BIONOMICS OF THE SPIDER

TIBELLUS OBLONGUS (WALCKENAER)

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ABSTRACT

A general investigation into the biology and ecology of the crab spider Tibellus oblongus was started in winter 1964/65 at the Imperial College Field Station, Silwood park in Berkshire. Research continued till autumn 1967 and covered the following areas:-

The life cycle and development characteristics of the spider were elucidated by laboratory rearing under varying environmental conditions in conjunction with the study of a field population throughout the three years. It was found to be biennial in development with a certain proportion of the population maturing each summer.

A population of the species in an area of typical grassland was studied and the characteristics and locations of the preferred microhabitats during the year were determined. The winter hibernation sites proved to be tussocks of the grass Dactylis glomerata L. which stayed warmer than adjacent areas. The spider's summer predation sites tended to be restricted to microclimatically unique "Special Areas" of mixed live and dead grass stems which formed a warmer and more humid environment than their surroundings.

Various aspects of the spiders' behaviour were studied in the field and in the laboratory. These included: mating, moulting incubation, aggregation, dispersal and defence.

Finally, the predatory behaviour of the species was examined in depth using the experimental component analysis technique and as a result, various modifications to the functional response model are suggested and integrated into the model to extend its generality to ambush predators of similar type to T. oblongus.

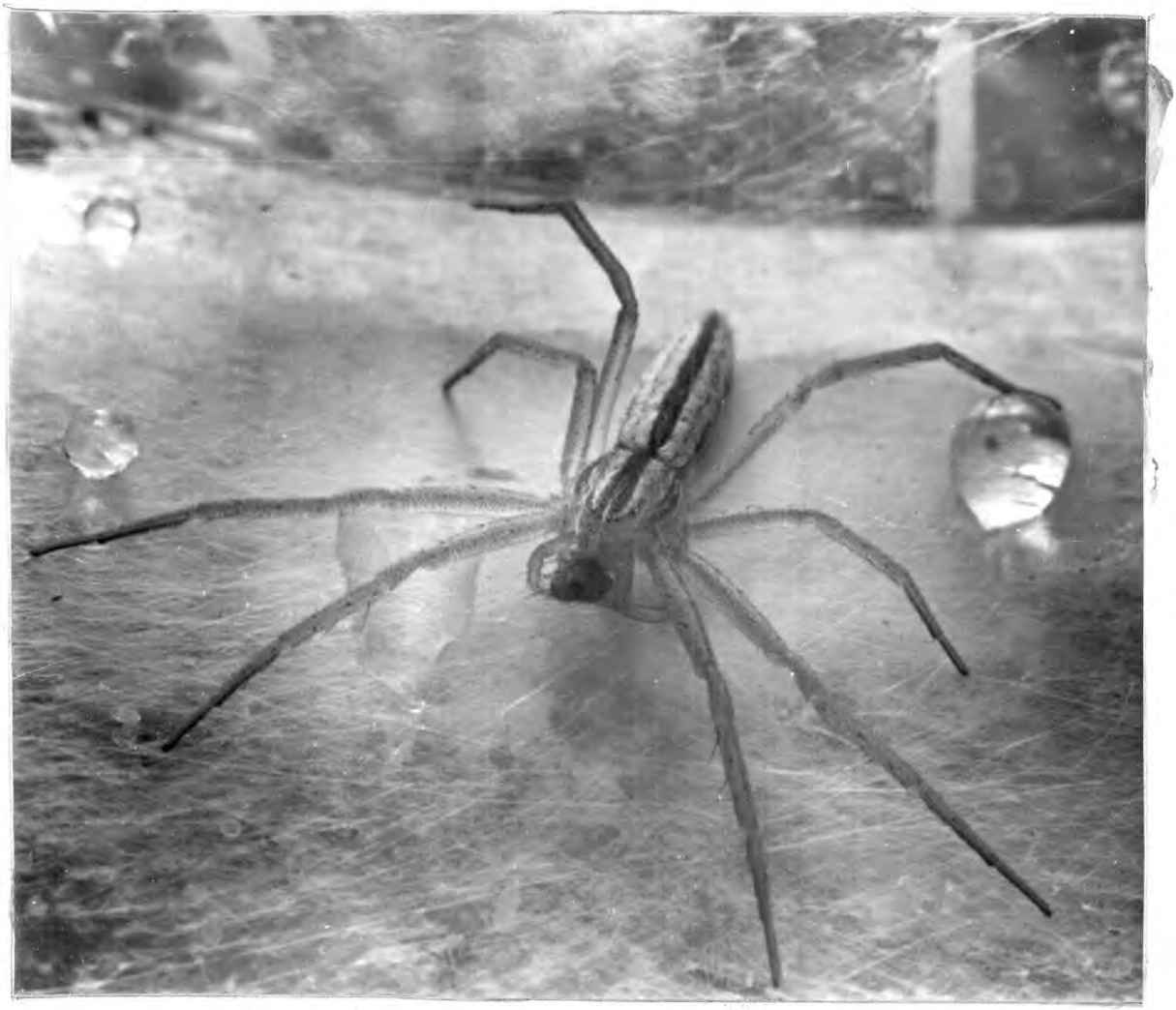


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TIBELLUS OBLONGUS

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SECTION 1
INTRODUCTION

The species T. oblongus (FIG 1) is distributed throughout Europe, Asia and in North America from Alaska across to Eastern Canada and south to Mexico, becoming scarcer in its southern limits (SCHICK 1965). In common with many spiders it has never been the object of intensive research, except as part of a community, despite its relatively unique morphological position within the family Thomisidae (SECTION 2), and its very common occurrence on coarse grasses and rushes, in damp places, on sand dunes and rough ground (LOCKET & MILLIDGE 1959).

At the Imperial college Field Station, Silwood Park, in Berkshire, a general programme of biological and ecological research was started in January 1965 and continued until September 1967. The aims were:-

to unravell the life history of the species-hitherto unknown-and to test the effects of various environmental conditions on its development,

to shed light on certain aspects of its behaviour especially those of ecological significance eg. microhabitat preferences-which were unknown, dispersal and aggregation behaviour, defense and predation, none of which had been studied in depth;

finally, during the later stages of the work described in this thesis, a detailed study was made of the predatory behaviour of the spider along the lines of the experimental component analysis technique developed and described by HOLLING (1966). During the course of this work it was hoped that broad ecological conclusions might be drawn concerning the predatory characteristics of other spiders and possibly other predators in general.

SECTION 2

TAXONOMY AND MORPHOLOGY

2.1 GENERAL CONSIDERATIONS

Tibellus oblongus (Walckenaer)

Classification:

Phylum	Arthropoda
Class	Arachnida
Order	Araneae
Family	Thomisidae
Genus	Tibellus

Called *Aranea oblonga* by C.A.Walckenaer 1802
Tibellus oblongus by A.R.Jackson 1911

General Characters of the Family Thomisidae (LOCKET and MILLIDGE 1959)

Typically crablike in appearance, abdomen long in *Tibellus* and *Thanatus*. Eyes are small, both rows are recurved. Legs I and II are long and stout and laterigrade except in *Tibellus*. The legs bear ventrally a variable number of paired spines and two tarsal claws. Chelicerae are small, bearing no teeth or one on the outer edge.

Genus *Tibellus* - E.Simon 1875

Carapace appreciably longer than wide. The anterior eyes with the posterior medium pair form a small, compact hexagonal group from which the posterior laterals are conspicuously removed.

The abdomen is long and cylindrical or cigar shaped. Legs are relatively long, bearing scopulae on both tarsi and metatarsi.

This genus contains two similar species: *T.oblongus* and *T.maritimus* (Menge), formerly confused with one another. They are very active spiders, found on coarse grasses and rushes. When disturbed, they run with great rapidity up the stems of grasses; when at rest they extend their four anterior legs forwards and the four posterior legs backwards along a stem, in this way becoming very inconspicuous. The two species can be separated with certainty only by their genitalia.

Tibellus oblongus

Length ♀ up to 10mm)
♂ up to 8mm) (LOCKET AND MILLIDGE 1959).

♀ 7.5 to 10mm)
♂ 6.6 to 8mm) (My findings agreed with the above)

This species is of a sandy or straw colour (♀) or greyish (♂) with a darker central band on the abdomen. It is usually devoid of spots (cf.T.maritimus).

Occurrence: very common on coarse grasses and rushes, in damp places, on sand hills and rough ground. Adult in summer.

Distribution: There has been much confusion in the past over the Tibellus species. There are five named species in France, some of which seem to be common to the whole of Southern Europe and reach as far north as Jutland. The French species T.parallelus (Chyzer and Kulchinski) is equivalent to our T.oblongus and the French T.oblongus is equivalent to our T.maritimus. This is because of historical reasons, not because they are difficult to distinguish. The French and English nomenclatures arose independantly and have only been reconciled recently. (Clark, verbal communication).

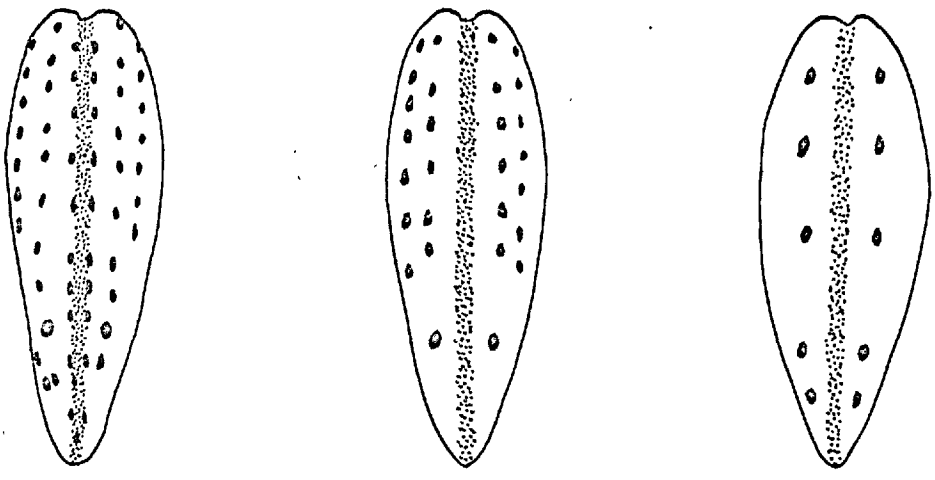
T.oblongus and T.maritimus are easily distinguishable by their genitalia, also T.maritimus is larger and of a more greenish tinge, it is plentiful only on sand dunes and marshes, (Duffey, verbal communication),(COOKE & COTTON 1961).

All the Tibellus spiders that were collected in Silwood Park were examined microscopically after death and not a single T.maritimus was found.

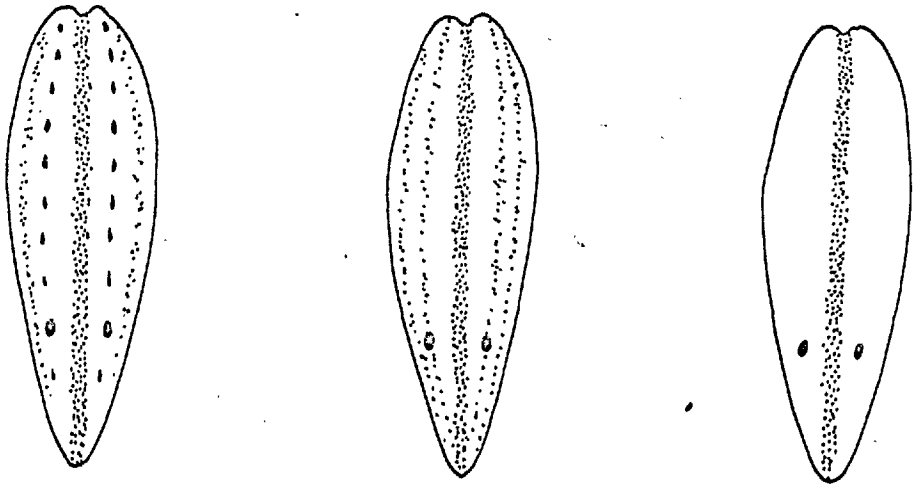
2.2 SPOT PATTERNS

LOCKET and MILLIDGE(1959) consider thatthe abdominal spot pattern can be used as a specific character, although not as an absolute one. The T.oblongus that were collected in Silwood Park ranged from "not spotted" i.e. two spots only, to

FIG. 2.
T.OBLONGUS ABDOMINAL PATTERNS



"SPOTTED"



"NOT-SPOTTED"

EXAMPLES FROM SILWOOD

"heavily spotted" i.e. about 60 spots. See FIG 2. The spotted individuals comprised about 20% of the population.

In order to clarify the relationship between the "spotted and the "not spotted" individuals, records were kept of their behavioural, physical and physiological characteristics. These were observed during experiments that will be described in later sections. The records of the "spotted" individuals are given in TABLE 1 and FIGs. 3 and 4 since they have a bearing on the taxonomy of the species.

2.2.1 Numbers collected are given in TABLE 1

2.2.2 Sizes at capture are given in FIG 4

The size of individuals that were collected varied greatly and the distribution of sizes in "spotted" and "not spotted" individuals did not differ significantly in the third and fourth Instars.

4th Instar males $\chi^2 = 4.56$ D.D.F.=2 n = 19

4th Instar females $\chi^2 = 0.625$ D.F.=2 n = 20

2.2.3 Time taken to first moult in captivity

The fourth Instar juvenile stages were placed in constant temperature rooms; one set at 20°C and another at 25°C. The time taken to the first moult by the "spotted and "not spotted" individuals was noted and compared. No statistical analysis was made as the number of individuals was low, but the histograms (FIG 3) indicate that there was no difference between the two types of individuals.

2.2.4 Behaviour

During the observations on mating (see SECTION 5.4.8), spotted females were mated with not spotted males and vice versa. Mating followed the same pattern, took the same length of time and the females were successfully fertilised in both cases. Unfortunately, none of the resulting offspring was reared to the stage where the spots were visible, so there is no information on the inheritance of the spot patterns.

TABLE 1.

Numbers of SPOTTED and NOT SPOTTED T.OBLONGUS found at Silwood Park Winter 1964/65

	SPOTTED			NOT SPOTTED			%Sample Spotted		
Instar	♂	♀	total	♂	♀	total			
3	6	5	11	23	29	52		21·1	
4	12	4	16	30	41	71		22·5	
							♂	♀	total
TOTAL	18	9	27	53	70	123	34·0	12·9	21·9

FIG. 3

Time taken to first moult by T.OBLONGUS found Winter 1964/65, put in const. temp.

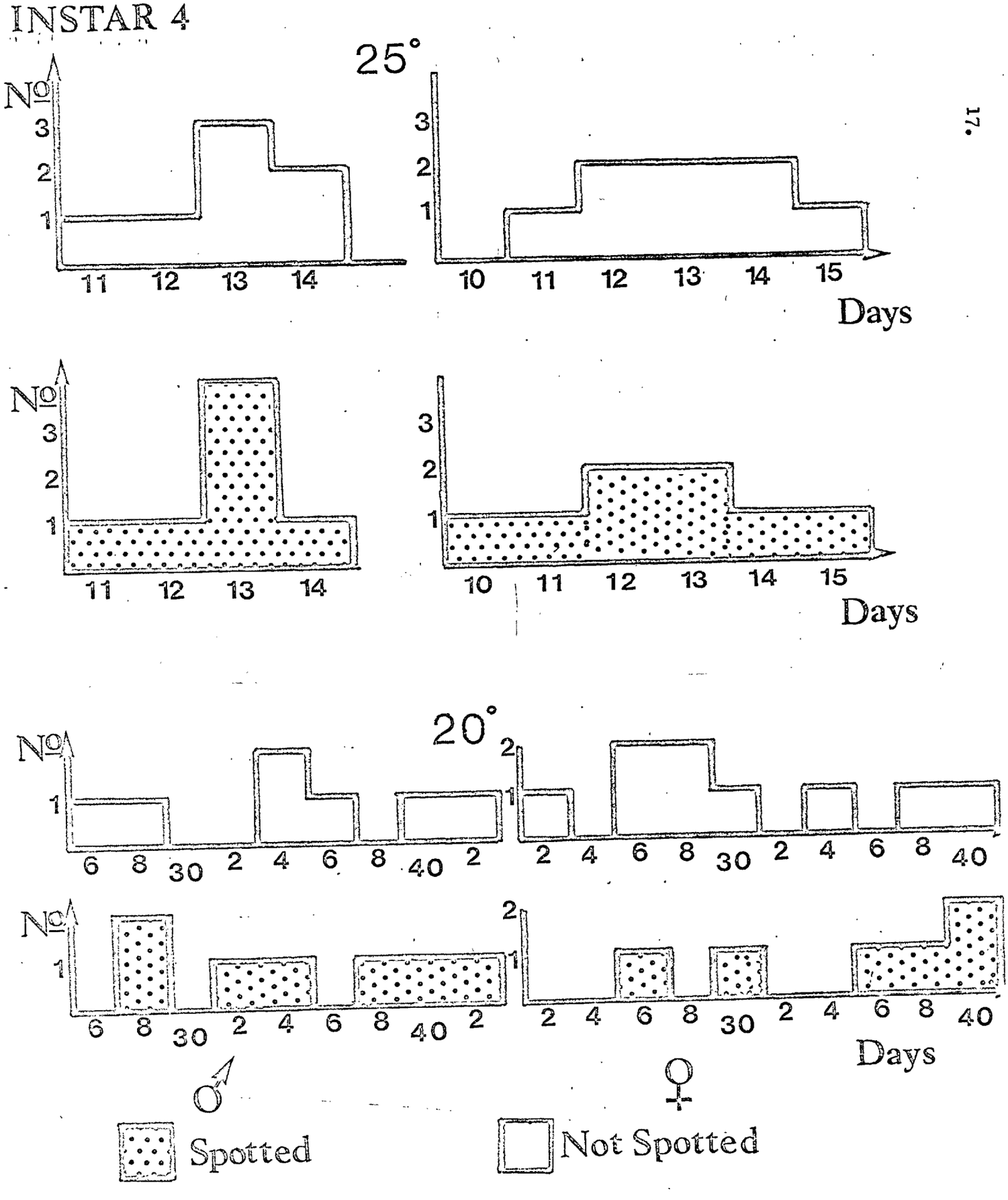
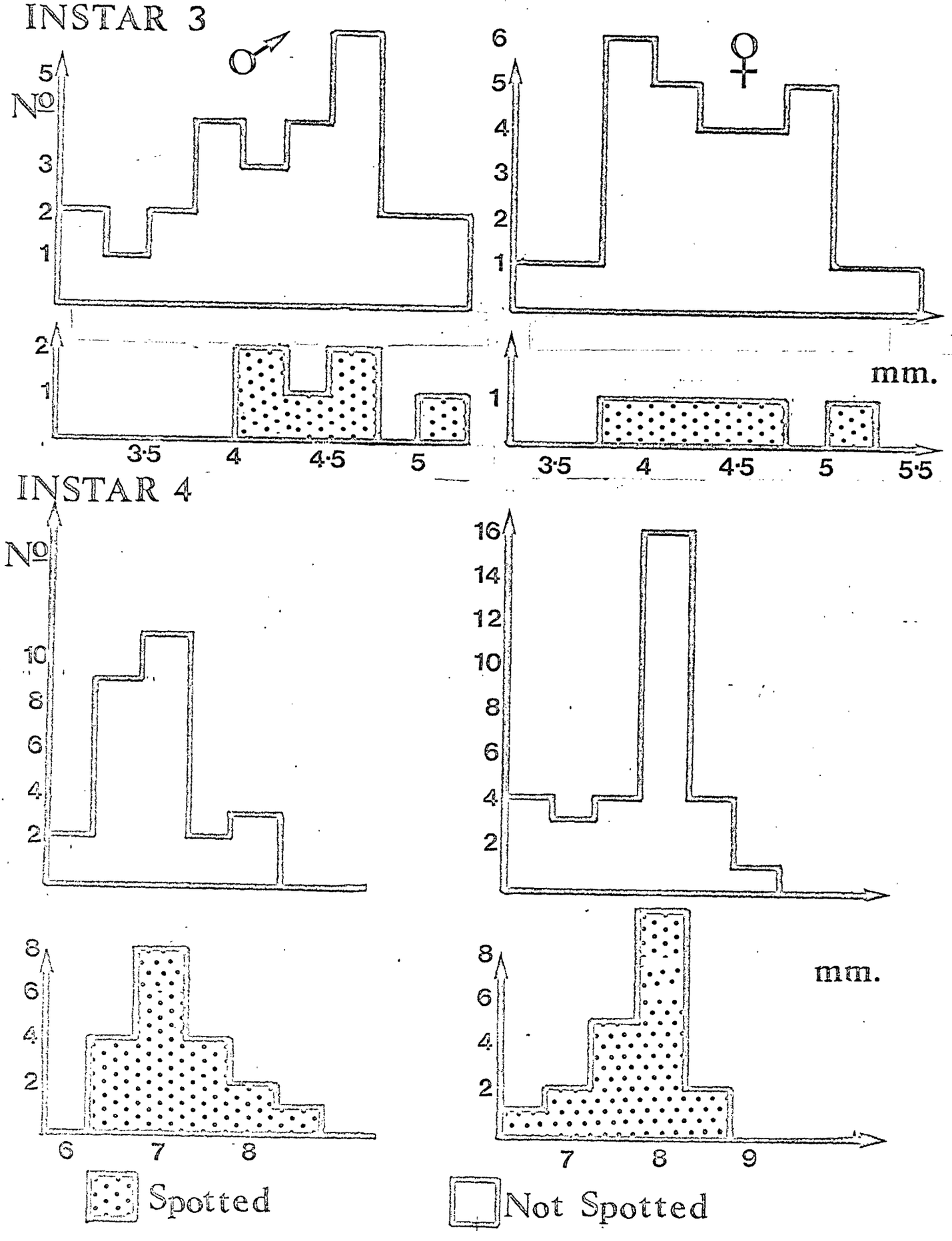


FIG. 4

Length of T.OBLONGUS from Silwood in Winter.



No major difference was seen in the predatory and defensive behaviour patterns, or in the length of incubation of the spotted and not spotted individuals.

2.3

CHANGES IN ABDOMINAL PATTERN

GABRITSCHEVSKY (1927) investigated colour changing in the related Thomisids Misumena vatia (Clerk) and M.aleatoria (Hentz) . Spiders of these species are generally found on flower heads of the same colour as their abdomen. He found that the background colour of the adult females could change from white to yellow and vica versa within three or four days, and that the colour change corresponded with the colour of the substrate. A yellow adult spider placed on white paper changed from yellow to white and a white spider changed to yellow when placed on yellow paper; also, he thought that this occured in both adult and juvenile males of M.vatia, M.aleatoria and Misumessus asperatus. (Hentz)

BRISTOWE (1958), noticed that white patches on the abdomen of the Linyphiid Floronia bucculenta (Clerck) contracted instantaneously to pinpoints when the spider was disturbed or dropped to the ground. He records a similar occurrence in an Australian Argiopid, Phonognatha wagneri. An instantaneous colour change also occurs in Tetragnatha extensa (Linnaeus) Tetragnathidae. When the spider is disturbed and drops to the ground amongst the grass stems, a network of black lines appears on the abdomen. In this way it becomes less conspicuous. In the case of the instantaneous colour changes, the abdominal pattern gradually reverts to normal in several minutes.

From a review of the literature and from my own studies three basic types of changes in abdominal colour andppattern have been recorded:

a) Gradual adaptation to substrate colour during the whole life of the spider, or at least the last three Instars.

e.g. Misumena vatia
M.aleatoria
Misumessus asperatus

b) Response to a change in the colour of the substrate over 3 to 30 days.

e.g. adult female M.vatia

c) Instantaneous colour change in response to a disturbance

e.g. Floronia bucculenta
Phonognatha wagneri
Tetragnatha extensa

Types a) and b) involve pigment deposition, type c) probably involves muscle action. All three types of change presumably have the function of making the spider inconspicuous. In the case of types a) and b) it seems probable that the adaptation is part of the predatory behaviour of the spider; the colour adopted makes it less visible to potential prey. Experiments by Bristowe confirm this. He placed either a black or a yellow pebble on each of a number of flowerheads, and he found that the flowerheads with a black pebble were visited by less flying insects than those with a yellow pebble. However, the colour change type c) seems to be a defensive reaction, occurring when the spider has been disturbed by a potential predator. The change in pattern operates by breaking up the outline in the case of Tetragnatha extensa and by matching the spider's colour to that of its background in the case of Floronia bucculenta and T.extensa.

The spiders recorded as showing type c) colour change depend on a web a catch their prey, so presumably their conspicuousness is less important than that of the Thomisids which attack prey which comes near them or lands on them.

When T.oblongus is in its normal predatory position amongst grass stems, it is camouflaged by its body shape, its overall colour and especially by the longitudinal stripes on the abdomen. The important function of the spots is probably to raise or lower the general colour tone of the spider according to the general colour tone of the surrounding grass. The surrounding grass can vary in tone according to the proportion of dead to live stems. Another possible function of the spots might be to break up the outline of the spider while it is lying in wait for prey or after it has performed its short escape run as mentioned earlier.

T.oblongus was therefore investigated for all three types of colour change.

JACKSON (1911) observed developing T.oblongus and thought that the spots disappeared with age. However, the difference in proportion on non-spotted to spotted individuals between the third and fourth Instars of spiders collected at Silwood Park was not significant, $\chi = 0.067$ See TABLE 1.

When the spiders collected in winter 1964/65 were placed in the constant temperature rooms, half were placed on a white enamel tray and half were placed on black paper. Although the numbers of spots on each spider were not recorded, at no moult did a spider which had been classed as "spotted" or "heavily spotted" became "not spotted" or "spotted" respectively. As far as I could tell, there was no change in the number of spots at any stage in the development, with one exception. At the last moult of the male, the abdomen of the emerging adult is covered by a coat of short, grey hairs. The adult males all appear to have the same greyish colour, regardless of whether they had developed from spotted or not spotted juveniles.

Whenever T.oblongus was disturbed or threatened in the laboratory, there was no change in the abdominal pattern during any stage of the defensive behaviour.

No evidence of the ability to change the abdominal colour or pattern was found in T. oblongus.

2.4 CONCLUSION

Although the comparison of the characteristics of spotted and not spotted individuals was not rigorous, it became apparent that the variation in abdominal pattern is not reflected in major physiological, physical or behavioural differences.

In the experiments and observations to be described in later sections the species is treated as being homogenous.

SECTION 3

LABORATORY REARING

3.1 SOURCE OF MATERIAL

During the three winters 1964/65, 1965/66, 1966/67, T.oblongus were collected from Silwood Park and brought into the laboratory for rearing. The spiders were collected from tussocks of the grass Dactylis glomarata L. where they were found to overwinter. This grass is widespread in Silwood Park.

The sizes and numbers of individuals from one tussock varies according to the method of extraction and according to the location of the tussock. Collecting was done on a dry day so that any spiders that were disturbed would not stick to the wet stems by capillary attraction.

Methods of Extraction

In the Field.

a. Sweeping

The sweep net was moved through the stand of Dactylis about six inches above the ground because the density of the lower vegetation prevented deeper penetration. Another disadvantage of this method was that the specimens were likely do be damaged when retrieved from the net.

b. Examination of the tussock by hand

The mass of dead vegetation surrounding the base of the tussock was separated and disturbed, any T.oblongus revealed were captured by hand or with a 'pooter'. The usual escape reaction of T.oblongus when disturbed is to run upwards and towards the light along the grass stems, but in cold weather this behaviour in not so pronounced; firstly, the spiders are lethargic because of the temperature, also they tend to move downwards when exposed to the cold air.

c. Vacuum sampling

The nozzle of the vacuum was moved through the dead vegetation at the base of the tussock and along the stems; the bag was then searched for T.oblongus. The electric vacuum could only be used within range of the power points in the field and T.oblongus was

not very abundant in this area. The hand operated vacuum was found to be too cumbersome and not powerful enough to extract much fauna from the base of the tussocks.

d. Shaking

This method is based on that of PEARCE (1948). The dead leaves surrounding each tussock were separated from the soil and litter on which they were lying and, together with the upright living stems and leaves, were cut off at a height of 15 cm from the ground, leaving only the basal vegetation of the tussock. The fibrous base of the tussock, together with this lower part of the vegetation, was then cut away from the underlying soil with a saw-toothed knife. (FIG 5).

The two parts of the tussock were then vigorously shaken over a sheet of dark green P.V.C. that had been spread on the ground. Dark green was chosen as a search substrate because this is the colour which gives the greatest contrast to the straw coloured T. oblongus. The majority of specimens were found in the basal part of the tussock which was turned upside down and held one hand on each side and rapidly pressed and pulled apart, as one would operate a concertina for example.

Extraction in the Laboratory

The tussocks, cut out as described above, were put in a polythene bag and brought to the laboratory.

e. Shaking

The tussock was shaken, as in the field, above a cleared, dark brown bench top, the debris shaken out was searched for the spiders.

f. Tullgren Funnel

The tussock was placed base downwards in a Tullgren Funnel of nine inches in diameter. The usual method of extracting small animals in this way, drives them out of the base funnel into a tube. However, in the case of T. oblongus the heat and light of the bulb and the ambient laboratory temperature activated the spiders of Instar 4 which moved up the grass stems and up the inner surface of the funnel and were collected round the upper rim of the funnel, usually within an hour or so.



FIG 5 **Sampling a Dactylis tussock**

The younger Instars were eventually forced out of the base of the tussock by dessication in the usual way.

The results of the different methods of collection can be seen in TABLE 2.

A comparison of the different collecting methods is not straight forward, since many variables were involved in determining the best method. The best method being simply that which gave the most specimens of the greatest variety for the least time and effort spent collecting. The relevant variables include: the number of tussocks sampled, the size, age, condition and location of the tussocks, climatic conditions at the time of sampling, the exact date of sampling, and whether the tussock had been sampled previously. An investigation into the effects of all these variables was impracticable, so information concerning the efficiency of the various methods was found in the following way.

Several tussocks were each subjected to a succession of extraction methods. They were first swept, then searched by hand, then put in a Tullgren funnel, then shaken in the laboratory. In a few of these cases, only the final shaking revealed any T.oblongus. It became apparent that shaking was the most efficient collecting method in winter, both as regards the total number of T.oblongus extracted and as regards least bias in the proportions of the three Instars found. There seemed to be no difference between the results of shaking in the field or in the laboratory, but most of the shaking was done indoors for convenience.

After these comparisons, the tussock shaking method was adopted as the source of specimens in winter. The great disadvantage of this method is that it destroys the overwintering places of T.oblongus and populations were found to be depleted in years following intensive collecting in a restricted area.

TABLE 2.

Numbers of T.Oblongus collected by various methods, Silwood Park OCT.→MARCH.

	FIELD				LAB.	
INSTAR	Sweeping	Hand	Vacuum	Shaking	Tullgren Funnel	Shaking
2				5	2	149
3		4		2		78
4	21	10	2	10	3	107
TOTAL	21	14	2	17	5	334

3.2 APPARATUS

During the first set of rearing experiments, 1964/65, it was decided to keep the spiders separated from each other for two reasons. Firstly, possible cannibalism would be avoided, and secondly, closer observations could be kept of the development of each individual.

The spiders were each kept in an 8 cm x 2.5 cm glass tube containing a small cotton wool ball to hold the water supply. The cork was bored with a $\frac{1}{4}$" hole and gauze was glued across the end of the hole inside the tube, this allowed air exchange. The spiders appeared to eat and drink quite normally in these containers. Food in the form of various species of adult, live Drosophila genus fruit flies, was introduced into the tubes from a pooter. The tube mouth was held downwards,,the spider was induced to run to the upper end of the tube by slight agitation, the cork was partly withdrawn and the flies blown in. A pooter made entirely of glass was used so that the number of flies to be blown in to each spider could be checked directly by sight. Water was injected into the cotton wool ball by means of a hypodermic syringe, the needle of which was inserted between the cork and the glass rim of the tube.

Usually, the spiders sat on the gauze-covered inner surface of the cork. Some individuals spun threads along the length of the tube and some appeared to spin a loose platform of threads at the upper end of the tube and sit on it. These preliminary observations suggested that T.oblongus spins a rudimentary web. However, later observations showed that this was not so, but that these spiders trail a thread when they move about in an environment new to them; it was only because the 8 cm x 2.5 cm. tubes were so small that the threads appeared to form a partly coherent network.

