Ph.D. THESIS

THE COMPARATIVE BIOLOGY OF THE ORB-WEB SPIDERS ZYGIELLA X-NOTATA AND ZYGIELLA ATRICA

BY

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ABSTRACT

The aim of this investigation is to compare the ecology and behaviour of the orb-web spiders Zygiella x-notata and Zygiella atrica. Differences between them in their choice of habitat, as cited in the literature, are generally confirmed by a preliminary field survey. Mixed populations do occur but hybridization has not been detected, although the close morphological similarity, especially in the immature stages, is emphasized. Field studies show that the species also build basically similar webs with respect to spider size, retreat position and habitat structure. However, the larger number of radii in Z. atrica middle instar webs is of interest. Life histories are compared in a two-year study of two natural populations and differences in mating behaviour are described.

In conjunction with the field studies, which include microclimatic measurements, laboratory experiments on the effects of temperature, humidity and feeding rates on development; humidity and temperature preferences; and changing reactions to light are detailed. Tolerances to temperature extremes, desiccation and starvation are investigated. These experiments indicate several differences between the species. Z. x-notata eggs hatch more quickly than Z. atrica at equivalent temperatures. Z. x-notata prefers higher temperatures and can also withstand greater extremes. At 25°C., for example, Z. atrica males show high mortality during the final moult. The preference shown for low humidities is more pronounced in Z. x-notata and it is more resistant to desiccation and also food deprivation. Limited feeding results in reduced size and increased instar length, but there is some compensation by reduction in instar numbers, especially for Z. x-notata.

In conclusion, the differences detected in morphology, life histories, webs, preferences and tolerances in both field and laboratory indicate that Z. x-notata is more adaptable, and this may well help to explain its wider and more varied pattern of distribution.

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CHAPTER I

INTRODUCTION

Spiders are a widespread, common and diverse group of arthropods. They have been reported from most parts of the world, occupying varied habitats in many different environments, and although essentially terrestrial, some species have become partially or totally aquatic. The distribution of spiders by environment is discussed by BRISTOWE (1939), for example, and literature on the subject is cited by TURNBULL (1973) in a very useful review on Araneomorph ecology.

That habitat structure and microclimatic conditions, which are often closely linked, may well influence spider distribution between and within habitats is acknowledged by numerous authors. DUFFEY (1966) stresses the importance of examining these factors when studying spider distribution. If a species is common in two quite different ecological habitats, the absence of competition from related species may be an added factor (DUFFEY, 1968). BRISTOWE (1929) and LUCZAK (1963) also recognise the influence of interspecifc competion on distribution.

In the case of actual site selection by web-building spiders, the site must provide microclimatic conditions suited to the physiological needs of the spider, scaffolding for the web, and an adequate food supply (TURNBULL, 1973). Although temperature (NØRGAARD, 1956; KRAKAUER, 1972), humidity (SAVORY, 1930; CLOUDSLEY-THOMPSON, 1957), light (CHERRETT, 1964; ENDERS, 1973), sunlight (POINTING, 1965), and wind (POINTING, 1965; EBERHARD, 1972), plus height above the ground (JONES, 1941; ENDERS, 1972) have been shown to influence the siting of webs, the structural characteristics of the habitat may be more important (LOWRIE, 1948; DUFFEY, 1962b; CHERRETT, 1964; ENDERS, 1973). The preference for dead rather than living vegetation (DUFFEY, 1962b; EBERHARD, 1972; ENDERS, 1972), the stiffness and rigidity of supports for the web (BRISTOWE, 1939; TILQUIN, 1942; LOWRIE, 1948) and the size of the space available (SZLEP, 1958) are known to affect site selection, at least in some spiders.

Different responses by different species to such factors may lead to horizontal, vertical and temporal stratification. Stratification in spiders has been recognised in field studies by various authors (ELLIOT, 1930; MUMA and MUMA, 1949; DOWDY, 1951; TURNBULL, 1960; DUFFEY, 1962a, 1962b, 1968; LUCZAK, 1963 and ENDERS, 1972). ELTON and MILLER (1954) have proposed a method for classifying habitats by structural characters useful when defining physical strata. TRETZEL (1955) points out that stratification in closely related or similar species within a community minimises competition between them. DUFFEY (1966) gives examples of closely related species which illustrate the three types of stratification mentioned above.

A survey of the literature on the orb-web spiders Zygiella x-notata (Clerck) and Zygiella atrica (C. L. Koch) (for synonyms see Table 1.) indicates distribution differences in relation to habitat. The aim of this study is to confirm that the differences do occur, to examine factors which may influence habitat choice, and to compare life cycles both in the field and under controlled conditions in the laboratory.

Although general information on the distribution and biology of the two species appears in the literature, and both are mentioned in species lists from field observations, no comparative ecological

Table 1. *Zygiella x-notata* and *Z. atrica* synonyms

Zygiella x-notata	Reference			*Zygiella atrica*	Reference		
	W	L&M	G		W	L&M	G
Aranea calophylla	+			*Aranea calophylla*	+		
" litterata		+					
Araneus x-notatus		+	+				
Epeira similis	+	+		*Epeira calophylla*		+	
				Eucharia atrica	+	+	+
Zilla californica			+	*Zilla atrica*	+	+	+
" Keyserlingi ♀	+			*" Keyserlingi*	+		
" litterata	+	+					
" x-notata	+	+	+				
				Zygia calophylla	+		
Zygiella litterata		+	+	*Zygiella (Zilla) calophylla*			+

W = WIEHLE (1931), L&M = LOCKET & MILLIDGE (1953), G = GERTSCH (1964)

field study seems to have been made. Comparative ecological experiments are few (SAVORY, 1930; DAVIES and EDNEY, 1952) and these will be referred to later. Unlike *atrica*, *x-notata* has been used extensively as an experimental laboratory animal in the study of orb-webs and web-building behaviour (WIEHLE, 1927; TILQUIN, 1942; KOENIG, 1951; PETERS, 1951, 1969; MAYER, 1952; WITT, 1956; LE GUELTE, 1964a, b; 1966a, b), the effect of drugs on web construction (WOLFF and HEMPEL, 1951; WITT, 1956; WITT and REED, 1965; BAZANTE, 1971), and learning in spiders (LE GUELTE, 1969). WITT, REED and PEAKALL (1968) have worked with orb-web spiders in the laboratory and much research, including that done on drug webs, is reviewed in their book.

The genus *Zygiella* (F. O. Pickard-Cambridge) is one of ten genera in Britain representing the Argiopidae, a family exclusively of orb-web spinners (LOCKET and MILLIDGE, 1953). (For discussion of the family name, see PLATNICK and LEVI, 1973). A total of twenty-two

Zygiella species is given by BONNET (1959) but many of the reported species should probably be assigned to other genera (GERTSCH, 1964). LEVI (1974) recognises fifteen species. The genus is represented in Britain by *Zygiella x-notata* (Clerk), *Z. atrica* (C. L. Koch) and the rare *Z. stroemi* (Thorell). The geographical distribution of *x-notata* and *atrica* in Britain is summarized by BRISTOWE (1939) and LOCKET, MILLIDGE and MERRETT (1974); and abroad by BRISTOWE (1939), GERTSCH (1964) and LEVI (1974). Both species are distributed all over the British Isles; *x-notata* is common in most places and *atrica* in many places and may be locally abundant (LOCKET and MILLIDGE, 1953). BLACKWALL (1864) seems to suggest that, at that time, *x-notata* was less widespread than *atrica* but there must be doubt whether the females of the species could then be separated.

Some of the more important examples of habitat preference are given in Table 2. These may perhaps be summarized as a preference by *x-notata* for man-made structures such as the outside of houses, sheds, fences and bridges, and when on shrubs, often close to such structures, while *atrica* prefers low trees, bushes and shrubs, commonly distant from human habitation.

Morphologically, the zygiellas are small to medium-sized orb-weavers with oval abdomens of grey, silvery or yellowish colouration (GERTSCH, 1964). Genus characteristics are given by COMSTOCK (1940), KASTON (1948), LOCKET and MILLIDGE (1953) and GERTSCH (1964). Descriptions of adult *x-notata* and *atrica* are given by these authors plus BLACKWALL (1864), McCOOK,(1893), WIEHLE (1931) and SAVORY (1935). The very close similarity in size and appearance between the adult female spiders is generally acknowledged. Illustrations of adult male palps and female epigynes for species identification are found in WIEHLE (1931), LOCKET and MILLIDGE (1953), GERTSCH (1964) and LEVI (1974). Means to separate earlier instars are not found in the

Table 2. Some examples from the literature of habitat preference by *x-notata* and *atrica*

Reference	*x-notata*	*atrica*
CUTHBERTSON (1926)	In a mixed wood near Glasgow, on low branches of trees, amongst undergrowth, especially in open parts of wood.	Similar.
SAVORY (1928)	In angles of doorways and window frames, inside and outside the house, never far removed from buildings.	On bushes and shrubs. Not found together with *x-notata*.
BRISTOWE (1929)	On an island in Co. Kerry, on all banks, bushes and stone walls. *Araneus diadematus* and *Meta segmenta* absent.	Overlap with *x-notata*, but not found on the same bush by the author.
NIELSEN (1932)	Near human habitations. On board-fences, often on staircases.	In forests, on bushes and low trees, especially spruce and pine. On stone-fences and old sheds.
SAVORY (1935)	Usually on walls, fences, window frames or door frames. When on plants usually holly or gorse.	On bushes and shrubs.
KASTON (1948)	May live in hedges. Prefers the outside of houses, fences etc.	May live on houses, but prefers shrubs and trees more than *x-notata*.
LOCKET and MILLIDGE (1953)	Most noticeable in window frames of houses, under shed eaves etc.	On gorse, bushes and low plants generally. On rocks close to high tide. Not so partial to human habitation but may be found there.
BRISTOWE (1958)	On window frames.	On shrubs far distant from houses.
GERTSCH (1964)	New England, U.S.A. :- on houses, barns, wharves, bridges, fences West Coast, U.S.A. :- similar, plus shrubs, trees, rock cliffs, and dirt banks along streams.	Habits much the same as *x-notata* but said to prefer trees and shrubs.

literature.

The webs of x-notata and atrica are characteristic of the genus in that they are roughly vertical, have an oval catching zone, the viscid spirals are absent from one sector of the web, and a signal thread leads from the hub through this sector to a tubular silken retreat (various authors). Small differences between the species in the average number of radii, size of free sector and the retreat are mentioned by WIEHLE (1931) and BRISTOWE (1941). The retreat is usually above the hub (McCOOK, 1889; TILQUIN, 1942; LE GUELTE, 1969; MARPLES and MARPLES, 1971), the hub is displaced towards the retreat (TILQUIN, 1942; LE GUELTE, 1966a,b) and the shape of the web changes with changing retreat position (SAVORY, 1952; LE GUELTE, 1966b). Sometimes there is no free sector (BLACKWALL, 1864; COMSTOCK, 1940; SAVORY, 1952) and this is said to occur in x-notata when the signal thread is greater than 40° to the web (WIEHLE, 1931) and in atrica when 90° (NIELSEN, 1932). BRISTOWE (1941) noted that the proportion of complete Zygiella webs on foliage increases through the autumn, and suggests that this may be due to the spiders moving further into the foliage with colder weather. DAHL (1885) and McCOOK (1889) were early workers to note that very young Zygiellae build complete orb-webs. From the almost circular webs (WITT, 1963; LE GUELTE, 1964a) the change to the normal web seems to depend both on maturation and the nature of the supporting frame (PETERS, 1969). The different ways Zygiellae then make their signal thread and free sector are described by BLACKWALL (1864), BERLAND (1927) and NIELSEN (1932). In general, much of the analytical work on the building and structure of 'Zygiella-type' webs has been carried out on two-dimensional x-notata webs built on frames in the laboratory (LE GUELTE, PETERS, TILQUIN, WITT), and such information is lacking for atrica.

Most of the information on the life cycles comes from non-comparative observations by various authors, often in different countries. The eggs are laid in the late summer or autumn in one (or more) egg cocoons (NIELSEN, 1932; JUBERTHIE, 1954; LE GUELTE, 1962); x-notata may lay up to five batches of eggs (WIEHLE, 1931). Two moults take place in the cocoon (JUBERTHIE, 1954; PETERS, 1969). Young x-notata emerge in April (WIEHLE, 1931; JUBERTHIE, 1954; LE GUELTE, 1962) while atrica emerge in May (NIELSEN, 1932). Laboratory experiments using x-notata indicate that the number of moults after emergence may vary from four in both sexes to five and six in males and females respectively, depending on the feeding rate (LE GUELTE, 1966b). PETERS (1951) quotes five moults for females. BLACKWALL (1864) quotes four moults after emergence for atrica, while KASTON (1948) states that this species moults five times. While x-notata matures from July (GERHARDT, 1926) or August (WIEHLE, 1931) onwards, atrica reaches maturity in August and September (KASTON, 1948) or September and October (NIELSEN, 1932). In controlled conditions with excess food, x-notata may mature in three months compared with the usual six months (LE GUELTE, 1963). Mating in x-notata has been observed in July (GERHARDT, 1926), August and October (LOCKET, 1926), and in atrica in September (or perhaps earlier) (GERHARDT, 1924) and September and October (NIELSEN, 1932). Mating behaviour in both species is described by GERHARDT (1924, 1926). The adults are killed by autumn and winter frosts (NIELSEN, 1932; BRISTOWE, 1941) although some x-notata may over-winter successfully (KASTON, 1948 quoting WIEHLE, 1929; BRISTOWE, 1941).

Microclimatic conditions at suitable web sites are closely linked to the physiological needs and tolerances of the spider (TURNBULL, 1973), yet comparative preference and tolerance experiments for these species are few. SAVORY (1930) in simple humidity gradient experiments showed x-notata prefers low and atrica high relative humidities at normal laboratory temperatures, but below 5°C. x-notata reverses its choice. SAVORY linked this behaviour with habitat preference. DAVIES and EDNEY (1952) found that the critical temperature of x-notata is higher than that of atrica, and that at higher temperatures, atrica in dry air loses weight much more rapidly than x-notata.

