Microdistribution of the Linyphiid Fauna.

Species	Heavily Grazed 8 Squares.	12 'Tussock' Squares
Centromerita sp.	1	61
Erigone dentipalpis	2	5
Dicymbium tibiale		28
Tiso vagans		3
Diplocephalus permixtus		3
Savignia frontata		3
Oedothorax fuscus		3
Silometopus elegans		2
Eboria fausta		1

7. Specific Distribution in a Given Vegetation Stand.

The problem of larger spider populations being associated with the thicker and more complex vegetation swards, was studied, by examining the distribution of hammock-web building spiders, in a fairly complex vegetation type, namely the *Calluna/Eriophorum* Blanket Bog flora.

For the purposes of this investigation, 6 arbitrary zones were recognised in the *Calluna/Eriophorum* vegetation, as shown in Plate 24:-

Zone 1. Consisting of green heather tips, leaves and flowers. (30-36 cms)

Zone 2. " " brown 'twiggy' heather stems. (22-30 cms)

Zone 3. " " heather stems, and green leaves of *Eriophorum vaginatum*. (8-22 cms)

Zone 4. " " procumbent heather stems and *Eriophorum* bases. (5-8 cms)

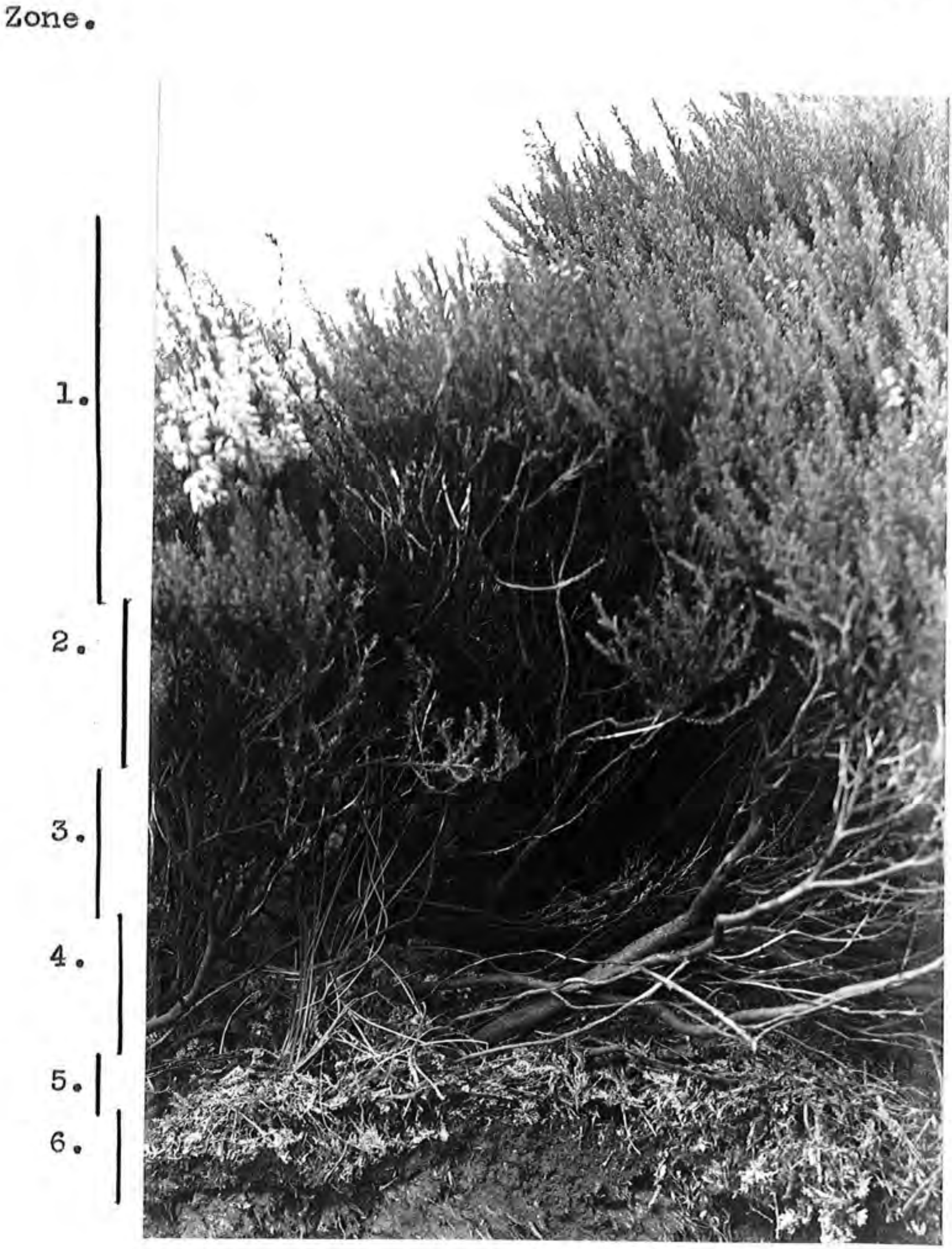
Zone 5. " " *Sphagnum*, or other moss heads, or the surface of heather litter. (5 cms)

Zone 6. " " *Sphagnum*, or other moss stems, or heather litter, often permeated by fungal hyphae; usually damp. (0-5 cms)

N.B. The measurements given refer to the original *Calluna/Eriophorum* 'type stand', and were found to vary greatly.

By careful inspection, the positions of hammock-webs were noted, and the spiders on them removed and identified. Unfortunately, the results shown in Table 73 deal with only small numbers of animals, partly because many

Plate 24.



Section through *Calluna/Eriophorum* Vegetation.

(From top of zone 1, to bottom of zone 6 = 36 cms.)

of the animals taken were immature and unidentifiable, and partly because of the extreme difficulty of capturing spiders from given webs, due mainly to their habit of dropping to the ground at the least disturbance. This table does however suggest a stratification of small Linyphiids in the low growing vegetation, a phenomenon which has been demonstrated by Weese (1924) on a larger scale measured in metres in a forest environment, and suggested by Duffey et al (1957) for tall Fen vegetation. Weese has suggested, after laboratory experiments, that web location is largely determined by mechanical and structural relations, rather than by microatmospheric factors, although light intensity may be important.

In any event, this stratum preference could account for some of the specific faunal differences found in different vegetation types, and in this respect, it is perhaps significant to note that the 2 species found in Zone 6, Centromerita sp. and Robertus lividus, were amongst the most ubiquitous, the former having been taken in 7, and the latter in 4 of the 8 habitats whilst the two species in the top layer of the vegetation, Bolyphantes luteolus, and Lepthyphantes zimmermanni, were much more restricted, being found in only 3 and 2 of the 8 habitats respectively, all of which were

TABLE 73.

Species stratification in Calluna/Eriophorum Vegetation.

Species	ZONE						Nature of Web.	Notes
	1.	2.	3.	4.	5.	6.		
Linyphiidae								
Bolyphantes luteolus	XXX	XXX					Medium mesh	Frequently in gap in canopy.
Lepthyphantes zimmermanni		XXXXX	XXX	XX			" "	Frequently below canopy.
L.angulatus				X			Fairly fine mesh	
Tapinopa longidens				XX	XXX	X	Very fine mesh Indeed	
Centromerita sp.						X	Fairly fine mesh	
Theridiidae								
Robertus lividus						XX	Tangle web	

X = One animal.

characterised by deep sward vegetation.

8. A Seasonal Examination of an Area of Calluna/ Eriophorum Blanket Bog.

A seasonal examination of the spider fauna of the Calluna/Eriophorum site previously described in Section VII 4 a, was made by sampling at monthly intervals, as more frequent sampling was not practicable. Sampling was in a grid, 50 yds by 20 yds. and laid out as 10 squares, 10 yds. by 10 yds. in 2 continguous rows of 5. The area upon which this trid was placed, can be seen in Plate 25.

(a) Uniformity of Plant Cover Within the Study Area.

The distribution of the two co-dominants, Calluna vulgaris and Eriophorum vaginatum was patchy, and it was found impossible to judge by eye, whether or not the proportions of the two remained reasonably constant over the 10 squares of the grid. Accordingly, a 2 ft. by 2 ft. quadrat was thrown down 10 times in each square, the percentage Calluna cover being estimated on each occasion. An analysis of variance was then performed on the data, comparing the variation within each square on the grid with the variation between grid squares. For data see Appendix II.

Plate 25.

Site of Calluna/Eriophorum Grid.

This gave an F. ratio of 1.268, and as the F. ratio at the 5% level was 1.8, it seems that the variation between grid square averages was commensurate with the cover variance as indicated by the variation within the individual grid squares. All this suggests that the 10 squares in the grid lay within a single type of Calluna cover.