During the weeks that the spiders were under observation, the interiors of the tubes became contaminated with spiders' threads, cast skins, dead flies and excretory products in the form of dry,

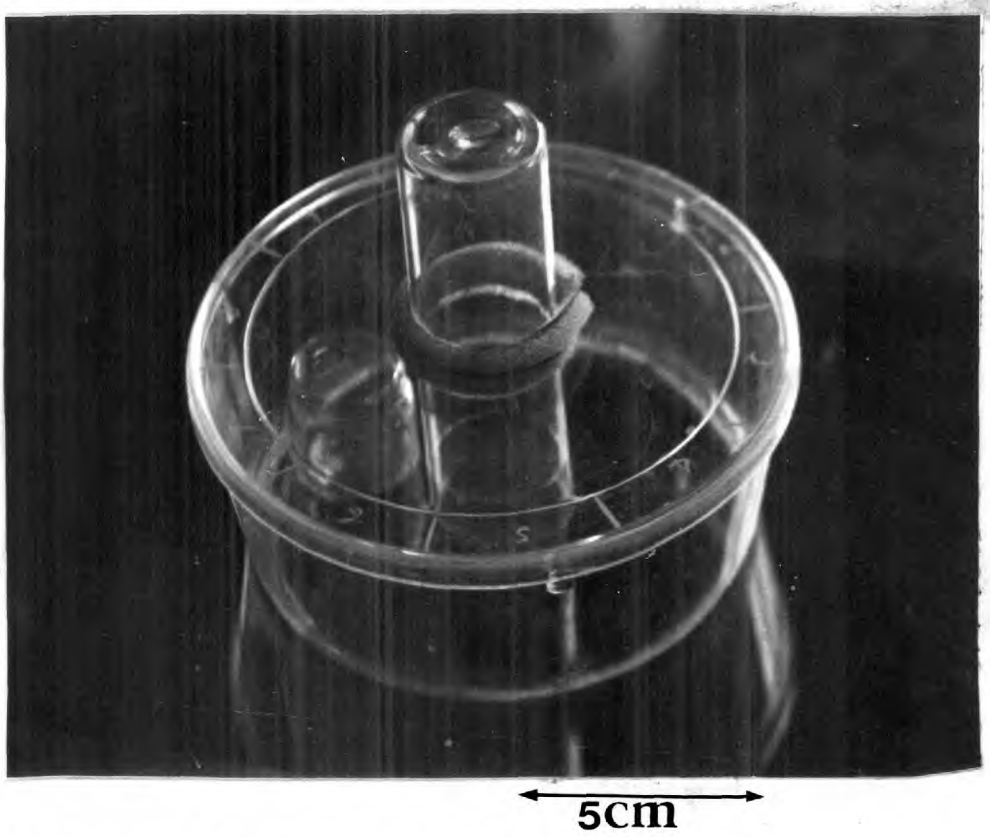
off-white spots about 2mm in diameter scattered over the inside of the tubes. Cleaning of the tubes was difficult and there was the risk of the spider either escaping or being damaged. Although T.oblongus moves very rapidly when disturbed, it can be handled fairly safely after a little practice because it always runs upwards when threatened and it will only leap when dangerously threatened.

During the second set of rearing experiments, an improved cage was developed, FIG 6.

The cage was originally a polystyrene dish of 10cm diameter and 5cm depth with a tight-fitting lid, the base was melted out with a hot ring, and a hole melted through the centre of the lid with a hot 8cm x 2.5cm tube. Flies were introduced into the cage in an 8cm x 2.5cm tube which was inverted through the hole in the lid and held in place by a ring of adhesive foam rubber half way along the tube. The flies were shaken onto the cage floor and the tube was left in position till the next feeding time. The water supply was in a glass dish, 2.5cm x 2.5cm, which stood on the floor of the cage and was refilled when necessary. The cage was stood on a sheet of glass which formed the floor.

The advantages of this type of cage were: the easy introduction of food and water, and the ease of cleaning, also the plastic was more easily gripped than glass, by the spiders. All the dead Drosophila and the excretory products of the spiders gathered on the floor of the cage, and since the spiders usually sat on the walls or on the roof, the whole cage could be lifted and transferred to a clean piece of substrate with little risk of escape or damage to the spiders.

These cages were used to hold about four individuals, it was found that there was no cannibalism when the spiders were well supplied with flies.



Rearing cage



Functional Response cage

FIG 6

3.3 AIMS

The aims of the rearing experiments were as follows:-

1) To determine the number of Instars during the normal development of T.oblongus.

2) To determine the stage of development of the over-wintering population.

3) To determine the rate of growth and food consumption of various instars of T.oblongus.

4) To determine the effects on the life cycle of:-
   a) Varying food supply
   b) Varying temperature
   c) varying day length
   d) Crowding

5) To determine the fertility and fecundity of the females.

6) To gather information on various types of behaviour:- feeding, moulting, reproduction.

3.4 METHODS

3.4.1 Sizes of Spiders

Two criteria for measuring the spiders' sizes were considered; length and weight. The measurement of length was chosen for the reasons given below.

The carapace of T.oblongus is relatively more sclerotized than the abdomen and it changes in size only immediately after moulting, whereas the soft abdomen can alter up to 20% in length and breadth, that is by about one millimeter in a fourth Instar female. The size of the abdomen is generally dependent on the food and water content of the individual. A thirsty fourth Instar female can expand by one millimeter in five minutes whilst she is drinking. Since weight is more or less directly proportional to volume, a 10% in length would correspond to a $(10\%)^3$ increase in weight; therefore length measurements are more reliable and not so subject to day to day fluctuations depending on the state of hunger and thirst of the spider.

Also, the transference of individuals into a weighing vessel is difficult and likely to lead to damage or escape.

All measurements and records of size of T.oblongus represent the length of the spider. The measurements were made by placing the cage containing the spider onto a sheet of graph paper, manoeuvring the spider into a horizontal position and noting the length in millimeters from the anterior point of the cephalothorax to the posterior point of the abdomen. In individuals up to 5.5 mm long, the length was assessed to the nearest 0.25 mm, above 5.5 mm it was assessed to the nearest 0.5 mm. These approximations were conveniently measured by the naked eye, they also tended to nullify the 15% changes in total length that can occur from day to day.

3.4.2 Dates of Collection

The latest date in the year that T.oblongus was found to be active on the vegetation surface was October 17th and the earliest was March 13th. The spiders used in the rearing experiments were collected between these two dates, and the period of time was termed "Winter". It was assumed for the analysis of the results that there was no significant change in size nor any external development of the spiders during the winter period. There remained the possibility of endocrinal development; this was not investigated. Individuals collected at various times throughout this five month period were regarded as being at a constant state of development. Experiments which showed that T.oblongus does not feed below 10°C ambient temperature verified this assumption; since the temperature at soil level in the grass tussocks where T.oblongus hibernates did not rise above 4°C. Also there is no direct radiation to raise the spider's temperature above that of its surroundings.

3.4.3 Environments

Various combinations of the variables listed previously were used as rearing environments. TABLE 3.

TABLE 3

Rearing Conditions of T.Oblongus

Temp. °C	Daylength Hrs.	Humidity	Food	Individuals per Cage
1	0	Max	/	1, 4
10	16	Max	Max	1
20	16	Max	Max	1
20	16	Max	Min	1, 4
25	18	Max	Max	1, 4
25	18	Max	Min	1
27	18	Max	Max	4
30	16	Max	Max	4
air temp.	normal	Max	Max	4

The temperatures listed in TABLE 3 are the air temperatures of the Constant Temperature rooms. The effect of the radiation from the overhead flourescent lighting during the hours of illumination tended to raise, slightly the air temperature inside the cages because of the "green house effect". The polystyrene cages transmit more infra red radiation than do the glass cages, so the temperature raising effect is not so pronounced. It was assumed that T.oblongus, being pale in colour, did not absorb much heat from incident light.

The maximum humidities are given because the cotton wool balls and the small dishes were kept well filled with water so as to maintain the humidity inside the cage at a high level but a few individuals were completely deprived of a water supply. The humidity in the C.T. rooms was between 60% and 70%.

3.4.4 Food Supply

Two levels of feeding, termed "maximum" and "minimum", were used with two sets of individuals. When maximum feeding was adopted, a constant, live supply of food was maintained inside the cage. This entailed the introduction of six to ten Drosophila per spider every two days. Minumum feeding consisted of the introduction of two flies every two days. The food requirements of the spiders is obviously different at 20° than 25°, however the same minimum feeding level was used in both sets: only the maximum supply varied with temperature.

Experiments with the minimum food supply could be conducted only in cages containing a single spider because of the danger of cannibalism.

The smaller spiders were fed with Aphis fabae (Scopoli) adult and young stages. The second Instar spiders fed readily on this prey and were given Drosophila when they had grown large enough to capture and subdue the flies.

The times recorded for dates of moulting are to the nearest 24 hours since the spiders were observed once a day.

3.5 RESULTS

The description of the various stages of T.oblongus as Instar 2, 3, 4, and adult that is used in the description of the results, is derived in the analysis, SECTION 3.6.

3.5.1 Conditions

1°C. Darkness. Maximum Humidity. No food.

These individuals were placed in cages in a refrigerator immediately on capture. They assumed the quiescent posture and were completely inactive, except, when disturbed, they moved sluggishly.

a) Ten 4th Instar individuals were put in the refrigerator on December 1st, and brought out on December 14th, thirteen days after capture. They revived immediately and assumed the predatory posture under the lamp. They were strongly phototactic. There was no size change. They were returned to the refrigerator after 20 minutes, and brought out on January 11th, fortynine days after capture, and revived as before. The cages were found to be criss-crossed with threads. The implications of this is that the spiders were active for some time after having been returned to the refrigerator on December 14th. The spiders were returned to the refrigerator and had all died within 2 days. Presumably the stress of the second revival had been fatal.

b) Seven 4th Instar T.oblongus were put in the refrigerator on January 13th, and observed every day, not taken out. Death occurred as follows: 43,49,51,54,61,63,66 days after capture.
Mean death point was 55 days. When there were four individuals in a cage; there was no interaction because the spiders were quiescent.

3.5.2 10°C. 16 hours daylength. Maximum Humidity. Maximum food.

Four 4th Instar males and four 4th Instar females were captured January 11th.

The spiders were not very active, but they did not assume the quiescent posture. All four males ate and grew slowly in length. Only one female ate and grew.

None had moulted after 62 days when the observations were discontinued.

TABLE 4

Changes in length over 62 days of T.oblongus at 10°C. Max. food supply.

Individual Males	mm	Individual Females	mm
A	7.5 - 8.0	E	8.5 - 8.0
B	6.5 - 7.5	F ate	8.0 - 9.0
C	7.0 - 7.5	G	8.0 - 7.5
D	7.0 - 7.5	H	7.5 - 7.5
all ate			

3.5.3 T.oblongus at 20°C. 16 hour day. Maximum Humidity. Maximum food.

a) Twenty five 4th Instar Individuals.

TABLE 5 T.oblongus at 20°C. 16 hour day. Maximum food. Number of days till first moult in captivity.

Date of Capture	Number of days till first moult in captivity	Mean no. days
October 25th	18,18,19,21,28,30,32,36	25
November 22nd	18,19,21	19
December 3rd	28,28,29,29	28.5
January 11-20th	18,25,26,26,26,26,28,32,40,52	30
Overall		27.5

There is no significant difference between the means for October and January. $t = 0.253$ $d.f. = 17$.

TABLE 6

Size Changes of T.oblongus at 20°C, maximum food.

	Size at Capture mm.	Size at Moult mm.	Change mm.
♂	5.5	7.0	1.5
♂	8.0	8.0	1.0
♂	7.0	7.5	0.5
♂	8.0	9.0	1.0
♀	7.0	8.0	1.0
♀	7.0	9.0	2.0
♀	6.5	7.0	0.5
♀	8.0	9.0	1.0

b) One 3rd Instar Female.

Moulted 23 days after capture.
Moulted to adult after a further 19 days.
6.0 mm at capture,
7.0 mm at first moult,
9.0 mm at second moult.

c) One 2nd Instar

Moulted after 26 days,
2.5 mm at capture,
4.0 mm at moult .

d) Four 4th Instar, 2♂♂, 2♀♀

Captured December 1st, kept at 1°C for 41 days, transferred to 20° and maximum feeding.

Two moulted 18 days after transference,
Two moulted 19 days after transference.

3.5.4 20°C. 16 hour day. Maximum Humidity. Minimum food.

Two cages of four adults, two males and two females, were deprived of food in order to study cannibalistic behaviour.

In a cage well supplied with food, when two individuals come into contact with each other there is not a strong reaction; they simply disengage themselves or ignore each other. The spiders will settle into the replete posture whilst in contact, but will not assume the predatory posture.

After five days of starvation, a female was seen to be eating a male. It is not known whether the female had been fertilised or not. Fertilisation is a stimulus for increased food consumption, however, during the observations on mating behaviour, well-fed individuals were used, and the male invariably survived the encounter.

During the starvation period the spiders became relatively more active; they spent more time moving about the cage and more time in the predatory posture. When two individuals came into contact, there was a short tussle and both usually escaped unharmed. Sometimes, one of the spiders was killed. A female, being larger, is likely to be the victor over a male, but males have been observed to overpower immature females.

3.5.5 25°C. 18 hour day. Maximum Humidity.

a) 19 2nd Instar individuals with a maximum food supply; one with minimum food. Results are summarised in FIG 7. None moulted into the adult stage.

b) 18 3rd Instar individuals, maximum food. Results in FIG 8 part 1. All moulted into the adult stage.

c) 12 3rd Instar individuals, minimum food, Results in FIG 8 part 2. None moulted into the adult stage.

FIG 7

Size and Day of Moulting of T.OBLONGUS at 25°C Max food. Each vertical line represents one spider.

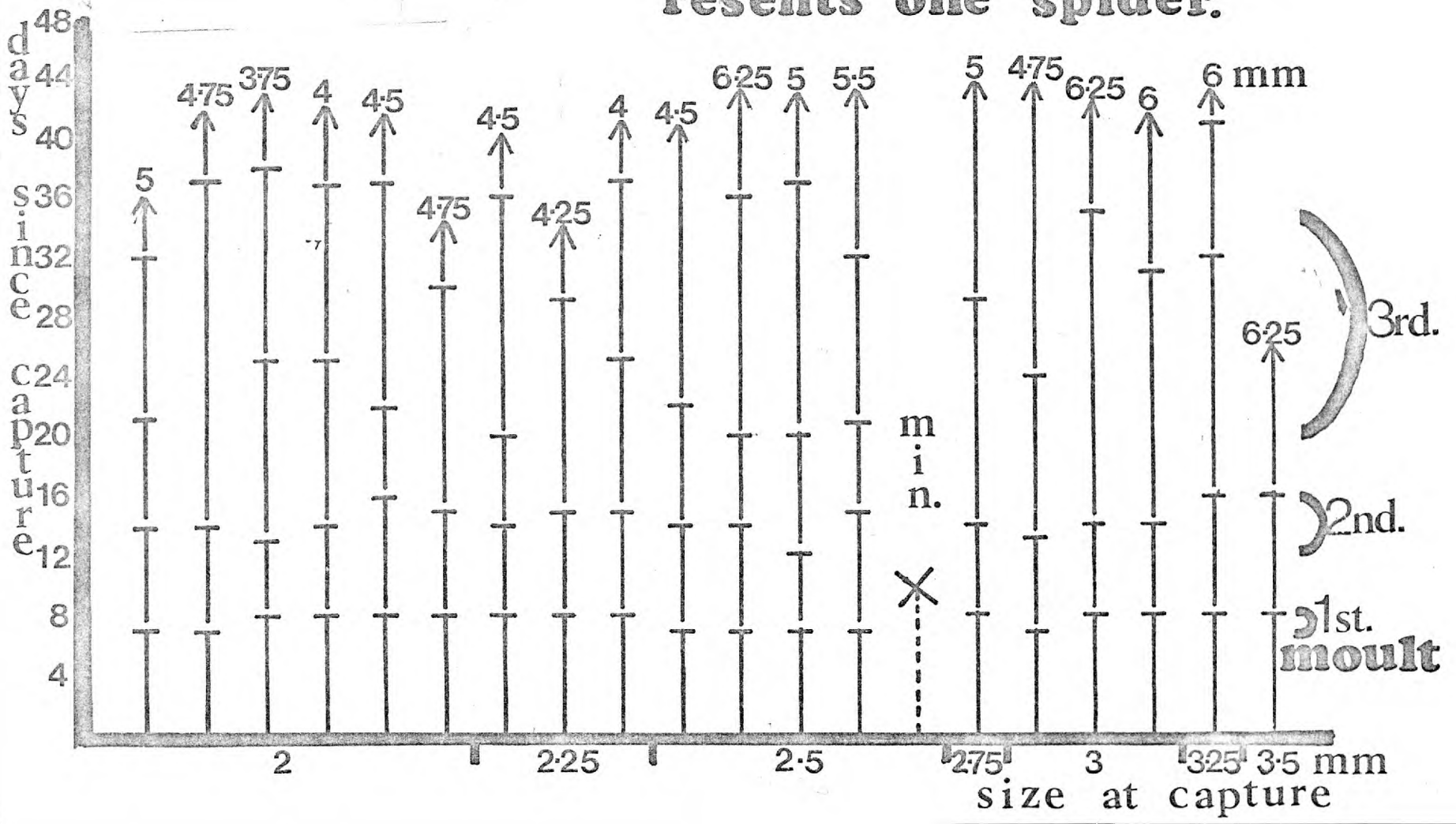
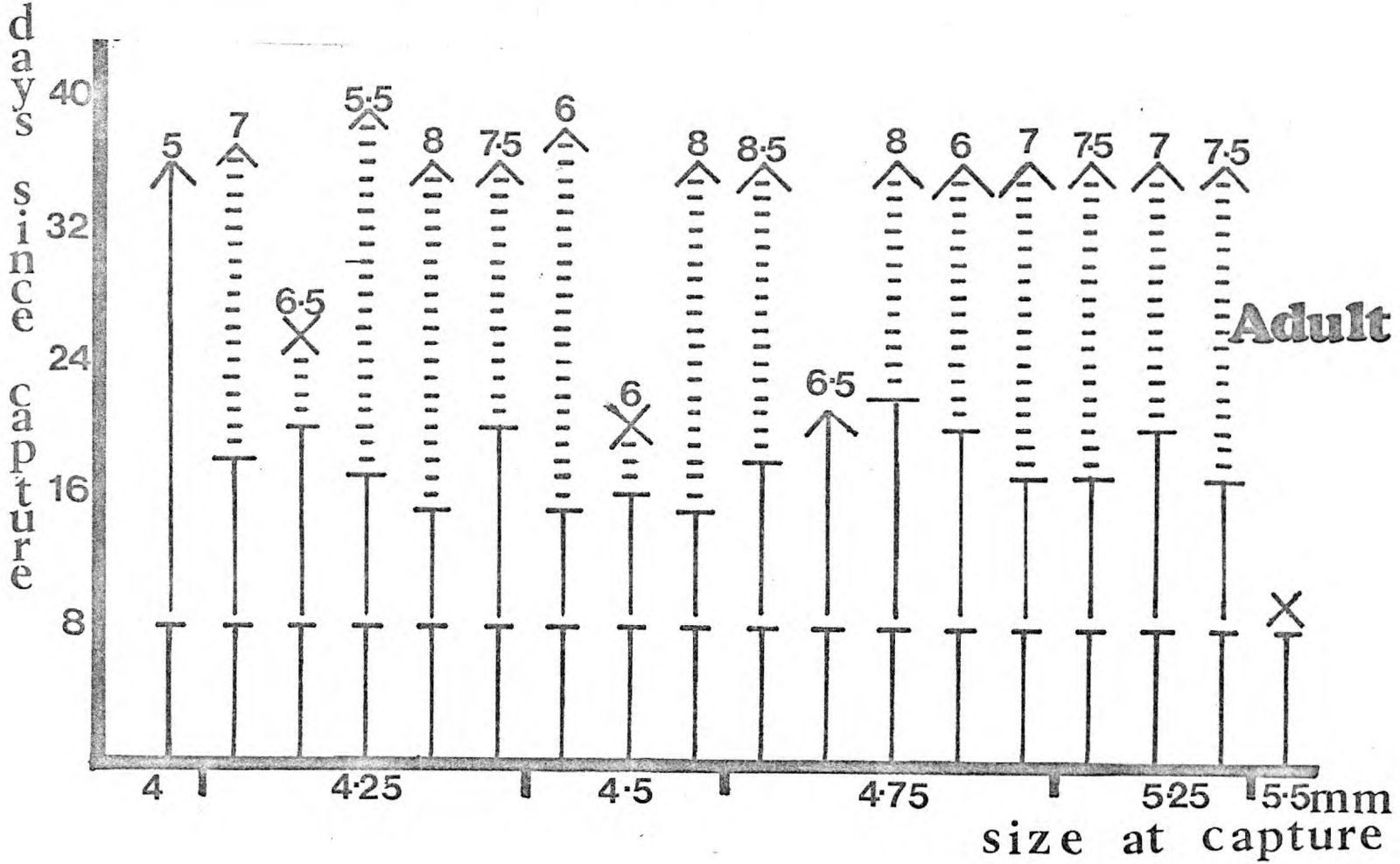


FIG 8

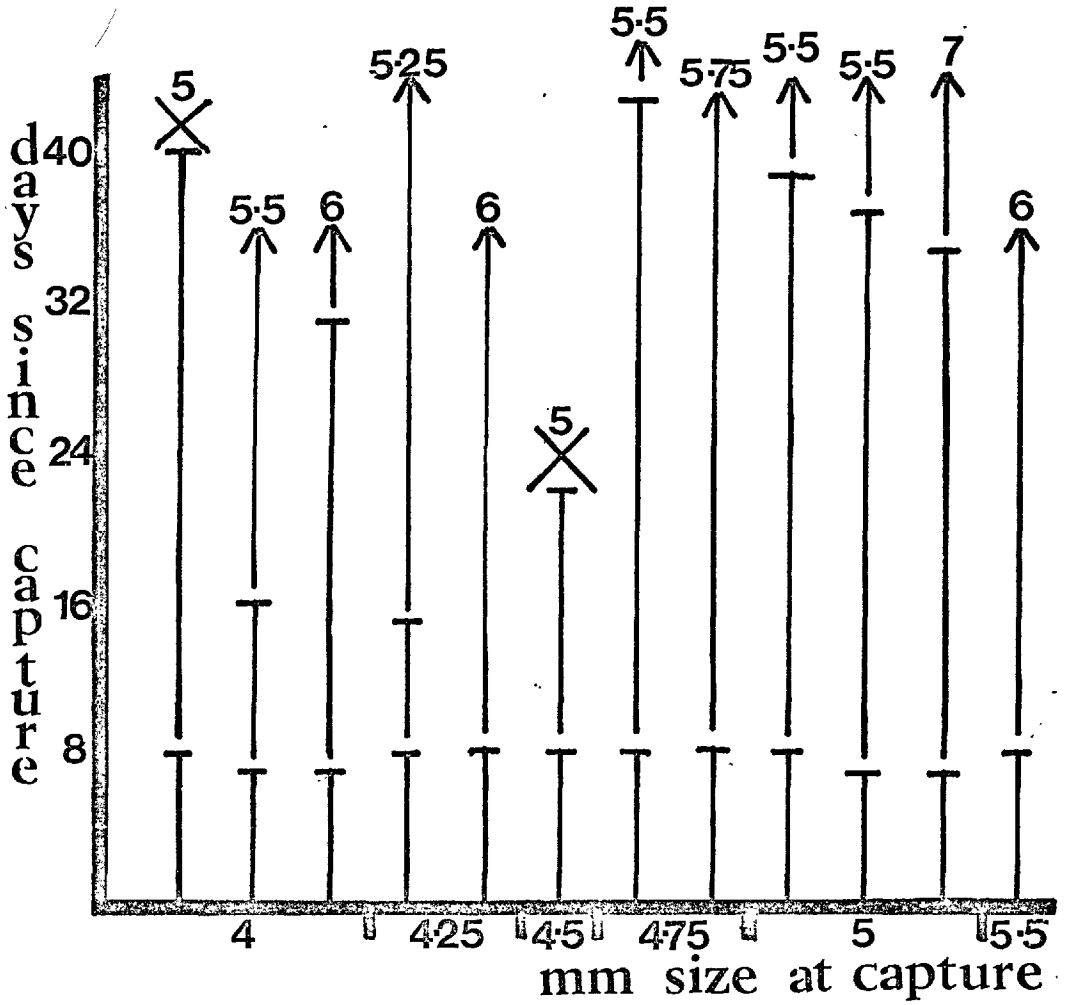
Size and Day of Moulting, T.OBLONGUS

Part 1 Max Food. 25°C



Size and day of moulting T.oblongus

FIG 8 Part 2 Min Food.25°C



d) 12 4th Instar T.oblongus at 25°C. All became adults.

TABLE 7 T.oblongus at 25°C. Number of days till First moult in captivity:-

Size mm	No. of days till first moult in captivity	Size of adult mm.
6.5	21	7.0
6.5	16	7.0
7.0	14	8.0
7.0	13	7.5
7.0	14	8.0
7.0	11	8.0
7.5	14	8.5
7.5	13	8.0
8.0	11	9.5
8.0	12	10.0
8.5	14	8.5

e) One 4th Instar, minimum food.
Moulted to adult after 12 days. 8mm to 8.5 mm.

3.5.6 TABLE 8

T.oblongus at 27°C. 18 hour day, Maximum Humidity, Maximum food. Days till first moult in captivity. Six fourth Instar individuals.

Days till first moult in captivity:

10
10
11
12
12
15

All moulted to adults.

3.5.7 30°C. 16 hour day, Maximum Humidity, Maximum food.
One male, one female, 4th Instar.
Both moulted after 11 days, mated shortly afterwards, and a fertile egg sac was laid.

3.5.8 Insectary rearing.
Air temperature, Maximum Humidity, Normal daylength, Maximum food. Put in the insectary January 25th.
Three 2nd Instar, died after 11,27 and 38 days respectively.
One 3rd Instar, died after 16 days.
Two 4th Instar,
One died while moulting after surviving 33 days.
The other survived till spring, and started developing then.

Four 4th Instar captured October 21st.
One died February 10th - 112 days.
One died February 14th - 114 days.
One died February 16th - 116 days.
One died February 27th - 127 days.

3.6 ANALYSIS

3.6.1 Life Cycle

Two more sets of data are presented here since they are essential to the analysis and understanding of the life history of T.oblongus.

FIG 9 shows the sizes of spiders captured in winter.

FIG 10 shows the occurence of the various Instars of T.oblongus throughout the summer. This latter information was gathered by observation in the field during sampling.

The size distribution of the over-wintering population shows three distinct peaks. None of the spiders was adult. This indicates the presence of three juvenile Instars. Since the first moult of a newly hatched T.oblongus spiderling is just outside the egg case, the smallest Instar found in winter was termed Instar 2, and the two larger ones Instars 3 and 4.

FIG. 9
Length of T. OBLONGUS from Silwood in Winter.

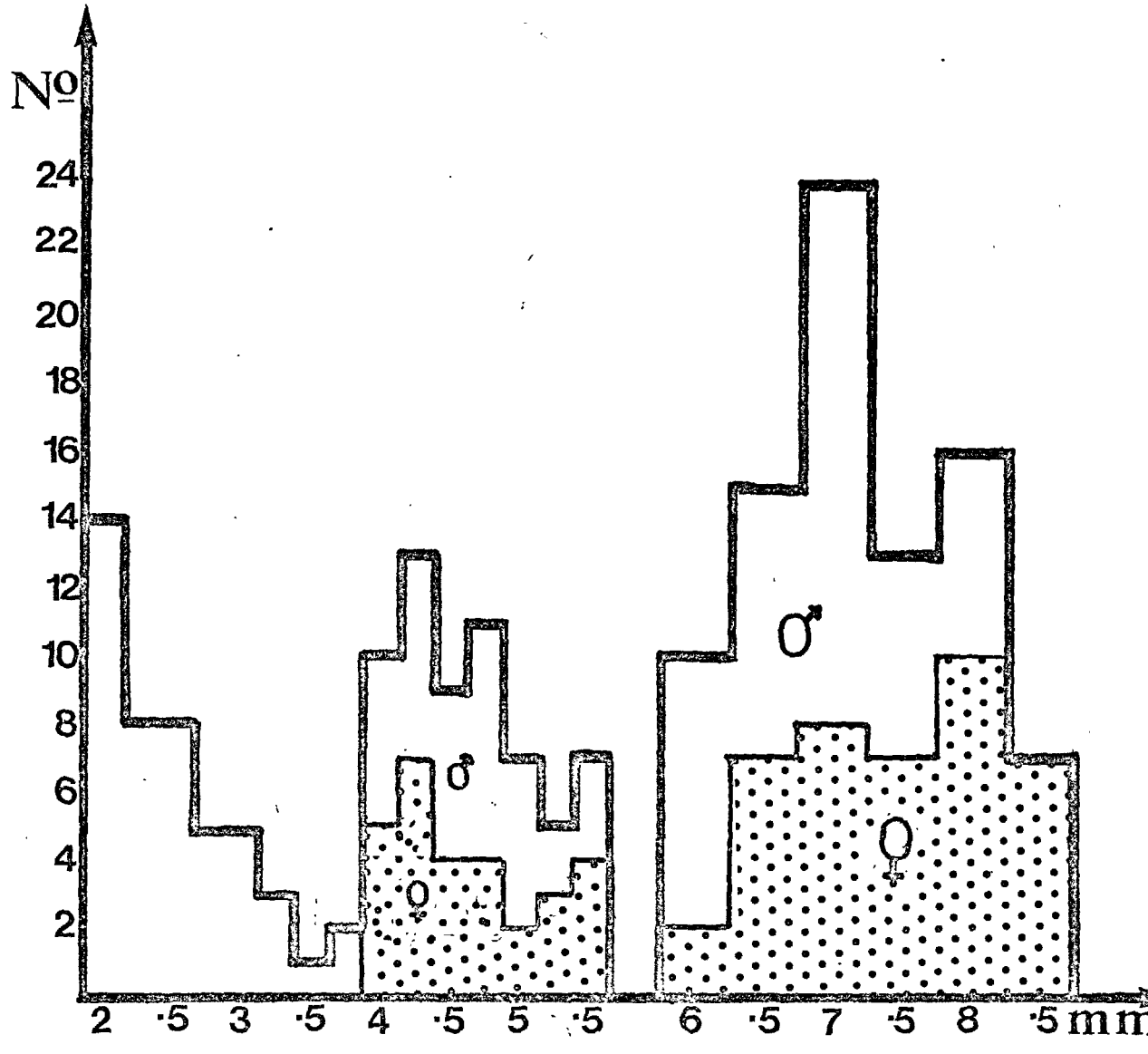
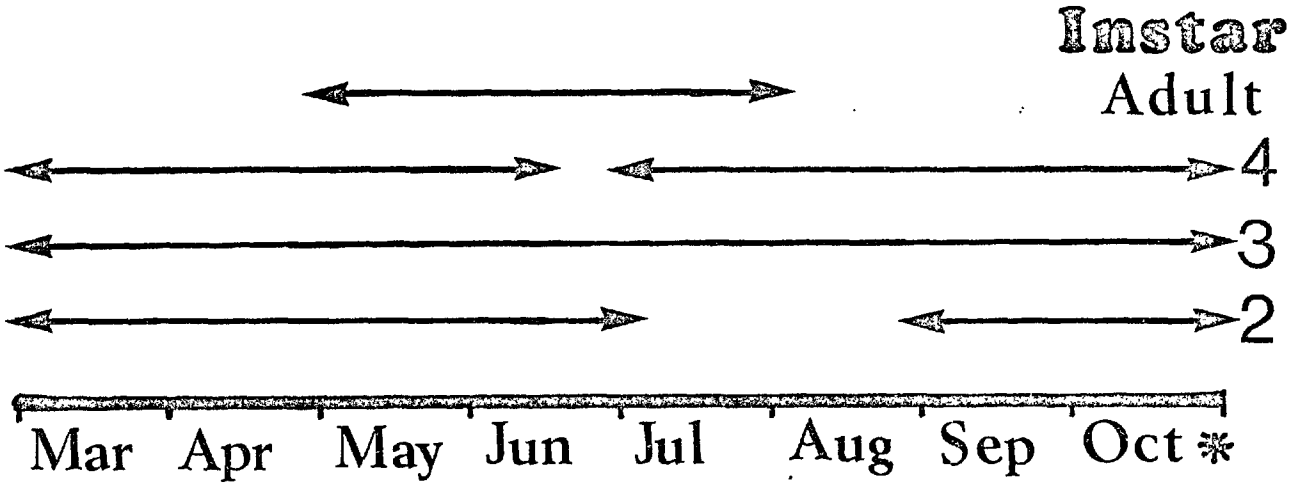


FIG 10

Occurrence of T.OBLONGUS at Silwood in Summer.



*Oct. to March identical

The smallest size seen in the field was 1.75 mm and this is only 0.25 mm bigger than the size of newly hatched spiders.

TABLE 9

Sizes of T.oblongus, captured in winter, Silwood Park

		Mean Length
Instar 2		2.46 mm
Instar 3	♂	4.60
	♀	4.63
		No significant difference
		t = 0.24
		d.f= 0.32
Instar 4	♂	6.93
	♀	7.45
		Differ significantly at 1% level
		t = 3.27
		d.f= 0.84

All the well fed Instar 4 individuals moulted directly into adults in captivity, and all but one of the well fed Instar 3 individuals became adult at their second moult FIG 8. This confirms the interpretation of the size distribution.

It is apparent that the normal development of T.oblongus involves four juvenile Instars, the first Instar lasting only a few hours in the immediate vicinity of the egg sac (see the section on reproductive behaviour).

As can be seen from FIGS 7 and 8 the number of days until the first moult in captivity of Instar 2 and 3 captured in winter is remarkably constant at about 7.5 days at 25°; whether at Maximum of Minimum food, there is no more than half a day's variation in this figure for any individual. The time to the first moult of Instar 4 into the adult stage, however, is longer and more variable having a mean value of 14 days, range 11 - 21 days at 25°C.

Instar 3 undergo their second moult into the adult stage at 25° after an average of 9.5 days ranging from 7 to 12 days, (FIG 8). Instar 2 undergo the second moult after 6.7 days, range 5 - 8 days.

It is interesting to note the increase in variation in moulting times of Instar 2 individuals in FIG 7. The variation in the time of the first moult is 1 day, in the time of the second, 4 days, and of the third, 15 days.

The series is not large enough to be analysed mathematically, but it would seem to be some kind of exponential increase in variation.

In the light of this information on moulting times one can trace the life of an individual on FIG 10.

It hatches in July and spends the first winter as Instar 2. In the following spring and early summer it moults to Instar 3 by the end of June, the individuals that over-wintered as Instar 2 have become Instar 3; in the late summer and autumn it MIGHT moult to Instar 4. It spends the second winter as Instar 3 or 4 and the following spring it becomes Adult directly or moults to Instar 4 and then into the Adult; by the end of May the individuals that over-wintered as Instar 3 and 4 have become Adults. Two apparent anomalies arise from this interpretation:

a) The Instar 2 individuals having over-wintered with the Instar 3 individuals are present in the field until the end of June, whereas before the end of June the Instar 3 individuals have moulted twice and become Adults. At 25°, Instar 2 and Instar 3 both took the same length of time to their first moult and Instar 2 individuals undergo their second moult about three days before Instar 3 individuals undergo theirs.