DUFFEY (1962b) showed that field-layer spiders including atrica are able to live without water for much longer periods than ground-living species. Two atrica specimens survived an average of 51 days in the laboratory without food or water. Excess feeding of x-notata in controlled conditions increases the number of instars (LE GUELTE, 1966b) and shortens the time to maturity (LE GUELTE, 1963), whereas limited feeding causes an increase in instar length (LE GUELTE, 1966b).

In view of the aims as outlined and the information already known regarding these species, the approach in this study is as follows. The spiders are compared morphologically throughout development primarily for identification purposes, and using this information, a survey on habitat selection in the field is carried out. Web-building behaviour is studied and structural characteristics of field webs and web sites investigated. Humidity, temperature and light preferences, and tolerances to starvation, desiccation and temperature extremes are examined. The rates of development under different conditions are studied in the laboratory and finally, comparisons are made of life cycles in the field.

CHAPTER II

MORPHOLOGY

Literature has been cited in which the chief diagnostic features of adult x-notata and atrica are given. Except for differences in the structure of the adult male palps and female epigynes, termed the genitalia (LEVI, 1974), the close similarity in general appearance of the species is emphasized. SAVORY (1935) and LOCKET and MILLIDGE (1953) do mention that living atrica usually have a red tinge to the anterior abdominal dark patches and edges of the folium. That spider colours may be lost quite rapidly in preservatives (KAIRE, 1963) might explain why many authors do not mention this colouration. GERTSCH (1964) quotes numbers and positions for spines on leg I of single mature specimens of both species. If even the tibial spines were characteristic, they alone would serve to separate mature males and females. GERTSCH also lists various linear dimensions of single adult x-notata and atrica specimens, but does not suggest that such dimensions could be used to separate the species. PETERS (1951) and LE GUELTE (1962) give the lengths of leg segments for different developmental stages of x-notata only. Information on differences between immature spiders is lacking, and therefore the need for a morphological investigation involving nymphs and adults of both species (nomenclature after VACHON, 1957) was considered necessary.

In addition to genitalia, colouration and appendage spines, other characters such as size and pattern, position of the eyes, and number, position and length of the trichobothria may be useful in spider identification (LOCKET and MILLIDGE, 1951). Various dimensions have also been used when comparing different species and developmental stages. They include carapace width (DONDALE, 1961; MIYASHITA, 1968; PECK and WHITCOMB, 1970; HAGSTRUM, 1971), carapace length (JONES, 1941; DONDALE, 1961), and body length, ocular quadrangle length and width, and femur II length (DONDALE, 1961).

Using the characteristics mentioned above, a preliminary morphological investigation of possible species differences was carried out on laboratory-raised spiders. Results suggested that there was no obvious single characteristic by which the two species could be separated throughout development. However, differences were noted in the colour and pattern of the carapace and abdomen at certain stages and also in the development of the genitalia. The numbers and positions of appendage spines in the adults showed variation, but insufficient spiders were used to eliminate spine characteristics at this point. Carapace widths and appendage segment lengths, although of limited value in species separation, did seem to be a useful pointer to developmental stage. Of these measurements, carapace width was the most convenient to take, but increases in tibia I length, for example, were relatively greater at each moult. Also, compared with other appendage segments, tibia I was longer than most and with the appendages in the natural position, the least difficult to measure. (Manipulation of appendages was kept to a minimum because of their easy detachment).

Following the preliminary investigation, certain characteristics were studied further, using spiders from as many different single-species populations as possible. The characteristics were colour and pattern of the carapace and abdomen, relative lengths of the appendage segments, development of the genitalia and the number and position of the appendage spines. In order that comparison could be made of field spiders at roughly equal stages of development, they were grouped according to tibia I length, as described below.

Determination of Stage Limits for Field Spiders.

Material and Method

Spiders from two large single-species populations were collected throughout 1971, x-notata from iron railings at Greenford, Middx. and atrica from Chobham Common, Surrey. Using a binocular microscope with an eye-piece micrometer, the lengths of both tibiae I were measured from the dorsal aspect to 0.05mm. and the average taken.

Results

These are presented in the form of frequency block graphs in Appendices 1 and 2, and stage limits derived from them in Table 3. These limits were used in all subsequent work on field spiders although it is acknowledged that they do not represent the true instar values for all spiders at all times.

Table 3. Field spiders - limits of tibia I length in mm. for each developmental stage.

Stage	Sex	Limits of tibia I length in mm.	
		x-notata	atrica
1	M + F	0.30 - 0.45	0.30 - 0.45
2	M + F	0.50 - 0.80	0.50 - 0.80
3	M + F	0.85 - 1.20	0.85 - 1.15
	M	0.85 - 1.40	
4	F	1.25 - 1.65	1.20 - 1.55
	M	1.45 - 2.10	1.20 - 2.25
5	F	1.70 - 2.15	1.60 - 2.00
	M	2.15 - 3.15	2.30 - 3.25
6	F	2.20 - 3.00	2.05 - 2.85
	M	3.20 +	

M + F = sexes could not be distinguished.

Allocation of Field Spiders to Developmental Stage

To aid recognition of stages in the field, spiders were compared in size with reference spiders, minus their abdomens, mounted in Canada balsam between microscope slides. Each specimen represented a stage upper size limit. Although the final reference was to tibia I length, the carapace width, abdomen colour and time of year were often useful when allotting a spider to a particular stage. Spiders were captured as follows. During the day when they normally occupied the retreat, the immature ones especially could be attracted to the web hub by directing small puffs of air or talcum powder at the web. Otherwise they were approached directly in the retreat with a small paint brush and captured as they escaped backwards through the rear exit. For examination purposes, each spider was placed in a 5 x 2cm. glass tube with a base of microscope slide glass. Using a white foam plastic stopper pushed up inside the inverted tube, the spider was trapped against the plain glass and viewed with a hand-lens. Spiders were returned to their webs unless laboratory examination was required.

Spider Pattern and Colouration

Material and Method

Many spiders of known species at all stages of development were compared for patterning and colouration of the abdomen and carapace.

Results

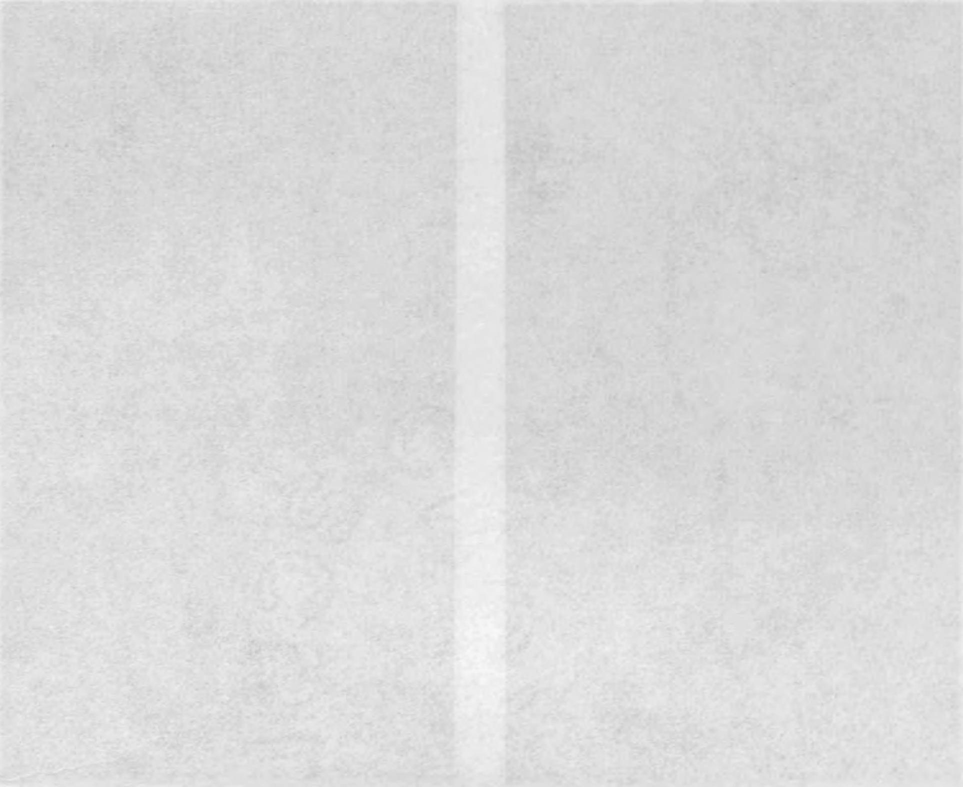
Figs. 1 and 2 show mature male and female x-notata and atrica taken from the dorsal and ventral aspects.

(A) Abdomen.

The shape and more especially the colour of the abdominal folium were found to be very variable in both species, the variation being greatest in the adult. Adult x-notata of both sexes varied from a

Fig. 4. Adult male and female *x-spinis* (linear magnification = 7)

Male - dorsal Male - ventral



Female - dorsal Female - ventral

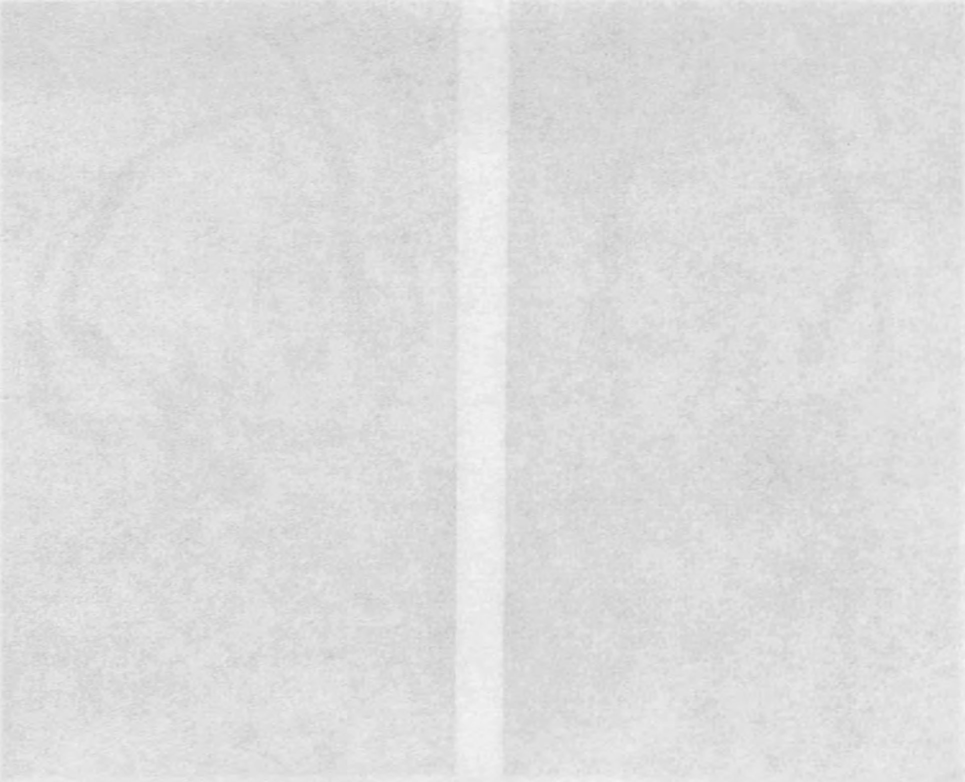


Fig. 1. Adult male and female x-notata (linear magnification = 7)

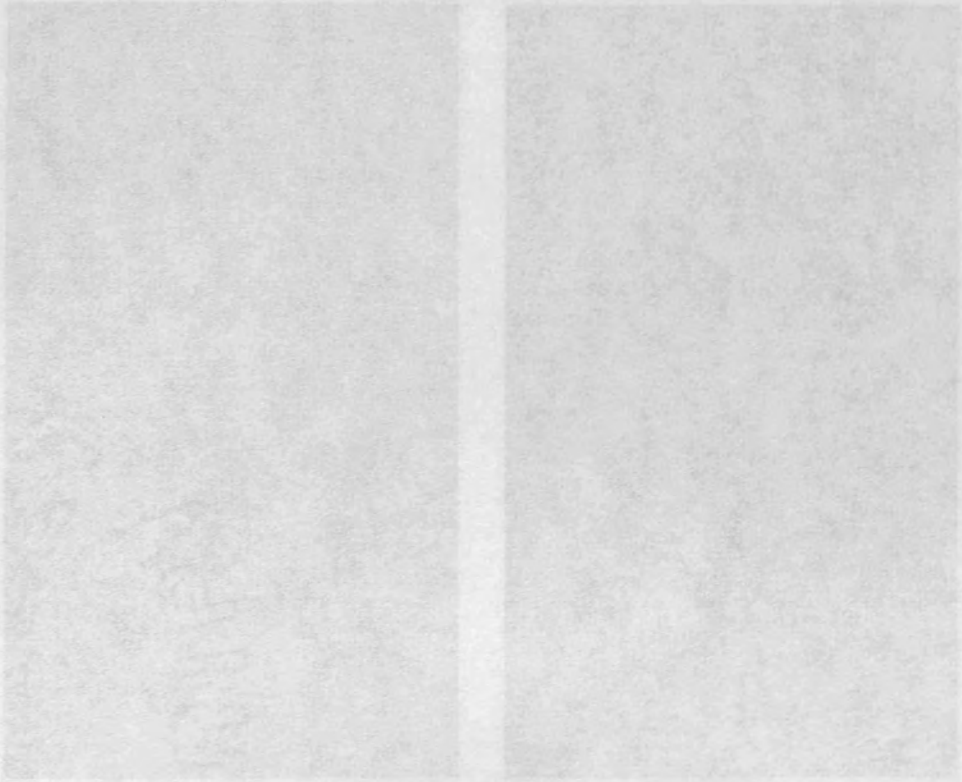
Male - dorsal

Male - ventral

Female - dorsal

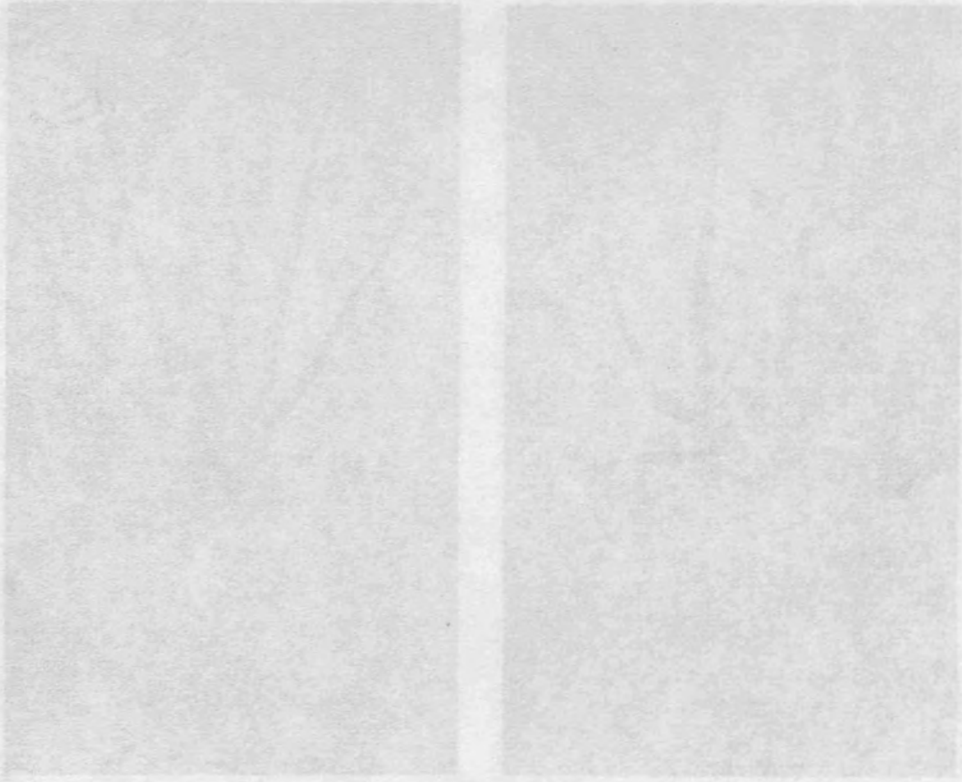
Female - ventral

Fig. 3. Adult male and female _aphids_ (linear magnification = 7)