(b) The Grid Sampling Technique.

On each sampling occasion, one sample was taken from each of the 10 squares within the grid, although within that square, its position was selected at random, by throwing the metal quadrat. This procedure, as discussed in Macfadyen (1957), ensures better randomization of the samples, and it is statistically important that samples should be taken without bias in the area under consideration. It also means that eventually, some conclusions can be drawn about the distribution, and variability of the spider population within the grid, on the basis of the grid squares. In all cases, once the samples were taken, they were carefully randomised in the extraction boxes of the apparatus, so making it possible to separate variation due to the differing populations of the grid squares, and the differing extraction efficiency, of the various units of the extraction apparatus, as will be discussed in the next section.

(c) Sources of Variation.

An analysis of co-variance was performed on the data, to find the amount of variation attributable to each of the following 3 factors, time, position on the grid in the field, and the position in the extraction apparatus. Results from 15 standard extractions were used, and are shown in Table 74, whilst the original data appear in Appendix IV, 1 and 2.

TABLE 74.

Sources of Variation in Spider Numbers.

Based upon 15 monthly extraction of 10 samples each, from the *Calluna/Eriophorum* grid.

Source of Variation	Sum of Squares	df	Variance Estimate	F	P
Date	1218	14	87	2.4	<.01
Grid posn.	540	9	60	1.65	>.1
Extn. posn.	472	9	52.44	1.45	>.1
Residual	4246	117	36.29		
Total	6476	149			

The only significant cause of variation was the time of the year when the samples were taken, whilst the least significant of the 3 factors investigated was the position of the samples in the extraction apparatus, suggesting that at least the various units in the apparatus gave comparable yields.

(d) Distribution of the Animals.

(i). In Space.

Following Salt and Hollick (1947), the spatial distribution of spiders was examined, and for each of the 15 sampling dates, a coefficient of dispersion was calculated, for the 10 samples taken. The results of this appear in Table 75, from which it is clear that on the majority of occasions, very significant aggregation was exhibited.

TABLE 75.

Spatial Distribution of Spiders in Heather Grid.
- 10 samples, 9 df.

Date	Coef. of Disp.	χ^2	P
1958			
5/8	1.073	9.65	>.3
26/8	5.508	49.57	<.001
23/9	2.178	19.6	<.05
22/10	2.961	26.65	<.01
17/11	2.778	25.0	<.01
16/12	4.078	36.7	<.001
1959			
21/1	3.231	29.08	<.001
20/2	2.904	26.14	<.01
8/4	3.202	28.82	<.001
29/4	1.714	15.43	>.05
27/5	1.539	13.85	>.1
3/7	5.035	45.31	<.001
21/7	1.318	11.86	>.2
17/8	6.889	62.0	<.001
14/9	2.766	24.89	<.01

(>1 = Underdispersion (aggregation) <1 = Overdispersion)

$\Sigma \chi^2 = 424.55$ with 135 df
i.e. total is highly aggregated.

N.B. Probabilities from these coefficients of dispersion were calculated by a χ^2 technique, to be found in Healy (1958).

Having established the fact of aggregation, its nature was investigated in Table 76, where it can be seen that the deviation from expected lies in an excess of small negative deviates, and a shortage of small positive deviates. That is to say that the aggregation takes the form of too many samples with slightly less than the mean value, and too few with slightly more. There is no evidence of really large aggregations, and this picture would be consistent with slight variations in the favourability of an admittedly 'patchy' environment. In this, these Linyphiid spiders appear to be conforming to a very common distribution pattern amongst animals; as Andrewartha and Birch (1954) p 568 write, when discussing natural populations, "It is generally true, with very few exceptions, that natural populations are distributed nonrandomly and that the departure from randomness is in the direction of excessive patchiness".

(ii) <u>In Time</u>.

The analysis of co-variance showed that of the factors examined, the only significant cause of variation was the time of the year, when the samples were taken, and in Figure 36 the monthly estimates of the spider popula-

TABLE 76.

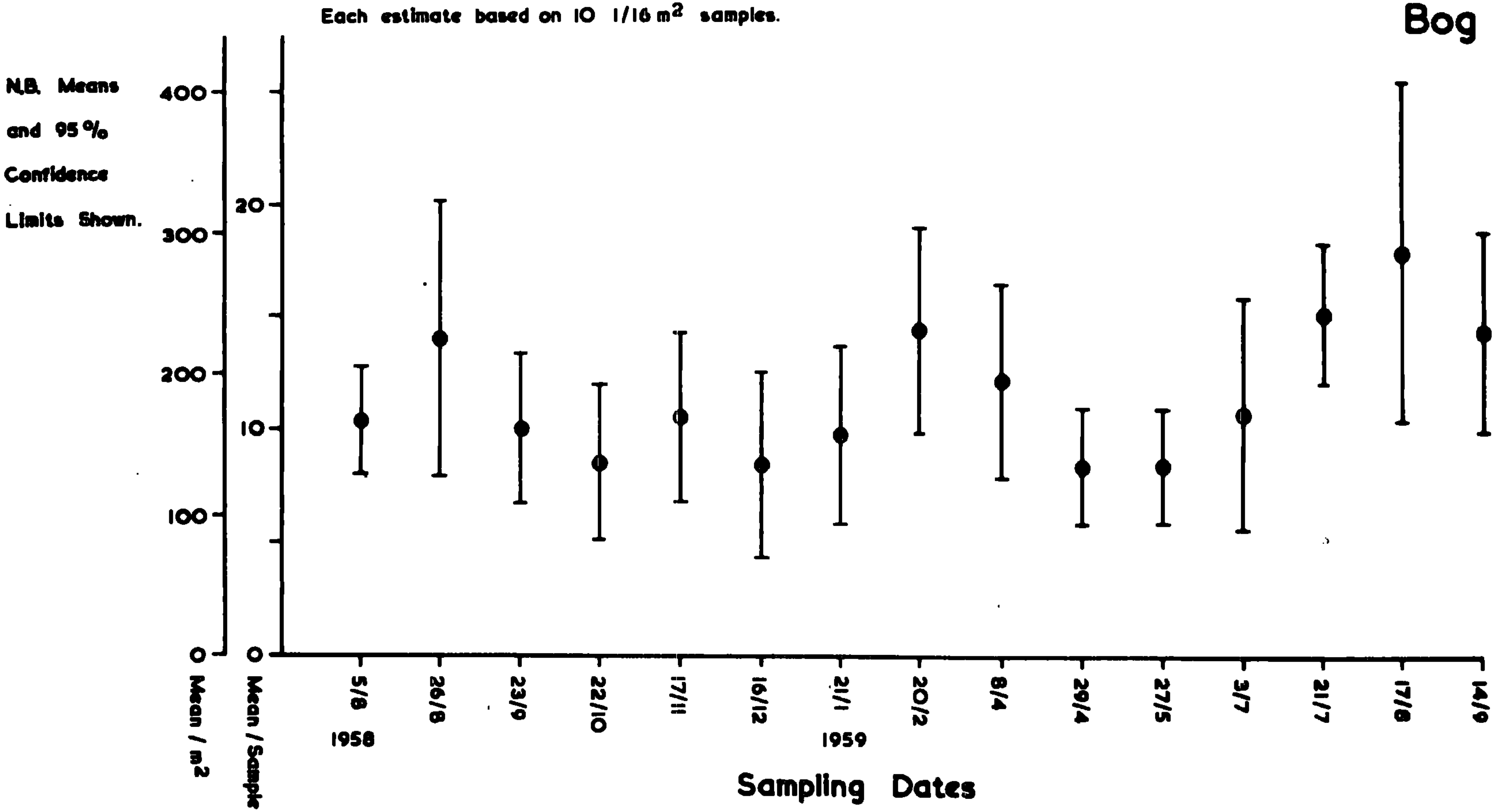
Nature of Aggregations of Spiders in Heather Grid.

Date	S.D.	Standard Deviation Classes.					
		-2	-1	0	+1	+2	+3
1958							
5/8	3.339	3	1	5	1		
26/8	8.782	2	3	3	2		
23/9	4.667	2	3	4	0	1	
22/10	5.017	2	4	3	1		
17/11	5.4	2	3	3	2		
16/12	5.854		6	2	2		
1959							
21/1	5.598	3	0	6	1		
20/2	6.467	1	5	2	2		
8/4	6.227	1	4	4	1		
29/4	3.772	1	6	0	3		
27/5	3.596	1	6	1	2		
3/7	7.306		8	0	1	1	
21/7	4.447	1	4	3	2		
17/8	11.56	1	6	1	1	1	
14/9	6.291	1	3	5	1		
Σ	Observed	21	62	42	22	3	
	Expected	20.39	51.19	51.19	20.39	3.22	

tion of the Calluna/Eriophorum site are graphed. The most striking feature in this Figure, is the apparent constancy of the spider fauna, thus the highest mean is only 2.14 times the lowest. This is to be compared with differentials of 3.27 in Bristowe (1939) p 206, and about 5.0, calculated from a Figure given by Duffey (1956). The reasons for this are not clear, but a comparable situation was found in Araneus cornutus, where the life

Fig. 36.