The explanation of this discrepancy between field observations and laboratory results can be found in the behaviour of the spiders. Instar 2 individuals, in summer, were invariably found beneath the surface of the vegetation amongst the grass stems and litter,

at or near soil level where the air temperature is relatively low; it rises to about 17° on a hot May day: however, the Instar 3 and 4 individuals were found on the surface where the temperature can reach 40°. This difference in the micro-environmental temperatures of the two Instars can account for the difference in development times in the field. Food availability can also affect development. A short calculation indicates the relative difference of food requirements of the two Instars; the figures and concepts used are great over-simplifications but the implication is valid.

Volume of Instar 2	2 cu.mm.
Volume of Instar 3	7 cu.mm.
Volume of Adult	25 cu.mm.

The predatory efficiency of T.oblongus is related to the area it can span with its legs.

Area of Instar 2	7 sq.mm.
Area of Instar 3	80 sq.mm.

so: for an Instar 2 to increase in size to Instar 3

Increase	Measure of Predatory Ability
5 cu.mm.	7 sq.mm.
about ratio 1:1	

for an Instar 3 to increase in size to Adult

Increase	Measure of Predatory Ability
17 cu.mm.	80 sq.m
+ 2 cast skins.	
about ratio 1:4	

There are, of course, constants that apply in both situations; rate of digestion and absorption, cell maturation, endocrinal development and energy expended in movement. Also there are unknown variables such as type and density of prey, and body temperature. But the indication is that the larger spider can grow faster.

b) The second anomaly is that adults are present in the field for a relatively short time, about 2 months when males and females are occurring together and able to reproduce, yet they develop from an over-wintering population consisting of two Instars, 3 and 4, of average sizes 4.60 mm and 7.20 mm respectively.

Collected in winter, Instar 3 reach the adult stage in an average of 17 days with two moults, and Instar 4 reach the adult stage in 14 days with one moult, at 25°C. This is not a large time difference and would easily be encompassed by the two months:- MAY/JUNE - occurrence of the adults. However, it is interesting to note the difference between the time taken for captured Instar 4 to become adult at 25° (14 days) and the time spent in the fourth Instar by individuals captured as Instar 3 (9.5) days, even though the Instar 4 individuals must have spent up to four months as Instar 4 the previous summer and autumn. Instar 4 captured in October became adult in the same average time as individuals captured in January.

The explanation of these phenomena probably lies with the endocrine complex of the spider and would involve research into the effects of cold periods, photoperiod and the hormone cycle generally.

The most recent information concerning neurosecretion in spiders is in the book 'Neurosecretion' by GABE(1966). He writes:-

> "The classical techniques employed in endocrinology do not appear to have been applied to the study of neurosecretion in Araneida; but the application of these methods would appear to be extremely difficult..... .....these indications obviously do not entitle us to assign any exact significance to the phenomena of neurosecretion in Araneida and fresh research would appear eminently desirable."

LEGENDRE(1959) and KÜHNE(1959) have found a distinct relationship between the state of the neurosecretory cells and maturing gonocytes.

Neurosecretory cells in Pardosa, Tegenaria and Araneus become charged with a product which stains with paraldehyde fuchsin as sexual maturity approaches, remain very active up to the time of copulation and oviposition and become progressively impoverished of secretion granules as the animals age.

Fasting did not affect morphology of the neurosecretory cells but in hibernation there was a disappearance of the product staining with paraldehyde fuchsin from the neurosecretory cells. The product reappeared when feeding was resumed.

Because of this scarcity of information, any explanation of the hormone system in T.oblongus must be purely hypothetical. Three hypotheses are put forward to explain the life history in terms of neurosecretory activity, in particular the development of adults from the over-wintering population consisting of Instars 3 and 4.

3.6.2 Hypotheses

a) When juveniles are captured in winter and placed at 25°C, there is an acceleration of the development cycle. This acceleration has a greater effect on Instars 2 and 3, which only take 7.5 days to their first moult in captivity, than on Instar 4 which takes 14 days to its first moult.

The impetus of this acceleration in the captured Instar 3 carries over into their fourth stage which lasts only 9.5 days. An equivalent series of events would take place in the field when the spiders came out of hibernation in Spring.

b) There is a cessation of the production of Juvenile Hormone in Instar 4 as they enter hibernation and an accompanying degeneration of the relevant glands. The glands must be restarted on emergence from hibernation, delaying the moult; whereas the Instar 3 glands are in hormone producing condition immediately on emergence from hibernation.

c) There is a hormone system cycle involved in the development of sex organs, both internal and external, which is separate from, and longer than, the normal moulting cycle and starts only after the second cold period: when Instars 3 and 4 are placed at 25° from hibernation, this event triggers off the sexual cycle in both;

so that although Instar 3 has to undergo two moults to become adult, its sexual development has started whilst it is still in Instar 3, therefore less time is spent as instar 4.

None of the Instar 2 captured during their first winter developed into adults, despite undergoing three or even four moults in captivity.

3.7. DISCUSSION

T.oblongus is biennial in development with two generations present in the field throughout the year, and a certain proportion of the population maturing and reproducing each summer.

Thelife histories of very few spiders are known in great detail; one reason for this is the lack of reliable rearing methods and another is the variation, within a species, of the number of Instars, the number can vary even amongst the offspring of a single female all reared under apparently identical conditions (BONNET 1930). Nevertheless the size distribution in the field of T.oblongus is consistent and obviously represents the presence of three juvenile Instars.

DONDALE(1961) analysed the life histories of the two Thomisids Philodromus rufus(Walckenaer) and P.cespiticolis (Walckenaer), which are related to T.oblongus, by means of size distribution in the field and by insectary rearing. He found a similar biennial pattern, however the situation was simpler than in the case of T.oblongus because the over-wintering population that matures the following spring consists of one Instar only, not two as found in T.oblongus.

Many other spiders reach maturity in Spring e.g. other Thomisidae, Salticidae, Theridiidae, Clubionidae and Lycosidae (GERTSCH W.J. 1949),(BRISTOWE 1958). Some of these mature in one year, others in two: in some species either or both sexes reach anatomical maturity in autumn and reproduce the following spring. There is no significant difference in the time taken to moult by

males and females of T.oblongus. The effect of temperature, humidity and photoperiod on spider development are little understood, there is evidence that some species are biennial in the Northern part of their distribution and annual in the Southern part. (PALMGREN P.1939), (BONNET P.1930).

The distribution of T.oblongus, although large geographically is probably restricted to maritime or semi-maritime climatic regions, and in the northern part of its distribution long day-length could compensate for lower temperatures.

A second group of spiders mature and reproduce in Autumn e.g. some Linyphia, Araneus, Zygiella, Argiope and Agelenopsis. Observations on several of the species in the group indicate a one year development time (BONNET P.1930), (DUFFEY E. 1956) (TURNBULL A.L. 1960); but there is evidence for a lengthening in at least two species, Araneus diadematus (Clerck) and A.circe (Sav. and Aud.) (WEIHLE 1931).

Thomisidae in general, not spinning webs, have a smaller prey catchment area that web-spinner or wolf spiders and this aspect of their behaviour may necessitate a two year development period, especially in cooler climates.

3.7.1 Rate of Growth

As a measure of the efficiency of the laboratory rearing methods, a comparison can be made of the sizes of various stages of T.oblongus in the field and the sizes of those same stages reached in the C.T. rooms by individuals captured at a younger stage.

a) Adults in the field.

A random selection of 20 adults, 10 and 10 from the field in early June was of average size: 8.9 mm.

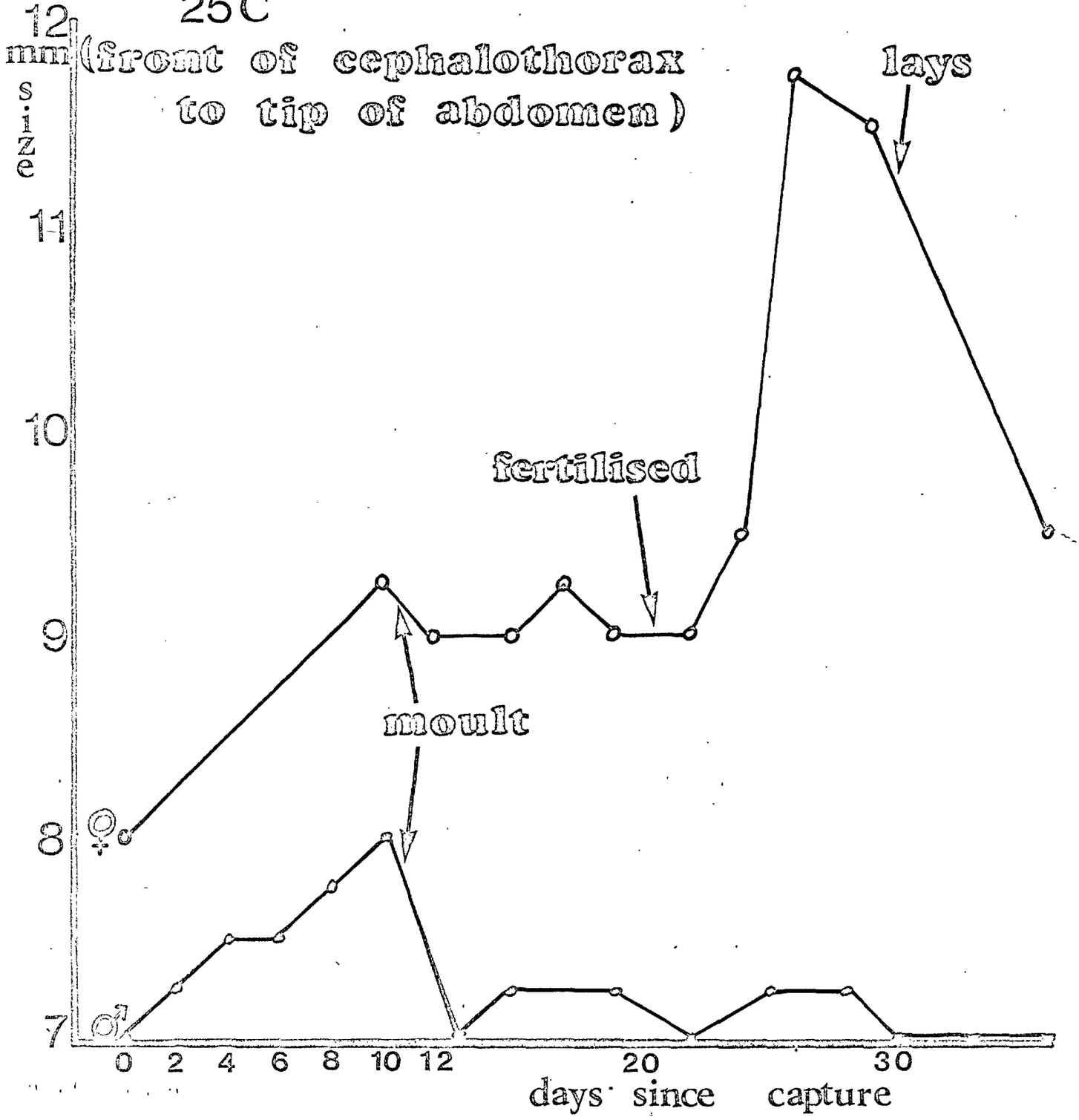
b) Adults reared from Instar 4 at 20°C are 8.1 mm long.
Adults reared from Instar 4 at 25°C are 8.2 mm long.

c) Adults reared from Instar 3 at 25°C are 7.0 mm long.

FIG 11

Size changes of T.oblongus

25°C



There is a significant difference between the sizes of adults in the field and the sizes of adults reared from Instar 4, and a further difference between the sizes of adults reared from Instar 4 and adults reared from Instar 3. Although the spiders were provided with as much food as they could eat, it must be concluded that laboratory rearing has an adverse effect on their rate of growth. Possible reasons for his are:-

a) Restricted diet.

b) Stress arising from the physical aspects of captivity including enclosure and contamination of the cage by waste products.

c) An acceleration of the ecdysis cycle at a faster rate than the growth process by the continuous high temperature.

In the light of this evidence, it follows that the information on fertility and fecundity gained in the laboratory may well be grossly unrepresentative of the field population.

The food consumption of T.oblongus could not be gauged accurately since the amount of food taken from each Drosophila killed and fed upon by the spider varied a great deal; sometimes the corpses were completely masticated and sucked dry, other times they appeared hardly touched, all stages in between were observed, however, a number of three to five adult Drosophila per day for a large Instar 4 spider is an approximate value.

A close record of size changes of a number of spiders was kept, and FIG 11 shows the size changes of two representative individuals.

The daily variation is apparent from the figure, as is the effect of fertilisation as a stimulus to the appetite of the female.

3.7.2 Effect of Minimum Food

a) Cannibalism SECTION 3.5.4

b) There is no effect on the number of days taken to the first moult in captivity (FIG 8) in Instar 3 or 4.

However, as can be seen if FIG 8, a poor food supply has a drastic effect on subsequent development. The second moult in captivity of individuals captured in Instar 3 was delayed by up to 24 days past the normal 9.5 days. None of them became adults and size increase was only an average of 1.00 mm after 40 days compared with an increase of 2.25 mm in fully fed individuals.

It is concluded that a full food supply is necessary for the spider to become adult when captured in Instar 3.

Captured in Instar 4, one individual moulted to adult after 12 days.

Captured in Instar 2, one individual died after 10 days. FIG 7.

3.7.3 Effect of Crowding

Cages holding four individuals were used in the experiments at 1°C, 20°C, 25°C and at outdoor temperature.

The spiders were not observed to interfere with each other to any great extent, except when minimum food was provided and cannibalism occured. When the spiders were fully fed they spent most of the time in quiescence or in the predatory posture separated from each other. They moulted and grew at the normal rate.

In order to study activity, the cages were marked off into radii and a record was kept of the spiders' movements. This is analysed in SECTION 5.4.5

3.7.4 Longevity

As can be seen from FIG 8, the majority of spiders can live for as long as 24 days as adults at 25°. A few individuals were fed and observed beyond this length of time.

TABLE 10
Length of Life of adult T.oblongus at various temperatures.

Temperature	Death Point days after final moult
25°C	45
	46
	49
20°C	51
	54

3.7.5 Fertility and Fecundity

Several adult females reared at 20°C, 25°C and 30°C were fertilised and laid eggs.

TABLE 11
The number of young produced by female T.oblongus at various temperatures.

Temperature	Number of Spiderlings
20°C	46,64,72.
25°C	88,32,35.
30°C	110,69.

At 30°C the two batches came from the same female.

SECTION 4

POPULATION SURVEY

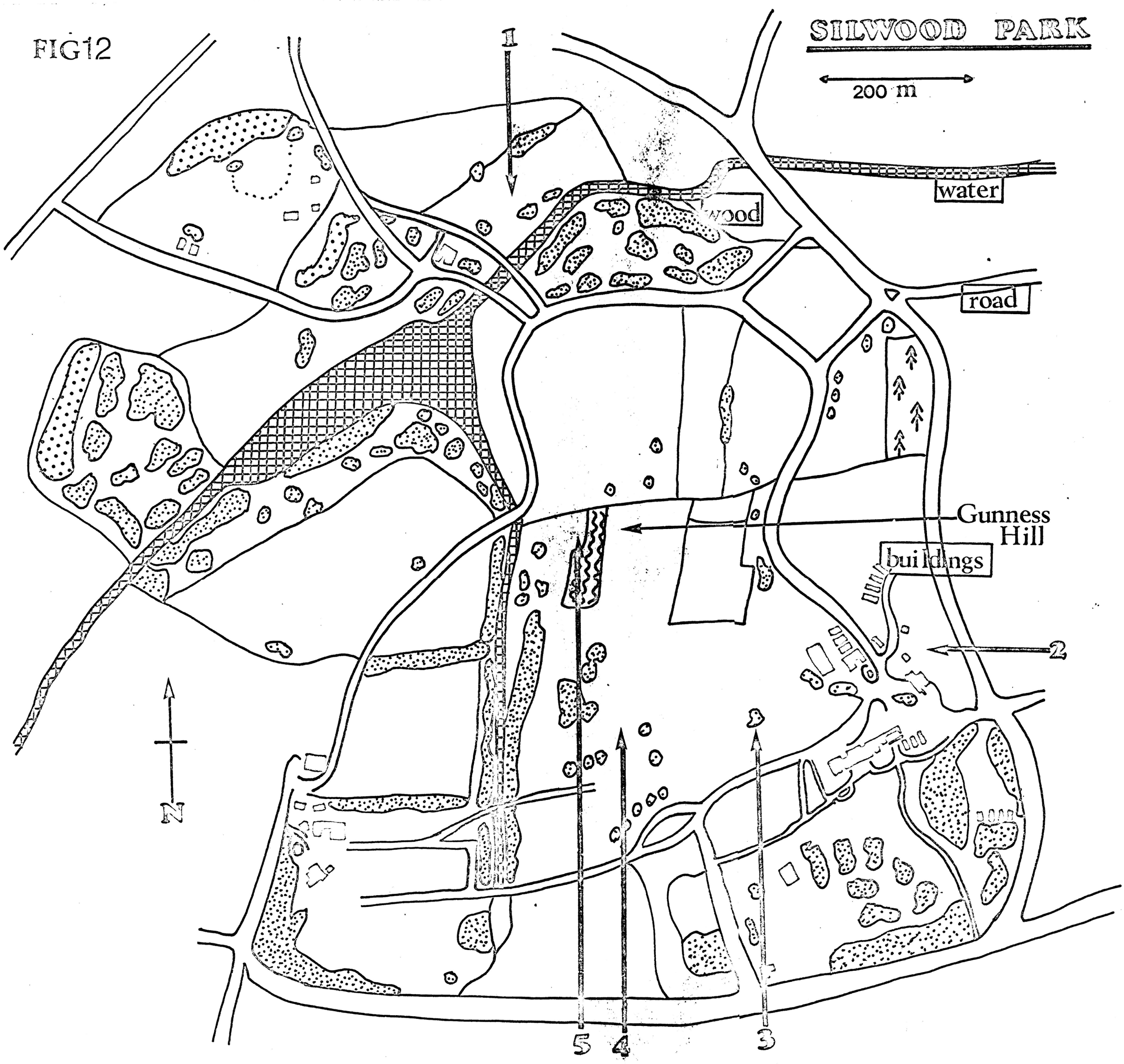
4.1 STUDY AREA

Populations of T.oblongus were studied and experimental specimens were collected in various areas in Silwood Park, Sunninghill, Berkshire.

Silwood Park is situated about one mile on the London side of Ascot, Berkshire, 51° 24'N and 0° 39'W, at an altitude of 64m. The area is about 48.5 hectares and was at one time mostly included within Windsor Great Park, but part of the grounds has been more or less cultivated or has formed part of a garden for some hundred years. The grounds mostly lie on beds of Eocene age, namely Bracklesham beds (gravel and some clay) on the east, and Bagshot sands (sand with some gravel) on the rest of the area. A good deal of the higher ground, including almost all the Bracklesham beds, is capped with Platean gravel. The soil is mostly a sandy gravel incorporating locally a good deal of clay but nearly always very light. It therefore dries out very rapidly after rain and the water table in summer is far below the surface and the vegetation tends to suffer during droughts. The greater part of the area is covered by acid grassland of a rather uniform type, dominated by Festuca rubra L. and Agrostis tenuis Sibth. with patches in which Holcus mollis L. forms closed stands. There are two patches of woodland and there are isolated trees elsewhere in the park.

Habitat studies were made and specimens taken from the five areas shown in FIG 12. Regular population counts were made in Area 4.

FIG12


SILWOOD PARK
200 m
1
water
wood
road
Gunness
Hill
buildings
2
N
5
4
3

AREA 1 - THE WATER MEADOW

An area of grassland, very damp but not swampy. Dominant vegetation is Holcus mollis L., Dactylis glomerata L.,and Juncus spp. L. It is sheltered from the wind by screens of trees and has a slight slope to the south-east.

Specimens of T.oblongus were taken from this area in winter and summer for laboratory experiments.

AREA 2 - NORTH GRAVEL

This is a level patch of rough grassland, about 300 m. long and 100 m. across, with a dry, slightly acid, sandy soil. Dactylis glomerata L., has colonised the area since it was left to become waste in 1955, and is now one of the most common grasses, together with Festuca rubra L., Agrostis tenuis Sibth, Holcus mollis L., H.lanatus L., Poa trivialis L., and P.pratensis L.

T.oblongus were taken in winter and summer.

AREA 3 - 'THE OAK PATCH'

A circular patch of unmown grass standing in the middle of a large area of mown grassland. It is about 26 m. across, 530 sq.m. in area and the vegetation is dominated by a large oak tree, the foliage of which covers all but a perimeter of 1.5 to 2 m. Vegetation is sparse beneath the tree's branches, denser at the perimeter: Holcus mollis, Agrostis tenuis, Festuca rubra, and Dactylis glomerata. This area was examined intensively for T.oblongus during winter.

AREA 4 -

This is the area where the population of T.oblongus was measured by various means during summer. The habitat was disturbed

as little as possible by trampling or digging up of tussocks. A full description of this area is presented in SECTION 4.3.

AREA 5

A dense stand of Dactylis glomerata at the top of a slight rise, partially sheltered from wind by broom plants to the east and south.

The tussocks are adjacent to each other over much of the area and this habitat provided a good supply of T.oblongus during summer.

The sampling of over-wintering populations of T.oblongus necessitates the partial destruction of the habitat as described in SECTION 2, therefore winter and summer populations had to be sampled in different areas. Area 1,2,3 and 5 were sampled in winter, and Area 4 was sampled in summer. Most of the habitat and microclimatic investigations were also carried out in Area 4.

4.2 WINTER SAMPLING

4.2.1. Over-wintering Sites

T.oblongus was found to occur in various types of grassland, regardless of the presence of Dactylis glomerata; however M.LUFF (verbal communication) reported many over-wintering species including T.oblongus inside tussocks of Dactylis, and there was found to be a concentration of T.oblongus around the single Dactylis tussock in Area 4 in autumn and spring; also the last and the first active T.oblongus found on October 17th and March 13th respectively were found on Dactylis. This evidence indicates that the hibernation site of T.oblongus is in the Dactylis tussock and examination of several tussocks confirmed this. However, T.oblongus is fairly abundant in areas devoid of Dactylis; dense stands of Holcus, and Agrostis were searched in winter but no T.oblongus were found; it was therefore decided to restrict winter sampling to areas where Dactylis was prevalent i.e. to Areas 1, 2, 3, and 5, on the assumption that T.oblongus in such a habitat would imigrate the small distance to the nearest tussock in order to hibernate.

The density of T.oblongus in summer in rough grassland is about three individuals per square metre, the discovery of a hibernating individual in such grassland would therefore involve the digging up of $\frac{1}{3}$ sq.metre of Holcus or Agrostis on average: whereas the average Dactylis tussock is only 1/30 of a sq.metre usually with 2 individuals of T.oblongus within the area.

Three sampling methods were adopted:-

a) Examination by hand.
b) Digging and shaking of the tussocks.
c) Tullgren funnel extraction.

These methods are described in SECTION 3.1. Digging and shaking was adapted as the most efficient method and the following samples were taken:-

1)	Area 1	6 tussocks	
2)	Area 2	36 tussocks	
3)	Area 3	30 tussocks,	1964/65.
		8 tussocks,	1965/66.
4)	Area 5	23 tussocks,	1964/66.

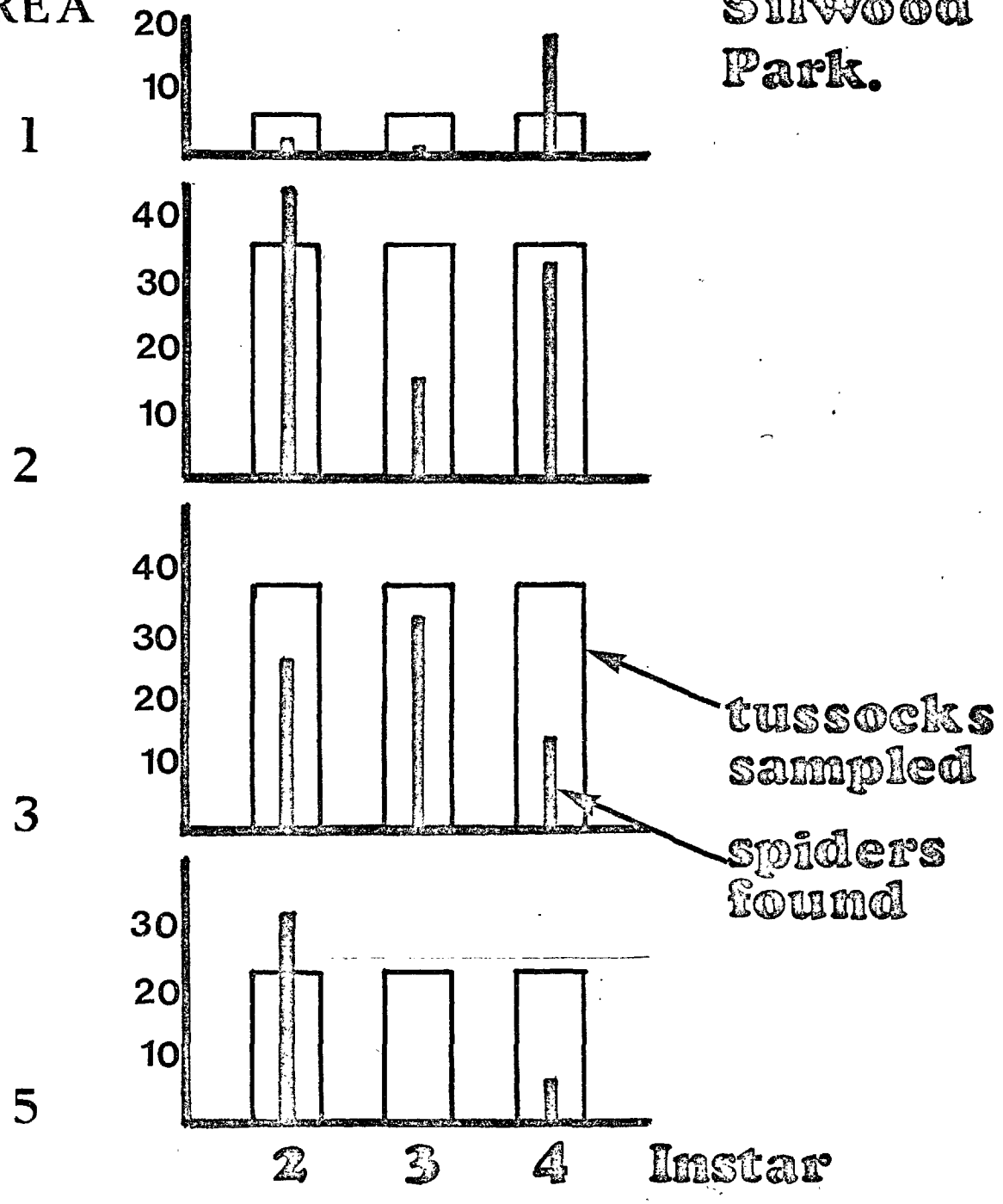
Only tussocks over 15 cm. diameter were sampled. The results of sampling are given in FIG 13 and TABLE 13.

As shown in TABLE 13, calculations of index of dispersion had shown that T.oblongus is distributed non randomly amongst the Dactylis tussocks of Silwood Park.

Intensive sampling of a small area such as the Oak Patch (Area 3) showed the same type of distribution.

The Oak Patch is not regarded as a typical habitat for T.oblongus because the grass cover is relatively sparse and most of the area is covered and shaded by the foilage of the oak tree, however it was chosen for intensive sampling because

FIG 13 Winter Sampling, T. oblongus Silwood Park.



of the abundance of Dactylis tussocks and because of its isolation in a large area of regularly mown grassland where T.oblongus did not occur. The nearest T.oblongus habitat to the Oak Patch is 30 m. to the south. TABLE 12 shows the results of sampling the Oak Patch.

TABLE 12

Winter sampling of T.oblongus in the Oak Patch.

a) 1964/65

No. of T.oblongus per Dactylis tussock	No. of tussocks
0	12
1	3
2	2
3	4
4	4
5	0
6	3
9	1
10	1
72	30

Average 2.29 spiders per tussock I.D. = 100 N = 29
Non random at 0.005 level.

b) 1965/66

No. of T.oblongus per Dactylis tussock	no. of tussocks
0	4
1	1
2	1
3	1
7	8

Average 0.9 spiders per tussock. This value is significantly lower than that for 1964/65 indicating a general depletion of the population caused by intensive sampling.

TABLE 13

Winter sampling of T.oblongus in Silwood Park.
Areas 2,3, and 5

Number of spiders per Dactylis tussock	Number of tussocks
0	33
1	10
2	4
3	2
4	6
5	0
6	4
7	0
8	2
9	2
10	1
16	1
132	65

Average 2.03 spiders per tussock.
The distribution was analysed by Fishers Index of Dispersion and found to be significantly non random at the 0.005 level. I.D. = 331 N = 64

4.2.2 Analysis

The distribution of T.oblongus amongst the Dactylis plants of Silwood Park is non random, also their distribution in the Oak Patch is non random and the spiders tend to be concentrated in relatively few grass tussocks.

The grass, Dactylis glomerata,is very variable in form, STAPLEDON (1928) divides the varieties into six ecotypes, varying in tussock profile and density,also varying in flowering time. Most of the Dactylis plants on the North Gravel (Area 2) resemble the "tussock ecotype" of STAPLEDON's classification: dense, erect plants, higher than wide, leaves long, very many barren tillers, with the panicles in tiers; flowering over a long period. The plants of the Oak Patch

however tend to be of the "cup ecotype": plants with the panicle tillers widely inclined from the vertical, wider than high, fewer barren tillers than tussocks, but can be lax or dense. The different ecotypes will have different microclimatic characteristics and they might differ in other characteristics which make them more or less attractive to T.oblongus as over-wintering sites.

North gravel sampling yielded 92 spiders from 36 tussocks, an average of 2.55 spiders per tussock. This is not significantly different from the Oak Patch average of 2.29 t = 0.5, N = 30 Other characteristics of Dactylis tussocks which might affect the distribution of T.oblongus are: age, size, ratio of dead to live material, position in relation to trees and water, nearness to neighbouring tussocks and the occurrence of other animals within the tussock.

Attempts were made to correlate the occurrence of T.oblongus with the size of the tussock and the nearness to the neighbouring tussocks in North Gravel. The tussocks were divided into two categories; large and small, larger and smaller than 20 cm. diameter respectively.
20 large tussocks yielded 53 individuals, average 2.65.
16 small tussocks yielded 39 individuals, average 2.44.
i.e. there was no significant difference between the numbers of spiders in these two habitats (χ^2= 0.28).

Six isolated tussocks, i.e. more than three meters from the nearest tussock were compared with six non isolated tussocks i.e. in contact with another tussock.

The isolated tussocks yielded 14 spiders, and the non isolated tussocks yielded 16 spiders. Again there was no significant difference.

In the Oak Patch, certain tussocks were noticed to contain dead oak leaves from the overhanging tree, this may have been associated with the tussock's position in relation to the tree or it could have to be due to the shape of the tussock, since flatter and dense tussocks could trap and hold more windblown leaves. These tussocks tended to be to the north-east of the area FIG 14, or it could have been due to the age of the tussock. Seven tussocks impregnated with oak leaves yielded seven spiders, the distribution being 0.0.0.0.2.2.3. spiders per tussock, and average of 1 individual per tussock. This gives a value of "t" of 8.0 with 6 d.f., which indicates a significant difference between tussocks impregnated with oak leaves and those which are not. This characteristic of tussocks only occurred in the Oak Patch, since the other areas had no tree cover.