Male - dorsal

Male - ventral



Female - dorsal

Female - ventral

Fig. 2. Adult male and female *atrica* (linear magnification = 7)

Male - dorsal Male - ventral

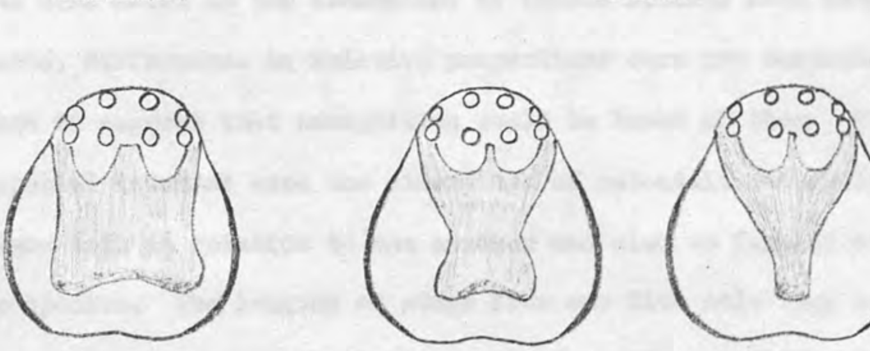
Female - dorsal Female - ventral

light grey folium with greyish-brown anterior patches and borders to steel grey and black. The folium of adult atrica was even more variable, from a silvery grey with prominent red anterior patches and red in the borders laterally and posteriorly to an almost uniform dull black colour. However, extensive dark pigmentation was uncommon even in adult atrica, and where it did occur, red colouration was found in relation to the anterior patches (except in two females), though a lens was required in some cases to see this. Red in these patches was noted in some second stage, more frequently in third stage, and in almost all later spiders. It was not found in x-notata at any stage. Red to orange/red pigmentation was noted on the lateral parts of the atrica abdomen, but it was also found to a lesser extent on some of the lighter coloured early and middle stage x-notata. Ventrally, atrica was generally more yellow in colour, and the dark ventral medial stripe less pronounced.

(B) Carapace.

Although not absolute, the shape of the central carapace pattern provided a useful guide in the separation of first stage spiders, as shown in Fig. 3.

Fig. 3. Typical first stage carapace patterns.



In older spiders, the shape of the carapace and carapace pattern tended to parallel those of the adult females and differences between them were not sufficiently consistent to separate the species with any certainty. The adult males acquired their rather distinctive carapace at the final moult.

Appendage Segment Lengths

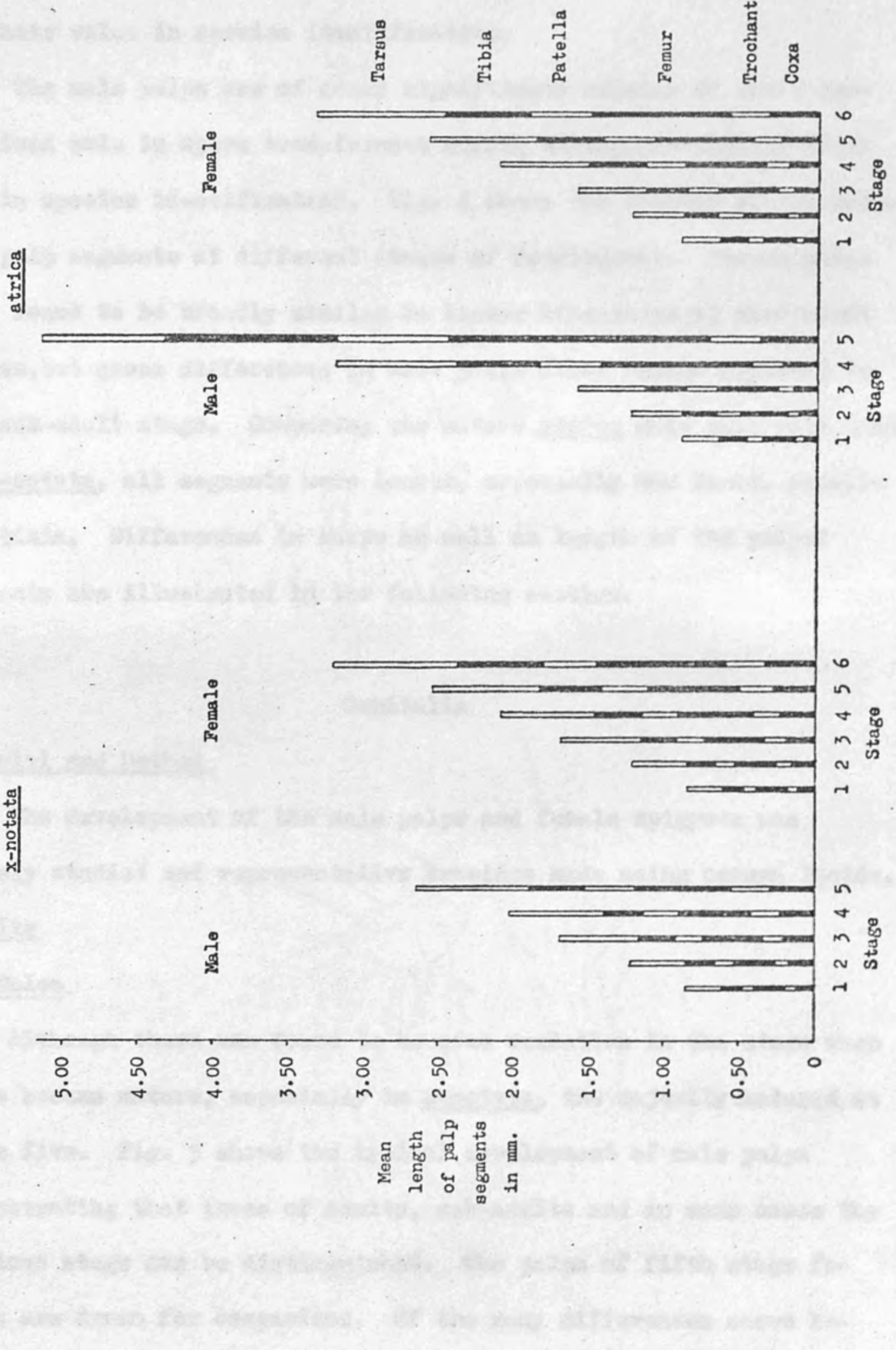
Material and Method

From the spiders collected in 1971, five average-sized spiders (as judged by tibia I length) were selected for each of the first three developmental stages and two groups of five for later stages when the sexes could be separated. They were killed with ethyl acetate vapour to leave the appendages limp (LOCKET and MILLIDGE, 1951). Under a binocular microscope, the appendage segment lengths were measured from the dorsal aspect to 0.05mm. accuracy, and the mean readings for each group compared for the two species.

Results

The mean segment lengths for the different developmental stages are given in Appendix 3. In the first three stages, the lengths of appendages and appendage segments were closely comparable in the two species. The relative segment lengths were too similar to enable the species to be separated by this method. Although minor differences were noted in the dimensions of female spiders from stage four onwards, differences in relative proportions were not consistent enough to suggest that recognition could be based on them. However, of special interest were the dimensions of sub-adult and adult male spiders both in relation to one another and also to females of the same species. The lengths of stage four and five male legs were greater than those of the females. At stages four and five in male <u>x-notata</u> and stage five in male <u>atrica</u>, the metatarsus of leg I was

Fig. 4. Mean lengths of pedipalp segments at different developmental stages (n = 5 for each stage)



longer than the femur. This is in agreement with GERTSCH's (1964) figures for mature males, but LE GUELTE (1962) in a detailed laboratory study on growth in *x-notata* found the male metatarsus to be shorter than the femur at all stages. Hence, differences in segment proportions may be more variable than results indicate and cast doubt on their value in species identification.

The male palps are of added significance because of their specialised role in sperm transference during mating and also of their use in species identification. Fig. 4 shows the lengths of the palps and palp segments at different stages of development. Female palps were found to be broadly similar in linear dimensions at equivalent stages, but gross differences in male palps first became apparent in the sub-adult stage. Comparing the mature *atrica* male palp with that of *x-notata*, all segments were longer, especially the femur, patella and tibia. Differences in shape as well as length of the palpal segments are illustrated in the following section.

Genitalia

Material and Method

The development of the male palps and female epigynes was closely studied and representative drawings made using camera lucida.

Results

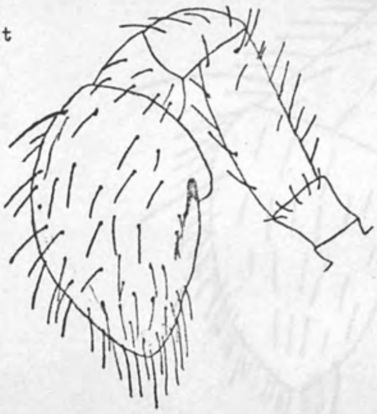
(A) Males.

Although there was found to be some variation in the stage when males became mature, especially in *x-notata*, the majority matured at stage five. Fig. 5 shows the typical development of male palps demonstrating that those of adults, sub-adults and in some cases the previous stage can be distinguished. The palps of fifth stage females are drawn for comparison. Of the many differences shown between sub- adult and adult palps, the darkening of the tarsus in