Monthly Estimates of the Spider Population of a Calluna/Eriophorum Blanket Bog



Each estimate based on 10 1/16 m² samples.

N.B. Means and 95 % Confidence Limits Shown.

cycle extended over 2 years, and it may be, that the cold, wet climate lengthens the life cycle, so blurring the annual population fluctuations.

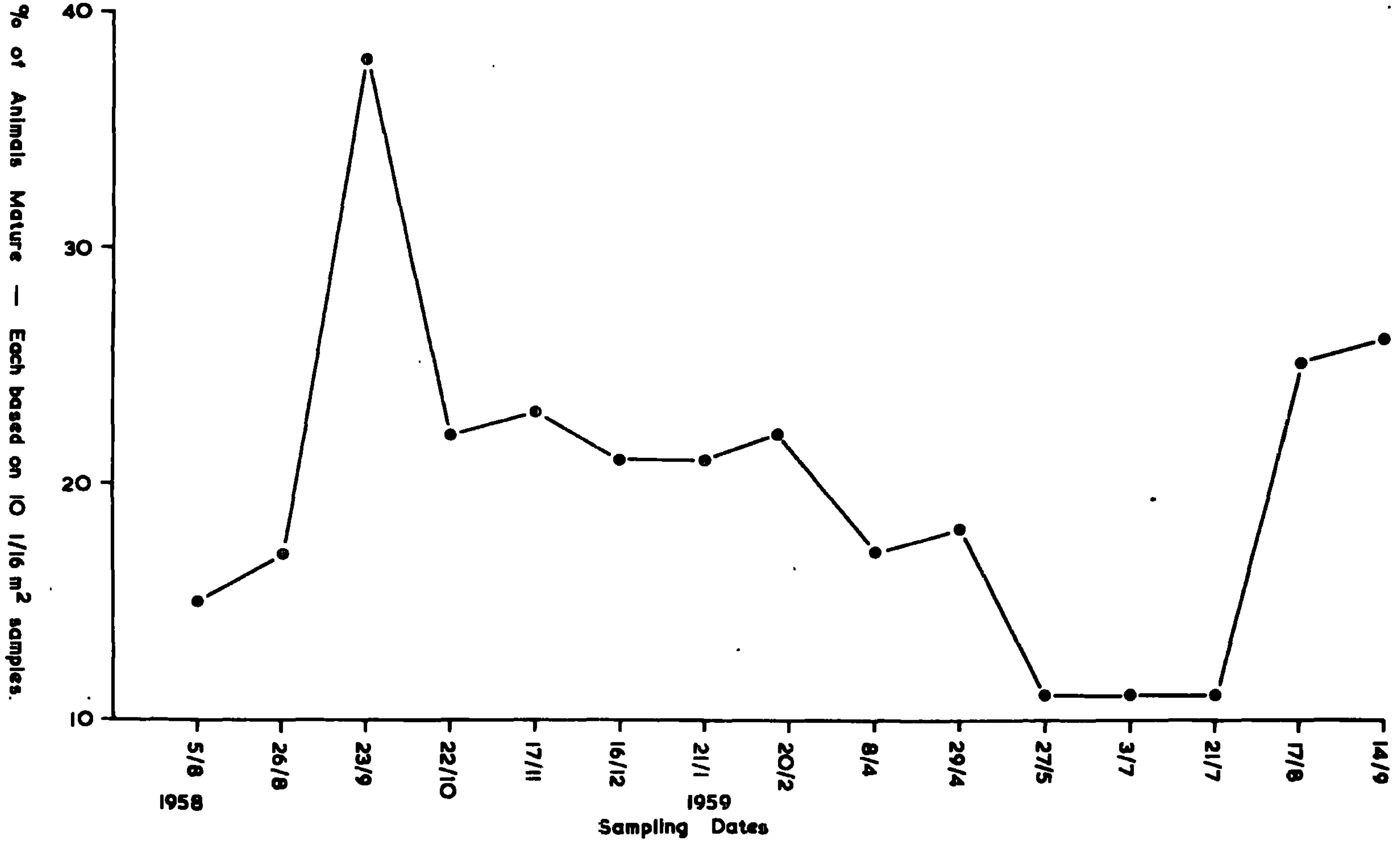
Both Bristowe and Duffey show population peaks in the August to October period, and in the present work, peaks such as these do appear in August. This is in contrast to the work of Turnbull (1957) who records a peak in June, probably due to his sampling methods which, as some of them involved beating and sweeping, would be very susceptible to the activity of the population; it is interesting to note here, that his lowest figures are for January, February and March. The lowest populations shown by Bristowe and Duffey occurred in May and June, whilst at Moor House, the lowest figures were for April and May (No June sample).

Figure 36 also shows a peak in February, at a time when Duffey describes an identical peak of juveniles, which he attributes to late winter hatching. In the present case however, the peak is associated with a slight decrease in the percentage of immature animals, and no explanation for it can be suggested.

In an attempt to show something more of the breeding biology of the Moor House Linyphiids, the percentage of mature animals, is shown in Figure 37 for all 15 sampling occasions. This picture shows a high percentage of

Fig. 37.

The Maturity of the Calluna / Eriophorum Spider Population



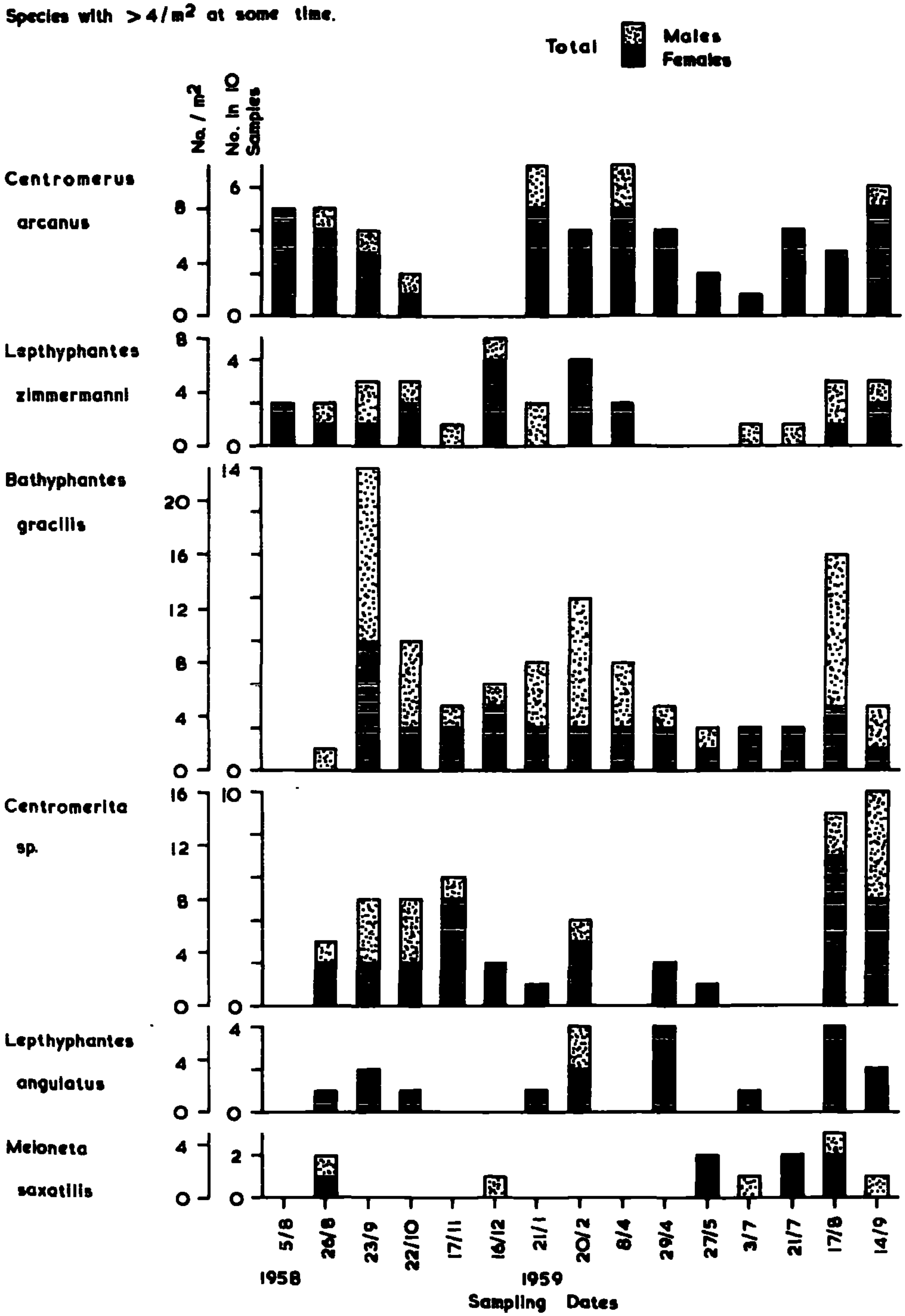
mature spiders in autumn, falling to a very low value in May, June and July, when the eggs are hatching, and the young spiderlings are growing up. This trend was found to be significant a homogeneity χ^2 on the mature/immature ratio, giving a χ^2 of 47.113 with 14 df and a probability $<.001$. According to Duffey (1955), the percentage of adults was never more than 48%, being highest in the winter, and lowest in the late summer, when in July it became less than 7%.