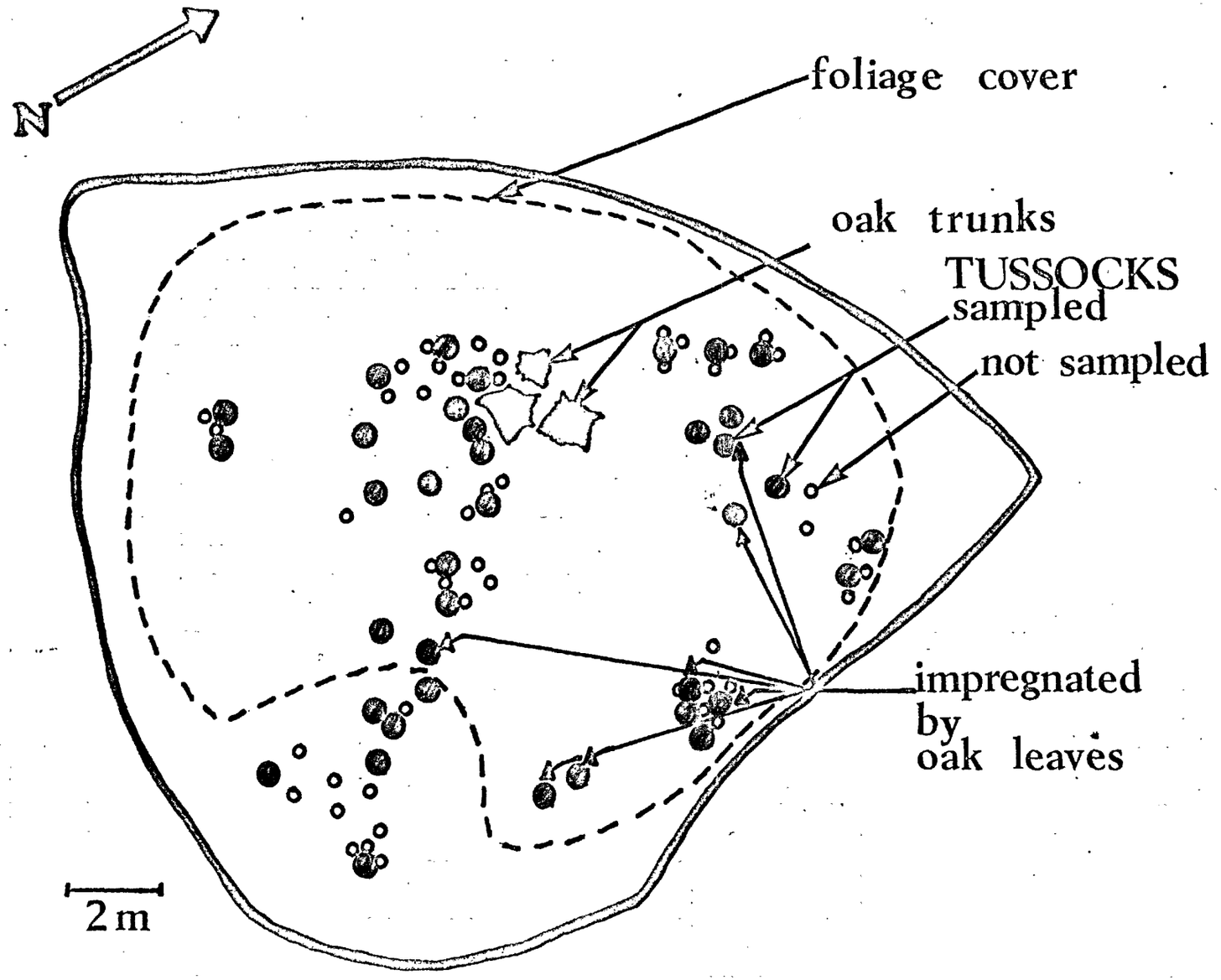
The six tussocks clear of overhanging foliage in the Oak Patch (FIG 14) yielded 14 spiders, and this was not significantly different from the general average.

Five tussocks from North Gravel, the bases of which were eaten into by mice which form tunnels in and around the base of the tussock surrounded by loose, dead vegetation, yielded 11 spiders, again a number which was not significantly different from the general average.

One possible reason for the concentration of T.oblongus in certain tussocks may be unrelated directly to the characteristics of the tussock. If the egg sac is laid the previous summer on the stems of a particular tussock the Instar 2 individuals hatching in August may not disperse far before hibernation; this would lead to a concentration of spiders in particular tussocks which are suitable as oviposition sites. However, a tussock often had no spiders whereas eight or nine were found in an adjacent one; also the larger Instars 3 and 4 were as non randomly distributed as the younger ones.

FIG 14

Sampling of T. oblongus, Oak Patch.



The only indication of a tussock's attractiveness to T.oblongus came from the negative correlation between the presence of dead oak leaves and that of the spiders, and this characteristic could not be investigated in any of the other areas.

A full, multiple correlation of all the variables may have provided more definite results concerning the spider's distribution amongst the Dactylis plants but further research is necessary for a full explanation.

4.3- SUMMER SAMPLING

The population of T.oblongus was studied in summer in Area 4. Microclimatic investigations were also carried out in this area. The purpose of the study was an attempt to determine the micro-environmental preferences of this particular spider, its prey and predators and its abundance in a typical area of grassland.

Two areas of open grassland, both fairly close to Silwood House, were considered as possible sites for investigation: the eastern slope of Gunness Hill and the crest of Elm Slope.

AREA 4 - (ELM SLOPE)

Description

A level patch of rough grassland, 36.6.m by 18.3 m, the longer side running north-west to south-east. It slopes slightly to the south-west, dropping 1.3 m in 18 m. It is on the southwestern brow of one of the highest points in Silwood Park (65m), but is sheltered by high trees on all but the Southwestern side, the vegetation has a tendency to slope towards the north-east.

The total area of 670 sq. m. consists approximately of $\frac{2}{3}$ Agrostis tenuis, $\frac{1}{7}$ Achillea millefolium, $\frac{1}{7}$ Festuca rubra and $\frac{1}{15}$ Holcus mollis. There is one tussock of Dactylis glomerata, about 100 oak saplings of $\frac{1}{3}$ to $1\frac{1}{3}$ m in height and a scattering of other typical grassland herbs. FIG 15 shows the area divided into sub-areas of vegetation of particular species. The sub-areas are not composed solely of the species indicated but are dominated by that species. Only in the case of Festuca which grows in dense clumps are other plants excluded.

Examination of Gunness Hill in autumn of 1964 had revealed that there was a population of Tibellus there, but Elm Slope (Area 4) was selected as there appeared to be more of the spiders there even though the vegetation of the two areas was similar. Elm Slope faces west whereas Gunness Hill faces east, Elm Slope has more clearly defined areas of different vegetation although it is more homogenous than Gunness Hill in that there are no large trees inside the area nor any thistles, also Area 4 is slightly dryer, Holcus mollis is less common except at the western boundary and there is no Juncus which is present on Gunness Hill.

Sampling methods

A preliminary investigation of the habitat showed that T.oblongus was fairly evenly distributed across Area 4; the larger Instars 3 and 4 were found on the surface of the vegetation and when the grass was disturbed and pressed down with both hands the spiders ran along the uppermost stems and could be easily seen and counted. Instar 2 individuals were found lower down amongst the bases of the grass stems and the stems had to be parted and the vegetation examined in detail at soil level in order to find them.

It was decided to carry out a random quadrat survey of Area 4 in order to assess the general population density of T.oblongus, any microhabitat preferences and to determine the occurrence of the various instars throughout the summer.

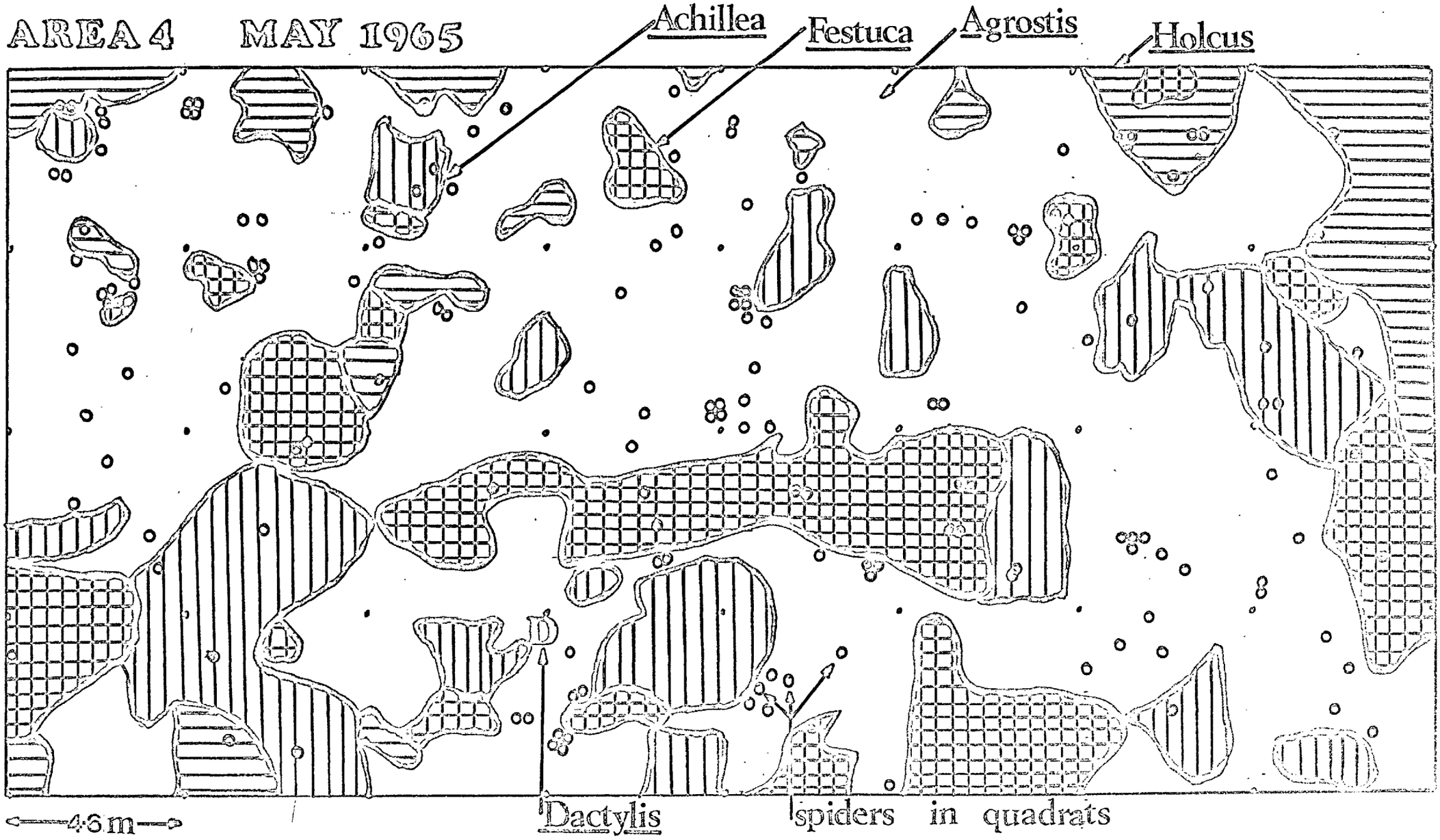

AREA 4 MAY 1965
Achillea
Festuca
Agrostis
Holcus
D
Dactylis
spiders in quadrats
4·6 m

FIG 15

The size of quadrat chosen was a wire square of 0.1 sq.m. This was a compromise between a larger size for the larger Instars since these individuals could be seen and counted in an area of twice this size, and a smaller size, which is more convenient for counting the smaller Instar because of the searching involved. A larger size would have been better for statistical reasons.

Area 4, was sectioned into a grid of 4.6 m squares, 32 in all, and canes were stuck into the ground at the intersections of the imaginary grid lines.

To ensure a random positioning of the quadrat, it was thrown into a particular square from a distance of about 5 m. The quadrat was made of springy wire and usually bounced and rolled between one and three metres in an unforseeable direction before coming to rest. The vegetation within it was searched for T. oblongus in the manner described. During each survey, the quadrat was thrownoonce into each of the 32 grid squares giving a sample ratio of 3.2 sq.m to 670 sq.m or 1:209.

A possible disadvantage of this method is the quadrat, in landing, might disturb the spiders and cause them to run away before being counted; however the quadrat weighed only a few ounces and usually landed gently after rolling, the disturbance of the grass was no more than that caused by a stron gust of wind; moreover the defensive behaviour of T. oblongus is to "freeze" at the first disturbance and to run only with continued disturbance especially if it coincides with a shadow. The quadrat does not cast a shadow whereas the investigator does.

This type of survey was carried out every few days from May 17th 1965 to August 17th 1965, usually in the late morning or early afternoon. Air temperature at a height of one metre was recorded, humidity at one metre was measured by means of a

wet and dry bulb hydrometer and recorded, whether the grass was saturated from recent rain and the total number of the various Instars of T.oblongus and the number in each quadrat was also noted. The results of this sampling are presented in TABLE 15 and condensed in TABLE 14.

TABLE 14

Numbers of T.oblongus found in quadrats in Area 4, May 17th to August 16th 1965.

No. of spiders per quadrat	No. of quadrats (0.1 sq.m.)
0	645
1	99
2	16
3	6
4	2
TOTAL 157	768

Mean 0.204 spiders per quadrat.
This distribution is significantly non random beyond the 0.005 level. I.D. = 1060 d.f. = 767.

There was an average of 0.204 spiders per quadrat, standard deviation was 0.476. This high value could be due to aggregation by the spiders as indicated by the index of dispersion test, or it could be due to the population density changing over the four months of the investigation.

Close observation of the spiders in the field showed conclusively that they aggregated in certain types of vegetation. However, this type of vegetation was only partially correlated with the species of plant. A cumulative record of the spiders found in quadrats between May 17th and August 16th 1965 is shown on FIG 15. The number of quadrats falling on each sub-area was not recorded, and a calculation of the probabilities of a proportional distribution of the quadrats over the different

TABLE 15

T. oblongus, quadrat survey, AREA 4 1965.

Date	May 17	19	19	20	20	21	25	27	27	31	June 2	2	2	3	4	4	10	10	11	14	25	29	July 19	Au 16
Time	12	12	15	10	12	15	15	12	15	15	11	12	15	10	10	15	10	15	12	12	12	12	15	15
Temp. °C	18	11	12	12	15	17	16	13	15	12	14	15	19	12	16	20	19	24	20	21	16	21	21	23
R.H. %	70	47	50	47	45	45				70	65	55	45	75	65	50	55	50		70				
Grass								W	E	T														
TOTAL	16	8	5	6	10	8	6	6	0	1	10	9	11	6	9	7	4	8	5	6	2	3	5	5
Instar 2	6		1	1	4	1	1	1			1	1	3	2	3	1		1	1	1				
3	8	6	2	3	3	3	4	1			4	3	5	1	3	2	2	5	1	3	1	2	1	1
4	1		1	2	2	3	1	3			5	3	2	2	3	2	1		1			1	4	4
A	1	2	1		1	1		1		1		2	1	1		2	1	2	2	2	1			
Distribution (max. in a quadrat)	4	2	1	4	3	2	3	3		1	3	1	3	2	2	3	2	3	1	2	1	2	1	1

types of vegetation would involve factors for the physical structure of the plants, the small bumps and dips in the terrain and the sizes and positions of the different sub-areas. It was assumed that there was a proportional distribution of the quadrats and a comparison can be made between the numbers of spiders found in each type of vegetation and the numbers that can be expected from a random distribution of the spiders.

Area 4 is 670 sq.m. and 157 spiders were found between the dates of sampling; the total of Agrostis sub areas was 427 sq.m. giving an expected number of 100 spiders, the observed being 113. The Holcus sub-areas totalled 57 sq.m. giving an expected number of spiders of 13, the observed 14. The Festuca sub-areas totalled 79 sq.m. the expected number of spiders, was 9 and the observed 16. There were 107 sq.m. of Achillea in which 14 spiders were found instead of the expected 25. A χ^2 value of 7.93 shows that the distribution of T.oblongus is significantly non random at the 2.5 level of significance in relation to species of substrate vegetation in Area 4. A comparison of the number of spiders found in Agrostis and that found in Achillea shows a more difinite deviation from the random, significant at the 1% level. The result of this calculation can only be regarded as an indication of the spiders's distribution because of the unknown distribution of the quadrats. Experiments were carried out to confirm the results of the calculation and the observations.

4.3.1 Choice of Substrate

The purpose of this experiment was to determine whether T.oblongus showed a tendency to position itself in a certain type of vegetation in the field during the late morning and early afternoon.

A wooden tray was used, 40cm. wide, 50cm long and 10 cm. deep. Two pieces of typical Area 4 vegetation were placed side by side in the tray, soil, litter and stems sloping in the same direction as in Area 4 i.e. north-east. The tray was placed on a lawn of short grass at noon on a

warm, sunny day and six Instar 4 spiders were released, three onto each of the two types of vegetation. See FIG 16. Two hours were allowed for the spiders to recover from the stress of being handled and to settle down into their predatory positions, then the vegetation was examined and the number of spiders in each type was recorded (It was hoped that none would escape over the sides of the tray, however some did but the results are not affected). Every combination of the four types of vegetation found in Area 4 was tried, three replicates of each. The results are shown in TABLE 16.

TABLE 16

Choice of Substrate Experiment Results

Plants in Tray	No. of spiders found on each species, 2 hours after release			total	Expected	χ^2
Replicate	1	2	3			
Agrostis	4	2	3	9	8.0	0.25
Holcus	2	3	2	7	8.0	
Agrostis	4	5	6	15	9.0	8.00
Festuca	2	1	0	3	9.0	
Agrostis	6	5	4	15	8.5	10.00
Achillea	0	0	2	2	8.5	
Holcus	4	5	5	14	8.0	9.00
Festuca	1	1	0	2	8.0	
Holcus	5	6	4	15	8.5	10.00
Achillea	0	0	2	2	8.5	
Festuca	2	1	5	8	8.5	0.06
Achillae	4	4	1	9	8.5	

There is a significant preference for the spiders to sit on Agrostis rather than Festuca or Achillea also to sit on Holcus rather than Festuca or Achillae.



FIG 16 **Choice of Substrate**

This experiment provided a strong indication of preference whereas the analysis of the population counts provided only a slight indication. The explanation of this discrepancy lies in the different time scales involved. The population counts continued over a period of four months whereas the experiment lasted only a week.

During the four months May 17th to August 17th, each of the three grasses produced inflorescences in succession; first the Holcus flowered, then the Festuca then the Agrostis. Associated with these reproductive phases were general changes in the physical condition of the grass areas namely the proportion of live green stems and leaves to dead or flowering non-transpiring stems. The occurrence of T.oblongus was found to be correlated with these changes. During the week of the experiment, the Holcus and Agrostis were both in the condition which proved favourable to the occurrence of the spiders i.e. a high proportion of brown, non-transpiring stems: these stems may be live, flower-bearing shoots or dead culms and leaves: whereas the Festuca was in the condition least attractive to T.oblongus having no long flowering shoots, and each tuft being composed of about 50% dead and 50% live stems.

As well as these differences in the occurrence of T.oblongus between different types of substrate vegetation, it was observed that their general abundance on the grass surface depended on the weather; they were absent or sparse on cool wet days and most of the population counts were done on warm sunny days when the air temperature at one metre was between 11°C and 24°C. The grass level temperature is a factor more relevant to the spiders and this was recorded from May 25th onwards, however since the sun and wind conditions were similar for all the population counts, the ground level temperature was correlated with the one metre temperature. This latter value was used in a multiple correlation designed to discover the relationship between spider activity in the field and temperature.

The correlation was carried out by the IBM 7090 computer at Imperial College using a program written by G.MURDIE.

A factor for the date was used as one independant variable expressed in terms of the number of days before August 17th from 80 to 0, temperature at one metre in ^{o}C was the other, and the number of spiders found in the quadrats was the dependant variable.

The correlation was significant at the 5% level, $F = 4.57$ for 2 and 15 d.f., however only 38% of the variation in numbers of T.oblongus was accounted for by the two factors temperature and date. The correlation coefficients were:

Temperature:Date	=	0.59
Number of spiders:Date	=	0.47
Number of spiders:Temperature	=	0.05

In an attempt to gather information concerning the behaviour of T.oblongus in relation to temperature and humidity, three correlations were tried using data from the population counts:

1. The proportion of the total sample in the most populous quadrat with temperature..To discover if temperature affected aggregation.

2. The proportion of the total sample in the most populous quadrat with humidity. To discover if humidity affected aggregation.

3. The proportion of Instar 2 individuals in the sample with air temperature. To discover if temperature affected different Instars differently.

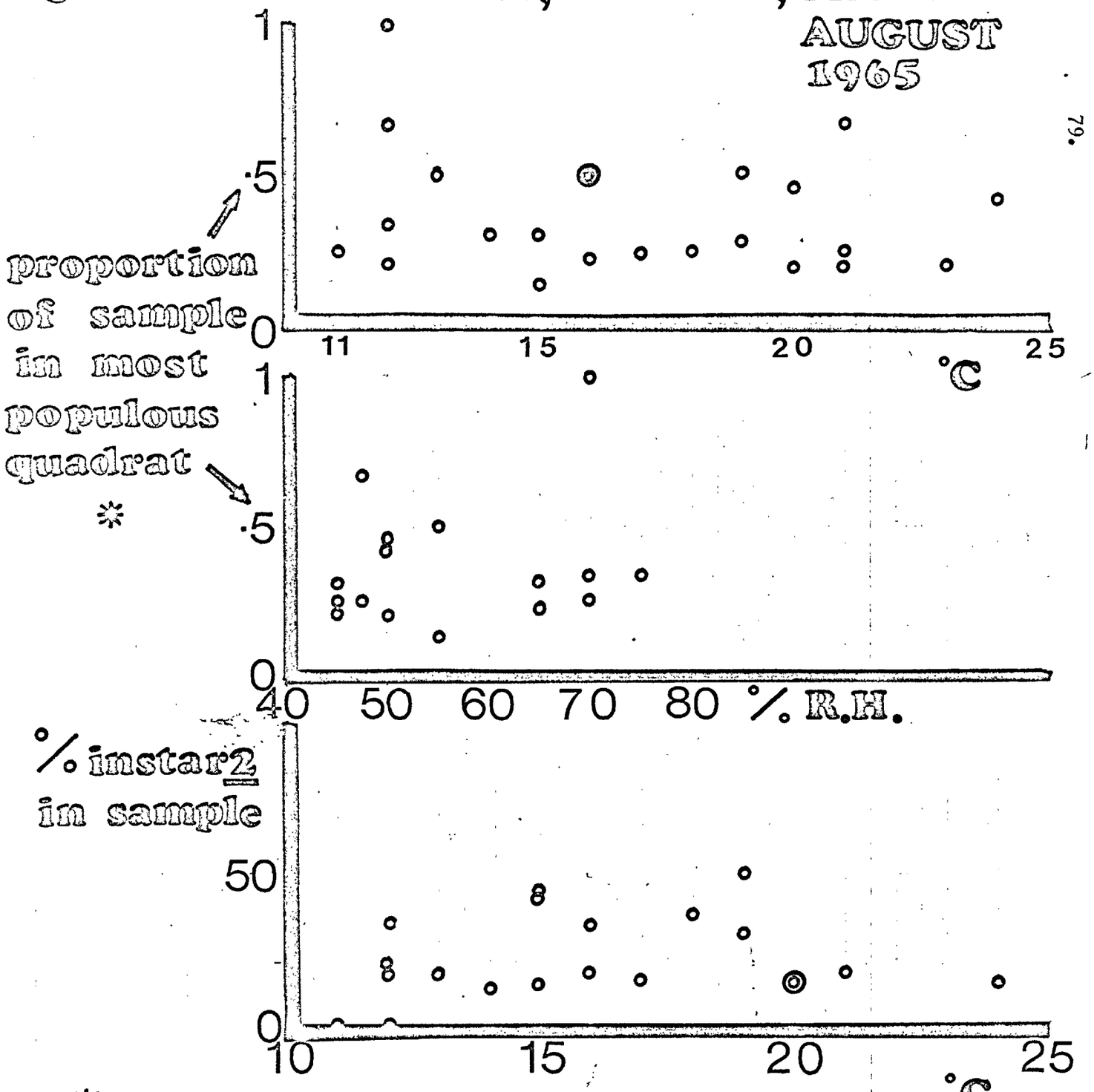
The calculated data is set out in FIG 17

In none of the three was there a significant correlation.

FIG 17

T. OBLONGUS,

QUADRAT SURVEY, AREA 4, MAY – AUGUST 1965



* No. of spiders in most populous quadrat divided by total No. of spiders in a sample.

4.3.2 Demarkation of Special Areas

In mid-August 1965, after the preliminary survey, Area 4 was inspected visually and a total of 6.0 sq.m in 14 small patches was marked out as "Special Areas." These special areas were patches of mixed live and dead grass which had been found to contain a much denser population of T.oblongus than the surrounding grass which was predominantly green; the stems tended to slope towards the north-east probably because of the prevailing southwesterly wind and because of the slight slope of the ground; the rest of the vegetation tended to be vertical.

The special areas in August 1965 were found mainly in Agrostis except for two which were in Festuca and the single Dactylis tussock. A random sample of 20 x 0.1 sq.m was taken seven times between August 17th and October 7th together with a 3.2 sq.m sample of the rest of the area in the manner described previously. The results are in TABLE 17. The samples were taken on warm sunny afternoons.

TABLE 17

Results of Sampling Area 4: August 17th to October 7th,1965.

	SPECIAL AREA 2.0 sq.m sample					NORMAL AREA 3.2 sq.m sample				
Instar	2	3	4	A	Total	2	3	4	A	Total
17/8	0	4	14	2	20	0	0	2	0	2
23/8	2	3	13	0	18	0	0	3	0	3
2/9	1	3	7	0	11	0	0	4	0	4
12/9	3	0	13	0	16	0	0	2	0	2
20/9	2	0	13	0	15	0	0	1	0	1
28/9	0	0	6	0	6	4	0	4	0	8
7/10	2	0	7	0	9	0	0	6	0	6
					TOTAL 95					26

A total sample of 14 sq.m of Special Area yielded 95 spiders, an average of 6.8 spiders per sq.m whereas the normal area yielded an average of 1.1 spiders per sq.m. However the ratio of numbers in special and normal varied from 15:1 to 4:3, so the difference is not consistent although it is highly significant.

4.4. SUMMER SAMPLING 1966

Throughout the summer of 1966, a record was kept of the changes in the pattern of the Special Areas in Area 4, observations were made on their microclimatic characteristics in relation to the rest of the vegetation and of the density of T.oblongus in them in relation to the rest of the vegetation.

4.4.1 Microclimatic measurements

Temperature measurements were made with a normal mercury bulb thermometer. This was adequate for the spatial requirements of the readings, the bulb is about the size of the body of an Instar 4, T.oblongus. When readings were taken, the bulb was shielded from direct sunlight but as little as possible of the surrounding grass was shielded and the Mercury level allowed to reach equilibrium before it was recorded.

4.4.2 Evaporimeter

The humidity was measured by means of an evaporimeter(FIG 18). This instrument in effect measures directly the evaporating power of its environment: it takes into account air currents and local saturation which neither cobalt thiocyanate paper nor the wet and dry bulb hydrometer do: also it is effective in a small space as compared with a Gregory hydrometer which is relatively bulky. The evaporimeter is very portable and convenient to use, except that its disadvantage is that it may saturate the microenvironment with water vapour; this would affect the rate of evaporation and hence the reading: however during calibration this source of error was not encountered.

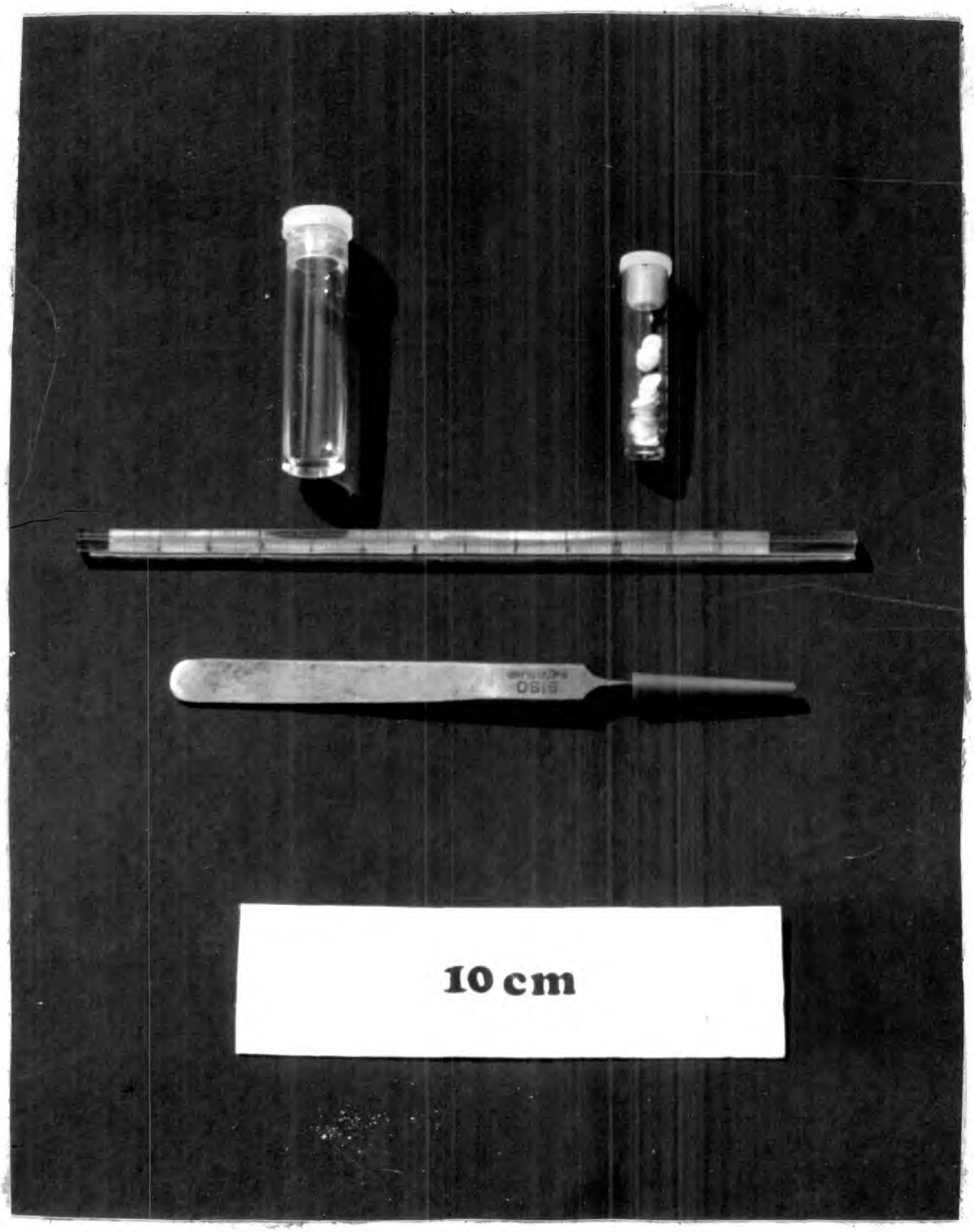


FIG 18 **Evaporimeter**

The evaporimeter is simply a length of glass capillary tubing full of water, with an evaporating surface at one end. The rate at which water leaves the tube is a measure of the evaporating power of the environment.

During the development of the instrument in the laboratory, two sizes of capillary tubing were tried:

a) 5 mm diameter, 0.5 mm bore.

b) 4 mm diameter, 0.3 mm bore.

The smaller tube was found to be more convenient because the surface forces inside it are larger in proportion to the mass of water, so the water does not move about and form droplets at the end of the tube so readily when it is moved or tilted. As an evaporation surface, three types of paper were tried:

a) Whatman Loose Weave filter paper.

b) Normal filter paper.

c) Washed cigarette paper. (Washed to remove any inorganic salts

A disc of each of these was punched with a number 3 cork borer, three tubes were filled with distilled water, a different disc was applied to one end ofeach tube and held there by capillary attraction the tubes were left adjacent to each other in the lab, and the movements of the menisci were recorded for two hours. More discs were cut and tried as before and it was found that the washed cigarettepaper gave the most consistent readings. The thicker filter papers were more likely to be unevenly crushed while being punched and handled and this could affect the rate of evaporation from them, whereas the cigarette paper being very thin was virtually uncrushable and all discs appeared homogenous and identical.

The final evaporimeter (FIG 18) was 13 cm long, 4 mm diameter, 0.3 mm bore tubing with a disc of washed cigarette paper of 4 mm diameter at one end and a thin strip of graph paper glued along its length for convenient observation of the movement of the meniscus. When it was used in the field, a small bottle of distilled water was taken together with about a dozen spare paper discs; the evaporimeter was filled by careful sucking from the

uncovered end, then a disc was applied to the other end by means of forceps to avoid contamination by finger grease, the tube was held level and allowed to stabilise and any droplet at one end taken into the capillary; then the evaporating surface was held in the microenvironment in question with the tube horizontal, the movement of the meniscus was recorded after five minutes.

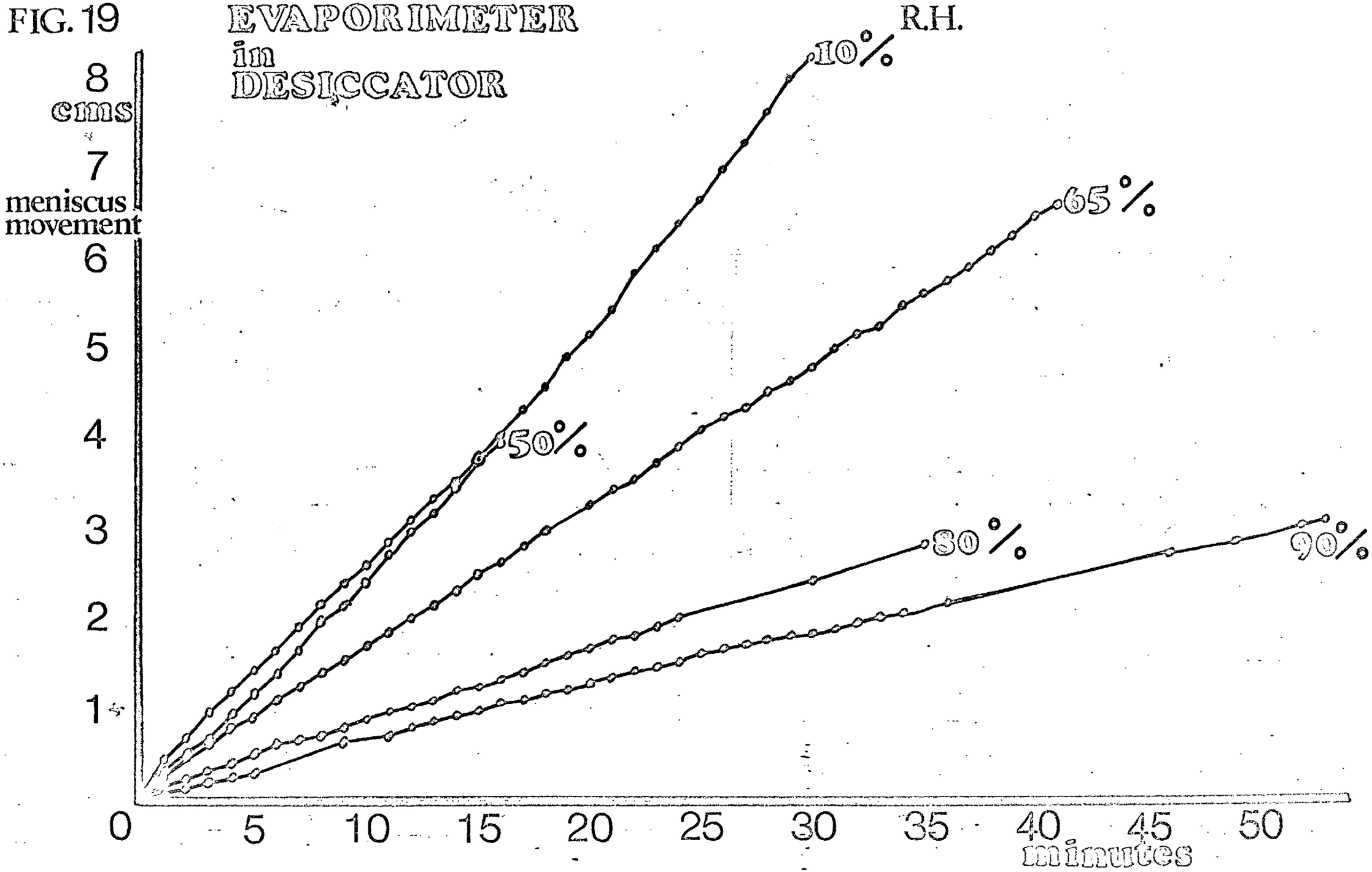
CALIBRATION

In order to discover an approximate relationship between relative humidity and the evaporimeter reading it was calibrated in the laboratory.