Fig. 5a. Development of <u>x-notata</u> male palp
- left, from side

Stage III

Stage IV
sub-adult



Stage V
adult

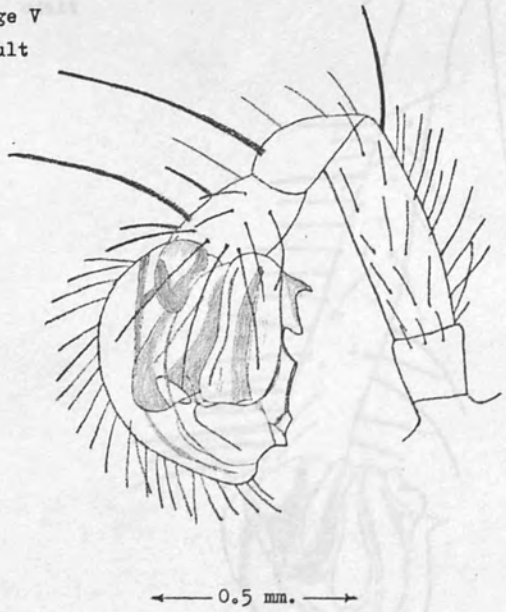


Fig. 5b. Development of atrica male palp - left, from side

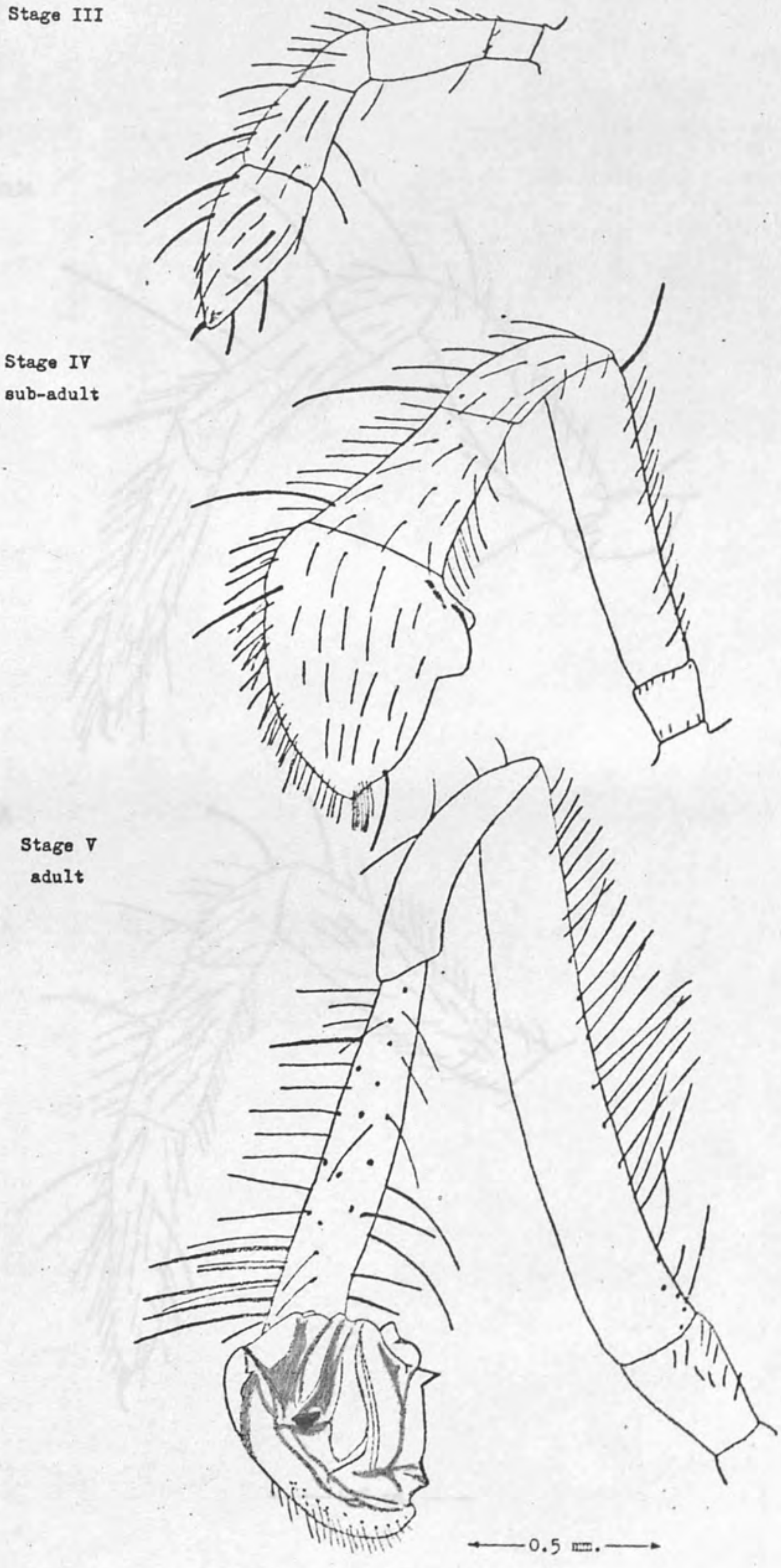
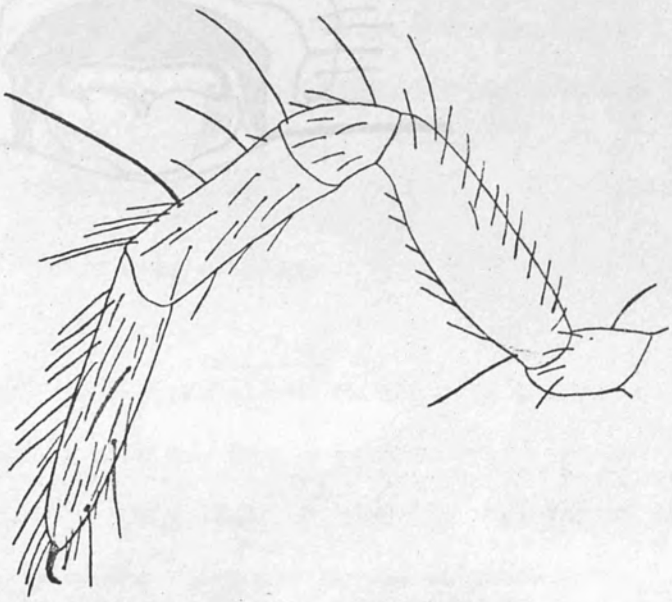


Fig. 5c. Stage V female left palps - for comparison

x-notata



atrica

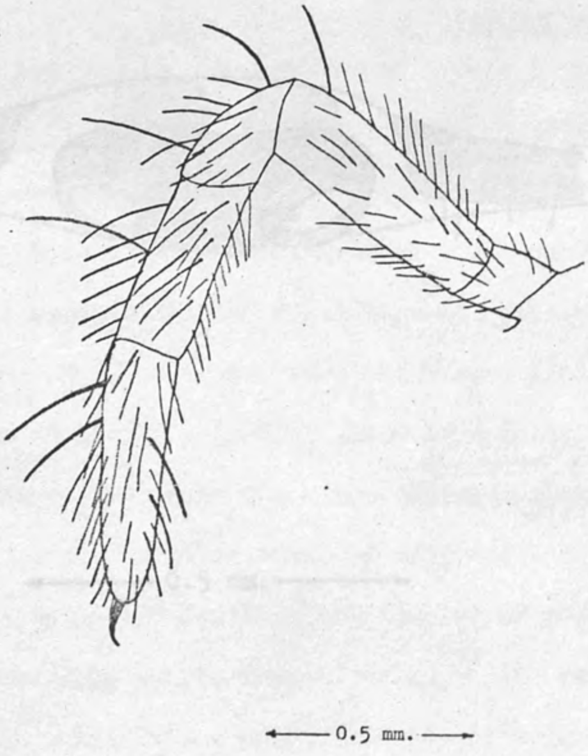
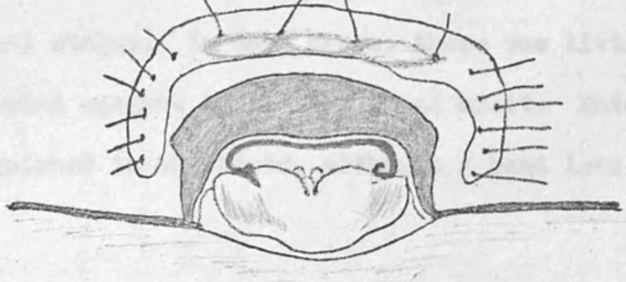
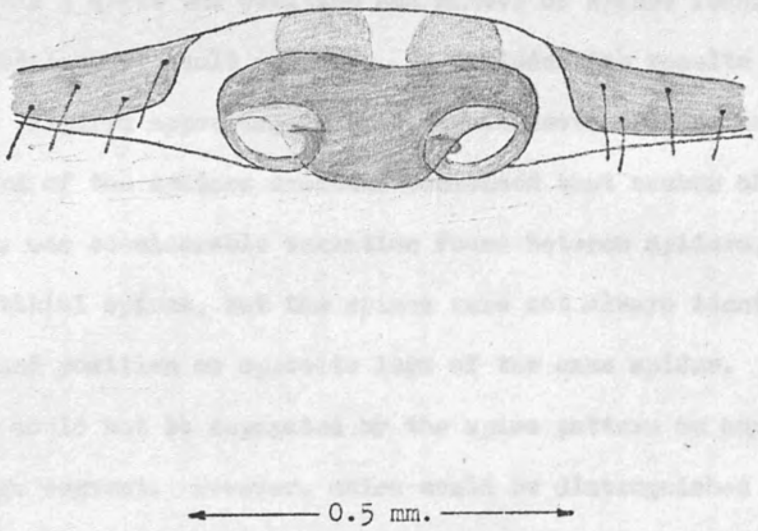


Fig. 6. Epigynes of mature females from the ventral aspect

(a) atrica



(b) x-notata



x-notata and of the whole palp, especially the patella and tarsus in atrica made separation easily possible in the field. The significance of the large difference in palp lengths will be discussed later.

(B) Females

Fig. 6 shows to scale adult epigynes of females maturing after five nymphal stages. In most cases, there was little indication of the developing epigyne before the final moult. Mature epigynes could be distinguished in the field, although a hand lens was normally required.

Appendage Spines

Material and Method

The number and position of the spines on the legs and palps were noted for groups of thirty male and female spiders from various localities. A dark spot on the cuticle marking the position of each spine was found useful when the spine had become detached.

Results

Table 4 shows the position and number of spines found on the palps and legs of adult spiders. It includes the results of GERTSCH (1964). Figures appearing in brackets indicate that no more than one third of the spiders examined possessed that number of spines. Not only was considerable variation found between spiders, mainly in the tibial spines, but the spines were not always identical in number and position on opposite legs of the same spider. The two species could not be separated by the spine pattern on any one appendage segment. However, males could be distinguished from females, males from males and females from females by patella I, femur II and metatarsus IV spines respectively. Where comparison of results can be made with those of GERTSCH (1964) some differences are apparent. However, the male x-notata and male and female

Table 4. Spines on the palps and legs of *x-notata* and *atrica* adults

Spine position	Pedipalp				Leg I				Leg II				Leg III				Leg IV				GERTSCH (1964) for comparison Leg I			
	Fx	Fa	Mx	Ma	Fx	Fa	Mx	Ma	Fx	Fa	Mx	Ma	Fx	Fa	Mx	Ma	Fx	Fa	Mx	Ma	Fx	Fa	Mx	Ma
Femur																								
Median																					1/2			
Dorsal	1	1	1	Hy	1+1w	1+1w	1+1w	2	1+1w	1+1w	2	1+1w	1+1w	1+1w	2	1+1w	1(2)+1w	2+1w	3(4)	2+1w		2	2/3	2
Prolateral					2	2	2	2	1	1	1	2(1)	1	1	1	1	1	1	1	1	2	2	2	2
Retrolateral					1	1	1	1(2)	1	2(1)	1	2	1	1	1	1	1	1	1	1	1	1	1	2
Patella																								
Dorsal	1w+1	1w+1	1	-	2w	2w	1w+1	1w+1	1	1w	1w+1	1w+1	2w	2w	2	2w	2w	2w	2	2w			1	
Prolateral							1	1			1w	1												
Retrolateral					1	1	1	1	1	1	1	1	1	(1w)	1	1	1	1	1	1		1w	1	1
Tibia																								
Dorsal	3	3	1	Hy	2w	2w	1+1w	1+1w	2w	2w	2	1+1w	2w	2w	1(2)	(1)+1w	2	1w+1	2	2	1	2	2	2
Prolateral	2	2			2	2	2	2	2	2	2	2	1	1(2)	1	1	1	1	1(2)	1	2	2	2	3
Retrolateral	1	1			2	2(3)	2	2	2	2(3)	2	2	2	2	2	2	2	2	2	2	2	2	2	2
Ventral					2p	(1)+2p	1+1p	(1/1p) +2p	1+1p	1+1p	1+1p	1(2)+1p	1+1p	1+1p	1(2)+1p	1+1p	1+1p	(1)+1 (1p)+1p	2+1p	2+1p	2p	3p	1+2p	3p
Metatarsus																								
Subdorsal																					2	2	2	2
Prolateral					2	2	2	2	2	2	2	2	2	2	2	2	2	1	2	2		2		
Retrolateral					2	2	2	2	2	2	2	2	1	1	1	1	2	2	2	2	2		2	2
Tarsus																								
Dorsal	2	2																						
Prolateral	3	3																						
Retrolateral	3	3																						

x = *x-notata*, F = female, p = pair of spines, Hy = many long hairs on palps,
a = *atrica*, M = male, w = weak spines, ( ) = found in less than one third of the spiders observed, 1/2 = 1 or 2.

The numbers of spines are written in the order proximal to distal.

atrica specimens of GERTSCH were sufficiently large to suggest that they had matured after an extra nymphal stage which might help to explain this. The spine pattern of sub-adults was found to be different to that of the adults, partly by reduction in the number of spines. Due to variability within and similarity between the species, separation with any certainty was not possible. This also applied to earlier stages where in addition some difficulty was encountered in distinguishing between spines and bristles. Thus, spines were of little real value in species identification. (See COOKE, 1965).

In summary, the investigation to find morphological differences between the two species for identification purposes has demonstrated not only their great similarity, but also wide intraspecific variation. No one difference was found which separated the species at all stages of development. Clear differences in sub-adult and adult male palps and in adult female epigynes, and the presence of red colouration in the anterior abdominal patches and folium edge in atrica middle and late stages have been mentioned. Separation of early stages is less certain although differences in first stage carapace patterns and the colour of the ventral abdominal surface have been described. However, the problem remains of the reliable identification of early stages in single and mixed populations.

Factors controlling colouration in these species have not been investigated in this study, although x-notata raised from laboratory-laid eggs and fed on Drosophila were found to be lighter in colour when adult than their dark parents collected from outside. All laboratory-raised atrica possessed the red abdominal colouration previously described. Of interest, PECK and WHITCOMB (1970) found that the colour of Cheiracanthium inclusum (Clubionidae) varied considerably depending on the type of insect food consumed.

or more usually by direct observation of the webs. Advantage was taken of early morning mists which made webs easier to see. Initially, some use was made of a fine water spray from a 'Spraymist' by ASL Airflow, Birmingham, but with experience this was no longer required. Talc from a puffer dispenser was invariably useful in showing up web details. Spiders were examined in the field as described previously. When necessary, they were transported back to the laboratory, either in separate glass tubes with foam plastic stoppers or in larger containers with some vegetation to minimise spider contact and cannibalism. If identification of young spiders was not possible at the site or immediately in the laboratory, either the sites were revisited later or the spiders were housed in individually labelled 7.5 x 2.0cm. glass tubes and fed on *Drosophila* until identification could be made.

Results

. The results of the survey are too many to give in full detail and therefore the following system has been adopted. Certain specific locations, habitats and populations are described which serve to illustrate important points regarding distribution, habitat preference and colour variation. These and other observations are then summarized to give an overall assessment of habitat choice within the geographical areas studied. Map references are from Ordnance Survey Maps of Great Britain, 1 inch = 1 mile.

(A) Populations of *x-notata* only.

(i) Iron railings - Greenford, Middx. (Map ref. TQ134836). A large population of dark *x-notata* was found on iron railings bordering the A40 trunk road where it crossed the Grand Union Canal. The railings extended on both sides of the road from the stone canal bridge for about 250 metres eastwards and 140 metres westwards. The road was raised above the surrounding open land and exposed to the prevailing winds. Occasional large Crataegus monogyna (hawthorn) bushes were growing close to or even through the railings almost exclusively west of the bridge, and it was here that most spiders were found, close to the bushes. The latter were not a reservoir for the spiders, as observation showed, but probably acted as a protective screen against high winds and strong sun. The actual physical form of the railings was also important in web site selection as discussed later.