In Figure 38, the number of mature animals of 6 species have been plotted throughout the 1958/59 sampling season, and again the absence of any obvious seasonal patterns of maturity is striking, and appears rather different from the descriptions of other workers in this field. Thus, Duffey (1956) extracted 10 *Bathyphantes gracilis* per M^2 in October and November, and none at any other time, whilst at Moor House, adults were taken during every month of the year, and Locket and Millidge (1953) p 366 write "Adult in Spring, Summer and Autumn". Again, according to Locket and Millidge, ~~and~~ the adult seasons for the other species studied here, are quoted:-

Centromerus arcanus - "Autumn, winter and spring".
Lepthyphantes zimmermanni - "At all seasons".
Centromerita bicolor - "Most of the year".
C. concinna - "Autumn and Winter".

Fig. 38.

Calluna / Eriophorum Linyphiids — Periods of Maturity



Lepthyphantes angulatus - "Late summer, autumn and winter".

Meioneta saxatilis - "Spring and summer".

Undoubtedly, collecting methods which depend upon the activity of the animals in the field, give a much clearer picture of sexual activity in the mature animals, as has been abundantly demonstrated by Tretzal (1954, 1955 a) but it seems, certainly in this area, that mature animals are often present throughout the year.

(e) Biomass Fluctuations with Time.

The 'dry' and 'wet' weights of all the spiders from the monthly Calluna/Eriophorum samples are shown in Figure 39, and as will be seen, they fluctuate in a wild, and inexplicable way. All that can be seen, is the decrease in the mean dry weight per animal, from winter to spring and summer, due presumably to the increasing numbers of young spiders in the population, hatching throughout this period.

9. Discussion.

The factors affecting the distribution of Linyphiidae in this area are difficult to establish, especially in a study such as this, concerned simply with empirical observations.

Monthly Spider Biomass Estimates from Calluna / Eriophorum Blanket Bog

Based on total weights of spiders from 10 1/16 m² samples

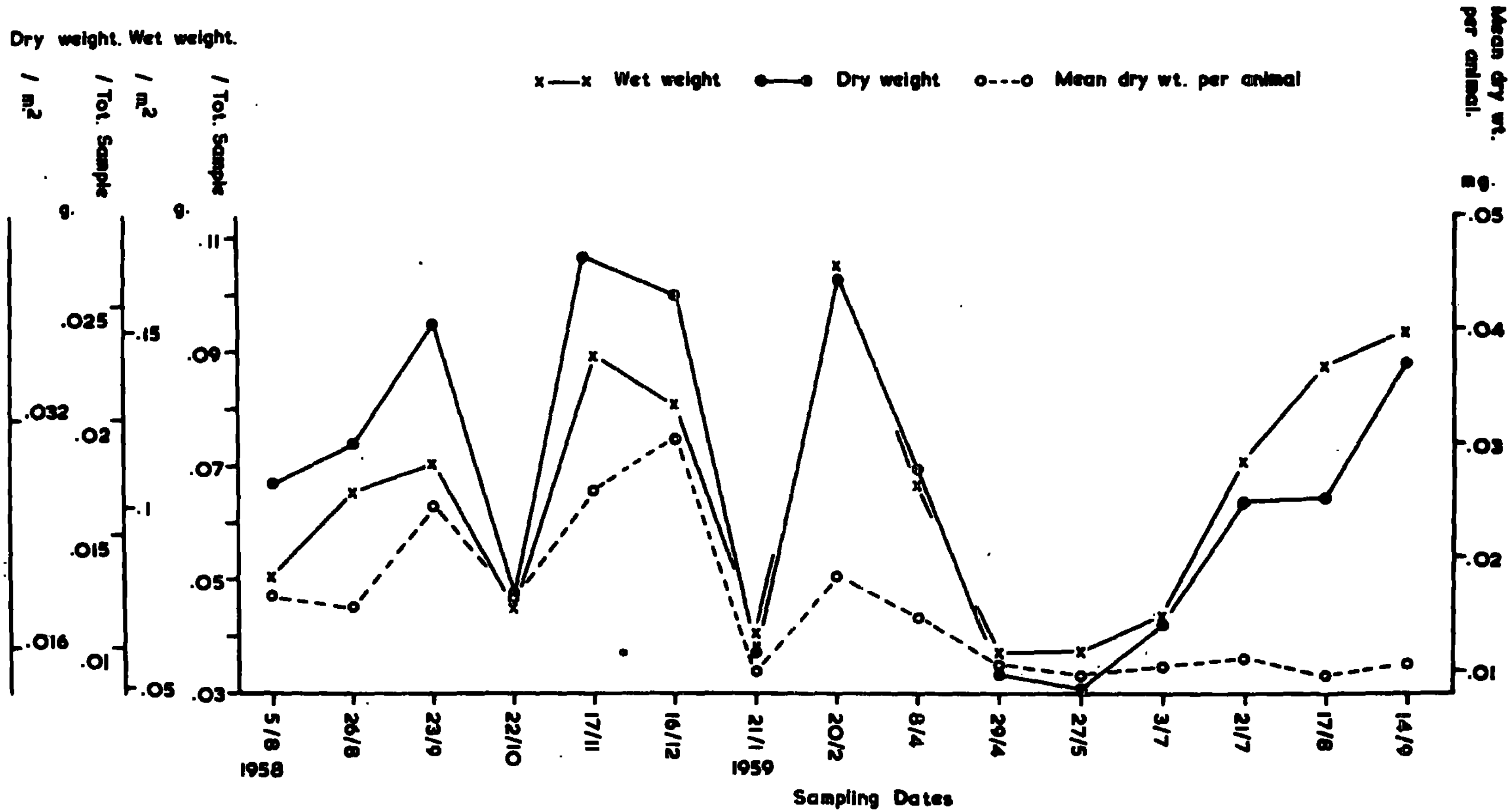


Fig. 39.

Individual species undoubtedly have specific requirements, limiting their distribution, and the dampness of the habitat, and the structure of the vegetation cover may be two of these. Indeed it is variation in specific requirements which makes the faunas of different habitats distinctive. However, despite the ecological radiation, which appears to leave no niches unfilled by spiders, the populations of different habitats also vary, indicating that not only are the different conditions in the 4 vegetation types causing one spider fauna to be replaced by another, but that the 'carrying capacity' of the different habitats also varies in respect of the number of spiders it supports.

The two most likely reasons for the variations in the 'carrying capacity' of different habitats are:-

1. Variations in available food.

2. Variations in the number of available places in which to live.

There are indications that the numbers of potential Arthropod prey do vary in a similar manner to the numbers of spiders, but this is not necessarily to be interpreted as a causal relationship, both may be reacting alike to a third set of factors. Indeed, the ratio of spiders to other Arthropods is not so close as to indicate an obligatory, neatly-balanced predator/prey relationship, and it does seem to be a characteristic of predators in stable, natural, environments, that the prey is not utilised to the maximum extent and a safety margin is left. Duffey (1955) was impressed by the apparent superabundance of potential invertebrate food, something also indicated by the imitation Linyphiid-web results quoted previously. As was shown for the orb-web spiders however, it is the availability of the prey which may be of greatest importance to a sedentary, net building animal like the spider. In this respect, the availbility of suitable places in which to live is important, and a decrease in the number of these might be expected to coincide with a decrease in their variability, and it is perhaps significant that the vegetation type with the smallest population (Grazed Limestone), supported the smallest number of species when collecting methods were standardised as in Figure 33, and that this relationship held up to the other extreme, where the Festuca/Nardus site supported both the largest population and number of species.