Solutions of various strengths of KOH were prepared, 100 cc of each solution in turn was poured into a desiccator, the lid was put on and the R.H. allowed to stabilize; then the evaporimeter was placed on the wire mesh six or seven centimeters above the surface of the liquid, the lid was put on the desiccator and the meniscus movement recorded every minute for about 35 minutes. The results are set out in FIG 19.

The results show a marked consistency in the evaporation rates and within the range 50% to 90% R.H. there is a regular differentiation in evaporimeter readings with the difference in R.H. Although the air in the desiccator is stationary, the danger of a sphere of saturated air round the evaporating surface depressing the evaporation rate does not seem to have materialised. During calibration, as soon as the hypothetical sphere comes into contact with the KOH solution surface it reaches equilibrium as the water vapour is absorbed into the solution, however the evaporating surface was six or seven cm above the KOH surface; a sphere of this diameter easily encompasses the microenvironments under investigation in the field, therefore the field results are regarded as reliable.

FIG. 19


EVAPORIMETER
in
DESICCATOR
R.H.
10%
50%
65%
80%
90%
8
cms
7
meniscus
movement
6
5
4
3
2
1
0
5
10
15
20
25
30
35
40
45
50
minutes

In 1965 I had underestimated the number of the younger Instars of T.oblongus in samples, so various specialised sampling methods were tried during 1966 in an attempt to obtain a more balanced survey of the species and also to determine more clearly the degree of stratification of the different Instars through the vegetation.

4.4.3 Stratified Pitfalls

Nine polystyrene dishes were used, 10 cm diameter, and 4 cm deep; 15 cc of ethylene glycol was poured into each forming a 1 cm deep liquid trap at the bottom.

The dishes were placed at three different levels in a typical stand of mixed live and dead Agrostis where T.oblongus was abundant; the uppermost dish was amongst the long sloping stems about 15 cm above soil level, the middle dish was level with the surface of the litter and shrivelled leaves at 8 cm and the lowest one was sunk into a shallow pit so that the rim was at soil level. Three traps were placed in each of three tussocks and were examined after one, five, eight and thirteen days. No T.oblongus were found, only a few Carabids and Lycosids. A T.oblongus deliberately placed in the liquid was trapped by it, apparently none had reached that far. The traps were rejected and removed.

4.4.4 Sticky Bands

Strips of commercial sticky band were cut, 10 cm by 3 cm, two strips were put in each of five typical Agrostis stands, one strip at a height of 10 cm facing upwards and outwards on the sunward surface of the grass covered by a single layer of about six stems; the second strip was placed amongst the litter at the base of the grass, from soil level to 5 cm.

The following morning, all the strips were empty; the slight smell of menthol emanating from them may act as a repellant, but a small Lyniphiid was seen to walk across the supposedly sticky surface without difficulty. The strips had caught nothing after six days and were removed.

4.4.5 Sticky Canes

Dr. Eric Duffey (verbal communication) recommended sticky canes as a trapping method. The gum on paper strips develops a non-adhesive surface after exposure to moisture whereas gum painted on canes maintains its stickiness through expansion and contraction and very slowly flowing down the cane, thus renewing the surface. A 20 cm band of "Sticktite" was painted on to 25 canes of 1 - 2 cm in diameter; the canes were stuck into the ground in and around the area frequented by T.oblongus, and were sloped parallel to the grass stems between 20^{o} and 40^{o} from the vertical. Five canes were placed in each of five tufts of Agrostis, one with its band from soil level to 10 cm, another with its band from soil level to 10 cm, another with its band from 5 cm to 15 cm, a third from 10 cm to 20 cm, a fourth from 15 cm to 25 cm and the fifth from 20 cm to 30 cm. After five days the canes had caught a few bugs, an ichneumon wasp and a young grasshopper, but no T.oblongus. A small spider was placed on to the gum, it was slightly repelled but walked across the surface easily then took off by means of an aerial thread. The canes were left out for several weeks, throughout the reproductive phase of T.oblongus in the hope that a female searching for an egg laying site may climb one. Eventually the gum was almost completely covered by trapped fauna of numerous types but no T.oblongus were found.

Sampling by marking and releasing was considered, as described by BAILEY 1951, but this was practicable only with the larger Instars. White paint was applied to the abdomens of several individuals but it appeared to disturb them probably because the abdomen is very sensitive to touch and is used in the detection of prey.

Since T.oblongus selects its microenvironment, it was considered that the disturbance involved in vaccuum sampling would have a destructive effect on the spiders habitat.

Because of these difficulties and because of the remarkable capacity of T.oblongus to avoid being trapped, the same imperfect sampling methods of 1965 had to be repeated in 1966.

4.4.6 Vegetation Pattern

The vegetation of AREA 4 was assessed visually each month from April to October and the percentage of dead vegetation was recorded. Although T.oblongus is not abundant in tufts of completely dead grass stems, the special area of mixed live and dead stems, where the spiders are abundant, form a close proportion of the dead vegetation. The changes that occurred in vegetation during April to October 1966 are given in TABLE 18.

TABLE 18

Changes in vegetation in AREA 4, 1966

	% of area appearing light brown	Composition		
		Holcus	Festuca	Agrostis
APRIL	23	5.5	3.0	14.5
MAY	17.5	0.5	2.5	14.5
JUNE	9	0.25	1.75	7.0
JULY	6	0.5	1.0	4.5
AUGUST	12	3.0	2.0	7.0
SEPTEMBER	30	8.0	8.0	14.0
OCTOBER	35	8.0	8.0	19.0

Early in the summer the dead patches are made up of normal leaves and stems that died during the winter; after the flowering time of the grass, the dead flower stems comprise most of the dead vegetation. The three minima in the values for the three grass species correspond to three flowering times: first Holcus then Festuca closely followed by Agrostis.

4.4.7 Microclimate

The vegetation of AREA 4 was subdivided into eight types.

a) Live Holcus

stands of live, photosynthesising Holcus stems and leaves, vertical and relatively diffuse, green in appearance. Stems 1 - 2 mm diameter, leaves up to 5 mm wide.

b) Dead Holcus

A gray mass of dry, dead leaves and stems, often horizontal.

c) Mixed Holcus

A mixture of the two above types.

NOTE - The flower stems of Holcus are green and photosynthetic at the basal 20 or so centimetres.

d) Live Festuca

A stand of thin, green leaves usually sprouting from a dense layer of shorter leaves and brown, shrivelled dead leaves. They point in various directions tending to the north-east.

e) Mixed Festuca

At flowering time long, pale brown reproductive stems rise above the surface of the normal vegetation.

leaves	0.75 mm - 0.5 mm diameter
reproductive stems	1.00 mm - 2.0 mm diameter.

f) Live Agrostis

Green stems and leaves in relatively dense bunches usually parallel, vertical or tending to slope northeastward.

g) Dead Agrostis

A mass of grey-brown dead stems and leaves invariably sloping north, northeast or east.

h) Mixed Agrostis

A close mass of parallel stems and leaves some green and photosynthesising, others grey-brown and dead, usually sloping northeast. The widths of the various components are variable up to 2 mm and there are flattened leaves intermingled.

Readings were taken with the thermometer and evaporimeter at a height of about 10 - 15 cm where T.oblongus was usually found.

A record of the microclimatic characteristics of these eight types during a typical sunny day in early summer is presented in TABLE 19.

These are the readings from a single day, June 4th 1966; the observations were repeated on other days and though the values were slightly different, the pattern was the same.

TABLE 19

Typical Microclimate readings from AREA 4, early June.

Source of Reading		Time of Day			
		09.30	12.00	14.30	22.00
Air at 1 metre	°C	12	16	17	10
	E	12	17	16	12
Live Holcus	°C	15	19	22	6
	E	6	12	5	4
Dead Holcus	°C	18	23	24	4
	E	7	17	12	0
Festuca	°C	17	23	27	6
	E	8	8	8	4
Live Agrostis	°C	18	23	24	8
	E	6	12	5	4
Dead Agrostis	°C	20	28	30	12
	E	9	25	12	2
Mixed Live and Dead Agrostis (special area)	°C	15	27	27	12
	E	5	8	8	4

E = Evaporimeter meniscus movement (mm)

At 9.30 hrs. the vegetation is already heated by the sun above the temperature at 1.0 metre though it is damper than the air. At 22.00 hrs (dusk) the ground is beginning to cool down faster than the air and only the dead and mixed Agrostis is retaining its warmth. The evaporimeter reading for the air at 1.0 metre is generally higher than in the vegetation because the air is moving past the evaporimeter but is almost stationary amongst the grass stems, whilst transpiration also keeps the humidity high. Live Holcus is the coolest and dampest environment

whilst dead Agrostis is the hottest and dryest; the readings for the mixed vegetation are the average of those for the live and dead of the respective species. Live Festuca becomes warmer and dryer by the afternoon than the other two species, because of the denser, darker litter within it and the more diffuse stems and leaves which are rolled thinner and semi-xerophytic.

On days following heavy rainfall or dew fall the dead Agrostis dried out and warmed up fastest, then Festuca, and lastly Holcus, which occasionally remained saturated the whole day even if the other two species dried out.

4.4.8 Distribution and abundance of T.oblongus summer 1966

Four times each month from May 1966 to October 1966, a sample was taken of the "special" and normal areas. Each sample consisted of the examination of ten squares of 0.1 sq.mm, in each type of vegetation the squares were chosen randomly, using a metal quadrat as before. The results are given in TABLE 20.

4.5 ANALYSIS

4.5.1 Microclimate

TABLE 19 shows the results during a typical sunny day in early summer when all the Instars of T.oblongus are relatively abundant and active in the field. The types labelled "mixed Holcus and "mixed Agrostis" are the Special Areas where T.oblongus is found in density greater by approximately four to one than in the rest of the vegetation; "mixed Festuca" does not appear until this species flowers in late June and early July and persists afterwards when the dead and dying flowering stems remain erect.

The important characteristic of the Special Areas in relation to the other areas is that they become warmer than the live grass and stay damper than the dead grass. Dead stems and leaves absorb the sun's radiation and heat up whereas live stems and leaves transpire, so dampening and cooling the surrounding air. A mixture

TABLE 20

Results of Sampling for T.oblongus AREA 4, 1966

One sq.m sample in Special Area (S), and Normal Area (N).

Date	Vegetation Type	Instar 2	3	4	A	Total	
April 4	N		3	5		2	
	S					6	
April 10th	N		3	3		1	
	S					5	
April 12	N		0	5		2	
	S					3	
April 25	N	3	2	3		3	
	S					5	
April Total	N					8	
	S					19	27
May 10	N		1	1		2	
	S		3	1		4	
May 16	N			1	♂	2	
	S		4	1		5	
May 20	N					0	
	S		5		♀♂	7	
May 30	N				♂	1	
	S	3	1			4	
May Total	N					5	
	S					20	25
June 4	N	1		3	♂	5	
	S	4	2			6	
June 12	N			♀	♀	2	
	S	1	4			5	
June 18	N					0	
	S				♂	1	
June 26	N				♂♂	2	
	S	1	2	3	♂♀	8	
June Total	N					9	
	S					20	29

TABLE 20 contd.

Results of Sampling for L. oblongus AREA 4, 1966

One sq.m sample in Special Area (S), and Normal Area (N).

Date	Vegetation type	Instar 2	3	4	A	Total	
JULY 1	N				♀	1	
	S	3				3	
JULY 7	N					0	
	S	1	3		♂	5	
JULY 11	N			1		1	
	S	3		2		5	
JULY 20	N		1			1	
	S				♂♂	2	18
AUGUST 2	N		6	4		2	
	S					8	
AUGUST 5	N					0	
	S					0	10
SEPTEMBER 25	N		3	6		2	
	S					7	
SEPTEMBER 18	N			6		0	
	S					6	
SEPTEMBER 25	N	1		4		1	
	S					4	
SEPTEMBER 30	N	4		6		0	
	S					10	
SEPTEMBER TOTAL	N					3	
	S					27	30
OCTOBER 4	N	2	1	1		2	
	S					3	
OCTOBER 10	N			3		1	
	S					2	
OCTOBER 16	N					0	
	S					0	
OCTOBER 23	N					0	
	S					0	
OCTOBER TOTAL..	N					3	
	S					5	8

of these two produces "optimum" conditions for T.oblongus, It was noticed that various types of Lycosid and Salticid spiders were abundant in these areas also, and many flying insects landed in them, especially Diptera. Some flies are known to be attracted to warm surfaces but these are mostly parasites of warm-blooded animals, the flies landing on the Special Areas may be just sunning themselves, raising their body temperature, or they may be in search of food. There are likely to be decomposing stems and leaves in the Special Area, especially late in the season and this would attract a whole complex of species of a food chain from bacteria and fungi through collembola, saprophytic beetles, and flies up to the higher predators, beetles and spiders. The cryptic coloration and posture of T.oblongus blends best with this type of vegetation with its intermingled parallel, green, and tan shadow components. So T.oblongus would seem to be adapted to the particular environment where its potential prey tend to congregate. However all stages of the spider were found amongst other types of vegetation; also certain Special Areas which appeared typical and had typical fauna and microclimatic characteristics were consistently devoid of T.oblongus . which was found to congregate on certain tussocks apparently identical to their neighbours from which T.oblongus individuals were absent. This could be explained by various factors: the microstructure of the particular grass patches devoid of T.oblongus may be unsuitable not having free water droplets for the spiders to drink, not being of the optimum density for the spiders, to prey or escape, not containing any decomposing matter, or there may have been no suitable places in the vicinity for the spiders to spend the night. T.oblongus usually disappeared from the vegetation surface at night although some Instar 4 individuals were swept on warm nights. Aggregation was investigated as a possible explanation(see SECTION 5.4.5) but the results were inconclusive.

4.5.2 Numbers of T.oblongus

The average density in the Special Area was 4.38 spiders per sq.m, varying from a minimum of 1.25 in October to a maximum of 6.75 in September: the average density in the 'Normal Area' was 1.35 spiders per sq.m, minima 0.75 in July, September and October, maximum 2.25 in June. The ratio of densities in Special to Normal Areas is consistent at about 4:1 from month to month, but since the total area of the Special Areas decreases through June to July and August (TABLE 20) the total number of T.oblongus must fluctuate correspondingly. The numbers of spiders sampled also reaches a minumum during this period and this further emphasises the decrease in population. July is the month during which the last of the individuals that over-wintered as Instar 2 emerge and moult, and all those that over-wintered as Instar 4 become adult and the adults are mating and reproducing. This is the period when predatory activity is at a minumum in T.oblongus, it is also the time when there are the lowest number of predatory sites, Special Areas, available.

Activity is resumed in September as the newly hatched Instar 2 individuals emerge and the newly moulted Instar 4 are active in the predatory sites, feeding in preparation for over-wintering. This corresponds to the dying off of the grasses and an increase in the number of Special Areas. The cold weather of October marks the disappearance of T.oblongus from the surface vegetation.

Adults were found from the beginning of May to the end of July; 11 males and 6 females in total. This is not a significant sex ratio when the variation in the results of single samples are taken into account.

POPULATION SURVEY

4.6 GENERAL CONCLUSIONS

T.oblongus proved to be a difficult animal to sample accurately for several reasons: first, the low general population level; second, the elusiveness of the species and its avoidance

of traps; thirdly, the difference in distribution of the various Instars; fourthly the biennial development cycle; and fifthly the daily and seasonal movements of the individuals are very sensitive to both climate and microclimatic conditions.

However, the investigation of the Special Areas of mixed live and dead grass stems showed significant microclimatic differences to the surrounding vegetation and a corresponding higher density of T.oblongus together with a higher density of its potential prey. Also the seasonal fluctuations in the prevalence and location of the Special Areas were found to coincide with the fluctuations in density and activity of T.oblongus.

The population of T.oblongus in winter was found to be concentrated in Dactylis tussocks, the microclimatic characteristics of which are known to be favourable for the hibernation of many Arthropod species. Certain Dactylis tussocks contained a significantly higher number of T.oblongus, the reasons for this were not discovered.

The tussocks have been shown to produce a more equable micro climate than Holcus or Festuca with a smaller range of temperature extremes at the 7.5 cm level and at soil level in summer and winter, after rain and under snow.(LUFF 1965)

SECTION 5

BEHAVIOUR

5.1 GENERAL CONSIDERATIONS

Like all the order Aranea, T.oblongus is a predator on other small organisms of similar or smaller size than itself. This aspect of the species' biology has an overriding influence on the whole of its behaviour. Also like many other spiders, it lives in temperate grassland of a fairly typical kind; however the structure and behaviour of the genus reflect its distinctive and unique ecological relationship to the other spiders in Britain.

As far as is known, all the family Thomisidae are ambush predators that neither build snares nor move directly in search or in pursuit of their prey; and all the genera whose predatory habits are known, tend to be confined to highly specialised location such as flowerheads or seeds while preying. One related tropical group is disguised as a bird's faeces in order to attract prey.

T.oblongus is an exception among the British Thomisidae; it preys in the same relatively generalised locations as the grassland Lycosidae and Salticidae, i.e. the patches of half-dead grass stems. This feature of its mode of life together with its structure and its use of its own body and legs directly to detect prey in the manner typical of the Thomisidae make it unique among British spiders.

In its relationship to its prey, the genus T.oblongus can be considered as a midpoint between the passive, sedentary snare-building families e.g. Argiopidae, Linyphiidae and Tetragnathidae and the active hunters e.g. Lycosidae and Salticidae.

A detailed analysis of the behavioural interaction between T.oblongus and its prey was carried out in the belief that a full understanding of this interaction is a pre-requisite to the understanding of the ecology of the species, and of others with similar modes of life. This analysis is described in SECTION 6 and is discussed in relation to the general predatory rôle of T.oblongus.

5.2. CLASSIFICATION

The aspects of the behaviour of T.oblongus that were studied can be categorised under the following headings:

a) Predatory Behaviour. Sources of information were: Observations in the field, experiments and observation in the laboratory. (Described in SECTION 6)

b) Defensive Behaviour. Sources of information were: Observations in the field, experiment and observation in the laboratory.

Mass Movements

c) Yearly migration cycle: Sources of information were: Observation and experiments on hibernation in the laboratory, and observation in the field.

d) Dispersal: Observation and experiment in field and laboratory, and experiments on aeronaut behaviour.

Individual Behaviour

e) Aggregation, i.e. orientation with respect to members of the same species. Laboratory experiments were carried out on this.

f) Orientation with respect to the physical environment: Sources of information were: observation and experiment in field and laboratory.

g) Moulting: this was observed in the laboratory.

Reproductive Behaviour.

h) Mating: this was observed in the laboratory.

i) Egg-laying: this was observed in the laboratory.

j) Incubation: this was observed in the laboratory.

5.3 POSTURE

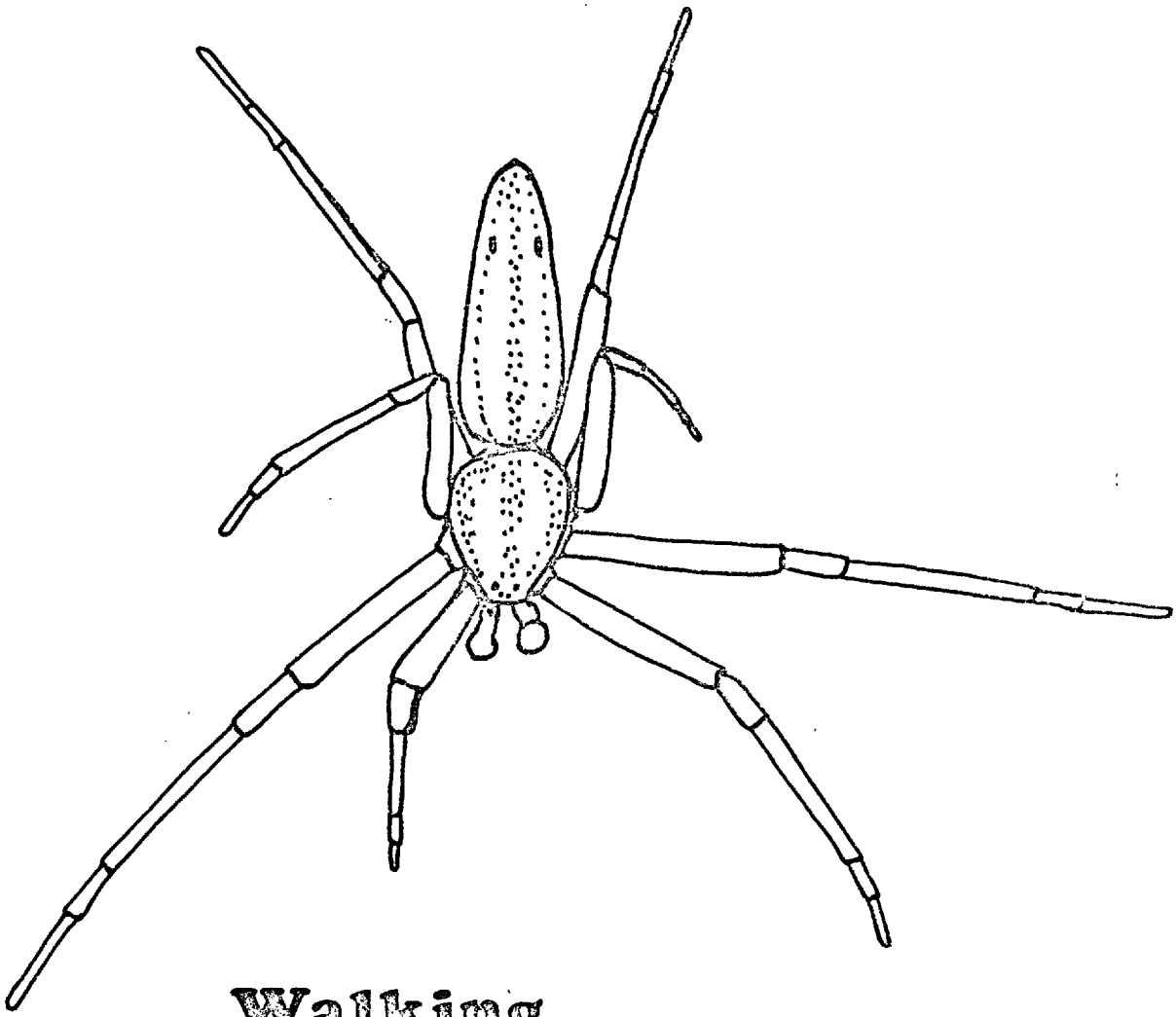
Although T.oblongus is very active in its immediate reaction to prey or predators, the individuals spend a high proportion of the time in a stationary, relatively fixed posture.

The postures were found to reflect the state of the individual; for example there were certain postures adopted during predation and others during hibernation. Therefore the postures could be used as a convenient term of reference during the behavioural observations and experiments on the species; they are referred to in the description and discussion which follow, however, a series of Figures 20 to 23 with brief descriptions is presented at this point for comparison.

The postures illustrated are extremes, intermediate positions were frequently observed which exhibited combinations of the following posture characteristics:-

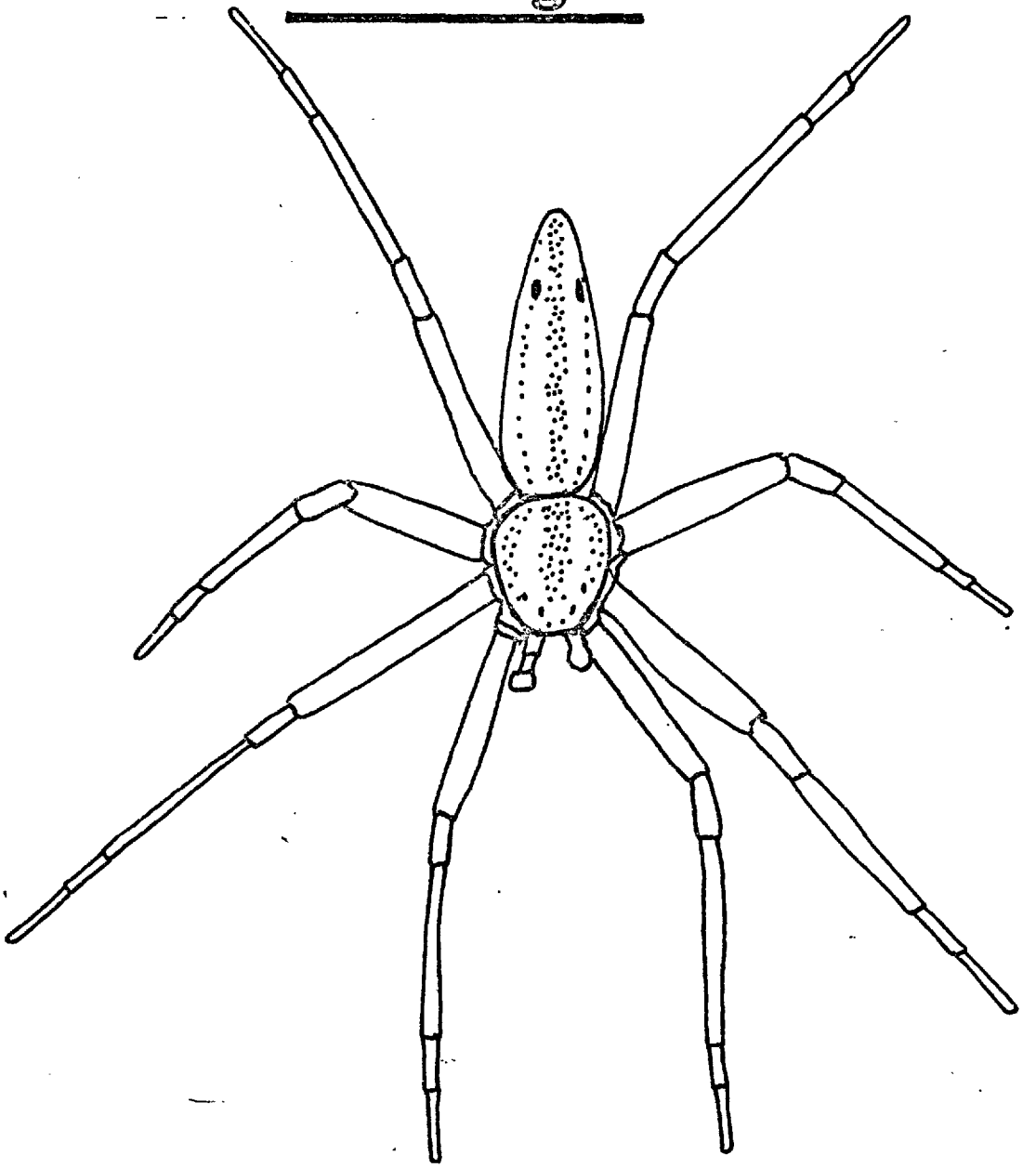
a) Walking (FIG 20)
Legs II, III and IV are used for propulsion while the first pair of legs are waved in a vertical place in front of the spider. The rate of movement of the front legs was found to be roughly proportional to the speed of walking, varying from one movement every two seconds to about four movements per second. It seems probable that the front legs are used to detect objects in the spider's path beyond the visual range, as was indicated by experiments on predation (see 5.6).

FIG 20 T.oblongus



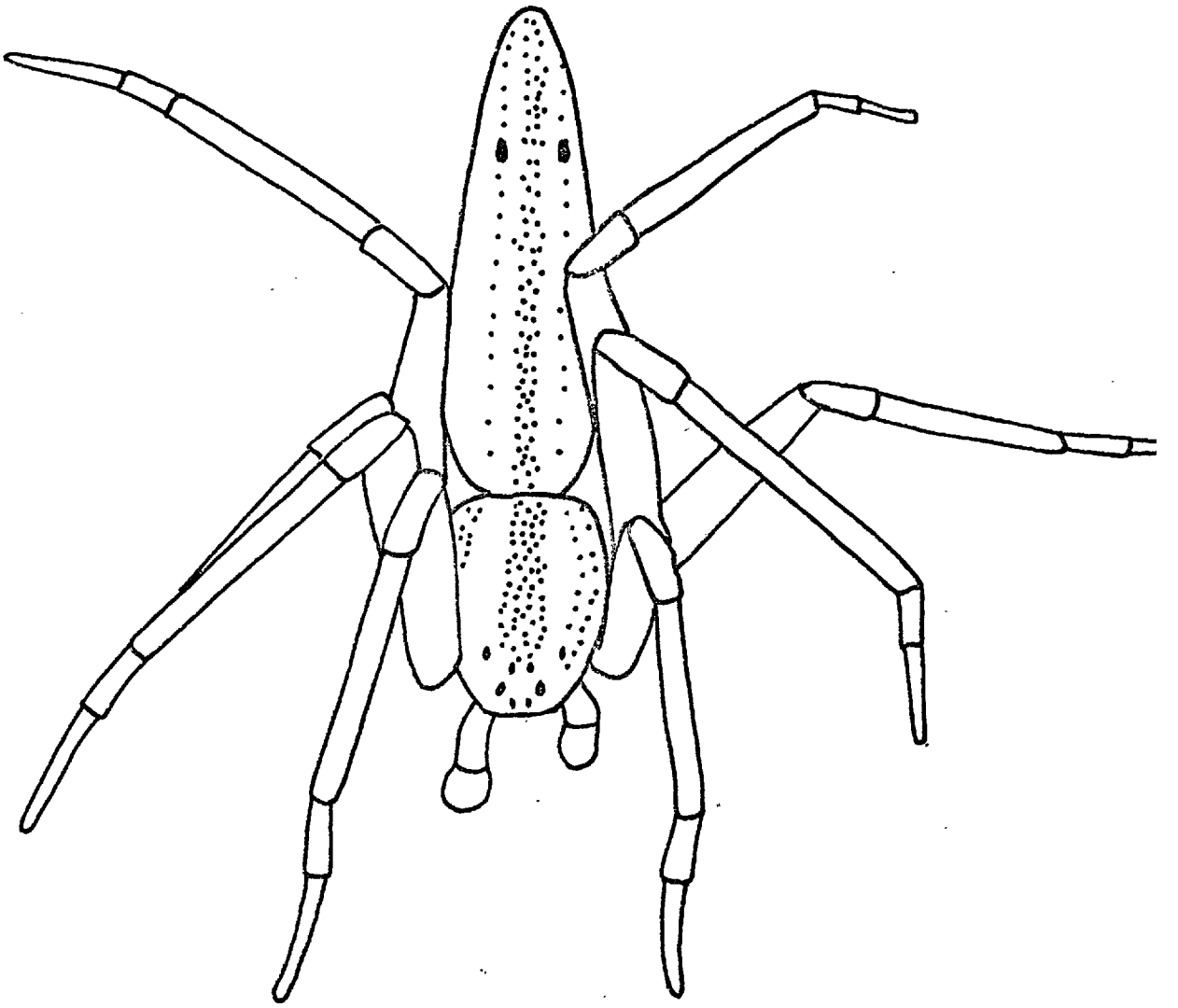
Walking

FIG 21 T.oblongus



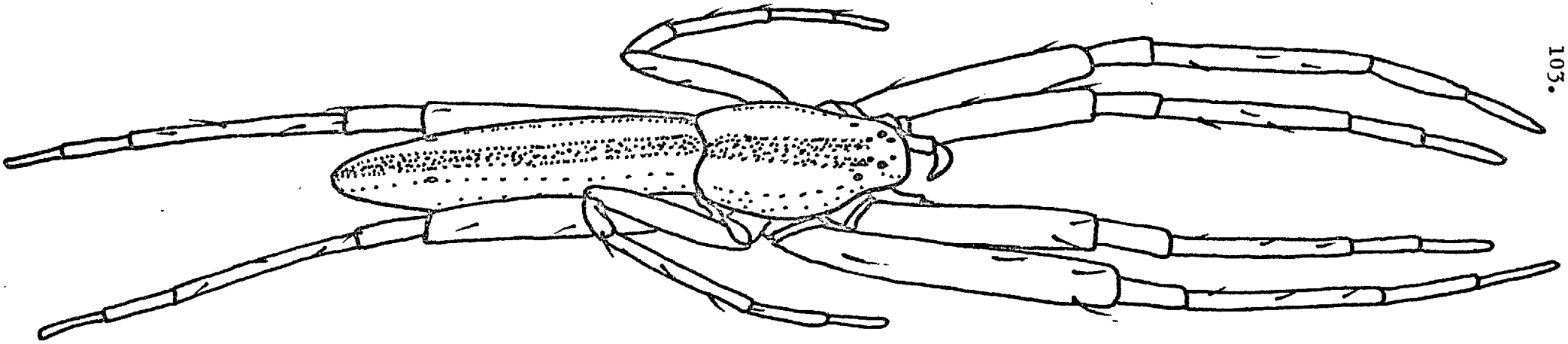
PREDATORY POSTURE

FIG 22 T.oblongus



DEFENCE POSTURE

FIG 23 T. OBLONGUS



HIBERNATION POSTURE

b) Hibernation Posture (FIG 23)

This posture was also observed when the spider was was replete, also when it was basking in sun or lamplight and it was adopted by the individual immediately on completion of the characteristic short escape run. It is likely that the posture has a camouflage function. Legs I, II and IV are held parallel to adjacent grass stems thereby combining with the longitudinal abdominal stripe to blend the spider with its background.

c) Defence Posture

All the legs are flexed over the carapace and abdomen probably to provide direct physical protection if the spider is attacked.

d) Predatory Posture

All the legs are extended so that they cover the greatest area for the detection of prey (see SECTION 6), or for the detection of threats during incubation.