(ii) Wire fence - Greenford, Middx. (Map ref. TQ145831). Early instar webs of dark x-notata were noted almost exclusively in the meshes of a wire fence. The fence measured approximately 18 metres by 1.4 metres high with mesh size of 5 x 5cm. The webs were on the top half of the fence and the retreats mainly situated where small loops attached the mesh to a supporting strand of wire, itself attached to concrete posts. Nearer maturity, no webs were found in the meshes but the spiders occupied retreats in holes and crevices in the posts with the webs stretching from the posts to the mesh. Being able to follow this sequence of events for several seasons, it became apparent that the size of the available space and the shape of the supporting structures for the web, the availability of a suitable site for the retreat usually above the web hub, and the willingness of the spiders to change retreat sites when necessary were all important factors in the choice of web site.

(iii) Taxus baccata (yew) hedge - Regent's Park, London N.W.1. (Map ref. TQ283827). Populations of dark x-notata were found on two hedges in Regent's Park, N.W.1. These established hedges, which were about 50 metres long and 1.8 metres high, ran roughly in an east/west direction. The webs were found in more or less equal numbers on the north and south aspects of the hedges but almost entirely on the upper two-thirds of each hedge. The webs of older spiders especially were built parallel to the faces of the hedges with the retreats behind the webs in the foliage. The percentage of webs without free sectors increased as the spiders developed through the season so that in September 1972, for example, 87% were without a free sector (200 webs). This appeared to be due to a changing relationship between the position of the web and retreat, partly as a result of normal growth of the hedge and partly to the repositioning of the larger retreats deeper into the foliage as the season progressed.

(iv) Ulex europaeus (gorse) near Denham, Bucks. (Map ref. TQ043858). During 1970, a patch of U.europaeus measuring roughly 20 metres by 4 metres on the central reservation of the A40 trunk road near rural Denham, Bucks. was found to be heavily populated by x-notata (a conservative estimate of adult females present in October 1970 would be over two hundred). The vegetation was very dark, possibly due to the effect of heavy traffic, and the spiders were once again of the dark grey/black type. This habitat has since been destroyed in extensive road improvements. The spacing and mode of growth of the rigid spines and shoots of U. europaeus made it an excellent support for webs and retreats, and it attracted much insect life as possible prey. One might also assume that the spines afforded some protection against enemies such as birds.

(v) Crataegus monogyna (hawthorn) hedge - Northolt, Middx. (Map ref. TQ112843). The four populations of x-notata so far mentioned were dark in colour. However, spiders found on a closely clipped C. monogyna hedge, approximately 80 metres by 2.2 metres high, were much lighter in abdomen colour, mainly a light brownish-grey. Typically, spider retreats were constructed on the underside of leaves.

(vi) Prunus spinosa (blackthorn) - Swanage, Dorset. (Map ref. SZ023774). Dry Purbeck stone walls as field boundaries were noted in the Swanage area. Extending towards the sea cliffs P. spinosa bushes were commonly found growing close to the walls. Although a small proportion of brownish-grey x-notata were noted on the walls, the vast majority were living on the bushes, and in fact were very common.

(B) Populations of atrica only.

(i) Ulex europaeus (gorse) - Chobham Common, Surrey. (Map ref. SU972652). Chobham Common, Surrey, is an extensive area of open, undulating heathland. Patches of U. europaeus are frequent, and there are isolated clumps of Betula verrucosa (silver birch) and a few Pinus silvestris (Scots pine). In certain parts, frequently on or near the tops of the undulations, atrica were commonly found on both living and dead U. europaeus. However, areas of U.europaeus have been periodically cut down or burnt, they have grown again, and this cannot be ignored when considering spider distribution. Early and middle instars were also frequently noted on the tangle of dead lower branches of B. verrucosa but not later ones, possibly because spaces were not large enough for the webs, or the sites for larger retreats were inadequate. A few webs were noted on P. silvestris. A large variation in abdomen colour from silvery grey and red to almost dull black was noted at Chobham, although there was some tendency for isolated groups to show less variation.

(ii) Ulex europaeus (gorse) near Cheltenham, Glos. (Map ref. SO953185). Far distant from human habitation, certain exposed patches of U. europaeus on the top of the Cotswold Hills near Cheltenham were heavily populated with atrica, although other apparently similar patches were not.

(iii) Mixed Crataegus monogyna (hawthorn) and Prunus spinosa (blackthorn) hedge - Egham, Surrey. (Map ref. TQ012718). This field hedge in open country was cut once a year in the autumn to a height of about two metres. Over several years, atrica were noted on this hedge, although not on an adjacent angle-iron farm gate, except for two adult females in October 1972 after the hedge had been cut.

(C) Populations of x-notata and atrica in close proximity.

(i) Agricultural shed on a Prunus domestica (plum) plantation - Cropthorne, Worcs. (Map ref. SP005448). Over several years, x-notata were noted under the eaves of a roofing felt-covered shed on a plum plantation. The shed was exposed to the sun and parts of the covering were at times almost too hot to touch. Scattered in the Yellow Egg plum trees, some very close to the shed, were atrica with the retreats mainly in the bunches of developing plums and accompanying leaves. The x-notata spiders were dark but atrica specimens were more red than any others observed anywhere.

(ii) Metal footbridge and Ulex europaeus (gorse) - near Ickenham, Middx. (Map ref. TQ063855). Many x-notata were found on a black metal footbridge crossing a trunk road near Ickenham, with atrica on U. europaeus about six metres from the bridge. In this case there was no overlap of the species although x-notata inhabited more U. europaeus about forty metres distant. Most x-notata specimens were slightly darker than the atrica.

(iii) Garden and field hedges - Thaxted, Essex. (map ref. TL612316). In the summer of 1973, x-notata were observed on assorted garden hedges along the Cambridge Road in Thaxted. As the road left the village, many atrica inhabited a bordering clipped C. monogyna hedge along its entire length. There seemed to be no overlap of the species.

(D) Overlap of x-notata and atrica populations.

(i) Crataegus monogyna (hawthorn) hedge - Southall, Middx. (Map ref. TQ142807). At Southall, a main road divided the local golf course into two. The road was bordered on both sides by 2.5 metre high C. monogyna hedges, each clipped next to the pavement but not to the golf course. Both species inhabited these hedges; some overlap was noted in 1973 although generally the two species were separated. Of interest was the observation that both were quite common on the clipped sides of the hedges but apparently absent from the unclipped sides. As noted earlier on C. monogyna, the spiders were not of the dark type.

(ii) Crataegus monogyna (hawthorn) hedge - near Denham, Bucks. (Map ref. TQ038857). In 1971, in a rural area with few houses, both species were noted on a 50 metre long, 1.5 metre high clipped C. monogyna hedge. The two were completely intermingled. In colour, the species resembled those at Southall. Unfortunately, this habitat was destroyed during motorway construction in 1972.

(iii) Ulex europaeus (gorse) hedge - near Ickenham, Middx. (Map ref. TQ062856). An 80 metre U. europaeus hedge formed the boundary between a small field and the A40 trunk road near Ickenham. The road and hedge were on a west/east incline. In 1970, it was noted that while atrica occupied a 25 metre section near the top of the incline, x-notata occupied the hedge lower down, possibly as an overflow originally from a nearby viaduct. There appeared to be no overlap. By 1974, the atrica region had been encroached upon by x-notata from below and above, probably from an adjacent wire fence and nearby buildings. Spiders of both species were intermingled on some bushes, and it appeared that x-notata were quite rapidly replacing atrica in this habitat. In colour, x-notata adults were somewhat darker than atrica.

The above observations and many others not specifically mentioned indicate the types of habitat chosen by the two species in the geographical areas listed. Of the two species, x-notata occupied a greater variety of habitats than atrica. It was commonly noted on man-made structures such as houses, sheds, fences of various kinds, gates, bridges and pylons, and on trees, bushes, shrubs and hedges often not very far from such structures. In one suburban garden, this species was observed at all stages of development on the following vegetation - Lonicera nitida hedge; Ligustrum sp. (privet) hedge; Crataegus monogyna hedge; Picea abies (spruce); Cupressus macrocarpa and Hydrangea macrophylla. Examples of other plants have been mentioned and the list could be extended.

Less common generally, atrica was abundant in certain localities. It was almost entirely found on vegetation, both living and dead, mainly away from human habitation and often, although not invariably, in exposed situations. Like x-notata, it was frequently observed on Ulex europaeus and clipped Crataegus monogyna, but overlap of the two species was limited.

Colouration was more variable in older than younger spiders, and in atrica than x-notata. No definite conclusions can be drawn from field observations, but it was observed that spiders on lighter coloured, open vegetation where the retreats were more exposed tended themselves to be lighter and more highly coloured. For example, x-notata established on Crataegus monogyna were noticeably lighter in colour than those on dense Taxus baccata and dark roadside Ulex europaeus.

CHAPTER IV

THE WEB

A *Zygiella* spider spends the greater part of its life building, destroying, occupying or at least remaining in tactile contact with its web, a structure of paramount importance in the trapping of prey. The habitat in which the spider is found must therefore have structural characteristics which make possible the construction and physical support of the web and retreat. It was decided that a study of behaviour prior to and during web building, together with an investigation into the position, size and structure of field webs might shed light on how web sites are selected, and indicate some of their common structural characteristics. Published information for *atrica* is very limited and that for *x-notata* is based mainly on spiders building on artificial two-dimensional frames under laboratory conditions.

THE RETREAT

Presence of a Retreat

After leaving the cocoon, early first nymph spiders of both species may build complete webs with no free sector, signal thread or retreat. They occupy the hub day and night. Others, perhaps from the same cocoon, build webs more typical of older spiders with a free sector and a signal thread running through it from the web hub to a silken retreat built by the spider. The spider is normally found in the retreat during the day and at the hub at night. McCOOK (1889) noted neighbouring young *atrica* webs, some with free sectors and some complete. LE GUELTE (1964a) found a similar situation in laboratory x-notata webs built on frames by spiderlings from the same cocoon. Whether x-notata spiderlings build a web with a free sector and signal thread seems to depend on age (MAYER, 1952; LE GUELTE, 1966b) and the type of framework for suspending the web which allows for construction of a retreat (LE GUELTE, 1964a; PETERS, 1969).

The following experiment illustrates the importance of age on the type of web built by first nymphs.

Material and Method

Forty first nymphs of each species were individually housed in 6 x 3cm. glass tubes at 20°C. and fed one Drosophila per day. Every morning, note was made of the presence and form of the webs and retreats, which were then destroyed.

Results

The results for 10, 12, 14 and 16-day-old nymphs are presented in Table 5.

Table 5. Web types of first nymphs at different ages.

Species	Age of nymphs in days	No. of nymphs	% with a retreat	Webs % with no web	 % with complete web	 % with free sector web
x-notata	10	40	100.0	95.0	-	5.0
	12	40	100.0	52.5	-	47.5
	14	40	100.0	40.0	-	60.0
	16	40	100.0	45.0	-	55.0
atrica	10	40	-	100.0	-	-
	12	40	-	67.5	32.5	-
	14	40	15.0	50.0	37.5	12.5
	16	40	22.5	52.5	25.0	22.5

By day 10, all *x-notata* had built retreats and the webs which followed had a signal thread and free sector. No *atrica* retreats or webs were built before day 12, the first webs were complete with no retreats and these were increasingly replaced by webs with free sectors after retreats were constructed. 40% *x-notata* and 50% *atrica* reached the second nymphal stage in less than 30 days without building a recognisable orb-web, just a thread tangle sufficient to entrap *Drosophila*. Such thread tangles were sometimes found in the field.

The form of the supporting framework also influences the type of web, as demonstrated below.

Material and Method

Ten 12-day-old nymphs of each species were placed on individual circular wire frames, 6cm. in diameter and 1mm. gauge. Each frame was supported vertically above water to reduce escapes, and any escapees were replaced by spiders of the same age. As controls, a similar number were placed on frames, each frame having a small cylinder of paper attached near the highest point to act as a potential retreat site. Webs and retreats were destroyed each day. *Drosophila* were fed to the spiders whether a web was produced or not.

Results

In the following eight days, 24 *x-notata* and 29 *atrica* webs were built by the experimental group, all complete, with no retreats. In the control group, 33 out of 38 *x-notata* and 16 out of 26 *atrica* webs had free sectors, signal threads and retreats.

The results for *x-notata* agree with those of PETERS (1969). Retreats were constructed first and the webs which followed had a free sector and signal thread. Where it was physically impossible to build a retreat due to the nature of the supporting structure, the webs were complete with no signal thread. For *atrica*, the ability to build a retreat and hence a web with a free sector and signal thread seemed to come at a later age, and this may be one reason why proportionately more early first nymph <u>atrica</u> field webs are complete on structures such as <u>Ulex europaeus</u> where potential retreat sites abound. Almost without exception, both species build a retreat after the first nymphal stage.

Siting of the Retreat

Except for the complete webs of some first nymphs, at least a partially completed retreat is constructed before the potential web site is fully investigated by the spider prior to web building. TILQUIN (1942) suggested that thigmotaxis, geotaxis and phototaxis are important factors in retreat site selection in <u>x-notata</u>. Both species tend to be positively thigmotactic and negatively geotactic as demonstrated by their locomotory behaviour when placed in large containers, for example. They come to rest in positions where later they may well build their retreats. The following experiment demonstrates such retreat positions.

<u>Material and Method</u>

Groups of ten adult female spiders were placed in non-illuminated glass tanks measuring 35 x 22 x 22cm. deep with sealed plain glass lids. The retreat positions were noted the following day.

<u>Results</u>

The retreat positions are given in Table 6.

Table 6. Position of adult female retreats in glass tanks

Species	Total retreats	% retreats in angles between walls and lid.	% retreats in angles between walls		% retreats elsewhere
			above ½ way	below ½ way	
<u>x-notata</u>	60	71.7	20.0	8.3	-
<u>atrica</u>	60	81.7	13.3	5.0	-

92% x-notata and 95% atrica retreats were located in the angles between the walls in the top halves of the containers or between the walls and lids.

The response to light was more variable and will be discussed elsewhere, although the tendency, especially in older spiders, was to settle in less well-illuminated positions.