Lowrie (1948) found a similar situation when studying the succession of spiders in dunelands, and associated increases in the populations, and numbers of species with the increasing complexity of the habitat, as the beech/maple climax was reached. As he says, the biotic and physical factors influencing the spider populations and faunas are difficult to disentangle, and it seems that the time has been reached, when laboratory experiments, in which animals such as spiders are cultured in 'habitats' of varying complexity, and with varying food supplies could usefully be undertaken.

VIII. NOTES ON OTHER ARANEAE FROM MOOR HOUSE.

Eight other spiders have been found on the Reserve, which belong to families not being specially studied; they are listed below, together with notes on their occurrence and habits.

Family *Dictynidae*.

Dictyna arundinacea (Linnaeus)

This is a cribellate spider, which combs out very fine threads over a tangle of radius threads, and the two or three individuals which have been found had built their lairs across the forks of dead *Calluna* shoots. The legs of passing insects are entangled in these threads, and their remains can often be seen, built into the fabric of the nest. Only females were found.

Family *Clubionidae*.

Clubiona trivialis C.L. Koch.

Only occasional specimens of this short-sighted, relatively unspecialised, hunting spider were taken from *Calluna/Eriophorum* and Limestone pitfall traps.

Clubiona diversa O.P. - Cambridge.

This species was found, only in small numbers, on the *Festuca/Nardus*, and Tees Alluvial sites, the previous Record from Westmorland being by Parker (1959) from Boltons Tarn, Crook.

Family Thomisidae.

These 'crab spiders' do not spin webs, but rely on ambushing their prey, and as a result, they can often be found in or among flowers where they kill the visiting insects. They also occur in many other habitats, and a specimen was found on close-cropped grassland on the summit of Cross Fell, where it was struggling with a large moth.

Two species were taken on the Reserve.

Xysticus cristatus (Clerck)

This species was occasionally taken in *Calluna/Eriophorum* samples and pitfall traps, and also in the pitfall traps on heavily grazed limestone.

Oxyptila trux (Blackwall)

The two females, were both captured in pitfall traps on the *Calluna/Eriophorum* site.

Family Agelenidae.

Antistea elegans (Blackwall)

This species forms a small sheet web in depressions in the ground, and appears to be associated with only the wettest places. Accordingly, it appeared to be common in the Valley Bog site, and the only other record, from a Limestone Grassland pitfall trap was that of a female, which must have wandered out of *Sphagnum* in a nearby flush.

Family Theridiidae.

x Robertus lividus (Blackwall)

This species was common in at least 4 of the sample sites, Calluna/Eriophorum, Juncus squarrosus, Festuca/Nardus and Valley Bog. It builds a type of scaffolding web not so highly developed as the Linyphiid hammock-web, low down in the vegetation, as shown in Table 73, and Forman (1951) associates it with the moorland habitat.

x Robertus arundineti (O.P. - Cambridge)

Only two females were taken, from the very wet valley bog site, and the only previous record for Westmorland was by Millidge and Locket (1955) for Martindale.

x The genus Robertus has been used throughout after Locket and Millidge (1953). However, Locket and Millidge (1957), write that the generic name Robertus (Cambridge 1879) must give place to Ctenium (Menge 1871), but in Locket et al (1958), they claim that nevertheless "....in view of usage, a case can be made out for retaining Robertus", and the matter must still be considered unresolved.

IX DISCUSSION.

In the three previous discussions, the more specialised topics in each section have been considered, and only general impressions of the study as a whole have yet to be examined.

Perhaps the most striking feature is the degree of ecological radiation or population interspersion as Elton (1949) calls it. Here is an example of a group of animals, which has become diversified ecologically to the extent that it appears to be exploiting, though not necessarily fully, all the habitats and food resources in the area. As a result few arthropods can be free of the danger of meeting, or being met and killed by a spider, at some point in their life histories.

The more detailed the analysis of ecological requirements, the more impressive do these subtle differences appear, as seen in the studies on M. merianae and A. cornutus, the various species of Lycosids, and the stratification and habitat preferences of Linyphiids. This phenomenon has been appreciated more and more in recent years as ecological techniques and the problems investigated have become more refined, and the present work simply adds data to a growing body of evidence. Field instances of this, in the considerable literature on the subject include comparative studies on the

Cormorant and Shag, and upon European birds of prey Lack (1945 and 1954); Lack's (1947) work on Darwin's finches; and the investigations of Hairstron (1951) on the distribution of Plethodon, of Shelford (1907) on tiger beetles, and of Dobzhansky and Pavan (1950) on Drosophila. Whilst amongst spiders, the work of Tretzel (1955a) and Luczak (1959) is of great importance.

In short, provided one looks at the ecology of animals in sufficient detail, all species seem to differ from each other in some respects at least, and everything in the present work supports this view.

It is the conclusions which are drawn from this situation that form the centre of much controversy and as the present work contains no data likely to resolve it, only a few general observations will be made. It has been customary to argue that different species exploit different resources of food, shelter and space, because if they had similar ecological requirements, they would have to compete for them with one another. It should be pointed out herethat 'competition' for any requisite implies that it is in short supply. So, as an explanation of ecological radiation amongst species, Darwin's struggle for existence is always seen by the proponents of this view, as primarily a struggle between the members of different species of animals, rather than the struggle of a species trying to survive in an unfavourable physical environment. Once this premise is accepted, and it is recognised that, in the words of Darwin, "As the species of the same genus usually have, though by no means invariably, some similarity in habits and constitution, and always in structure, the struggle will generally be more severe between them, if they come into competition with each other, than between the species of distinct genera", then attention is focused on the ecological relations of closely related species in the hope that they will reveal something of the forces which produce ecological radiation. A thesis of Gause, paraphrased by Allee et al (1949) as "...two species with identical ecology cannot persist together in the same area....", the wording of which has been frequently adapted, as shown by Gilbert et al (1952), stands at the heart of this view, but it should be noted that Gause (1934) himself was more concerned with ecological than taxonomic similarity, as shown in the following extract, "This once more confirms the thought mentioned earlier, that the intensity of competition is determined not by the systematic likeness, but by the similarity of the demands of the competitors upon the environment".

Although interspecific competition offers one explanation of ecological radiation, it is by no means the only possible one, thus Andrewartha and Birch (1954) write, "If we assume with Lack that related species have differentiated in geographical isolation, the chances are that they would also have developed different habits and preferences, so that when they were later brought into the same territory, they would select different sorts of places in which to live. It is not obligatory to suppose that these preferences were developed as a result of "competition"." In other words, different species would be expected to have some differences in their ecological requirements.

Again, there is some evidence that if a species extends over too wide an ecological range, it may split up into groups with slightly different characteristics, a point which is tacitly accepted when we look for 'physiological races'. This phenomenon has been described in Butterflies by Ford (1945) who claims that subspecies, and eventually species, as described in morphological terms, can develop at the ends of clines, and it would be interesting to see if this was accompanied by ecological divergence. Other examples of ecological radiation preceding speciation are those of Frost (1955) who quotes the apparent ecological division of the char in lake Windermere into separate Spring and Autumn spawning populations, for reasons unknown; and a similar phenomenon amongst species of trout in lake Ochrid in Yugoslavia.

As a variety of possible explanations of ecological radiation can be put forward, no single one can be assumed to be self evidently true, and thus the part played by interspecific competition must be demonstrated in an overwhelming number of cases, if the statement by Hutchinson and Deevey (1949) that "The generalization... that two species with the same niche requirements cannot form mixed steady - state populations in the same region has become one of the chief foundations of modern ecology", is to be substantiated.