5.4 DESCRIPTION AND DISCUSSION

5.4.1 Predatory Behaviour (see SECTION 6)

5.4.2 Defensive Behaviour

Definition: the reaction of the spider to a possible predator.

A part of the defensive behaviour of T.oblongus has been mentioned by BRISTOWE (1958) when he described the characteristic response by T.oblongus to a continued or second threat in the field. This particular response is one of several distinct reactions shown by the species to disturbance; it is the most characteristic reaction and also probably of the most ecological significance,

this will be discussed below.

It was found that the falling of a shadow across the ocular area of T.oblongus a disturbance of the substrate or a combination of these two stimuli produced a slight defensive response in a previously undisturbed individual which is in the predatory posture. The spider drew its legs slightly inwards and appeared to be poised in a state of readiness to react. Further disturbance produced the distinct T.oblongus reaction described by Bristowe: the animal runs upwards and towards the light at high speed (about 7cm per second) for a few seconds then suddenly stops and adopts the "camouflage posture" (FIG 23) lying along a grass stem or a similar position in the laboratory, such as a beaker rim, the edge of a bench or on a ridge of corrugated cardboard.

There was found to be no change of colour during the spider's defensive reaction in contrast to Tetragnatha extensa(SECTION 2.3)

Further extreme threat, for example lightly striking the spider, caused it to assume the extreme defensive posture(FIG 22) with the first three pairs of legs drawn up over the carapace and abdomen. The function of this posture appears to be to protect the cephalothorax and abdomen from physical damage. An individual that had been frequently disturbed assumed this posture more readily.

The structure and coloration of T.oblongus make it difficult to be detected visually by humans and presumably, by other animals with similar modes of vision, in its normal habitat, which consists of a mixture of parallel live and dead, green and tan grass stems. The selective advantage to the species of this structure and colour could be that potential prey are not frightened away. However the posture of the spider immediately after its short escape run strongly indicates that the structure and colour of T.oblongus evolved at least in part, as a defense against predators which detect their prey mainly by sight.

Predators of this type that would be most likely to come in contact with T.oblongus are: other spiders, lizards, birds, toads as well as predaceous insects e.g. carabids. No conclusive observations were made in the field and all the above list can be regarded as possible major predators; however spiders rarely attack prey of the size of T.oblongus and the fact that Tibellus responds to a shadow indicates that birds might be important. Birds are known to prey heavily on spiders; the gut contents of Rooks, Jackdaws, Swifts and Starlings have been found to contain the remains of spiders' exoskeletons, especially Lycosids (Verbal communication E.Duffey)(OWEN & LEGROS 1954), and although T.oblongus has never been identified specifically amongst these remains, Lycosids inhabiting the same situations as T.oblongus have been. HAMILTON(1941) reported spiders amongst the cut contents of small forest mammals in the Eastern United States. AVERY(1966) reported that the common lizard's principle food was spiders in the West of England. The abundance of lizards in the Study areas is not known, LESCURE(1964), determined that spiders constituted 2.7% of the prey of the common toad. No toads were ever seen in the areas under investigation.

5.4.3 Yearly Movements

T.oblongus performs marked movements in mass at different times during the year. This can be inferred from a comparison of the results of the winter and summer population surveys. In summer, the species is widespread over the whole of the grassy areas with variation in density corresponding with the grass species and vegetation type as discussed in SECTION 4: however in winter, all the Instars of T.oblongus are concentrated in tussocks, particularily in Dactylis. At Silwood, the transitions from one habitat to the other appear to take place in late October and early March. The migration of the whole population was spread over a period of 2 to 3 weeks.

In the field, T.oblongus emerged from the tussocks earlier in certain areas but these areas did not differ markedly in daylength or temperature from the areas where emergence was late, i.e. they occurred on both north facing and south facing slopes.

Observations in the laboratory during the winter sampling when T.oblongus was being extracted from Dactylis tussocks in Tullgren funnels indicated that the spider became phototactic after being warmed up. The spiders then emerged onto the upper surface of the tussock where they basked in the light.

An experiment was set up in the insectary in an attempt to study these movements in greater detail.

A box of polystyrene was constructed and soil and vegetation were placed in it to form a simplified replica of the structure of a typical Dactylis tussock(FIG 24). A thermometer was inserted in each of the 4 strata and the model was placed in the insectary in direct sunlight during February 1966.

Individuals of 4th Instar T.oblongus, in various conditions, were placed into the model at different times of day and a record was kept of the temperatures of the 4 strata and of the movements of the spiders.

The main possible sources of error in this experiment were as follows:

a) The microclimatic conditions in the model tussock were not identical to those in a tussock in the field; however, the temperature readings taken from the model were found to correspond to readings from similar strata in tussocks in the field although the differences between strata were less marked in the model. TABLE 21.

b) The differences between light intensity in the different strata of the model were less pronounced than those in a field tussock as incident light penetrated through the polystyrene walls of the box.

For this reason the model was positioned in the insectary so that the upper strata were more strongly illuminated than the lower ones.

The spiders were unavoidably disturbed during collection and during their introduction to the model tussock. This disturbance was kept to a minimum.

FIG 24

MODEL DACTYLIS TUSSOCK

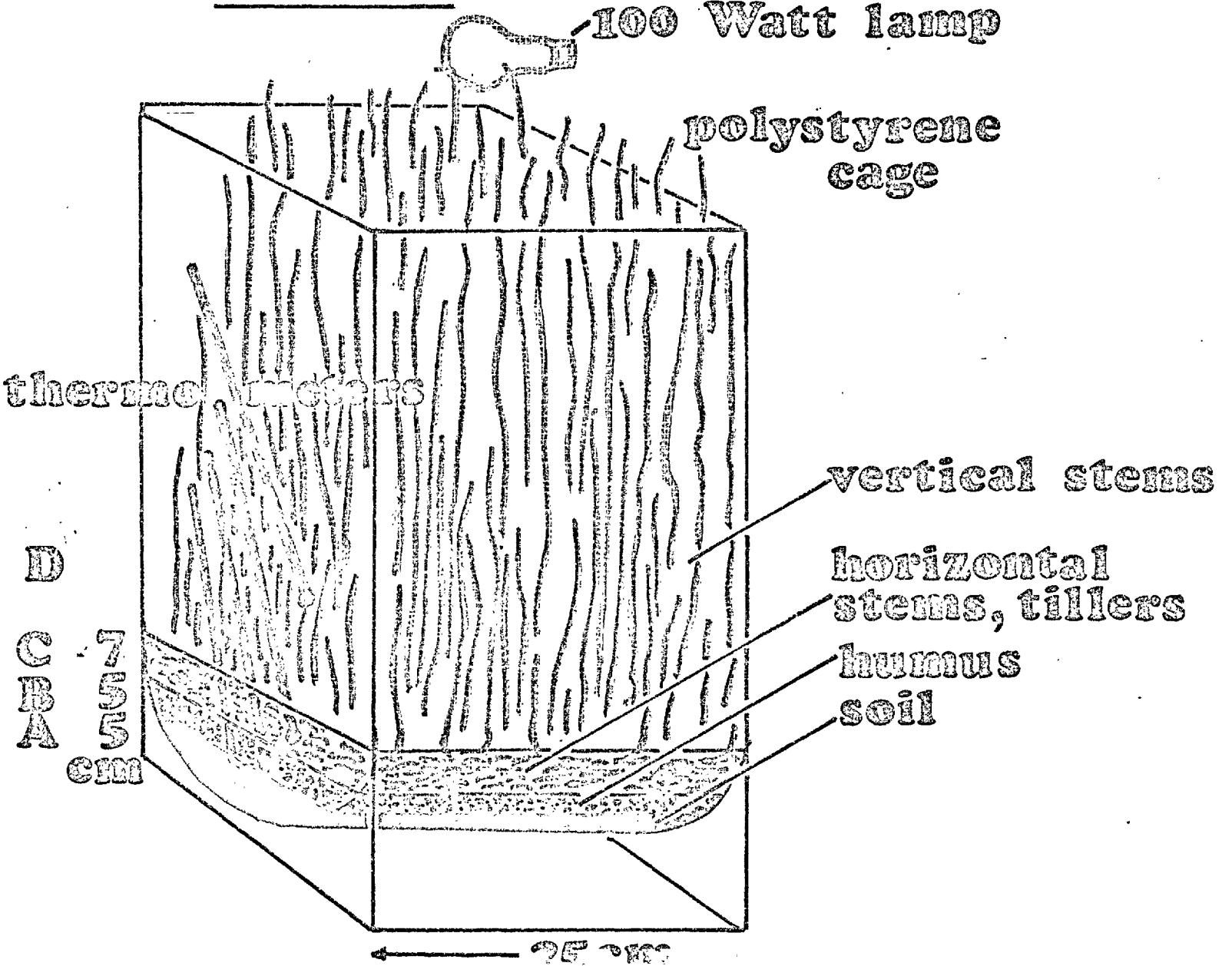


TABLE 21

Examples of temperatures in Model *Dactylis* tussock in Insectary February 1966

Stratum	°C				
D	7·8	9·2	8·9	10·8	stems
C	7·2	9·4	8·9	10·5	tillers
B	6·8	8·9	8·6	9·6	humus
A	5·9	8·0	7·7	8·3	soil

As a maximum variation of light and temperature between the strata of the model occurred on sunny days, the observations were carried out on such days.A 100 watt bulb was placed 10 cm above the cage in order to accentuate the gradients of light and temperature. A set of typical temperature readings from the model throughout an experiment is presented in TABLE 21.

4th Instar T.oblongus individuals were introduced into the model tussock. The spiders were in two conditions namely:

a) Individuals that had just been collected from their hibernation sites in the field.

b) Individuals that had been collected beforehand and placed in the laboratory at 20° for one hour.

The spiders were positioned at the interface between strata C and D, i.e. at the base of the vertical stems and observations were carried out on one individual at a time so as to avoid possible affects of aggregation behaviour. Typically the behaviour of a spider was as follows:

a) In condition a) the individual was sluggish and made no fast or positive movements.

If the spider was disturbed strongly by hand, it crawled downwards to the B/C interface, beneath the horizontal stems and tillers. In some instances the spiders crawled to that position when left in the model overnight.

b) A spider in condition b): The individual was relatively more active and invariably crawled up the vertical stems and basked in the light. If strongly disturbed by hand, it ran upwards rapidly, in the characteristic T.oblongus fashion. If left overnight in the model an individual in this condition did not crawl back into the tussock.

CONCLUSIONS

The behaviour of T.oblongus in the model implies that a change of temperature is important in stimulation the spider to emerge from its hibernation site. After emergence the spider climbs upwards

and towards light and basks in the sun (thus raising its body temperature.) This pattern is consistent with field observations on the emergence of the spider after hibernation.

Another spider known to exhibit mass seasonal movements is Lycosa lugubris (Walckenaer), which moves into open areas at two distinct times during the year. The reasons for these movements are:

a) General increase in the range of the adult.

b) The females use sunlight in the open areas to incubate the eggs. (EDGAR 1968).

The first reason could not be applicable to T.oblongus since the whole population migrates.

Further research is necessary to determine if sunlight incubation is a factor involved in the selection of egg laying sites by adult T.oblongus.

5.4.4 Dispersal

Like the majority of epigeic arthropods, T.oblongus inhabits specialised environments which are geographically separated, and a method of dispersal is necessary for the species to colonise as many of the available locations as possible.

Theoretically distinct from this colonisation - dispersal is the dispersal of young arthropods from the site where the eggs hatch. In the case of many spiders however, the two types of behaviour overlap or coincide. Juvenile spiders of many species disperse, in summer, by means of gossamer throughout boreal and temperate Europe and other parts of the world, leaving the site of hatching and colonising new habitats at the same time.

However, Thomisids were not recorded as playing any great part in these dispersal movements at Wytham (DUFFEY 1956) and T.oblongus has never been recorded from aerial samples of arthropod populations including the aerial sampling by suction trap carried out at Silwood.

The movement of young T.oblongus from the egg sac was observed in the laboratory at 20°C, 10 hours daylength i.e. in photoperiod corresponding to that in the field(FIG 25).

The egg sac with the incubating mother was placed in the apparatus on Day 1.

The majority of the eggs hatched overnight of Day 1 to Day 2, and the spiderlings underwent their first moult on the egg sac. By Day 3, three spiderlings had reached the edge of the Petri dish, and had left a thread connected to the egg sac. On Day 4, five individuals had reached the edge of the Petri dish, three individuals had reached the pins, still trailing silk. All the spiderlings exhibited typical T.oblongus behaviour, lying in the predatory posture along a pin or along the rim of the Petri dish.

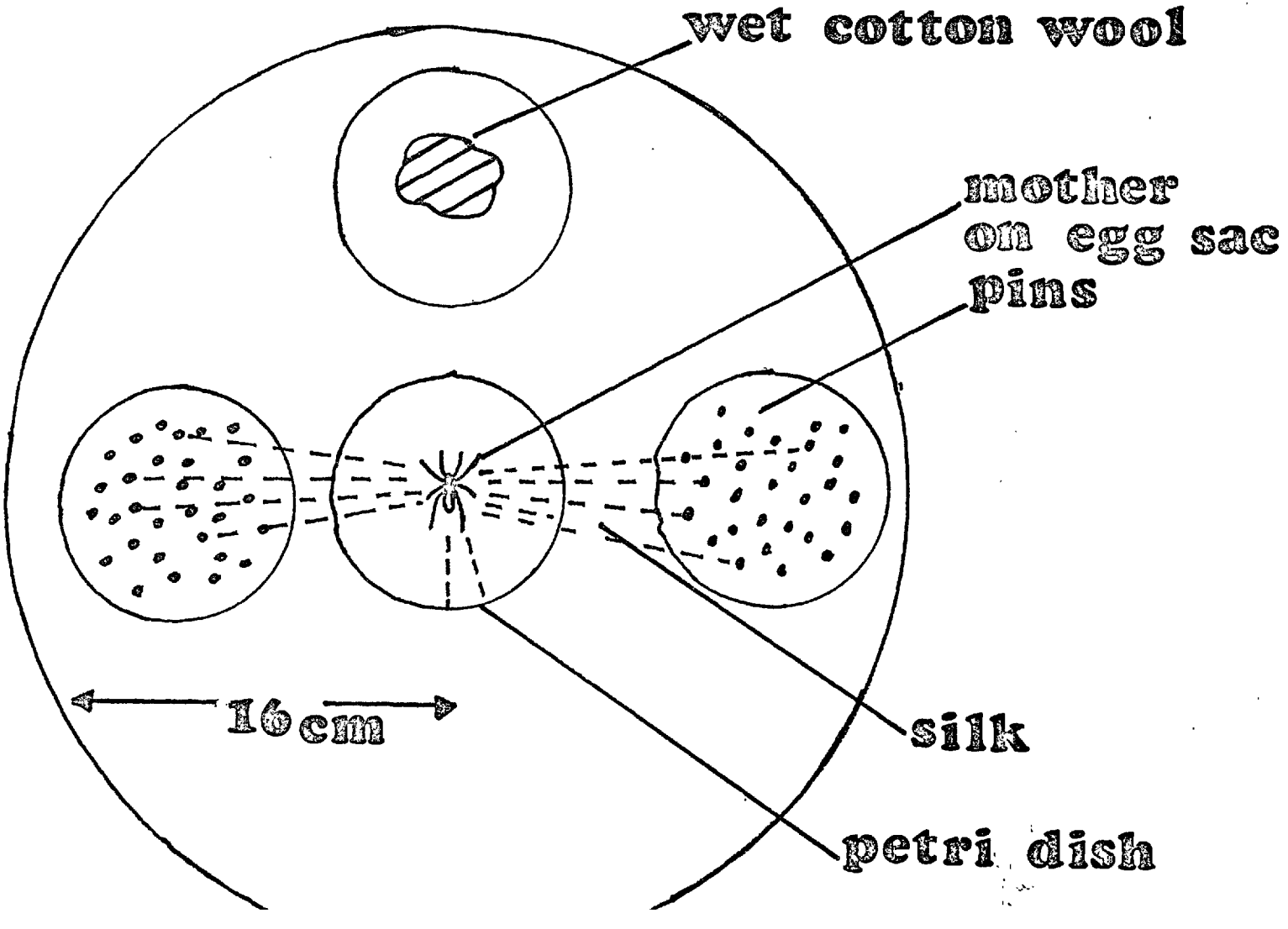
By Day 5, eight individuals had reached the side of the pneumatic trough, six were on the pins, seven on the side of the petri dish and ten still on the egg sac. This even dispersal of the brood continued till the last spiderling left the egg sac on Day 7 and by Day 10 all the individuals had left the pneumatic trough completely.

A network of silk strands was built up by the spiderlings, stretching from the egg sac to the sides of the petri dish, to the pins and to the edge of the trough, most of the strands were radial in direction and the spiderlings were seen to walk along these, outwards and inwards but in general getting further from the egg sac.

Throughout the period of dispersal the mother was not seen to leave the egg sac, Drosophila were fed to her periodically. Similar dispersal behaviour was reported by R. McHUGH(1964) after he observed the brood cluster of Araneus diadematus(Clerck) the brood was not guarded by the female. An egg sac together with

FIG 25

Dispersal of young TIBELLUS



the incubating female was taken from a rearing cage in the laboratory and placed in AREA 4 in a Dactylis tussock at a height of 35 cm, however the adult and the egg sac had disappeared the following morning and the behaviour observed in the laboratory was not confirmed in the field.

During population sampling of AREA 4 and during general observation of the vegetation, T.oblongus individuals of Instars 2 and 3 were found walking about amongst the grass stems trailing threads in spring, summer and autumn.

Habitats usually unsuitable for T.oblongus, such as short mown grassland and a Broom Patch, adjacent to areas supporting a population, were searched in order to find dispersing T.oblongus individuals, but none was found.

CONCLUSION

On the basis of the laboratory experiment and the information from observation it appears that T.oblongus disperses by normal walking during the 2nd and 3rd Instar.

This method of dispersal can easily distribute the species from one specialised area to another within a continuous stretch of grassland but difficulties must arise in the colonisation of isolated habitats. Natural barriers such as woodland and rivers would be formidable obstacles owing to the restricted use of silk as a means of transport. The aerial dispersal method employed by many spiders appears to be much more effective for this purpose.

The normal walking rate of Instars 2 and 3, which was observed in the laboratory and in the field is in the range: 2mm per second to 1 cm per second. The duration of these Instars in the field comprises 12 months of activity. Table 22 shows estimated distances walked.

TABLE 22

Estimates of the distance travelled by T.oblongus during the normal life span of Instars 2 and 3 in the field.

Time spent active	100%	50%	10% of active time spent walking
All days and nights	300	150	30
All days	150	75	15
T.oblongus seen active	75	37	7

kilometres

During observations in the field, T.oblongus individuals were, occasionally discovered in the act of walking; however the quadrat sampling method disturbed the spiders so an accurate estimate of the percentage of the time they spent walking was impossible. A reasonable allowance for feeding and resting periods as well as the time spent in moulting could be made and seven kilometres was calculated as a conservative estimate of the total distance travelled. A possible maximum would be in the region of 100 kilometres.

SKELLAM(1951) gives a formula which relates these estimates to the general rate of geographical expansion of a growing population.

$$R = (na^2 \log N)^{\frac{1}{2}}$$

where

R is the radius of the whole population

"a" is the root mean square distance of daughters about the parent

N is the final population after "n" generations (assuming Malthusian population growth characteristics)

This formula is obviously highly generalised and many other factors are involved in the dispersal process, however in substituting the values for T.oblongus the following result can be derived:

An area the size of mainland Britain could be fully exploited by T.oblongus in as little as 2,000 generations after initial colonisation.

5.4.5 Aggregation

Since it was not possible to ascribe the concentration of T.oblongus in particular Dactylis tussocks to differences in physical environment, aggregation due to mutual attraction was investigated as a possible explanation.

Concentrations of spiders were most marked during hibernation, but they also appeared on sites of predation in summer.

AIM:

An experiment was set up in the laboratory, the aim of which was to discover if the spiders tended to rest in contact with each other, rather than separately, during hibernation.

The rearing cage (FIG 6) was used for the experiments, the circumference was divided into 10 equal arcs of 3.2 cm i.e.approximately the length of a 4th Instar T.oblongus in hibernation posture.

Four individuals of Instar 4 were placed in each of two cages which were put in the insectary on November 22nd. Observations continued till January 20th.

The spiders maintained the hibernation posture throughout the period of the experiment but were found to move about sporadically.

On 40 occasions between November 22nd and January 20th the positions of the four spiders were recorded. The four arcs they were in were noted and when any one had changed position, a movement was recorded. Contact between individuals was also recorded.

RESULT:

Cage A: In the 40 observations, 56 movements were observed. If these movements were random then individuals would have come into contact with each other eight times. In fact contact occurred 12 times.

The probabilities relating to this result were as follows: there are 10 possible locations - the arcs on the circumference of the cage

At each random rearrangement of the 4 objects, the probability of any two ending up in the same location i.e. in contact is 0.469 with a standard deviation of about 0.2. The total number of movements of the spiders(56), can be considered as $\frac{56}{4}$ complete rearrangements; this is an approximation. It follows that the

expected number of contacts is 8 with a standard deviation of 4. Therefore the 12 recorded contacts was not a significantly high figure.

This analysis is open to criticism but it was not thought worthwhile to carry out a more exhaustive analysis.

In cage ♂, 68 movements and 10 contacts were recorded. Nine contacts were expected by chance and the number observed is not significantly higher.

CONCLUSION

This experiment was designed to test whether T.oblongus individuals aggregated in physical contact with each other. It is possible that T.oblongus can detect the presence of other members of the species by other means such as chemical sensitivity; this possibility was not investigated and the definite conclusion that can be drawn from the experiment is that T.oblongus individuals do not tend to hibernate in physical contact with each other. Whether or not another factor concerning the presence of other individuals is involved in their aggregation is not known.

5.4.6 Orientation with respect to Physical Environment.

The behaviour of T.oblongus in response to light, temperature, humidity and gravity in so far as it is involved in hibernation, predation and incubation is discussed under the relevant headings in other sections.

5.4.7 Moulting

Moulting was observed several times and photographed in the laboratory. It followed the pattern typical of the Araneae described by BRISTOWE(1958) and many others.

The individual becomes quiescent several hours prior to the onset of edysis and ceases to feed.

The shedding of the skin is accomplished within ten minutes and two stages in the process are illistrated in FIGS 26 and 27. Ten minutes after the old skin is finally discarded the spider can bend its legs and assumes the defensive posture and chews the ends of its legs. One hour later the spider is preying and feeding normally.

5.4.8 Mating

Complex mating behaviour has been described in many spiders, the ♂ performing strange and specialised actions in order "to neutralise" the predatory responses of the ♀ (BRISTOWE AND LOCKET 1926).

The same basic problem exists in the case of T.oblongus, the ♂ has to distinguish himself from prey; however, the sensory equipment of the ♀ is of such short range that the ♂ must pacify her extremely rapidly and in very close contact with her.

In the case of most spiders, during the reproductive period, the adult female remains relatively stationary and sedentary, preying in the normal way while the adult male walks around actively searching for a female; BRISTOWE (1958) states that there is a greater chance of them coming into contact in this way than if both were moving. However, MOSIMANN(1958) points out that if two animals are moving in a 2-dimensional space each with velocity V, then their relative velocity is 1.2732V, and since the number of encounters - θ is proportional to relative velocity:

$$\theta = 2rvn$$

r = detection radius
n = density
v = velocity

Then Bristowe's argument would not appear to hold true.

FIG26 T. OBLONGUS MOULTING

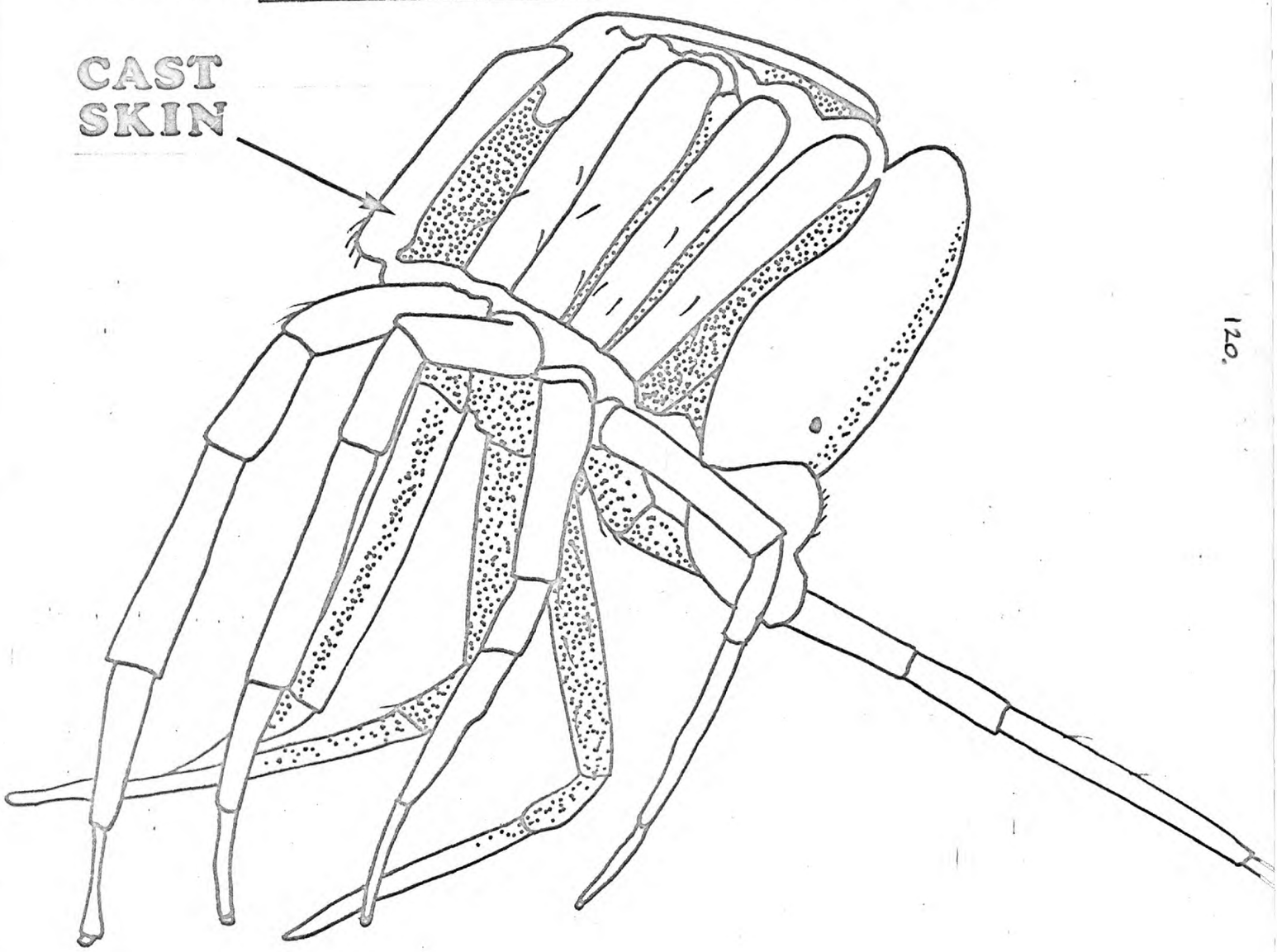
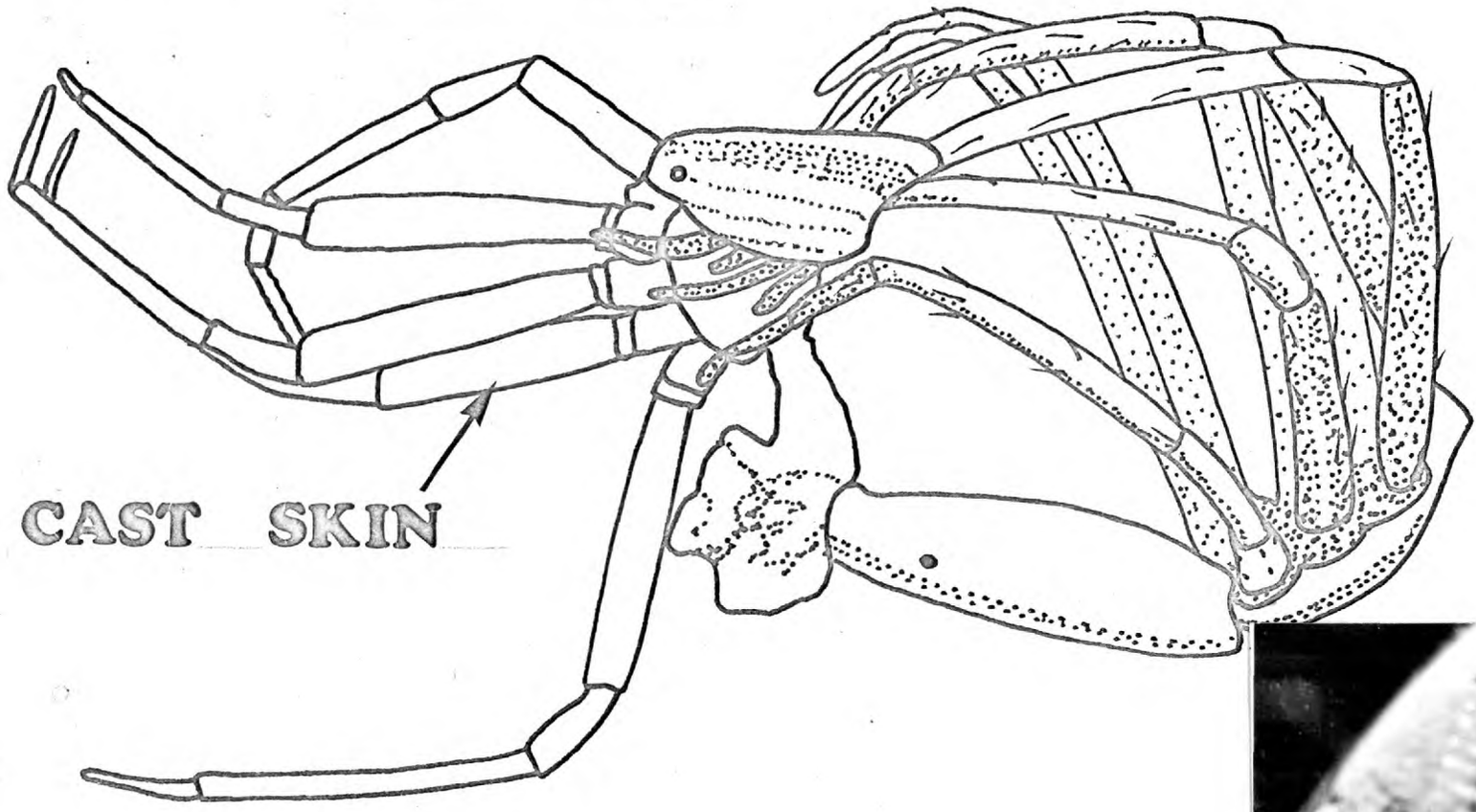




FIG27 T. oblongus MOULTING





The adult female T.oblongus is generally more sedentary than the male throughout her adult life so it is probable that the overall pattern of a mobile male searching for a stationary female holds true for T.oblongus. However during the observations of mating in the laboratory, a tube containing a female was placed end to end with one containing a male and after this disturbance both individuals were equally active and often both were in motion when they came into contact.

The reason the adult female spider is usually more sedentary than the male is probably connected with the fact that predation is more efficient when the spider is in a fixed location. In the case of web building species this is obvious, but I think it is very likely in the case of T.oblongus also where the stationary predatory posture contrasts strongly with the mobile walking posture. Therefore the decrease in the number of sexual encounters due to the female remaining stationary is compensated by the higher predatory efficiency of the population as a whole.

At the instant of contact the behaviour of the two individuals changed rapidly as follows:

a) the female detected the male by tarsal contact.

b) the female lunged towards the male as if he were prey.

c) before the female completed the attack, the male gripped the patella of the second , or third leg of the female with his jaws although the fangs did not appear to pierce the cuticle.

d) the female immediately became completely immobile with all the legs raised and half flexed.

e) the female remained immobile during the subsequent fifteen to twenty-five minutes while the male continued with the method of copulation that is typical of the Araneae. The palps were inserted alternately into the epigyne, sperm being transferred in this way.
After copulation the male walked away and a few seconds later the female became active and walked away from the site of copulation.
The transfer of sperm from the male sex organs to the palps was never observed.

DISCUSSION

In a particular discrete environment, there exists a theoretical minimum population - of any animal - which is reproductively viable; i.e. the population is dense enough so that a sufficient proportion of the females are found and fertilised by the males for the population to reproduce itself.