Building the Retreat

The retreat itself is an open, silken tube of diameter somewhat greater than the spider abdomen and of length about twice that of the whole animal. It is expanded at both ends but more so at the entrance where the signal thread is attached. (When occupying the retreat, the spider faces this entrance with a first tarsus normally resting on the signal thread). In building the retreat, the spider lays down a number of longitudinal and diagonal threads attached to the structure to which the retreat will be firmly anchored. Towards the centre of this elongated three-dimensional framework, it builds the tubular wall of the retreat from inside by attaching silk to the frame threads in turn as it rotates, dabbing each thread with its spinners. This operation is interrupted from time to time by the laying down of additional frame threads. The retreat is often added to later. Typically, more silk is used by x-notata and therefore the wall is more dense and opaque. The structure on which the retreat is built must provide attachment points for the frame and anchor threads and yet allow access to the retreat from both ends. Retreats may be built on suitably wide concave surfaces but not on isolated flat or convex ones. These factors alone restrict the number of potential retreat sites. Larger spiders build larger retreats, and therefore a site suitable for a small spider may be unsuitable for a large one and vice versa.

One important factor in the time taken to build a retreat (or web) is temperature. An x-notata retreat completed in 15 minutes at 23°C. may take over twice as long at 15°C.

WEB-BUILDING

Initial Stages in Construction

There is some indication from the literature (for example, LE GUELTE, 1966b) that x-notata on a two-dimensional frame begins construction of a completely new web from its retreat site. However, it was decided to follow the early stages of web-building in both species on potentially three-dimensional frameworks, as these are more typical of the natural situation in the field. For convenience, and to prevent spider escape, the structure used was in fact the walls, top and base of the glass tanks mentioned earlier. After allowing ten mature female field spiders of each species to occupy separate tanks and build retreats and webs, the webs were destroyed. Winged Drosophila were introduced into each tank and this frequently induced at least some of the spiders to commence web-building within the hour. Destroying the new webs after a few threads were laid down often resulted in the spiders commencing construction once again after an interval of a few minutes. Hence the opportunity to study the early behaviour in web-building was increased.

Although there was a basic pattern of building behaviour common to both species, no two webs were built in exactly the same way. During or following the construction of the retreat, or just prior to web-building, the spider may move up to several centimetres from its retreat along a supporting structure, lay down a thread and return. More than one thread may be placed in this way eminating from around the retreat entrance. In some cases no such threads are constructed.

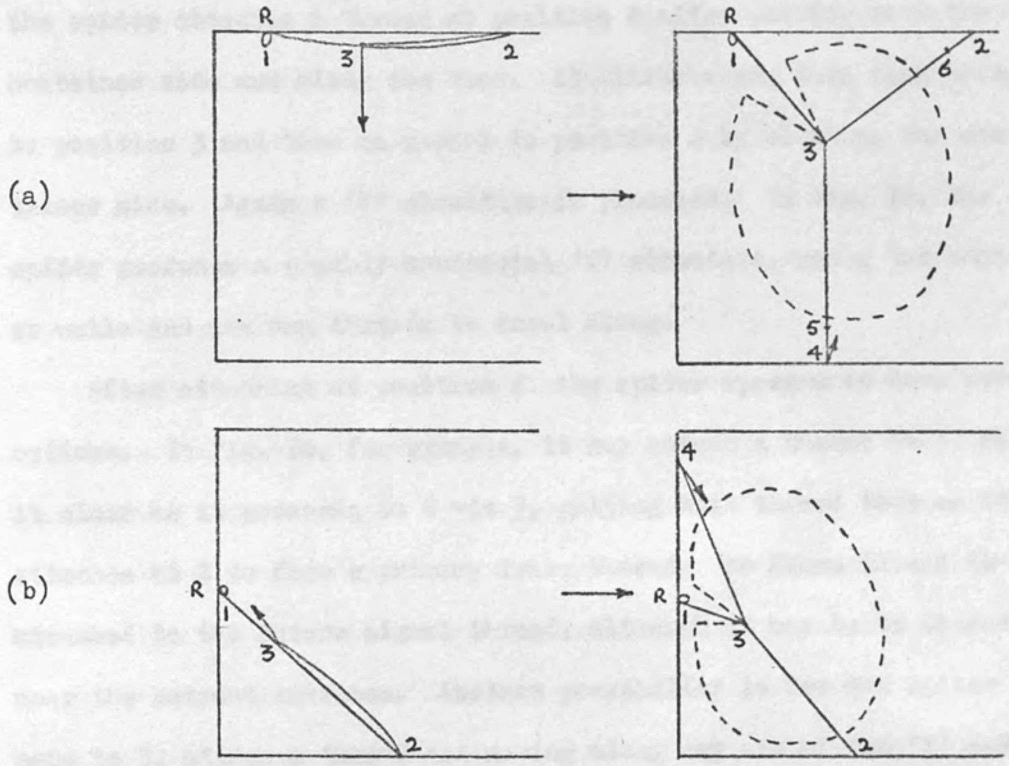
Although this behaviour could be to anchor the retreat entrance more firmly, it may be more of a preliminary exploration of the potential web site. The threads also provide 'footholds' when web-building proper commences, and other threads produced during earlier wanderings may be utilised for this purpose. WITT et al (1968) describe exploratory behaviour prior to web-building in *Araneus diadematus*, although ENDERS (1972) found none in *Argiope aurantia*.

Some field webs suggest web construction proper may involve the initial building of the classical orb-weaver's bridge thread, from which the web is partly suspended. This was not found to be so for the webs constructed in the glass tanks, and it is on these webs that the description of web-building is based. The first real move by *Zygiella* is to attach a thread to the retreat entrance and then to construct on the frame available a 'Y' structure of threads (initial fork). The arm connected to the retreat forms the future signal thread and the other two, the primary web radii. The three arms meet at the future web hub. The 'Y' structure is constructed whether the retreat lies in the plane of the future web or not (see Figs. 7a,b,c). In all three examples, the attachment at 3 (future hub) is nearer to 1 (the retreat) than 2, and this places a restriction on the length of the future signal thread. When the retreat is roughly in the plane of the web, the hub is displaced towards the retreat. The hub becomes more central as the angle between the signal thread and the web increases. However, the relative length of the signal thread still holds good and no small-framed webs with long signal threads were observed.

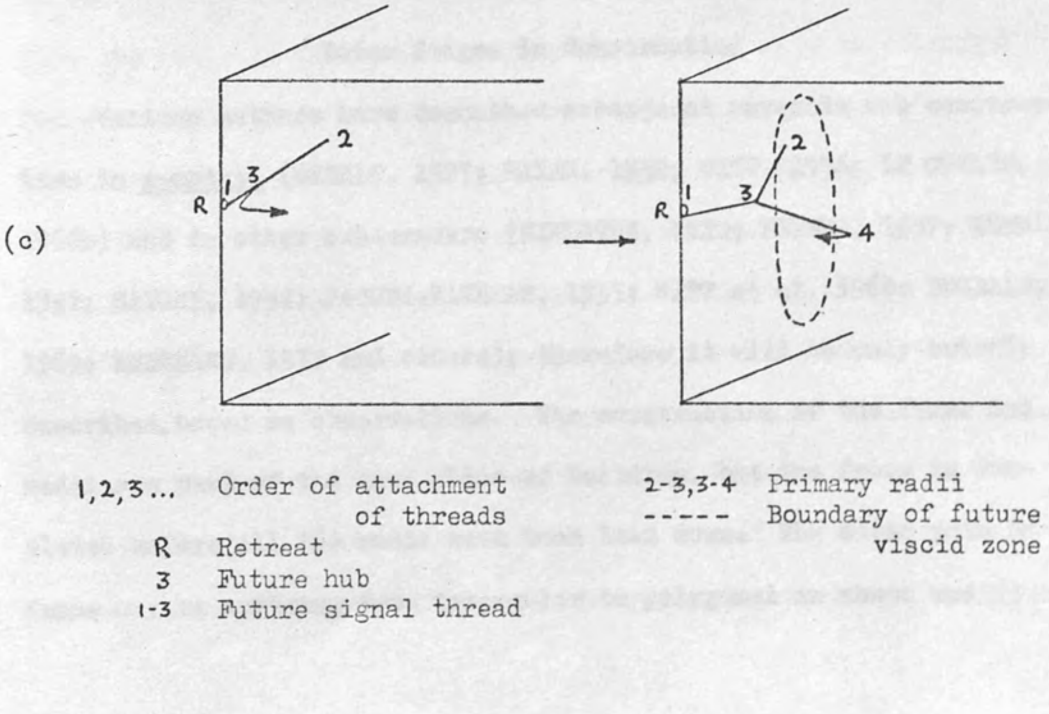
In Fig. 7a, the spider after attaching a thread to the retreat moves to position 2, holding the thread away from the container top with a hind tarsus. After attaching the thread, it moves back along it to position 3, a point nearer to 1 than to 2. The portion of the thread from 2 to 3 appears to be reinforced and not replaced during

Fig. 7. Examples of early moves observed in web-construction

Retreat in the plane of the future web -- lateral view



Retreat behind the future web -- lateral view



1,2,3...	Order of attachment of threads	2-3,3-4	Primary radii
R	Retreat	-----	Boundary of future viscid zone
3	Future hub		
1-3	Future signal thread		

this process. The spider then drops under gravity, controlling its fall by gripping the thread produced with a hind tarsus, and attaches it to the container base under tension at position 4 so that the 'T' structure is pulled into a 'Y' structure as indicated. In Fig. 7b, the spider attaches a thread at position 2 after walking down the container side and along the base. It climbs along this taut thread to position 3 and then on past 1 to position 4 by climbing the container side. Again a 'Y' structure is produced. In Fig. 7c, the spider produces a roughly horizontal 'Y' structure, using the container walls and its own threads to crawl along.

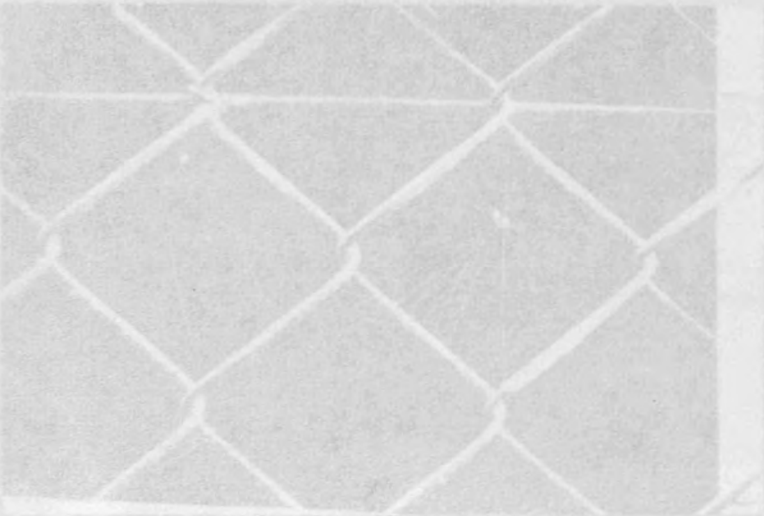
After attaching at position 4, the spider appears to have various options. In Fig. 7a, for example, it may attach a thread at 5, hold it clear as it proceeds to 6 via 3, pulling this thread taut as it attaches at 6 to form a primary frame thread. No frame thread is attached to the future signal thread, although it may be to threads near the retreat entrance. Another possibility is for the spider to move to 3, attach a thread and moving along any arm of the 'Y' and out onto the container, produce another radius. These are two of many early moves noted in the construction of the radii and frame threads.

Later Stages in Construction

Various authors have described subsequent moves in web construction in x-notata (WIEHLE, 1927; MAYER, 1952; WITT, 1956; LE GUELTE, 1966b) and in other orb-weavers (HINGSTON, 1920; PETERS, 1937; KOENIG, 1951; SAVORY, 1952; JACOBI-KLEEMAN, 1953; WITT et al, 1968; DUGDALE, 1969; EBERHARD, 1972 and others); therefore it will be only briefly described, based on observations. The construction of the frame and radii are part of the same phase of building, but the frame is completed before all the radii have been laid down. The outer primary frame may be anything from triangular to polygonal in shape and secondary frame threads commonly brace the more acute angles between the primary ones. The radii, which extend from the hub to the innermost frame threads, tend to be laid down successively in opposite halves of the web. The spider uses an existing radius as a path from the hub to the frame and either replaces or strengthens the new radius on the return to the hub. During and at the end of this phase, the hub is enlarged by the spider connecting the radii with threads, partly in the form of a tight spiral. The spider now builds the widely spaced non-viscid temporary spiral moving outwards from the hub towards the periphery.