The importance of interspecific competition in determining the ecological distribution of some species, has been shown by Brian (1952) for ants, but despite an abortive statistical approach to this problem by Elton (1946), Williams (1947, 1951), Moreau (1948) and Bagenal (1951), further evidence of interspecific competition has been sparse. The difficulties of arguing from ecological radiation to an explanation based upon Gause's hypothesis have been pointed out by Gilbert et al (1952). "...as this hypothesis is concerned with ecologically similar animals not living together -

whatever this means - it is difficult to derive supporting evidence from ecologically different animals which do not live together." Even where one species is apparently replacing another, as for example, the replacement of the red by the grey squirrel - Shorten (1954), and *Gammarus duebeni* by *G. pulex* - Hynes (1954) the actual requisite for which competition is occurring has not been elucidated, its existence having only been inferred. This is also true in the zones where closely related species overlap, in their distribution as in the species of *Plethodon* described by Hairstron (1951), and the distribution of planarian species in streams - Beauchamp and Ullyott (1932). It is true that laboratory studies, such as those of Moore (1952) on *Drosophila*, Gause (1934) on protozoa, and Park et al (1941) on grain beetles, have shown competition to be important in determining which species shall survive within the limits of the experimental vessel, but it is not clear how these results can be applied to the problem of the causes of ecological radiation in the field. This point has been stressed by Gilbert et al (1952) who write "...when one tries to extrapolate from culture to field conditions, the delimitation of a population becomes a stumbling block."

Commenting on Gause's thesis as the theoretical basis for explaining all ecological radiation, either in terms of present competition, or where this cannot be detected, as evidence of competition having occurred in the past, Andrewartha and Birch (1960) write "A growing number of ecologists is becoming unwilling to accept the so called law as a general principle of natural population". Be this as it may, there is it seems, good reason for examining each case on its merits. In the particular instance discussed in this work, it is unlikely that the ecological differences between the two distantly related species of orb-web spinning spiders, Meta merianae and Araneus cornutus, have arisen by mutual competition, as their habitats are normally so different, that it is only the peculiar juxtaposition of dark peat overhangs, and water filled erosion channels lined with overhanging Calluna and Juncus effusus in this particular area, which has brought them together at all.

In conclusion, some general reflections on the status of spiders in the Moorland fauna as a whole might be appropriate.

As a result of his investigations on the feeding habits of Linyphia triangularis, Turnbull (1960 a) writes "L. triangularis is evidently a truly polyphagous predator. It is able and willing to feed on a wide range of species; in fact there is no evidence to demonstrate that it will not feed on any species available to it". Where feeding habits have been studied in this investigation, as in Meta merianae and Araneus cornutus, this observation seems to hold, and in this area, the group can be considered as being general arthropodan predators. This qualitative picture was summed up previously by saying that "few arthropods can be free of the danger of meeting, or being met and killed by a spider, at some point in their life histories". The quantitative picture is much more difficult to assess, and with the present data, even a crude approximation can only be attempted in the case of the orb-web spinning spiders.

Coulson (1956) studying the predatory effect of the Meadow Pipit (Anthus pratensis) on Tipula subnodicornis, estimated that there would be 3,600,000 adult T. subnodicornis available on 10 acres, the territory of one pair of birds, and of these well under 1% would be taken as food. Comparable estimates of the predatory effect of orb-web spinning spiders, the group most obviously adapted for catching these animals are roughly as follows. The maximum estimate of captured Tipulids, judging from remains in the cocoons of A. cornutus, was 15. If these are all assumed to be T. subnodicornis (which is untrue), and M. merianae is considered as taking a similar number which is again probably an over-estimate, this figure can be multiplied by 75, the maximum number of 'large' webs capable of catching these animals ever recorded for the 3 sites in 3 years. A figure of 1125 T. subnodicornis is then obtained. The webs on these 3 sites form the bulk of the orb-web spider population in an area 5280 sq. yds, in extent, an erosion area it should be noted, which was selected because of its large numbers of orb-web spinning spiders. According to Coulson (1956) 392,727 (3,600,000 X 5280/48400) Tipulids would be available, of which the maximum estimate of 1125 taken by spiders, represents well under the.58 of 1% quoted by Coulson for the Meadow Pipit. This, of course, only means that the orb-web spinning spiders are not important predators of Tipula subnodicornis, and as it is probable that some are taken as they emerge from their pupae by Lycosids, the total 'spider effect' for even this species is not known. However, it does suggest that inter or intra specific competition for food is unlikely to be important in orb-web spinning spiders, a situation which could be inferred from the relative sizes of the stationary web catching areas, and the general space available in which potential prey can fly unmolested.

Despite this, it is hard to believe that the Linyphiids present in numbers of up to $400/m^2$ with a biomass of possibly .2 gm, in some vegetation types, are unimportant predators, but a true assessment of their role must await specialist estimates of the numbers and biomass of the various potential prey, backed up by quantitative feeding experiments on the spiders.

With regard to animals preying on spiders, the common frog (*Rana temporaria*) is the only predator which has been observed, however the viviparous lizard, *Lacerta vivipara* is common in the area, and Smith (1951) states that it is particularly fond of spiders. As, by virtue of their numbers, these predators cannot exercise significant control over spider populations it must be admitted that the controlling factors continue to remain a mystery, the only clue in the case of *M. merianae* being the apparent importance of the 'reproductive potential', which fluctuates so violently, and for unknown reasons, from colony to colony, and from year to year.

In short, it would appear that a general review of this sort serves mainly to disentangle some of the problems worthy of further investigation.

X SUMMARY.

1. A study was made of the spider fauna of the Moor House National Nature Reserve, Westmorland, an area of high Pennine Moor, of approximately 4,000 hectares.

2. Of the 71 species recorded, 17 are thought to be additions to the published records for Westmorland. The family structure of the fauna was most similar to that of Iceland, which is to say that it shows a sub-arctic pattern.

3. Only 4 species of orb-web building spiders were found, two of which, Meta merianae and Araneus cornutus were common. A. cornutus lives in a silken retreat spun amongst heather tips overhanging erosion channels and in clumps of Juncus effusus, whilst M. merianae spins no retreat, and is restricted to the underside of dark peat overhangs, where its web is spun.

4. Desiccation experiments on adult females showed that A. cornutus was more resistant to desiccation than M. merianae. The field habit of A. cornutus was drier than that of M. merianae, although field experiments suggested that sheer physical inability to survive in the other's chosen habitat was probably not a determining factor in distribution.

5. Laboratory experiments on light reactions indicated that whilst adult females of A. cornutus and M. merianae preferred light, and dark conditions respectively, the position differed in the young, where both species reacted positively to light, a situation which corresponded with field observations.

6. Three sites were chosen on which to study 'colonies' of orb-web building spiders, counting, marking, measuring and recording the position of all webs, being performed regularly.

7. In M. merianae, the webs appeared to be distributed randomly along the peat edge sites in respect of each other, although certain areas could be classed on vegetational and topographical grounds as consistently suitable or unsuitable for web spinning, Evidence of 'site tenacity' was also presented.

8. By applying Dyar's growth law to measurements made on immature animals taken from measured orb-webs, it was estimated that M. merianae passed through 6, and A. cornutus through 7, instars.

9. Both species overwintered in at least two stages; as young first or second instar spiderlings, and as mature adults.

10. In *A. cornutus*, egg maturation began in May, the peak month for egg-laying being June, and it appeared that if the eggs remained healthy, the mortality associated with hatching, the subsequent communal life, and the first moult was quite low.

11. By relating web area to instar, a method of estimating the age distribution of a colony from measurements on the webs was devised, and studies on this confirmed the view that *A. cornutus*, and possibly *M. merianae* took two years to mature.

12. Web spinning fluctuated with season, virtually no webs being recorded for 5 months of the year.

13. As a rule in these two species, webs were renewed each evening, the old web being actively destroyed. As an overall figure for 2½ seasons, the average percentage of new webs each day was 79 and 82 for *M. merianae* and *A. cornutus* respectively.

14. The amount of web spinning activity was found to vary considerably from night to night in *M. merianae*, and this was related to the mean air temperature at the time of spinning.

15. Web destruction was likewise found to be connected with mean air temperature, but there was a suggestion that the threshold temperatures for these two activities differed; web destruction proceeding at temperatures which were not suitable for the subsequent spinning of

a new web.

16. Examination of web spinning in the field showed that activity commenced with the onset of darkness, and took most of the night.

17. Populations were estimated from the maximum number of webs seen in any one day in the month, and by comparing the ratio of 'adult' to 'first or second instar' webs at the end of the season, some measure of the 'reproductive potential' of each site was judged. This was found to fluctuate violently from site to site, and from year to year.

18. The 'availability of food' in various sites was assessed by the use of 'artificial webs', and it was found that the gullies in which the spiders spin were not favourable places for catching prey.

19. No evidence of a relation between fluctuations in web spinning activity one evening, and the availability or prey the following day could be found.

20. A prey catalogue for M. merianae and A. cornutus was compiled, based on observations throughout the study period.

21. An attempt at qualitative and quantitative analyses of the prey of A. cornutus was made, and it appeared that Tipulidae formed the main bulk of the food, with Empididae and Trichoptera also important.