From observation of T.oblongus, the range of mutual detection by the two sexes appears to be limited to about two centimetres, so that the minimum population density is probably comparatively high. However the other factors involved in this aspect of the spider's population dynamics e.g.

a) the rate of movement of the two sexes in the field during the reproductive season.
b) the relative concentration of the two sexes in the "Special Areas".
c) the proportion of encounters leading to successful fertilization;

All these factors, and others, need a detailed analysis before definite ecological conclusions can be drawn from the reproductive behaviour of the species as a whole.

The research involved in this analysis was beyond the scope of the work described in this thesis.

5.4.9 Egg Laying

Immediately after copulation, the appetite of the female increased dramatically (see FIG 11) and the abdomen grew up to 50% in length and breadth during the subsequent three to six days. At 25°C the egg sac was laid seven to ten days after copulation.

The typical appearance and position of the T.oblongus egg sac in the field is described by BRISTOWE(1958): the silken sac containing the eggs joining several grass stems at a height of about 20 cm and the female sitting on the sac guarding it. Similar sites were observed at Silwood Park, but the sequence of events before, during and after egg laying was studied in the laboratory.

a) the female spun a dense silk pad about 3 cm. in diameter on a vertical surface such as the side of the rearing cage.
b) the female sat on this pad for about 12 hours.
c) the egg mass was laid; 35 - 110 eggs in a relatively diffuse mass, 1.5 cm in diameter.
d) a layer of silk was produced which covered the egg mass.
e) the female sat on the egg sac invariably head downward in the predatory posture.

The female remained at the egg laying site till all the spiderlings hatched and dispersed, up to three weeks at 25°C. In some cases the appetite of the female then increased again and after 4 or 5 days' feeding, a second egg batch was laid on top of the old egg sac. These eggs were incubated and hatched, the spiderlings were guarded during dispersal. No female was observed to produce a third batch of eggs.

5.4.10 Incubation

The eggs were incubated continuously by the female for several days until hatching, which occurred in 11 - 15 days after laying at 25°C. All the eggs appeared to hatch within 24 hours of each other and then the dispersal behaviour occurred while the female continued to guard the site(SECTION 5.4.4).

Throughout the period on incubation the female was never seen to leave the egg sac, she accepted food in the form of Drosophila and water if it was placed in contact with her or with the silk of the egg sac. She was very sensitive to contact on the legs by possible prey or predators, which is typical of T.oblongus throughout its life. However, the incubating female responded to any disturbance of the silk covering of the egg sac up to a distance of two centimetres from her body.

After the dispersal of some of the young had taken place and silk strands lead away from the sac, the female responded to an object touching these strands up to 8 cm away from the egg mass. She detected the direction of the disturbance immediately and attacked any object close to the eggs or young. This is an interesting observation in relation to the well known theory of evolution of web building by spiders, that the webs which are used to snare prey evolved from the protective silken covering of the egg sac (BRISTOWE 1939-41).

During normal walking a spider showed no reaction to a disturbance of the thread, if it was trailing one so it is apparent that this is the only period during the life of T.oblongus that silk was used to extend the sensory range of the individual. The direction of the disturbance was detected immediately, but it was not possible to discover if the strength of the disturbance was detected by means of the silk as many other spiders do because the female T.oblongus attacked any object such as a forceps, a pencil, or finger. She was very tenacious and persistent harassing was necessary to force her away from the egg sac.

When the surface on which the egg sac lay, was tilted, the female became disoriented and made a series of short forays of five to eight cm in various directions trailing silk and returning to the original site.

On occasions after the famale had been forced away from the egg sac by threat or by tilting, she mistook other objects such as a cast skin, a group of Drosophila corpses, or a rough edged hole in the plastic side of the cage for the egg sac, and settled down on them as if incubating.

As has been shown in the case of other spiders, Lycosids and Dolomedes for example, discrimination by the female T.oblongus of what is and what is not the egg sac is very limited.

5.5. ADDENDUM

Unless otherwise stated, the spiders used in the laboratory observations were captured during their 4th Instar and reared at 20°C or 25°C, undergoing their final moult in captivity.

Major life processes such as ecdysis and all the components of reproduction were carried out successfully by T.oblongus in the laboratory environment; therefore it is reasonable to assume that the behaviour patterns were not grossly distorted by the artificial conditions and that the laboratory observations of the behaviour of T.oblongus were a reliable indication of its behaviour in the field.

SECTION 6

PREDATION ANALYSIS

6.1 INTRODUCTION

During the course of the work described in this thesis, several salient facts emerged concerning T,oblongus as a subject for ecological research.

a) Three years was a relatively short time in which to amass reliable facts concerning total population densities and to attempt a straightforward correlation with climatic or other large scale environmental factors.

b) The species was present in fairly low numbers in the locations under investigation and the specialised sampling methods that were tried during the summer of 1966 failed to yield satisfactory results.

c) Only limited information arose from field observations concerning the identity and characteristics of the normal prey and predators of T.oblongus.

d) The reproductive characteristics of T.oblongus, in the field especially fecundity, proved difficult to ascertain.

The population surveys together with the experiments and observations in the field during 1964, 1965, and 1966 revealed the life cycle of the spider and the characteristics of its preferred habitat as well as several important behavioural features. However, the information gathered could not be used to derive any meaningful, generalised conclusions on the population dynamics of the species as a whole, because of the reasons set out above. It was therefore decided to concentrate on an investigation of the predatory behaviour of T.oblongus along the lines of the experimental component analysis technique developed and described by C.S.HOLLING(1959a, 1959b, 1961, 1963, 1964, 1965, 1966).

It was cosidered that this would provide further information on the biology of Tibellus.

Although the component analysis approach to ecological research has been developed within the last decade almost exclusively by C.S.Holling, functional response investigations have been carried out by other workers, notably by MORRIS(1963) on Podisus maculiventris (Say) and by HAYNES AND SISOJEVIC(1964) on Philodromus rufus (Walckenaer). Evidence of a functional response by spiders to changes in density of the Spruce Budworm is put forward by LOUGHTON,DERRY & WEST(1963).

With regard to T.oblongus, the work involved a series of behavioural experiments and observations culminating in a carefully designed experiment to determine the functional response of the species to changing prey density. As a result it was hoped to achieve a contribution to the growing body of information on the functional response of predators in general; the degree to which the findings could be applied to other predators depending on how exemplary was T.oblongus in the details of its predatory behaviour.

6.2 PREDATORY BEHAVIOUR.

The prerequisite to the design of an effective functional response experiment was a thorough study of the behaviour of T.oblongus in relation to its prey. The three basic components involved are:

a) The time the predator and prey are exposed to each other.
b) The mechanisms by which T.oblongus detects and captures its prey.
c) The details of the time taken in handling, consuming and digesting the prey.

These three components cover wide and intricate aspects of the spider's behaviour and a great deal of experimental work would be necessary to clarify all the exact details. In the work described in this thesis, a fully comprehensive study was impracticable and several approximations and assumptions had to be made; these are made clear in the relevant subsections.

6.2.1 The time predator and prey are exposed to each other.

Throughout the life of a T.oblongus individual, the time that the spider is exposed to potential prey varies. The following factors affect this exposure time:

a) The acceptability, to the spider, of the prey in the immediate environment.

Laboratory observations showed that whereas the larger Instars of T.oblongus would accept a variety of prey readily, the smaller Instars fed reluctantly and would not attack anything larger than an aphid.

In the field, the general movement upwards through the vegetation strata during the life span by each spider was undoubtedly reflected in changing characteristics of prey encountered. Therefore generalisation is difficult, however, it is reasonable to assume that the larger the T.oblongus individual grows, the higher the proportion of animals encountered could be considered as potential prey.

b) Moulting activity - While the individual was occupied by moulting, it showed a lack of interest in prey for a total of about two days, before, during, and after ecdysis in the laboratory. It is reasonable to assume that this cessation of feeding also occurs in the field.

c) Dispersal - Laboratory observations revealed that when a prey individual was encountered by a walking spider, its capture was much less likely than when it was encountered by a spider in the predatory posture. The area covered, at any one time, by a walking spider was less than that covered by a preying one. For these reasons, the process of dispersal discussed in theprevious section, could be considered as having the overall effect of reducing the time each T.oblongus was exposed to prey.

d) Hibernation - At the onset of hibernation the T.oblongus individuals left the normal summer predation sites to spend the winter in grass tussocks: also they adopted the

hibernation posture, radically different from the predation posture. Laboratory observations never revealed a spider capturing prey while at a temperature below 9°C or while in the hibernation posture.

In the overwintering condition, the spiders therefore could be considered as totally unexposed to potential prey.

e) Unsuitable weather - Throughout the active season of the spider, the individuals were sparse or absent in the "Special Areas" during cold or wet conditions. It is probable that exposure to prey, and predatory activity were correspondingly reduced. Moreover, the presence of the spiders in the "Special Areas" was not governed by an intrinsic diurnal rhythm because they were discovered there on unusually warm nights.

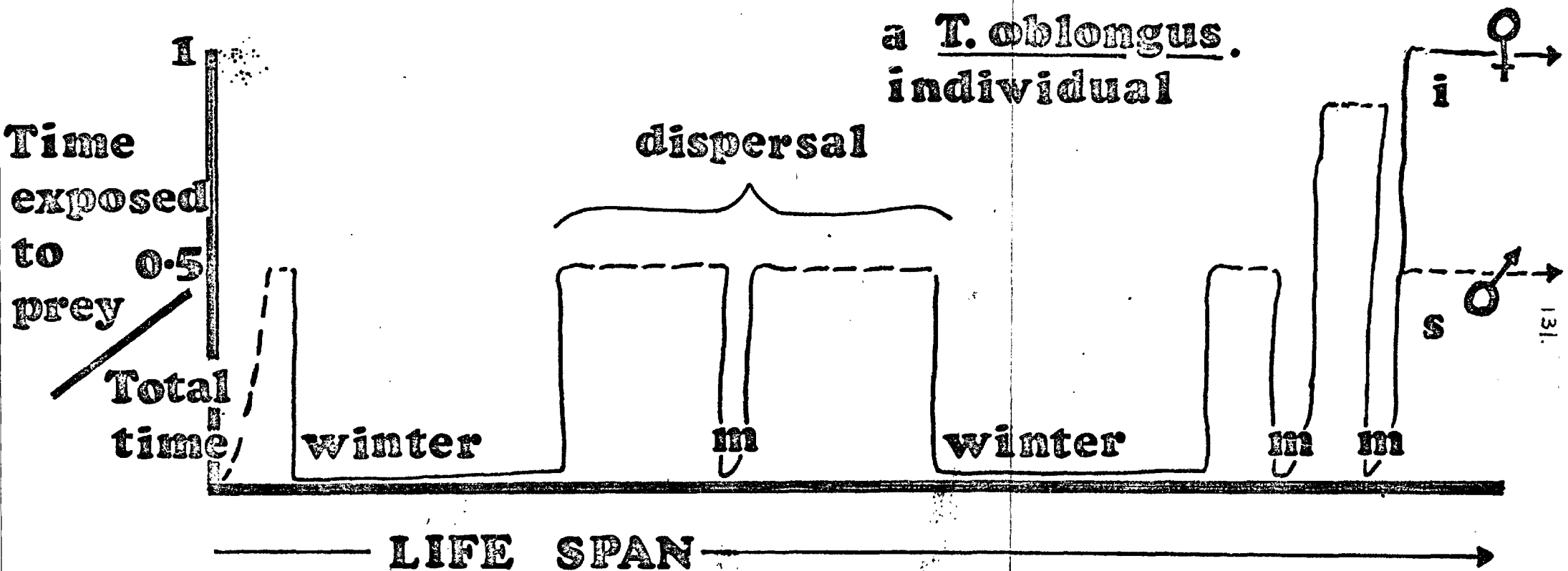
f) Mating Search - The activity of the adult males in searching for females as discussed in the previous section had the same effect as dispersal activity in cutting down the effective time the individual was exposed to prey.

g) Incubation - While the adult female was sitting on the egg sac, she was invariably in the predatory posture, attacked prey very readily and was in a position, in the field, that led to contact with potential prey fairly regularly. Her effective exposure to prey could be regarded as total throughout the incubation period.

Quantitive studies of the factors outlined above were not attempted. FIG 28 is a graphic summary of their inter-relationship within the lifespan of the spider expressed qualitatively.

The individuals chosen for the functional response experiments were adult females, unfertilised. At this period of the lifespan the fool requirements were relatively stable, all moults having been completed, all dispersal having been completed and the spiders spent a high proportion of their time in the predatory posture with minimal interference from other intrinsic behaviour patterns.

FIG 28 GENERAL PREDATORY ACTIVITY of a T. oblongus. individual



Gaps in the line represent nights and days unsuitable for predation.

m = moult.
i = incubation
s = mating search

6.2.2 The mechanisms by which T.oblongus detects and captures its prey.

Predatory behaviour by the spider was studied in detail in the laboratory during summer, using individuals of the 4th Instar and adult females that had been captured in the field and had spent at least 10 days in the laboratory at 20°C to become accustomed to the conditions.

TURNBULL(1960) states that most spiders are capable of feeding on almost any suitable size prey they encounter, and this held true for T.oblongus; at various times it was seen to be feeding on: lepidopterous larvae, aphids, other spiders, Dipterous flies, nabids and other T.oblongus individuals.

The prey used for the behavioural observations were adult Drosophila melanogaster, which the spider took readily. These flies have characteristics that have been found to trigger off predatory responses in other arthropods, such as: beating wings to which many spiders respond(BAYS 1962),(WALCOTT AND VAN DER KLOOT 1960) (H. AND M. CRINGS 1956), and a jerky walking movement wich stimulates the praying Mantis Hierodula crassa Giglioto (RILLING et al.1959). Drosophila was also very convenient to breed.

The interaction of the spiders and flies was observed in a covered plastic petri dish, to which neither animal had difficulty clinging. The dish was placed on graph paper, for closer observation. The spiders were introduced into the cage several days before observations began, to allow for accustomisation.

As means of prey detection, there were four main possibilities that merited investigation:

a) Silken strands in a more or less coherent web.

b) Vision.

c) Vibration reception i. Airborne
ii. Surface vibration
iii. Vibration transmitted by threads.

d) Tactile reception.

These mechanisms and combinations of them are known to be used by other spiders for the detection of prey so experiments and observations were carried out to determine their use by T.oblongus. In order to isolate these various responses, several artificial stimuli were applied to the spider. The total range of stimuli used during the investigation of predation was as follows:-

a) Live, active adult Drosophila.

b) Drosophila held in forceps by the wings.

c) Drosophila rendered moribund by CO^2.

d) Dead Drosophila.

e) Wingless Drosophila.

f) A horsehair bristle.

g) A tuning fork of 500 C.P.S.

Conclusions concerning the spider's behaviour were built up after many, varied observations using different stimuli and combinations of stimuli. Rather than a long list of detailed and relatively unrelated observational descriptions, there follows a series of generalised conclusions derived from a synthesis of all the observations.

The following findings emerged:

a) Posture - T.oblongus invariably reacted to the presence of prey while in the predatory posture(FIG 21), occasionally while walking but never while in the hibernation posture (FIG 23). This last posture was adopted when the spider was replete, also after the short defensive run.

b) Rhythm - There was no evidence of a diurnal rhythm in the predatory behaviour of T.oblongus. In the laboratory, spiders were observed in the predatory posture and capturing prey at all times during the 24 hours. What is more, T.oblongus individuals were captured in the field from time to time on warm nights in the Special Areas and were observed preying near a mercury vapour lamp at night.

c) Silk Strands - Live flies, walking and beating their wings were placed on threads attached to the spider's legs and abdomen; the spider showed no reaction whatsoever. This was in marked contrast to the behaviour of the incubating female which was able to detect the direction of any disturbance in the network of threads that surrounded the egg sac to a distance of eight cm. The spiders did, in fact, produce a network of threads in the Petri dish which appeared to form a partly coherent web. It was concluded that this network was a by-product of exploratory behaviour, since for several hours after their introduction into the Petri dish, they walked round the circumference trailing a silk strand and attaching it to the substrate every three or four centimetres. These threads had no function in the detection or capture of prey.

d) Vibration - Throughout the observations, a fly that was beating its wings elicited no different a response from the spider than that elicited either by a fly that was walking on the substrate or by one that was held in the air close to the spider and unable to beat its wings.

Many other species of spider react to vibration transmitted either through the air or through the substrate, and it is probable that two different types of receptor are involved (H. AND M. FRINGS 1966). CLOUDSLEY-THOMPSON (1959) reported that Dolomedes reacted to a tuning fork and to a buzzing fly held in the air three or four cm away.

A tuning fork of 500 C.P.S. was held near T. oblongus in the air and on the substrate but no response was forthcoming. WALCOTT AND VAN DER KLOOT (1966) showed that vibrations of 300 to 700 C.P.S. produced the greatest response in many spiders and the buzz of many insects is in this range, although that of Drosophila is significantly higher (about 2000 C.P.S.). Spiders that do not construct

webs generally do not react to airborne sounds (CHRYSANTHUS 1953) and other workers have obtained negative results with Lycosids CLOUDSLEY-THOMPSON (1959).

It was concluded that T.oblongus does not react specifically to vibration whether airborne or in the substrate.

e) Vision - T.oblongus occasionally reacted to an approaching fly at a distance of up to five mm beyond the ends of the legs in any direction, attacking it. It did not react to a dead or moribund fly at that distance, nor to a fly held in forceps by the legs. The spider reacted only to a fly on the surface in the same plane as itself, never to a fly walking on a surface above, however close. However, a fly often walked towards the spider between the legs, approaching to within three or four mm of the cephalothorax and escaped unattacked and apparently undetected.

HOMANN (1928,1931,1934) studied the use of vision by various spiders and showed its importance in Lycosids and Salticids. He also studied two Thomisids Misumena and Xysticus, reporting that the former showed a reaction to a flying Pieris at 20 cm and the latter detected a housefly at 12 cm, the primary eyes fixing the insects position by muscle movement after the secondary eyes had reacted to the motion of the insect. This was a method of detection similar to that of the Lycosids. These distances seem rather large when one considers that the range of attack by the Spiders in question is limited to about four or five cm, although POULTON (1934) reported Misumena approaching prey. Eye movements in response to prey movement was never observed in T.oblongus and the apparent oblivion of the spider to prey at very close range, even when starving, indicates that direct vision plays very little part in the overall system of prey detection by the species. The fact that the species was found preying at night supports this.

YOUNG AND WANLESS(1967) in their study of the fluorescence of various spiders' eyes, concluded that, in general spiders with poor sight and a marked preference for shaded conditions demonstrate strong fluorescence in all eyes. However, in two species only, one of which was T.oblongus, none of the eyes were at all fluorescent; whereas Xysticus cristatus and X.kocki showed medium fluorescence in all but the anterior medians.

T.oblongus is the British Thomisid with the longest leg span in all directions, while having a cephalothorax and abdomen not of significantly greater mass than the other larger species. The cephalothorax and abdomen are also relatively elongated in T.oblongus and it seems probable that the use of the legs and body to detect prey directly has become predominant, in this genus, over the use of the eyes and that it represents an extreme position amongst the Thomisids in this respect, at least in Britain.

f) Tactile Sense - When in the predatory posture, the spider invariably reacted immediately, or within 1.5 seconds, to a fly; whether the fly was active, moribund or dead, as long as the fly came in contact with the tibia of any of the legs. The reaction was almost immediate if the fly came into contact with any of the other leg segments, the abdomen or the cephalothorax.

The pattern of attack was similar regardless of the point of contact; the spider lunged towards the fly very rapidly, gripped it with the first two pairs of legs and injected poison through the fangs. The fly, still being gripped, succumbed after a few seconds. Feeding started immediately, except in special circumstances to be described later.

When a mounted bristle was touched against a tibia, the spider attacked it. The response to repeated contact abated after four or five attacks but renewed when the bristle was touched against a different part of the body, or legs.

One spider had one of the third pair of legs which was stunted, probably regenerated during the final two Instars, it did not react to a contact on the stunted leg.

g) Special cases - When a large number of flies was released into a Petri dish containing a hungry spider and many of them made contact in a short space of time, the attack response was inhibited. The spider abandoned the predatory posture and walked away.

When a spider had been deprived of food for up to four or five days, it attacked a single fly and fed on it, ignoring further contacts with prey. As the period of starvation increased from five to twenty days, however, the spider attacked a second, third, fourth or even a fifth fly while still feeding on the first one. These subsequent flies were bitten and injected with poison and held under the cephalothorax while feeding continued. After having injected three or four flies, the spider's poison had a reduced effect through either scarcity or dilution, consequently the fourth or fifth fly attacked invariably remained active after the bite and often escaped from beneath the spider.

Prolonged starvation, above thirty day's deprivation, had the effect of reducing the number of concurrent captures, and an extremely hungry spider attacked and fed on only one fly at a time.

h) Summary - Spiders of the family Thomisidae are known to be ambush predators, pouncing on their prey at short range and not relying to the same extent on vision or silk threads as do other families.

The comparitively elongated body and legs of the genus T.oblongus together with the unusual findings in regard to the fluorescence of their eyes support the following conclusion: the most important means by which T.oblongus detects the presence of prey is by direct tactile reception mainly via the tibiae.

There was evidence that vision played some part in detection but that it had a minor and inconsistent role.

The predatory posture of T.oblongus, all the legs spread out over the substrate with the widest possible spacing is an adaptation to increase the prey catchment area.

The area covered by an adult female of average size in the predatory posture is about 6 sq.cm, the area covered by a walking spider at any one time is about half that figure; also in the hibernation posture the area is 2 to 3 sq.cm.

The way that this area can be considered in relation to predatory effectiveness varies according to the direction of movement of the prey. If the prey is a flying insect that lands randomly in the vicinity of the spider, then the probability of it landing on the spider in the predatory posture is double the probability of it landing on the spider in the hibernation posture, i.e. directly proportional to the area spanned by the spider in each case. However, if a walking prey is moving towards a T.oblongus individual on a two dimensional surface, the relative probability

of the encounter of the two postures varies according to the direction of approach of the prey. A lateral approach gives the same probability of encounter whereas an anterior approach gives a probability ratio of about 3:1. That is a walking prey approaching a T.oblongus individual from an anterior or posterior direction would be three times as likely to come in contact with an individual in the predatory posture.

In the most frequent predatory habitat that T.oblongus was found in the field, the stands of parallel, sloping, mixed, live and dead grass stems, the spiders usually aligned their bodies parallel to the grass stems. It is possible that prey species tended to move along, rather than across, the stems, but even allowing for an even distribution of the probabilities of prey approaching T.oblongus from all directions, an individual in the predatory posture is more likely to be encountered than one in the hibernation posture.

Therefore the predatory posture is functionally more efficient regardless of the characteristics of the prey's locomotion.

DISCUSSION.

During the period of captivity, the amount of time the T.oblongus individual spent in thepredatory posture varied according to a fairly well defined pattern. When the spider was first put into the Petri dish in the laboratory, it walked around the inside of the dish trailing a thread for several hours. The thread was attached to the surface, usually the underside of the lid at intervals of three to seven cm. The circular shape of the dish combined with the regular pattern of thread attachments to give the appearance of a semi-coherent web structure. However, on investigation it was discovered that this was purely artificial.

After the first twelve hours or so of captivity, the spider spent more and more time in the predatory posture and during the second to sixth day the majority of the time was spent preying. However, if no food was given to the spider it became more and more active during the subsequent days, more responsive to disturbance in general and more phototactic. This activity increased steadily and predatory activity decreased correspondingly during the following thirty days as long as observations continued. A similar pattern of behaviour was described by TURNBULL(1964), Achaearanea tepidariorium C.L.Koch, selected sites for webs apparently randomly with respect to prey occurrence but a site was abandoned if it yielded too little prey. The spiders used air currents to move from one site to another whereas the prey they eventually discovered had been attracted to that position by light. In the case of T.oblongus the phototactic response during starvation was probably combined with other responses not apparent in a petri dish, which in the field would lead it to favourable predation sites, probably the Special Areas(SECTION 4).

Many species of spider have been found on sampling to be distinctly concentrated in space and time, and the mechanisms by which this concentration is achieved and its role in the ecology of the various species has been the subject of some discussion. The main arguable point is whether the prime impetus for the selection of certain locations and seasons by a spider species is solely physical habitat characteristics, structural or climatic, or whether the spiders respond directly to prey occurrence and are accordingly active at the appropriate place and time.

DABROWSKA-PROT(1966) noted a correlation between predatory activity, including the building of webs and the presence of spiders in their webs, of Tetragnatha montana(Simon),and the daily and seasonal occurrence of its primary food source - mosquitoes. The direct stimulus for the spiders' activity was not discovered. TURNBULL(1966) relates the migratory movements of several species of spider to physical conditions with little emphasis on predatory efficiency. Also KAJAK(1965) states that in a meadow the important factor governing the numbers of two web-spinning spiders, Araneus cornutus Clerck and A.quadratus Clerck, is the presence of suitable microhabitats, not food availability. However, the well known occurrence of may Thomisids on flowerheads(HOBBY 1930), together

with camouflage colouring, indicates that the choice of habitat is related to the presence of prey, either by direct stimulus or by means of an evolutionary process.

Also to be born in mind are the specialised physical mechanisms by which many spiders detect and capture their prey e.g. webs, vibration reception and direct tactile reception, these must be related to the structure of the microhabitat in which the species is found.

In 1965 I observed a continuous interconnected network of spiders' webs measuring two metres by one metre by four metres composed of countless different types of web and species of spider, situated beneath a battery of bright lights which, at night, attracted hundreds of flying insects. The spiders may all have happenned on this web site by movement random with respect to prey occurrence but there is no doubt that they had congregated in the most favourable predation site for many kilometres around.

KNULLE(1953) states that the distribution of the species of spiders depends on physical features of the plants, for example their height and morphology and DUFFEY(1968) and (1966) stresses the importance of microhabitat structure in detemining the social status of a species from one community to another throughout the geographical range.

Research by BREYMEYER(1966) indicates that the degree of penetration of a habitat by wandering spiders is affected by competition with other epigeic predatory Arthropoda.

The three major factors which must be considered as affecting the presence of spiders in a certain place at a certain time are:-

a) Microhabitat characteristics, structural and climatic.

b) Presence of prey, the effect may be by direct behavioural response on the part of the spider, or by means of natural selection favouring those spiders which chose a time and place where prey was abundant.

c) Presence of competing predators.

there can be no absolute, generalised answer to this problem, however I think it is very probable that the factors that effect the predatory activity, in space and time, of many spiders including T.oblongus are factors which cause them to prey in a favourable place at a favourable time; favourable in that prey density is high at that time and place.

Despite the phylogenetic homogeneity of the order Araneae, there is a wide diversity in the modes of life of spiders. Very many habitat preferences and predatory strategies are exhibited and any generalisation concerning spiders as a group would be dangerous. However the order has had a long period of evolution in conjunction with its insect prey and this together with its essentially polyphagic nature may well have led to a balanced interdependancy of the numbers and behaviour of spiders with the occurrence of suitable microhabitats and the numbers of potential prey, many stabilising factors being involved. ITO(1964) states that spiders might reduce their metabolic rate when starved to a degree that has never been attained by many primary consumers; this is another factor contributing to a balanced predator/prey relationship providing the necessary cushioning effect between the microhabitat requirements on the one hand and the need for food on the other.

6.2.3 The time taken in handling, consuming and digesting the prey.

As previously described, the attack by the spider was very rapid and the fly was bitten and rendered inactive a fraction of a second after detection. Feeding started immediately except when the spider was already feeding on a fly that had been previously captured, in which case the more recent captive was kept under the cephalothorax. Up to four adult Drosophila were kept under the cephalothorax at one time and the spider fed on them in turn, discarding a husk before progressing to a fresh corpse. The length of time spent feeding on a particular corpse varied from between 10 minutes and one hour with the average at about half an hour.. The factors affecting this were not investigated but were related to the size of the fly, the hunger of the spider and the number of corpses held in reserve.

The conditions of the discarded corpses was investigated as a guide to the length of time the spider had spent feeding on each one and to the amount of food taken from each.

The discarded husks varied between two extremes:-

a) Only one part was sucked dry and flattenned, the head, or the abdomen.

b) The whole animal was completely masticated and virtually unrecognisable.

All conditions between these extremes were observed, and there was found to be a correlation with the time the spider had spent feeding on each one, although not a simple, direct one.

It was decided that a detailed investigation of the weight of prey eaten under various circumstances was too complex to produce useful results in the time available. The cessation of the time elapsing after feeding before the next attack varied considerably from minus 10 minutes to six hours depending on the state of hunger of the spider. A detailed analysis was not attempted. A fuller analysis on the above factors is desirable as a preliminary to a functional response experiment, however this was impractical and the estimates and corrections made are described later.

6.3 The Functional Response of Tibellus oblongus.

The experimental component analysis of predator/prey interrelation has been developed and described by HOLLING(1963). The experiments and analyses performed by him involved the building of a mathematical model, comprising many separate equations, which described the interaction of several components. Holling extracted these components from a generalised predator/prey confrontation and they were supposed to describe and explain the relationship between the two types of organism completely. He studied the components experimentally using small mammals(HOLLING 1961)and the praying mantid Hierodula crassa Giglio Tos as predators(HOLLING 1966). He claimed that, as a result of the basic approach, the final model was of such a generalised nature that it would apply to virtually any predator/prey situation and this claim has been tested by MORRIS(1963) and HAYNES & SISOJEVIC(1964) and corroborated to a limited extent. Their experimental results were satisfactorily described and explained by Holling's model at least in part, since the full invertebrate model had not yet been developed.

The functional response of a predator is the reaction by an individual predator in the number of prey attacked to changes in prey density. The response of the predator population, the numerical response, was to be studied subsequently.

The aims of the investigation of T. oblongus in this context were twofold:-

a) To determine if the Holling model applied to this particular predator.

b) Assuming the model was relevant, to draw inferences concerning the ecological characteristics of the spider.

METHOD

The chosen experimental prey was the same species as was used in the general predation investigation, for the same reasons, D. melanogaster.

T. oblongus is an ambush predator, awaiting its prey and pouncing on it from short range, therefore contact between the spider and its prey is a result of prey movement rather than movement by the spider.

One of the basic components in Holling's model is the rate of search by the predator;in the case of T.oblongus, movement by the prey profoundly affects this component.It has been discovered that the movement of various animals is affected by their density:Musca domestica individuals for instance move less at high densities(HOLLING 1966) whereas D.melanogaster individuals move more(HAYNES&SISOJEVIC 1964).This fact was recognised in the case of the two ambush predators whose functional responses have been so far studied and correction factors relating prey densities to prey velocities were applied in the final analysis.

In order to obviate this type of correction factor for T.oblongus and Drosophila,the experiment was designed in such a way that the velocity of the prey could be both controlled and accurately recorded.The apparatus which was developed for this purpose is illustrated photographically in FIG 6 which shows an exploded view of the cage,and diagramatically in FIGS 29 &30.The cage where the animals came in contact with each other was mounted so that it could be rotated at various speeds by a Kymograph machine connected to it by a system of simple gears.

Within the cage,the space where the spider and flies were active was the space between the inner wall of gauze and the outer wall of polystyrene,in effect a band between two cylinders,one inside the other.The dimensions of this space were as follows:-

the circumference of the inner cylinder....28cm
the width of both cylinders..... 4cm
the depth of the space between them....0.5cm
the total volume...57cm^3.

The interior of the cage was maintained at a constant, high humidity by means of wet cotton wool inside the inner cylinder,and it was illuminated by a 100 watt bulb 15cm above the top of the cage.

FIG 29

FUNCTIONAL RESPONSE APPARATUS.