If the signal thread is in or near the plane of the web, the spider usually doubles back after attaching the thread to the radius next to the signal thread, or very occasionally to the signal thread itself. In any case, such pendulum movements may be necessary near the periphery in the region usually below the hub or at least opposite to the retreat when the hub is very eccentrically placed. If while building the temporary spiral two radii are found to be too far apart for the spider to bridge the space, it may stop and quickly lay down a new tertiary radius from that point, giving the appearance of a forked radius, then go on to finish the spiral, which terminates before the frame is reached. The temporary spiral acts as a bridge between radii during viscid spiral construction and also holds the radii in place (EBERHARD, 1972). It is destroyed as the viscid spiral is built. After a short rest, the spider commences to lay down the viscid spiral moving inwards from near the periphery to the hub. More spiral are laid down in the commonly larger, lower part of the web. The spider doubles back on itself many times, in each case just before reaching the frame, although spirals are sometimes attached to the frame itself. When the spider touches the signal thread with a front tarsus, it usually attaches the spiral in two places to the radius

Fig. 5.— Different stages in web-construction



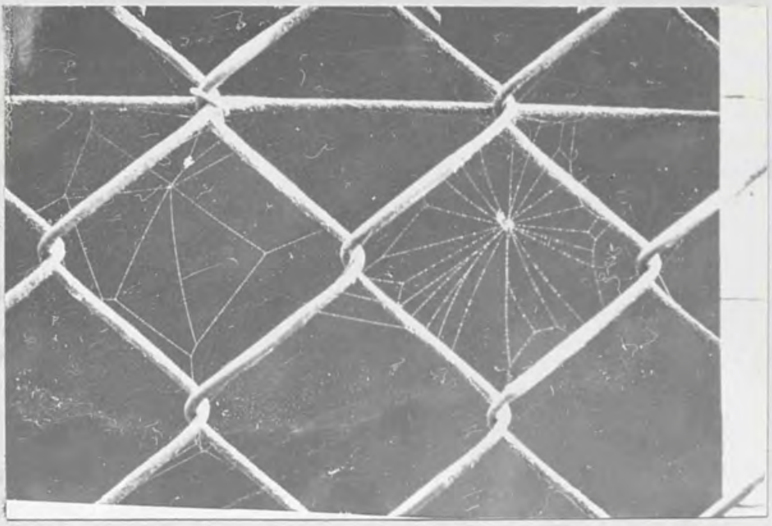
(a) Construction
of frame
and radii

(b) Completion
of temporary
spiral

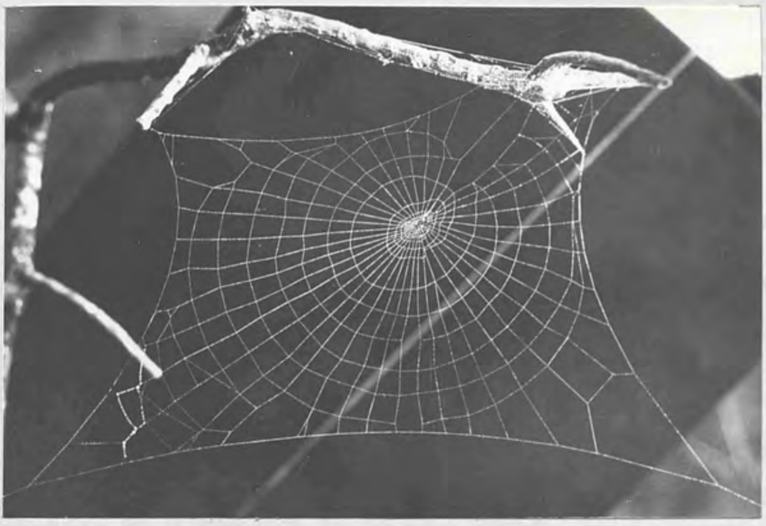
(c) Completion
of web

Fig. 8. Different stages in web-construction

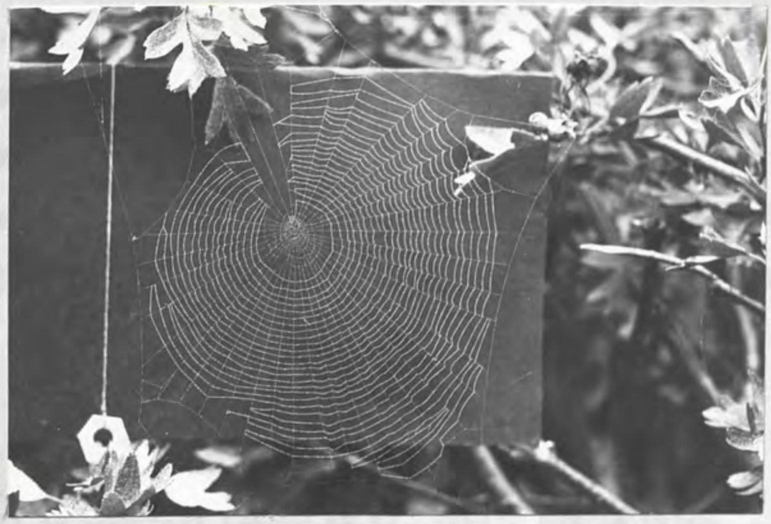
(a) Construction of frame and radii



(b) Completion of temporary spiral



(c) Completion of web



next to the signal thread, then doubles back to do the same on the other side, and so on, leaving a free sector with the signal thread running up the centre. In younger spiders, the signal thread may be treated to a varying extent as a normal radius and viscid spirals attached to it. When the spider finally reaches the vicinity of the hub, it abruptly moves across the strengthening zone onto the hub and the viscid thread is anchored there. On moving from the hub to the retreat via the signal thread, any spirals which have been attached to the signal thread are severed. If the signal thread is at a large angle to the web, the spider does not come into contact with it during viscid spiral construction and a complete web results. Thus, the presence of a free sector depends on the angle of the signal thread to the plane of the web.

BERLAND's (1927) description of the way *x-notata* constructs the free sector by building at least some spirals across it during web construction and then later severing them is too generalised. Typically, in older spiders, when the signal thread is roughly in the plane of the web, no viscid spirals cross the free sector at any stage.

For different stages in web-construction, see Fig. 8a, b and c.

Construction of a New Web in an Old Frame

In the field, both species commonly, although not invariably, build new webs each day before dawn (MARPLES and MARPLES, 1971). First nymphs build at any time. Spiders, in destroying the old web, often leave the frame threads and attach the new radii to them (McCOOK, 1881, for example). *Zygiella* also leaves the signal thread. Working outwards from the hub, a number of radii and linking spirals are severed, gathered in by the front legs as the spider moves outwards and rolled into a ball by the palps. In most laboratory *Araneus diadematus* the ball is consumed (BREED et al, 1964), but is often discarded by field *Zygiella*, possibly due to a covering of dust. As a group of sectors is removed, a new radius is laid down, roughly bisecting the space. The spider moves back to the hub from where it commences to remove another group of sectors immediately, or after a time interval. Clearing the old web may take from several minutes to several hours. Construction of the new web may follow clearance immediately or later.

Influence of Incident Light during Web-Building

Early in web-building, at the initial fork stage or soon afterwards, the approximate position and inclination of the future web and its relationship to the retreat can be recognised. The shape and form of the structure on which the web is built is a major but not sole factor in determining these characters. The restriction on the length of the signal thread in relation to other linear web dimensions has been referred to, and the importance of gravity indirectly demonstrated. The direction of incident light was also found to influence the direction chosen for the plane of the web, as the following experiment demonstrates.

Material and Method

Ten adult female spiders of each species were placed in two 35 x 22 x 22cm. glass tanks covered with black cloth, except for the face lying parallel to a window four metres distant. Each day, the covers were removed and the webs noted as to whether they were more or less than 45° to the incident light. The webs but not the retreats were destroyed, the tanks turned through 90° and the covers replaced.

Results

The results are presented in Table 7. χ^2 tests show that for both species, the plane of the web was significantly nearer 90° to the incident light than parallel to it ($P < 0.001$ in both cases).

This is in agreement with TILQUIN (1942) for orb-web spiders in general but at apparent variance with SAVORY's (1952) description of orb-web building in the laboratory.

Table 7. Position of webs in relation to incident light

Species	Total webs	% webs	
		0° - 45° to incident light	46° - 90° to incident light
x-notata	62	22.6	77.4
atrica	52	25.0	75.0

FIELD WEBS

An investigation was carried out in 1972/3 on a large number of webs from single-species populations in different habitats. It was hoped that the information gained from retreat and web positions and web sizes might relate to ecological differences between the species. A study was made of the number of web radii because of the wide range of values quoted by various authors yet the implication by some that the radii may be used to separate the species. Data was obtained at the web-sites and from photographs of webs printed to scale.

Web Photography

Photographs were taken of a selection of webs in different habitats, to give a hundred usable prints for each spider stage. However, it was impossible to make a completely random choice due to web damage and position, and the difficulty in obtaining clear photographs when no dark background could be placed behind the web. The camera used was a Praktica IV reflex type with a Tessar 2.8/50 lens, and 35mm. Ilford FP4 film. The shutter speed was 1/100th. sec. Flashlight was not used; a light meter was found unnecessary. Prior to photographing a web, talcum powder was puffed onto it. A background of plain black cloth pinned to a board, or occasionally plain black card, was held behind the web where possible. A plumb line of adjustable length and position was suspended from the top edge of the slightly tilted board to indicate the vertical on the photograph. A known focusing distance was pre-set on the camera. This was dependent on the size of the web, but 0.4 metres was commonly used because the backcloth could easily be held behind the web with one hand while operating the camera with the other. In addition, all but the larger webs could be photographed at this distance, and the depth of focus was very small. Because of the structural nature of the web, accurate focusing could be achieved by careful movement of the camera. The web was photographed at right angles to the web plane. A convenient large linear dimension was measured on the web to the nearest millimetre as a future check on web size.

The webs were printed to scale, the majority to actual size. On the prints, angles were measured to 1° , linear dimensions to 1mm., and using an 'Allbrit' planimeter, areas to $0.1cm^2$.

Position of Webs and Retreats.

Height of the Web above the Ground

The types of habitat in which the two species are found (see CHAPTER III) give an indication of the range of heights of their webs above the ground. However, TILQUIN (1942) did suggest that *x-notata* webs are not built below 60cm. Whether the height increases with instar in *Zygiella* as it does in *Argiope aurantia* (ENDERS, 1972) is not clear, but TURNBULL (1960) noted in a stand of oak immature *atrica* in the field layer only, whereas adults were also in the lower canopy.

Web height in both species was investigated further.

Material and Method

In various habitats throughout the season note was made of the general positions of webs, and where appropriate, vertical heights of web hubs above the ground were measured with a marked plumb-line, pole etc. Special attention was paid to adjacent and mixed populations of the two species.

Results

In situations where both species were found, no significant differences in web height were noted either between the species or during development. However, the geometry and rigidity of the supporting structures and the size of spaces available for web-building were important factors in web site selection. On vegetation, these often changed through the season due to normal plant growth. Occasional webs were found within 20cm. of the ground, but no anchor threads were attached directly to it. Webs on shrubs and garden hedges up to two metres high were mainly located on the upper two-thirds, eg. 96% on a 1.8 metre high Taxus baccata hedge in June, 1972. Those on man-made structures were often suspended from horizontal supports such as the tops of window and door frames, shed eaves and ledges, thus their heights above the ground were determined. Whether webs are built at the tops of tall trees is not known but x-notata webs were commonly found on tall buildings. On isolated structures such as sheds and shrubs, there was no evidence to suggest that specific aspects were particularly favoured by either species.

Inclination of the Web to the Vertical

Although BRISTOWE (1941) states that Zygiella webs are vertical or only very slightly inclined, and x-notata consistently builds webs on vertical frames in the laboratory (see works of PETERS, WITT and

LE GUELTE, for example), a few almost horizontal webs were observed in the field. It was decided to investigate further web inclination for both species in natural habitats.

Material and Method

From assorted habitats, 100 webs were randomly selected for each developmental stage. Using a clinometer (CLOUDSLEY-THOMPSON, 1967), the angle of the web to the vertical was measured to the nearest degree. For the rather cone-like webs where the retreat was well away from the web plane, the latter was taken as the line joining the upper and lower frame threads.

Results

As Fig. 9 shows, over 80% x-notata and 73% atrica webs were within 10° of the vertical, and 96% and 89% respectively within 20°. Reference has previously been made to the influence of gravity during web construction, and this was reflected in small inclinations of the finished webs. The more nearly horizontal webs seemed to be built where there was no support conveniently below the retreat or hub area, but where the spider could reach satisfactory attachment points without dropping down on a thread.

Position of the Retreat in Relation to the Web Hub

Retreats of x-notata (TILQUIN, 1942; SAVORY, 1952; LE GUELTE, 1969; MARPLES and MARPLES, 1971) and atrica (McCOOK, 1889; SAVORY, 1952; MARPLES and MARPLES, 1971) are usually found above the hub. This must be one of many factors reducing the number of possible web sites and even habitats. It was therefore decided to study retreat positions for both species.

Material and Method

Using photographs, the angle of the signal thread to vertically

Fig. 9. Inclination of webs to the vertical
(spiders at all stages of development)