22. Seven species of wolf spiders were recorded from the Reserve, all belonging to the family Lycosidae.

23. Pitfall trapping in 4 vegetation types showed differential distribution between 'wet' and 'dry' habitats of the 4 most common species. Thus *Pirata piraticus* was restricted to the wettest areas, whilst *Lycosa tarsalis* was found only in the driest, *Tarentula pulverulenta* seemed to be ubiquitous, and *Lycosa pullata* was most frequently associated with the *Juncus Eriophorum* Moor Edge.

24. The results of laboratory experiments on the ability of these species to withstand desiccation fitted in well with the field data, *P. piraticus* being the least, and *T. pulverulenta* the most resistant of the 3 species tested.

25. Intensive pitfall trapping on a grid 40 ft. by 20 ft. sited on an area of heterogeneous vegetation cover showed that *P. piraticus* exhibited a very strong preference for wet, *Sphagnum* covered areas, and that this could readily be detected in an area only 800 sq. ft. in extent.

26. Activity peaks as recorded by pitfall trapping, coincided with the periods of mating activity, and the predominance of males caught was in part a reflection of their active searching for females.

27. Population estimates for the pitfall trap grid varied from 212 ± 4.38 to 62 ± 9.17 males, during the course of 2 seasons' work.

28. 'Artificial webs' designed to simulate the hammock webs of Linyphiid spiders suggested that the potential prey of these animals depended upon the vegetation type, and season, but consisted principally of Collembola, Nematocera, Hemiptera, and Acarina.

29. 52 species of Hammock-Web building spiders were recorded, which, although they showed no close correspondences with the faunas of any particular country, contained a higher than normal proportion of forms associated with mountains.

30. A sampling technique was devised for studying this group of animals, in which 10 turfs 21 cms X 30 cms were cut on each sampling occasion, and extracted by a lateral heat extraction apparatus, modified after Duffey.

31. Various heating regimes were investigated, and finally a 5 day extraction period was adopted as standard procedure.

32. Humidity and temperature gradients were measured throughout the apparatus, and it was found that these tended to drive the animals into the water-filled trough.

33. The reactions of the various animals groups to the heating regime were studied. Each group seemed to have a characteristic emergence pattern.

34. These emergence patterns appeared to be affected by the season, and in the case of spiders by the age of the animals.

35. Although the extraction efficiency of this method was compared with that of other techniques for spiders, an estimate of absolute efficiency could not be made.

36. The problem of 'constancy of errors' was investigated with reference to one particular source of error, and it was found to fluctuate with the animal group. Within a given group however, it also fluctuated with season, age of the animals, spider species, the vegetation type being extracted, and other causes which could not be found.

37. Four main vegetation types were studied, and both qualitative and quantitative differences in their faunas were detected.

38. The spider populations in the four areas simply mirrored the general arthropod populations, and it was suggested that being an easily extracted group, it might be used as an index of faunistic productivity, in so far as general litter-living arthropods are concerned.

39. Heavy grazing pressure on limestone grassland in the area was associated with a marked reduction in the spider, and general arthropod faunas.

40. In an area of closely grazed alluvial grassland interrupted by tussocks of *Nardus stricta* and *Juncus effusus*, the spider fauna was in the main restricted to the tussocks of denser foliage.

41. Detailed examination of a stand of *Calluna/Eriophorum* blanket bog vegetation indicated that the Linyphiid species were ecologically separated within the vegetation according to the stratum in which they most frequently spun their webs.

42. A seasonal examination of the Linyphiid fauna of the *Calluna/Eriophorum* vegetation was undertaken using a grid sampling technique, and it was found that the only significant cause of variation in spider numbers was the time of the year when the samples were taken.

43. Within this relatively uniform area, the population showed significant aggregation, there being an excess of small negative deviates.

44. A high percentage of mature spiders was found in Autumn, falling to a very low value in May, June and July when the eggs were hatching, and the young spiderlings growing up.

45. When the number of mature animals of individual species was studied, the absence of any obvious seasonal patterns of maturity was as striking as it was inexplicable.

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XII. APPENDICES.

APPENDIX 1.

Homogeneity of Spider Emergence Data.

- Based on Heather Grid Samples.

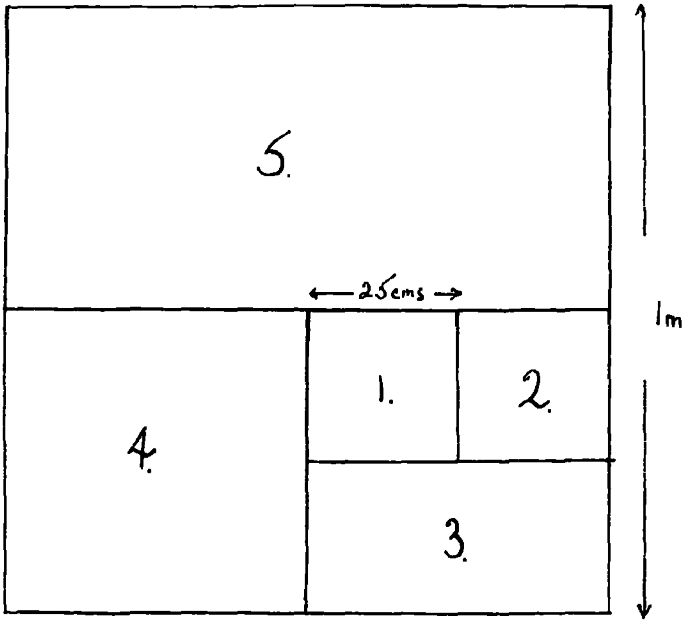
Date		Extraction Day					Σ
		1.	2.	3.	4.	5.	(4 df)
5/8/58	No.	19	10	4	26	11	70
	χ^2	.526	.085	1.062	13.74	8.14	23.553***
26/8/58	No.	28	16	20	16	23	103
	χ^2	.788	.5	10.616	.411	5.501	17.816**
23/9/58	No.	13	5	5	9	16	48
	χ^2	.352	.25	.04	.007	.111	.76
22/10/58	No.	12	3	0	5	25	45
	χ^2	.266	1.396	4.28	1.249	4.63	11.821*
17/11/58	No.	14	3	5	8	25	55
	χ^2	.146	2.417	.01	.411	1.29	4.274
16/12/58	No.	12	5	2	3	25	47
	χ^2	.133	.205	1.365	3.62	3.736	9.059
21/1/59	No.	11	1	4	9	23	48
	χ^2	0	4.41	.071	.007	1.81	6.298
20/2/59	No.	7	16	4	7	56	90
	χ^2	9.058	1.563	2.429	5.396	16.757	35.203***
8/4/59	No.	8	4	4	9	29	54
	χ^2	1.567	1.306	.253	.073	4.544	7.743
29/4/59	No.	3	4	2	9	17	35
	χ^2	3.168	.069	.531	1.076	1.472	6.316
27/5/59	No.	12	3	10	21	18	64
	χ^2	.499	3.41	2.51	7.459	1.161	15.039**
3/7/59	No.	34	20	6	14	24	98
	χ^2	5.839	4.108	1.183	.838	3.731	15.699**
21/7/59	No.	30	25	18	25	28	126
	χ^2	.037	4.496	3.012	.179	6.83	14.554**
Σ	No.	203	115	84	161	320	883
Σ	χ^2	22.379 *	24.215 *	27.362 **	34.466 ***	59.713 ***	168.135 ***

* = <.05 ** = <.01 *** = <.001 (48 df)

APPENDIX II. 1. Notes on Techniques.

Braun Blanquet Analyses of the 4 Principal Habitats.

The total area examined for each analysis was 1 metre square, and this was divided up :-



The areas were examined in turn as numbered.

The B B Cover Index was used, and a Key to this is set out below.

BB 5 = Cover >75%
BB 4 = " 50 - 70%
BB 3 = " 25 - 50%
BB 2 = Abundant, but cover only 5 - 20%
BB 1 = Scarce or scattered, cover very small
BB X = Isolated.

N.B. After the first square, only the cover of new species is recorded.