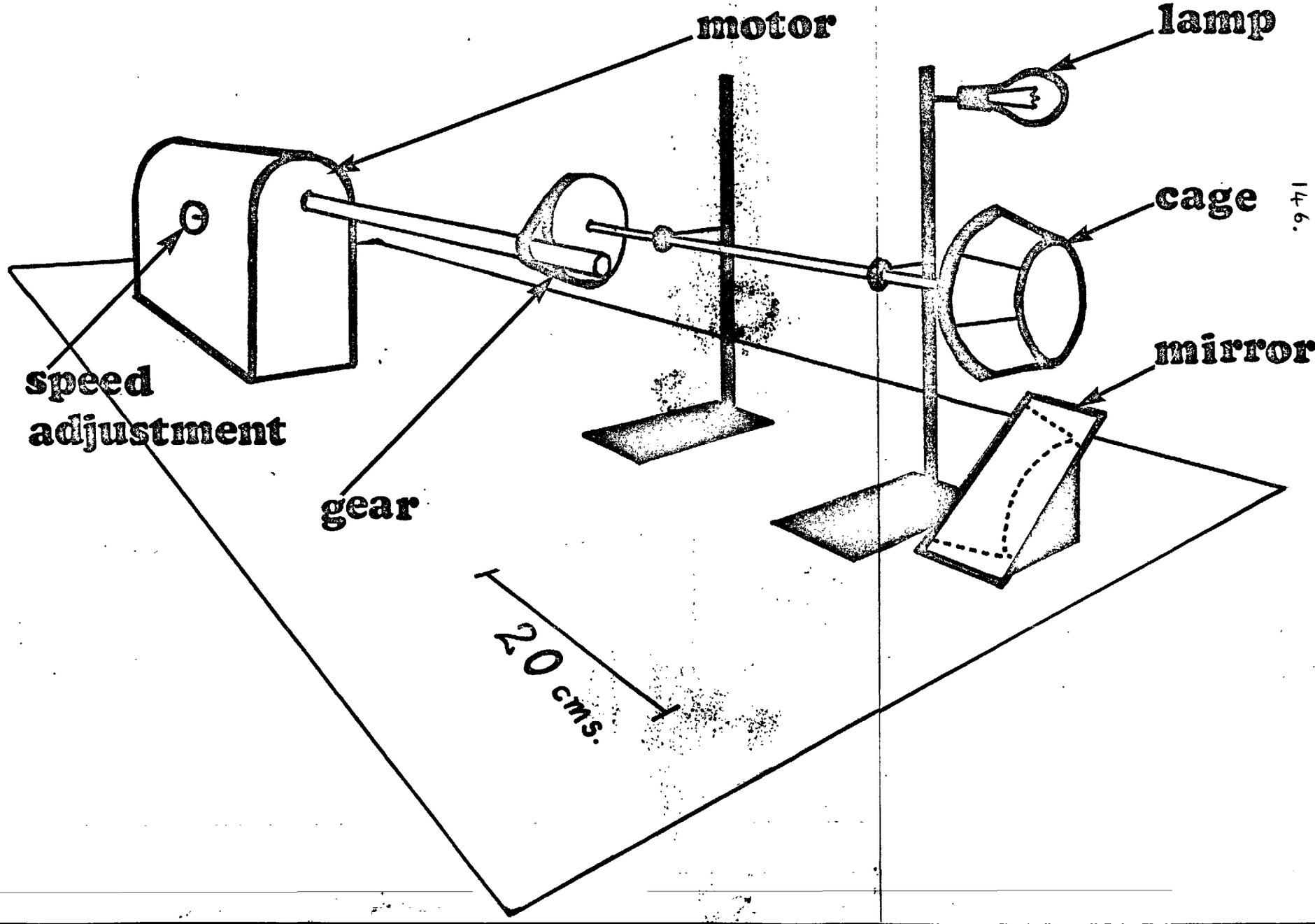
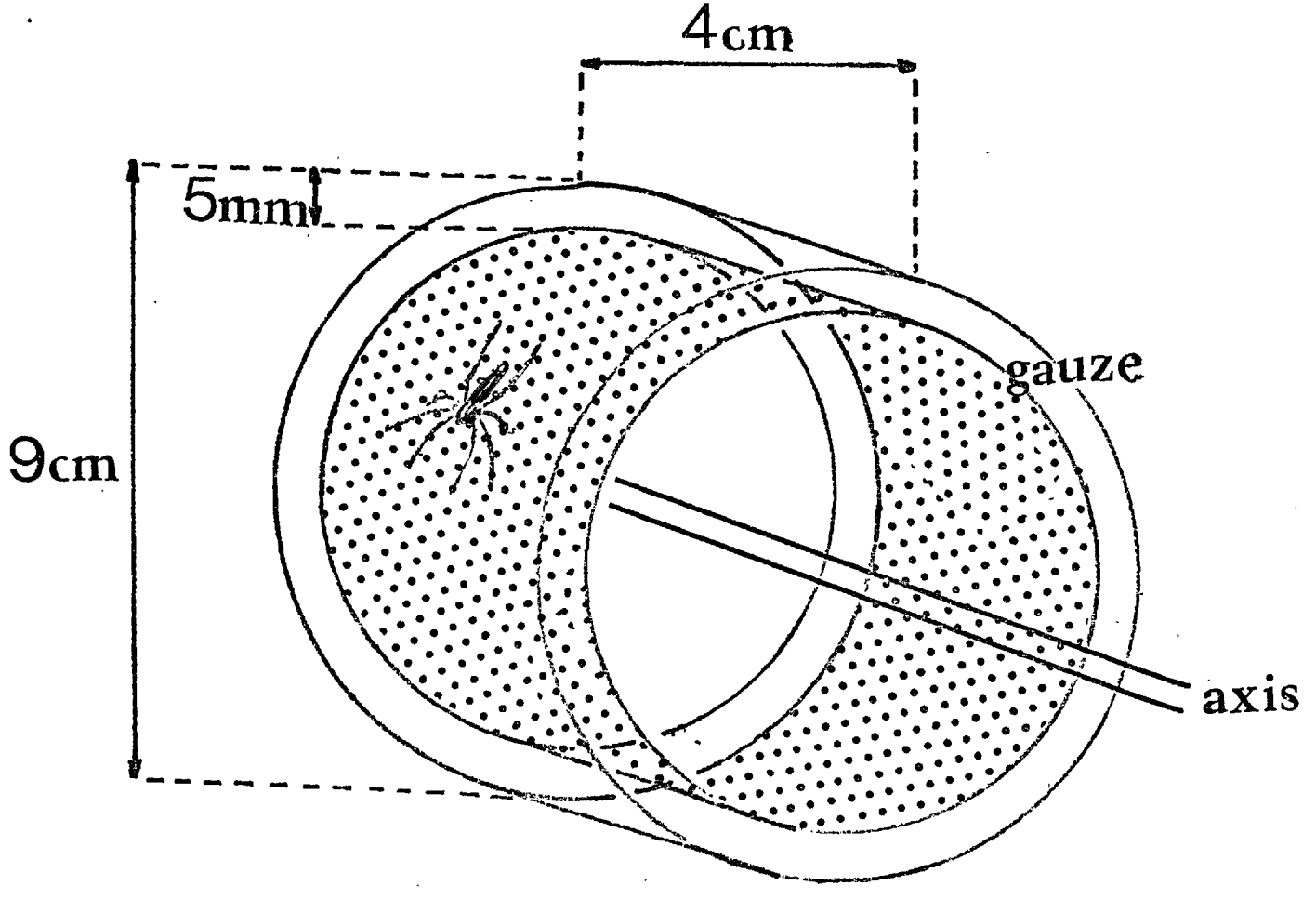


FIG 30 FUNCTIONAL RESPONSE CAGE

Oblique view



The whole apparatus was kept in a constant temperature room at 20° C.

The spiders used in the experiments were unfertilised adult females which, having finished moulting and not yet having mated, had a fairly constant basic food requirement. Individuals deprived of food during the 25 days prior to the experiment as well as individuals that had been feeding normally up to the experiment were used.

EXPERIMENTAL PROCEDURE

A spider was introduced into the cage through one of the stoppered holes and the rotation machinery was started. After a variable period of activity the spider positioned itself in the predatory posture on the gauze inner wall and was carried round with the cage. There was no evidence that the spider was disturbed into aberrant behaviour by the continual motion of the cage. When the spider had become accustomed to the environment, up to 6 hours after its introduction, the rotation machinery was stopped long enough for a number of flies to be put in through the stoppered hole. The rotation machinery was restarted and the light above the cage was lit.

The spider remained stationary on the gauze and was carried round with the cage as before, whereas the flies being negatively geotactic and positively phototactic tended to remain in the uppermost part of the cage, directly beneath the light bulb. In order to stay in this position they had to walk and fly in short bursts in the opposite direction to the rotation and at the same average speed. In this way the spider was carried through the group of walking flies once for each rotation of the cage, and since the rotation speed could be accurately controlled by the control on the Kymograph machine, the speed of the flies in relation to the spider could be both controlled and accurately recorded.

When the flies were from an old culture or when they were tired during the later stages of each experiment they could not walk fast enough to stay at the top of the cage and were occaisionally carried round with it. For this reason the measure of the flies' velocity that was recorded was the number of times a line through the spider and parallel to the cage axis was crossed by flies in a typical 30 minutes of the experiment.

This measure is termed the "Fly Velocity Value" hereafter referred to as the FVV.

So as to ensure that this value remained constant during each experiment, when a fly was attacked and put out of action by the spider a fresh fly was put into the cage as soon as possible in an attempt to keep the number of free flies constant.

As there was no evidence of a diurnal feeding rhythm in T.oblongus the experimental duration was a continuous 24 hour period and it was assumed that the spider's feeding pattern was unaffected by time alone.

At the end of the experiment, the corpses of the flies in the cage were examined. They were divided into two types:-

a) Attacked, bitten and eaten.
These corpses had at least one part obviously sucked dry by the spider.

b) Attacked and bitten.
These were flies which although dead, did not appear to have been fed upon since all segments were of normal shape. In the case of starved spiders these corpses were being held under the cephalothorax when the experiment ended, or had fallen from that position during the experiment. Also included in this category was a fly upon which the spider was feeding at the end of the experiment.

From experiment to experiment a different FVV was achieved by varying the rotation speed of the cage and by varying the total of free flies within the cage, from 2 to 8.

Spiders feeding normally up to the experiment are termed Normal spiders, and spiders deprived of food during the 25 days prior to the experiment are termed Starved spiders.

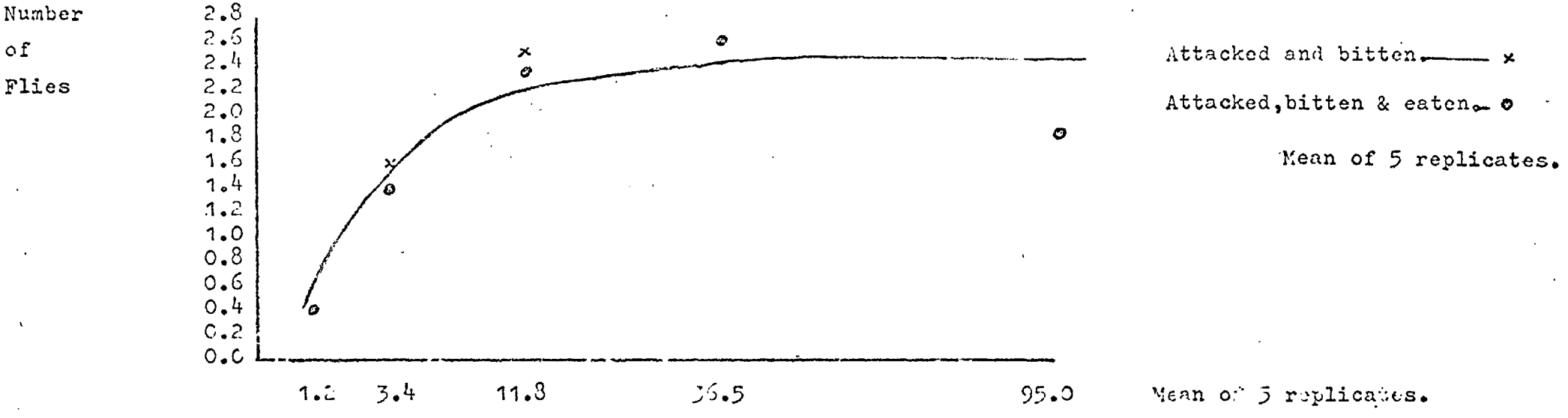
RESULTS

The experimental results are shown graphically in FIGS 31 & 32.

The variation between replicates is not included, for clarity; it was much higher in relation to the mean at the lower ranges of the FVV.

Attacks by the spider which were unsuccessful ie. which did not result in a bite were not recorded since the cage was not under observation for the full 24 hours. From general observation the proportion of unsuccessful attacks to successful attacks was about 5%.

FIG 31 The Functional Response of T.oblongus, spiders feeding normally up to the experiment.

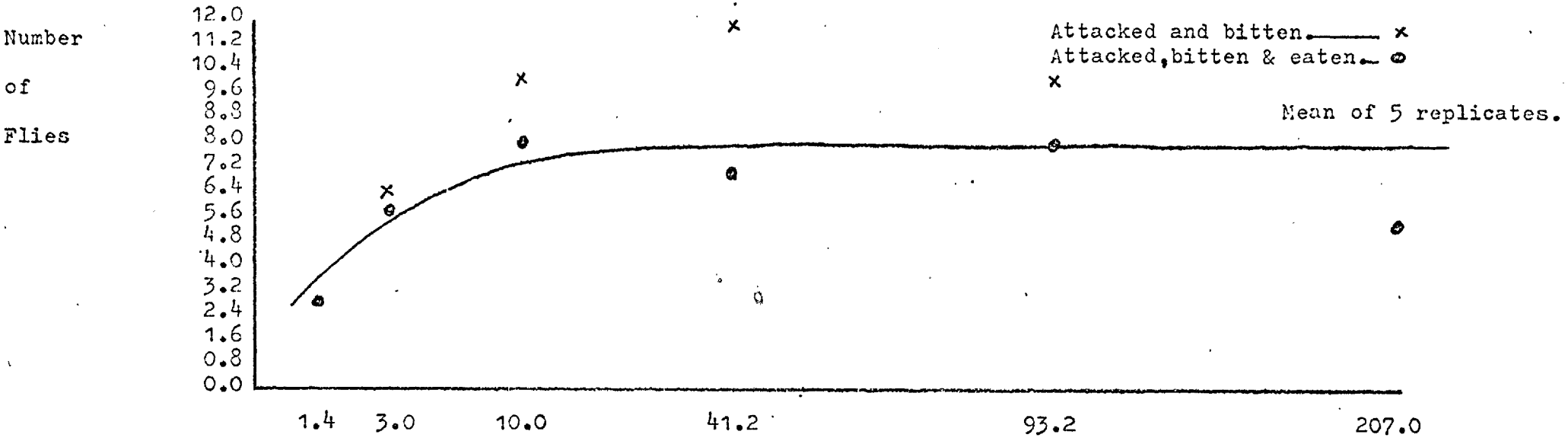


Fly Velocity Value-the number of times an imaginary line through the spider parallel to the cage axis is crossed by flies in a typical 30 minutes of the experiment.

Experiment duration-24 hours.

The points are the experimental results, the curve is calculated from the Basic Functional Response Equation.

FIG32 The Functional Response of T.oblongus, spiders deprived of food the previous 25 days.



Experiment duration-24 hours.

The points are the experimental results, the curve is calculated from the Basic Functional Response Equation.

ANALYSIS

The following points which are apparent from the results are listed here, they will be discussed in greater detail later:-

a)The experimental results for both Normal and Starved spiders approximately follow a curve which shows a negatively accelerated rise to a plateau.This was termed a Type 2 response by HOLLING (1959).This indicates that the experimental technique that was adopted ie. the replacement of prey density by a value for prey velocity- FVV, was a valid substitution for this type of ambush predator.

b)The marked difference between the Normal and Starved spiders in the number of flies eaten at the 'plateau' level of their respective curves indicates the importance of the hunger component in the functional response of the species.

c)The number of flies eaten at the highest FVV is lower than the number predicted by the basic functional response curve for both Normal and Starved spiders.This discrepancy indicates the action of a further component which has been identified by Holling but not yet investigated by him -ie. Inhibition by Prey.

d)The proportion of flies attacked and bitten to flies attacked,bitten and eaten is higher for starved spiders than for normal spiders.This reflects the fact that hungry spiders tended to capture up to five flies while still feeding on one. The spare corpses were kept under the cephalothorax and some were dislodged by the rotation of the cage,these fell free and remained at the bottom of the cage untouched by the spider.

Point a)...The functional response curve.

An attempt was made to describe the experimental results in terms of the three basic components of predation whose relationship is expressed in the Basic Functional Response Equation:-

$$y = \frac{Tt \cdot a \cdot x}{1 + abx}$$

Where,

y is the number of prey attacked.
x is the density of the prey (expressed as FVV in the experiments with T. oblongus).

And three three basic components of predation are:-

a --- the rate of successful search,
b --- the time the predator spends handling each prey,
Tt --- the time the predator and prey are exposed to each other.
This value was a constant 24 hours in all expts.

(HOLLING, 1959a).

The values used in the equation were:-

FOR NORMAL SPIDERS	FOR STARVED SPIDERS
b = 9.5 hours	b = 3.0 hours
a = 0.04	a = 0.2

The curves resulting from these substitutions are superimposed on FIGS 31 & 32.

The close correspondence to the experimental results is apparent (except for the number of flies eaten at the highest FVV).

The basic functional response equation is therefore a fairly accurate description of the response of T.oblongus.

In order to test whether it affords a coherent explanation of the predatory behaviour of the spider, the values of "a" and "b" can be examined for both normal and starved spiders.

The rate of successful search - "a" can be defined in in terms of the subcomponents:-

i) The reactive distance of the predator for prey.

ii) The speed of movement of the predator.

iii) The speed of movement of the prey.

iv) The capture success.

(HOLLING 1963).

With regard to subcomponent i), a replete spider had a reactive distance effectively of zero since flies could walk all over the spider without being attacked, whereas a hungry spider had a reactive distance equal to the range spanned by its legs, cephalothorax and abdomen since a fly coming in contact with it anywhere was attacked.

With regard to subcomponent ii), the speed of movement of the predator was zero for both normal and starved spiders, reflecting the fact that T.oblongus is an ambush predator.

The speed of movement of the prey, subcomponent iii), was effectively the FVV which covers the same range one to a hundred for both normal and starved spiders.

Although no quantitative observations were made on capture success, subcomponent iv), it can be assumed that it has a similar value for both normal and starved spiders.

HOLLING(1966) has developed a set of equations which describe the interaction of the above components and subcomponents with hunger and the various values for T.oblongus could be substituted in each one. Moreover the spider represents a simplified and extreme position in several of the interrelationships eg. having zero velocity and having a reactive distance for prey no larger than the span of the legs regardless of the degree of hunger: for these reasons a quantitative analysis of the component "a" for T.oblongus would be a relatively simple task. Its usefulness however would be severely limited since the interaction of component "b"(the time spent handling each prey) with hunger was not investigated in sufficient detail for the full invertebrate model to be used. The qualitative comparison of the values of the subcomponents of "a" that has been described above, is sufficient to show that the difference in the values of "a":-

0.04 for normal spiders

0.2 for starved spiders

is reasonably explained by the difference in subcomponent i), the reactive distance, which is zero for normal spiders and about 6 cm^2 for starved spiders.

Component "b",the time spent handling each prey,can be defined in terms of the subcomponents:-

i)The time spent pursuing and subduing each prey.

ii)The time spent eating each prey.

iii)The time spent in digestive pause after a prey is eaten and during which a predator is not hungry enough to attack.

(HOLLING 1963)

Subcomponent i) is only in the region of a second for T.oblongus in any condition that one was ever observed attacking a fly,a hungry spider pursued and subdued a fly no faster than a normal spider.Again the spider represents an extreme position in this respect as compared with many other types of predator.

Subcomponent ii),the time spent eating each prey,varied greatly for both normal and starved spiders,also according to the size of the fly.A more thorough investigation of this subcomponent was desirable but not possible.Since the rate of extra-corporeal digestion must be taken into account,an average time of 50 minutes spent eating each prey must be assumed as the value of this subcomponent for both starved and normal spiders.

Subcomponent iii),if called "a digestive pause after having eaten the prey" is a misnomer to some extent in the case of T.oblongus because of the extracorporeal digestion of the prey that takes place simoultaneously with the prey being eaten. The value of the subcomponent however,is expressed as the length of time after having eaten a prey,is a second prey attacked. In the case of normal T.oblongus individuals a mean value of 9 hours is appropriate but for a starved spider the value could be as low as MINUS 50 minutes when a second prey was captured 50 minutes before the spider had finished eating the first.

It is apparent that in the case of this predator, and in the case of certain web spinning spiders which wrap prey in silk and store them, a fourth subcomponent of "b" -the time spent handling each prey -can be identified. A subcomponent with which Holling has never dealt, it can be called:-

subcomponent iv) The time spent saving each captured prey prior to eating it.

For normal spiders this subcomponent had a value of zero since they never captured surplus prey. For starved spiders however the situation is more complex.

Considering the functional response curve at the plateau level, during the course of the experimental period each spider on average attacked and captured about 11 flies and had eaten about 8 of them with 2 or 3 still being held under the cephalothorax at the end of the experiment. Assuming that the spider held a stock of 2 or 3 flies on average throughout the experiment, then the series of events, from the viewpoint of each fly was as follows:-

attacked and captured,
held under the spider for 50 minutes, 3rd in line,
held under the spider for 50 minutes, 2nd in line,
held under the spider for 50 minutes, 1st in line,
being eaten for 50 minutes,
discarded.

The subcomponent under consideration comprises the second, third and fourth items in the above list, for the average fly a total of 2 hours 30 minutes.

The first three flies to be attacked, bitten and eaten however were not saved for so long prior to being eaten.

Therefore in this particular experiment the value of subcomponent iv) can be calculated as the mean value of the first eight flies to be attacked, bitten and eaten as follows:-

subcomponent iv)	for	the	first	fly	to	be	captured	is 0 minutes
"	"	"	second	"	"		50	"
"	"	"	third	"	"	"	100	"
"	"	"	fourth	"	"	"	150	"
"	"	"	fifth	"	"	"	150	"
"	"	"	sixth	"	"	"	150	"
"	"	"	seventh		"	"	150	"
and "	"	"	eighth	"	"	"	150	"

The overall mean is 112 minutes spent saving each captured prey prior to eating it.

A combination of all these subcomponents of component "b" gives values of 9.5 hours and 3 hours for the average time spent handling each prey by normal and starved spiders respectively.

These are the values used in the calculation of the curves which are superimposed on FIGS 31 & 32.

The above discussion covers point d) of the initial list.

The preceding examination of the components "a" and "b" in the basic functional response equation, although of a more qualitative nature than was ideal, indicates that Holling's approach, with a slight modification for this type of predator, is both an accurate description and offers a logical, cosistent explanation of the predatory behaviour of T. oblongus in response to changing prey density.

A more rigourous mathematical treatment of the analysis was not possible in the time available since detailed studies of the effect of hunger on the various subcomponents would have been necessary.

Returning to point c) of the initial list, the lower than predicted number of flies attacked at the highest FVV: on the evidence of general observation it was decided that this was the effect of a component of predation which Holling has identified but has never investigated...."Inhibition by Prey".

MORRIS(1963) investigated this component in relation to the prey species Hyphantria cunea, Drury, where the component took the form of a deliberate defensive behaviour pattern in reaction to its predator Podisus maculiventris. In the case of T. oblongus and D. melanogaster however, the component took a different form.

It was observed during the experiments that when the spider came into contact with several flies within a fraction of a second, it did not attack but walked away, only resuming the predatory posture after several minutes without further disturbance. The spider's attack response was inhibited by the prey.

The probability of the requisite number of flies coming in contact with the spider increased with increasing FVV for two reasons. Firstly there tended to be more flies in the cage and secondly they tended to be bunched together more when the cage was rotating rapidly at the higher FVV's.

In the field the probability of a similar occurrence would increase rapidly with increasing prey density, especially in the "Special Areas" where the spider preys and which are relatively crowded with prey.

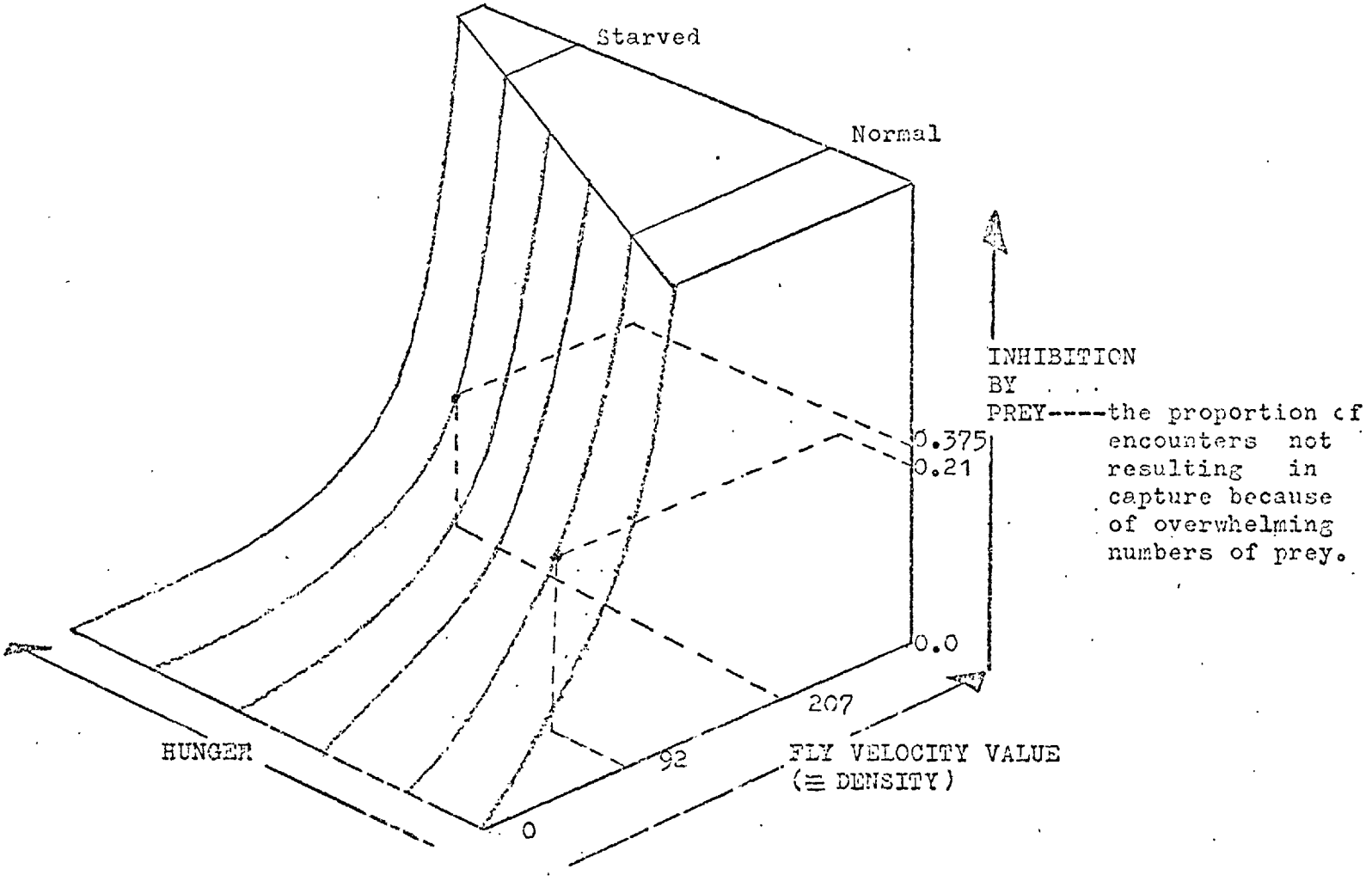
Inhibition by prey, if it is to be integrated into the functional response model, can be expressed as the proportion of encounters not resulting in capture because of overwhelming numbers of prey. This proportion would increase with increasing FVV and with increasing fly density.

There is evidence from the experimental results that the susceptibility of T. oblongus to this type of inhibition decreases when the spider is hungry, since at an FVV of 93.5 to 95 the normal spiders were inhibited from attacking the flies whereas the starved spiders were not. The starved spiders were inhibited at an FVV of 207. A detailed study of the interrelation of the component inhibition by prey with the other components of predation would be necessary for its integration with the main part of the functional response model, however the experimental results with T. oblongus indicated that the general form of its interrelation with changing prey density and with hunger is as expressed in FIG. 33.

At a particular level of hunger, the degree of inhibition increases with increasing fly density or FVV, also at a low hunger level the same FVV or fly density induces a higher degree of inhibition than at a high hunger level.

The experimental results are represented as the two points on the graph.

FIG 33 The general form of the interrelation between INHIBITION BY PREY and Prey Density and Hunger in T.oblongus.



DISCUSSION

The degree of generality of the component analysis approach appears to have been extended to another predator/prey confrontation in the light of the results for T.oblongus and D.melanogaster.

The descriptive power of the basic functional response equation can be seen in FIGs 31 & 32 and the examination of the various subcomponents involved in the response provided a reasonable and coherent explanation of the spider's behaviour.A full test of the explanatory power of the Holling model could not be made without a detailed study of the effect of hunger on all the sub-components and a synthesis of the separate relationships into a complete daily feeding cycle as Holling did for the Mantid (HOLLING 1966).This was impracticable in the time available,but the more qualitative examination that was carried out provided valuable information.

Firstly,the experimental design which allowed accurate control and measurement of the velocity of the flies in relation to the spider provided a useful short cut during the analysis because no correction factor relating prey density to prey velocity was necessary. The disadvantage was that the validity of the results could not easily be extended to a field situation because of the artificiality of the rotating cage environment. To take a wider view,a prey species in the field which, although abundant,moved very little would not come in contact with the spiders very frequently.If the prey species were to suddenly swarm or to move faster generally, then an ambush predator like T.oblongus would be much more likely to take a toll of the population.

So it is important that the two variables prey density and prey velocity be clearly distinguished for this type of predator, including web spinning spiders and other Thomisids which are completely dependant on prey movement for predatory success.

Inhibition by prey occurred at the higher FVV's and could well occur in the field occaisionally, especially in the Special Areas which, as discussed previously, attracted many arthropods at the time T.oblongus was preying. It is too small and too random a factor to have very much ecological importance for T.oblongus, but it seems likely that the evolution of swarming, shoaling and herding behaviour patterns in some prey species may have depended on it.

The "mutual interference constant" introduced by HASSELL & VARLEY (1969) into the Nicholsonian model of parasite/host interaction and which represents the reduction in the parasites' area of discovery as parasite density increases, is theoretically distinct from this component. It is related to parasite density as opposed to prey density, also it has been derived inductively rather than arising from direct observation, the details of its behavioural manifestations are under investigation.

In order to explain the difference in the results between normal and starved spiders it was necessary to invent and name a subcomponent:-the time spent saving each captured prey prior to eating it. Holling has never distinguished this factor specifically but it fits into the structure of the model perfectly. The characteristics of the subcomponent were developed and it was integrated into the basic functional response model as part of the definition of handling time, component b. There is a marked

ecological significance to the subcomponent in species like T.oblongus which save or store captured food prior to eating it.Animals in this category include those web spinning spiders which wrap surplus prey and feed on them up to several days after capture.

Of all the subcomponents of component "b",the time spent handling each prey.(p 157) ,this is the only one which allows a hungry individual any flexibility in this part of its functional response.The time spent in pursuit and subjugation is likely to be the same for normal and starved web spinners,and for other ambush predators in general including Thomisids,as it is for T.oblongus.The time spent eating each prey could well be limited by extra-corporeal digestion and the pharyngeal pump mechanism, a hungry spider,in other words,could eat no faster than a relatively replete one.The time spent in digestive pause is only meaningful in the case of Normal spiders,which leaves the new subcomponent as representing the only way in which a hungry predator can alter "b",the time spent handling each prey.By the variations in the subcomponent and the corresponding variations in the component,the predator is able to exploit a short term increase in prey density by handling each prey faster,also to provide a food reserve in case of future prey scarcity.

With regard to the overall implications of the component analysis approach to the study of predation in particular and population dynamics in general,Holling himself has developed and discussed these to some extent in all his published papers,especially in HOLLING (1965). In that paper he uses the logical implications of the model to point out that factors governing populations should be classified not as either density dependant or density independant agents,but as density dependant and density independant effects since the same agent can have either effect according to other circumstances.

In the light of Holling's approach ,and results, the classical controversy concerning the two types of population regulating factor mentioned above,would seem to be to a large extent redundant,despite its resurrection specifically in relation to the Holling model by HASSELL (1966).

It would be plagiaristic to repeat Holling's arguments here,the best contribution is merely to say that the behaviour of T.oblongus in relation to its prey conforms to the pattern that he predicted,from the point of view description as well as explanation, and this finding adds a little weight to the various implications he has derived and published.

SECTION 7

Summary and General Discussion.

The preceding sections of the thesis deal in turn with relatively distinct aspects of the biology of T.oblongus. Because of certain characteristics of the spider's biology, observations and experimental results in the laboratory tended to be complementary to those in the field. Moreover as particular findings arose, the general direction of the research changed, the major shift in emphasis, during the later stages of the work, being concentrated on a study of the species' predatory behaviour using the component analysis approach. The reasons for this are set out in the introduction to Section 6.

The results from the various fields of investigation are discussed separately under the relevant headings, particularly in in relation to the ecology of the species and only a general summary is given below.

The variations in the spiders' abdominal pattern were not reflected in major physical, physiological or behavioural differences. The species is biennial in development with a certain proportion of the population maturing each summer. This type of life cycle is similar to that of some other Thomisids whose life histories have been studied. Laboratory rearing was found to have an adverse effect on the individual's rate of growth although the laboratory environment did not appear to distort the spiders' behaviour. The volume of food supply was critical for the normal maturation of an individual in the laboratory, the usual four juvenile instars were extended to five at least in starved individuals and at least to six in spiders captured as instar 2 and kept at constant high temperature. Several individuals in a cage did not interfere with each other in the presence of a full food supply.

Investigation of a field population revealed a significant microclimatic difference between the locations where T.oblongus was abundant in both summer and winter and the surrounding locations. However; this does not fully explain the distribution of the spider.

Observation and experiments on the behaviour of the spider indicated the significance of its postures, especially in conjunction with its coloration during the defense reaction which may have evolved in response to predators using vision.

T.oblongus individuals did not tend to hibernate in contact with each other.

A change of temperature was found to be important in stimulating the spider to emerge from its hibernation sites.

There was no evidence of aeronautical behaviour in the species ,but a simple mathematical analysis showed that the effectiveness of walking as a means of dispersal was marked.

In the laboratory,the sequence of events during ecdysis was photographed and mating behaviour was described,as was egg laying and incubation.

The general pattern of predation during the life cycle of the spider was assessed and the machanisms by which it detected prey were found to be mainly tactile with vision playing a minor and inconsistent role.Silk was used only during incubation to extend the sensory range of the individyal.The spiders habitat preference in relation to predatory opportunity was discussed.

The functional response of T.oblongus to changing prey density was elucidated in the laboratory and the component analysis approach of Holling,together with its resulting equations,were found to provide both an accurate description and a logical explanation of the response.A new subcomponent of the time spent handling each prey is suggested,namely the time spent saving each captured prey prior to eating it. This subcomponent in the context of the functional response model explains the difference in behaviour of Normal and Starved spiders.It also reveals the importance of prey storing activity by ambush predators in general.

The general form of the interrelationship between "innibition by prey",hunger,and prey density is suggested on the basis of limited experimental evidence in conjunction with probability theory.

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