2. Calluna/Eriophorum Site.

Braun Blanquet Quadrat A. (Back rt. hand corner square 6)

Species	Square Number 1	2	3	4	5
Angiosperms					
Calluna vulgaris	3				
Empetrum nigrum		X			
Eriophorum vaginatum	2				
E. angustifolium	X				
Bryophytes					
Aulocomnium palustre	X				
Calypogea trichomanes	X				
Lophozia floerkii	X				
Plagiothecium undulatum	X				
Pleurozium scherberi					X
Polytrichum commune	X				
Ptilidium ciliare	X				
Rhytidiadelphus laureus					X
Sphagnum cuspidatum ag.	2		N.B 4		
Lichens					
Cladonia sp.		X			
Lichen A - unidentified		X			
" B - "		X			
" C - "					X

Braun Blanquet Quadrat B. (Back lt. hand 8, overlapping 3)

	Square Number				
Species	1	2	3	4	5
Angiosperms					
Calluna vulgaris	4				
Empetrum nigrum	1				
Eriophorum vaginatum		2			
E. angustifolium	X				
Rubus chamaemorus					X
Bryophytes					
Aulocomnium palustre		X			
Calypogea trichomanes	X				
Lophozia floerkii	X				
Plagiothecium undulatum	X				
Rhytidiadelphus laureus		X			
Sphagnum cuspidatum ag.	X				
S. rubellum	5				
Moss A - unidentified	X				
Liverwort A "		X			
Lichens					
Epiphytic lichen - unidentified	X				
Lichen A "		X			
Lichen B "			X		

Braun Blanquet Quadrat C. (Back rt. hand corner square 5)

Species	Square Number				
	1	2	3	4	5
Angiosperms					
Calluna vulgaris	4				
Empetrum nigrum			X		
Eriophorum vaginatum	2				
E. angustifolium				X	
Bryophytes					
Aulocomnium palustre	X				
Calypogea trichomanes	X				
Lophozia floerkii	X				
Plagiothecium undulatum	X				
Rhytidiadelphus laureus	X				
Ptilidium ciliare	X				
Sphagnum cuspidatum ag.	3				
Lichens					
Lichen A - unidentified	X				
" B - "	X				

3. - <u>Juncus Site</u>. - <u>30/7/59</u>.

Species	Square Number				
	1	2	3	4	5
Juncus squarrosus	8				
Agrostis tenuis	X				
Agrostis canina	2				
Festuca ovina	6				
Galium hercynicum	3				
Carex nigra	X				
Luzula campestris				X	
Potentilla erecta				X	
Eriophorum angustifolium					X
Nardus stricta					X
Plagiothecium undulatum	2				
Polytrichum commune	X				
Rhytidiadelphus laureus			X		
Hipnum cupressiforme			X		
Aulocomnium palustre					X

4. - <u>Festuca/Nardus Site.</u> - <u>30/7/59</u>.

Species	Square Number				
	1	2	3	4	5
Nardus stricta	8				
Festuca ovina	4				
Agrostis tenuis	3				
Agrostis canina	X				
Luzula campestris	X				
Galium hercynicum	2				
Polygala vulgaris	X				
Anthoxanthum adoratum			X		
Hipnum cupressiforme	1				
Rhytidiadelphus laureus	X				
Polytrichum commune			X		
Splanchnum ovatum				X	

5. - Rough Sike Limestone - Grazed - 29/7/59.

Species	Square Number 1	2	3	4	5
Selaginella selaginoides	2				
Thymus drucei	4				
Potentilla erecta	3				
Trifolium repens	3				
Luzula compestris	2				
Galium hercynicum	X				
Rumex acetosella	2				
Euphrasia confusa	X				
Achillea millefolium		X			
Carex caryophyllea		X			
Veronica officinalis		X			
Cirsium sp.			X		
Prunella vulgaris			X		
Viola riviniana				X	
Cerastium vulgatum					X
Viola lutea					X
Alchemilla vestita					X
Cardamine pratensis		X			
Festuca ovina	8				
Agrostis tenius	5				
Anthoxanthum adoratum	X				
Rhacomitrium lanuginosum	X				
Polytrichum commune	3				
Mnium undulatum	X				
Mnium punctatum			X		

APPENDIX III.

Variation in Plant Cover on Heather Grid.

% Heather - Cover estimations on a 2' x 2' quadrat.

Grid Square	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.
	4	6	9	9	8	3	8	9	5	5
	6	6	6	5	7	1	5	5	8	8
	9	5	5	3	9	6	4	3	8	4
	7	4	5	5	8	5	5	8	8	7
	5	8	4	5	7	4	8	8	7	8
	7	4	6	8	7	4	6	8	9	5
	6	4	8	5	5	2	8	6	4	7
	6	8	9	6	6	9	3	7	5	5
	5	9	6	9	7	9	7	6	7	9
	5	8	8	9	8	4	8	5	7	7
Sample Totals	60	62	66	64	72	47	62	65	68	65
Means	6	6.2	6.6	6.4	7.2	4.7	6.2	6.5	6.8	6.5

Total No. of items = N = 100. Total of all items = T = 631

Grand Average = 6.31

APPENDIX IV.

Analysis of Variation. -

1. Time and Extraction Position.

Spiders from Heather Grid.

Date	Extraction Unit Number. 1	2	3	4	5	6	7	8	9	10	ΣX	$(\Sigma X)^2$
1958												
5/8	13	10	7	11	12	13	12	15	5	6	104	10816
26/8	27	5	18	16	3	21	8	9	7	26	140	19600
23/9	20	7	5	11	10	8	9	14	12	4	100	10000
22/10	12	12	4	17	1	7	3	8	8	13	85	7225
17/11	9	10	13	17	12	12	8	19	3	2	105	11025
16/12	5	15	13	3	20	9	8	3	4	4	84	7056
1959												
21/1	1	15	10	16	4	14	10	15	10	2	97	9409
20/2	9	14	11	5	13	25	19	18	8	22	144	20736
8/4	18	17	6	8	23	9	13	16	4	7	121	14641
29/4	5	8	13	6	3	14	7	13	8	6	83	6889
27/5	7	8	11	8	15	7	6	13	3	6	84	7056
3/7	5	6	9	10	5	8	8	8	28	19	106	11236
21/7	13	11	11	7	17	15	18	20	17	21	150	22500
17/8	9	4	14	30	12	21	17	44	15	12	178	31684
14/9	15	10	17	15	10	24	20	19	11	2	143	20449
ΣX	168	152	162	180	160	207	166	234	143	152	1724	210322
$(\Sigma X)^2$	28224	23104	26244	32400	25600	42849	27556	54756	20449	23104	304286	

$\Sigma X^2 = 20290$

2. Time and Grid Position.

Date	Grid Number									
1958	1	2	3	4	5	6	7	8	9	10	Σ X
5/8	15	12	10	12	6	7	13	13	11	5	104
26/8	18	5	7	27	26	9	21	3	16	8	140
23/9	8	12	20	14	4	9	10	5	7	11	100
22/10	3	8	12	8	7	13	12	1	17	4	85
17/11	13	19	2	9	10	12	17	3	8	12	105
16/12	20	9	3	13	8	4	4	3	15	5	84
1959											
21/1	2	10	14	15	4	16	10	10	15	1	97
20/2	9	11	25	22	13	14	5	8	19	18	144
8/4	13	17	9	16	7	18	8	23	6	4	121
29/4	13	6	3	13	6	14	7	5	8	8	83
27/5	8	8	7	7	3	15	13	6	6	11	84
3/7	8	9	8	5	5	6	10	8	19	28	106
21/7	18	11	15	20	21	17	13	7	17	11	150
17/8	21	44	30	9	14	17	15	4	12	12	178
14/9	15	10	15	10	17	24	11	2	19	20	143
Σ X	184	191	180	200	151	195	169	101	195	158	1724
$(\Sigma X)^2$	33856	36481	32400	40000	22801	38025	28561	10201	38025	24964	305314

Analysis of Variance - Working.

Correction Factor = T^2/N = 2972176/150 = 19814.

Tot. Sum of Squares = 26290 - 19814 = 6476 with 149 df.

Bet. Unit Sum of Squares = 304286/15 - 19814
= 472 with 9 df.

Bet. Date Sum of Squares = 210322/10 - 19814
= 1218 with 14 df.

Bet. Grid Sum of Squares = 305314/15 - 19814
= 540 with 9 df.

Residual Sum of Squares = 4246 with 117 df.

This data has then been summarised in Table 74.

APPENDIX V.

Since this thesis was prepared, an interesting paper has been published by Witt and Baum (1960), on the changes in the orb-webs of spiders during growth.

By breeding Araneus diadematus in the first instance, measuring the web catching area, (area of the viscid spiral) and recording the number of spirals and radii, during the ensuing months, the web changes during maturation were followed.

14 animals were studied, but it is unfortunate that in the resulting mean measurements on the webs, no mention is made of the instar of the spiders, or the point at which they became mature. This makes the results difficult to interpret, and the levelling off of the 'increase in area' curve after August was probably due to the maturing of the animals at this time.

The finding of a simple relationship between leg size and web size confirms the present results, and the discovery of a similar relationship between body weight and mesh size, though outside the scope of the present work is of great interest, and should be checked against field observations.