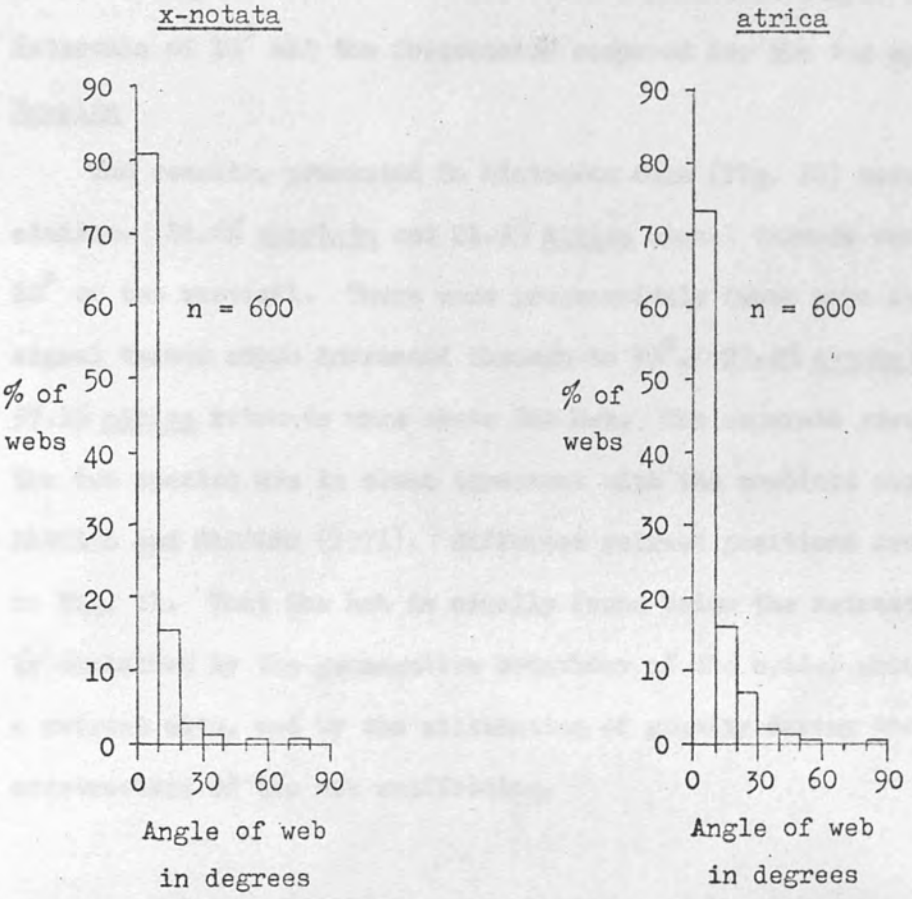
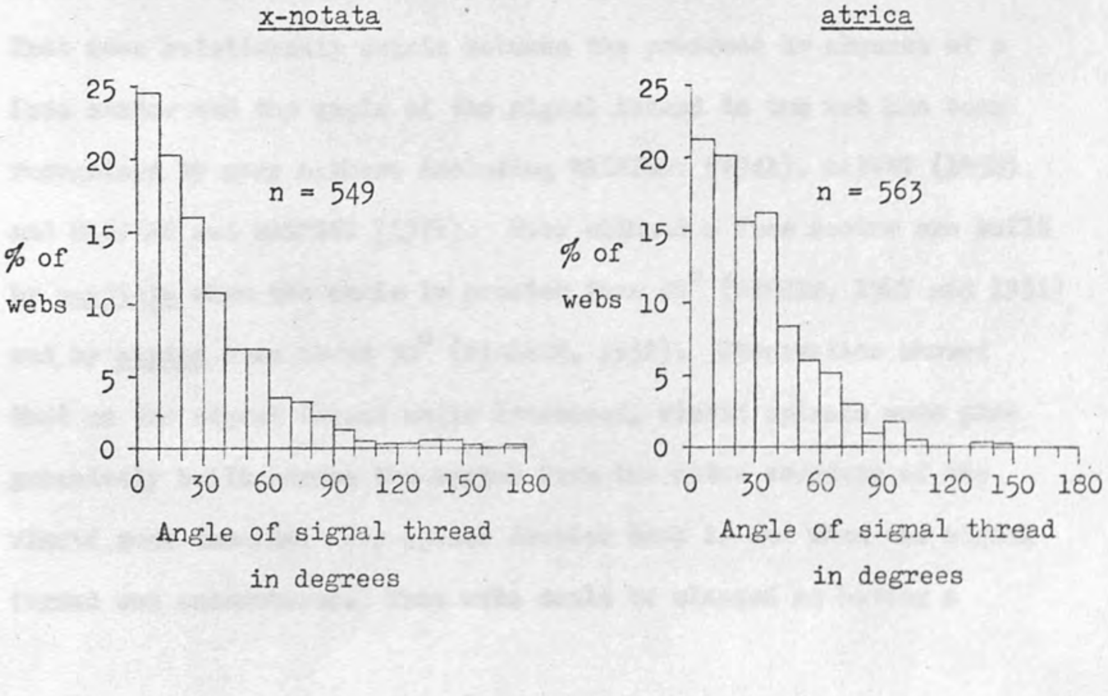


Fig. 10. Inclination of the signal thread to vertically upwards as seen from directly in front of the web
(spiders at all stages of development)



upwards, as seen from in front of the web, was measured on numerous webs built by spiders of all ages. The angles were placed in group intervals of 10° and the frequencies compared for the two species.

Results

The results, presented in histogram form (Fig. 10) were very similar. 24.6% x-notata and 21.3% atrica signal threads were within 10° of the vertical. There were progressively fewer webs as the signal thread angle increased through to 90°. 95.4% x-notata and 97.1% atrica retreats were above the hub. The separate results for the two species are in close agreement with the combined results of MARPLES and MARPLES (1971). Different retreat positions are shown in Fig. 11. That the hub is usually found below the retreat is partly explained by the geonegative behaviour of the spider when selecting a retreat site, and by the utilization of gravity during the early construction of the web scaffolding.

Relationship between the Position of the Retreat and the Presence of a Free Sector

Early workers, BLACKWALL (1864) for example, noted that the retreat and signal thread were not always in the plane of the web. That some relationship exists between the presence or absence of a free sector and the angle of the signal thread to the web has been recognised by many authors including BRISTOWE (1941), SAVORY (1952) and MARPLES and MARPLES (1971). Webs without a free sector are built by x-notata when the angle is greater than 40° (WIEHLE, 1927 and 1931) and by atrica when about 90° (NIELSEN, 1932). Observation showed that as the signal thread angle increased, viscid spirals were progressively built across the sector from the outer boundary of the viscid zone inwards. The spider doubled back if and when the signal thread was encountered. Thus webs could be classed as having a

Fig. [illegible] Different retreat positions in relation to the hub

(a) Retreat
above
the hub

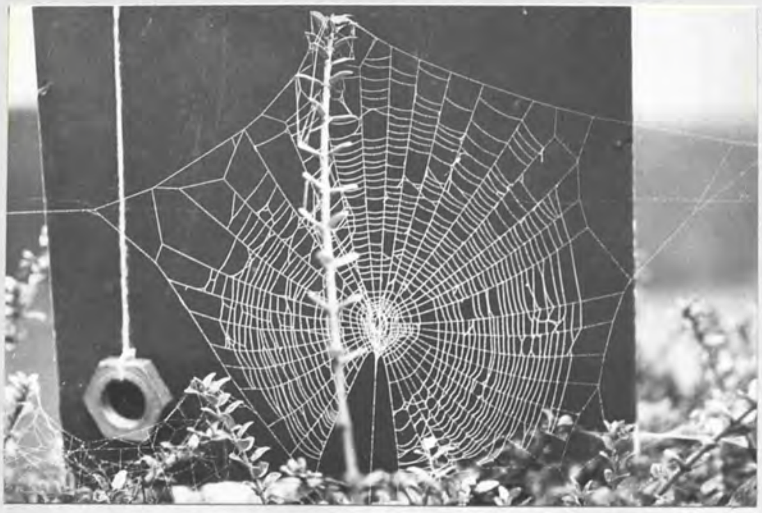
(b) Retreat
level
with
the hub

(c) Retreat
below
the hub

Fig. 11. Different retreat positions in relation to the hub

(a) Retreat above the hub

(b) Retreat level with the hub



(c) Retreat below the hub

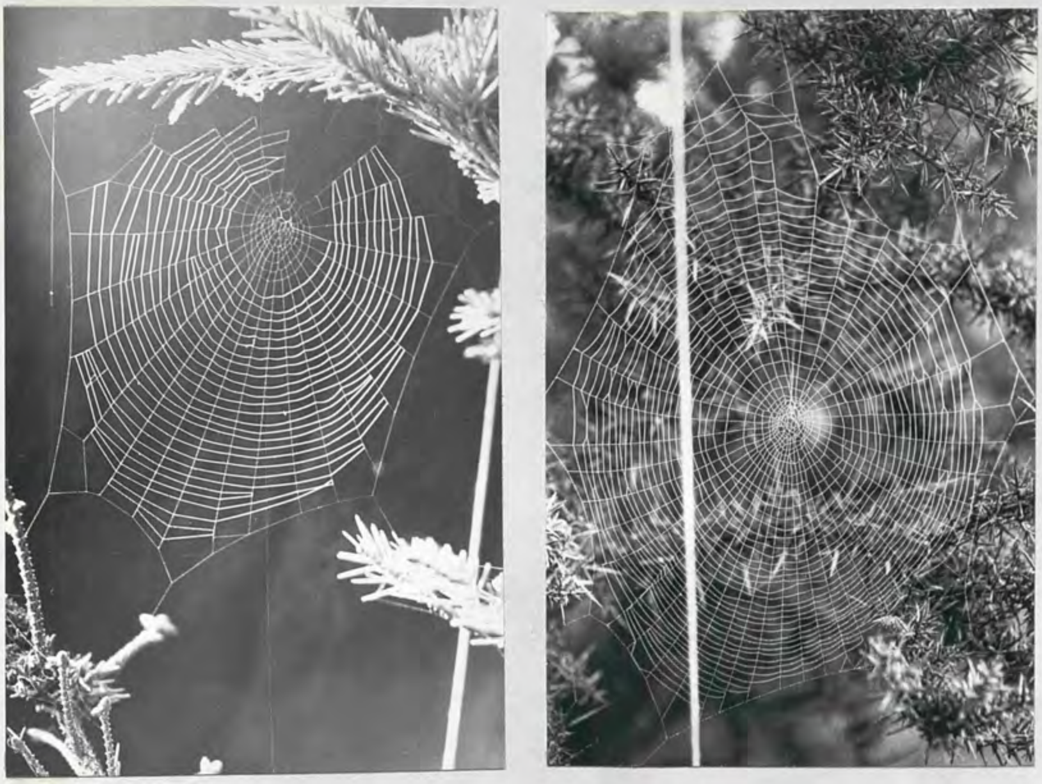
[illegible] free sector: complete, incomplete or
no free sector

(a) Complete free sector

(c) No free sector

(b) Incomplete free sector

Fig. 12. Examples of webs with a complete, incomplete or no free sector



(a) Complete free sector

(b) No free sector

(c) Incomplete free sector

complete, incomplete or no free sector (see Fig. 12a, b, c).

Material and Method

Numerous webs of both species at all developmental stages were selected from different habitats. A half-moon protractor, with the 0° - 180° line forming its base, was used to measure to the nearest degree the smallest angle of the signal thread to the web. The webs were classified as above.

Results

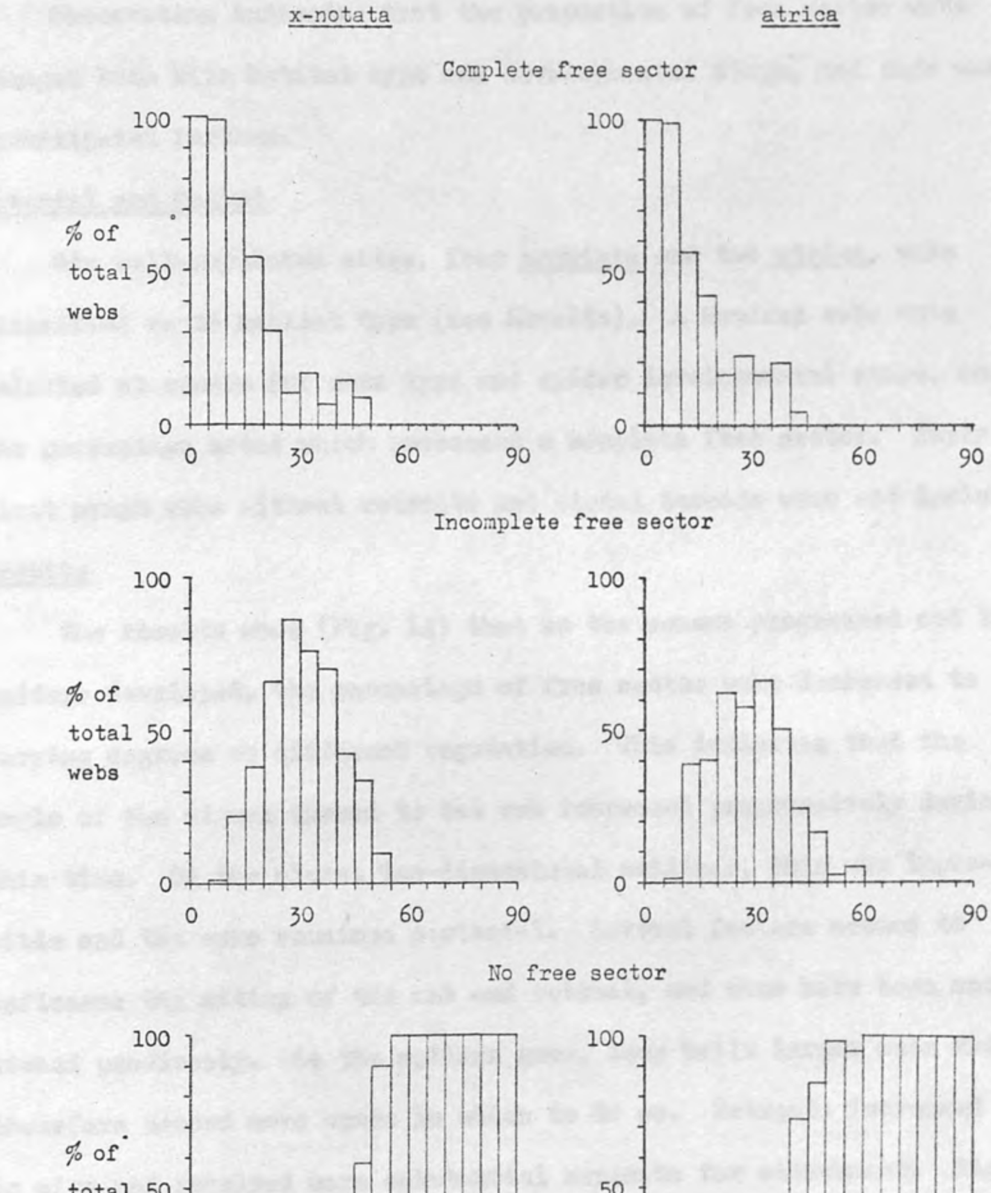
The results are presented in histogram form in Fig. 13. They show that there was no abrupt change from one web type to another as the angle of the signal thread increased, but each type could be associated with a particular range of angles. For x-notata and atrica respectively, these were from 0° to 19° and 0° to 14° for free sector webs; 20° to 39° for incomplete free sector webs; and 45° to 90° and 40° to 90° for no free sector webs. The results as a whole were similar for the two species.

For each species, combined results (not presented here) for the first three developmental stages compared favourably with those for older spiders, and this suggests that the relationship between the web type and the signal thread angle varies little as the spider develops.

Occurrence of Free Sector Webs in Different Habitats

In the literature, webs tend to be classed as either having or not having a free sector. SAVORY (1952) observed that in August on ornamental shrubs a small proportion had no free sector. Such webs on gorse and cupressus hedges become more common through the autumn, the spiders probably moving further into the foliage to avoid cold weather (BRISTOWE, 1941). MARPLES and MARPLES (1971) noted a greater

Fig. 13. The relationship between the form of the free sector and the angle of the signal thread to the plane of the web


x-notata

atrica

Complete free sector

Incomplete free sector

No free sector

proportion of complete webs on holly than on soft-leaved shrubs, while those on buildings were almost invariably sectorial. All linked the web type with retreat position.

Observation indicated that the proportion of free sector webs changed both with habitat type and developmental stage, and this was investigated further.

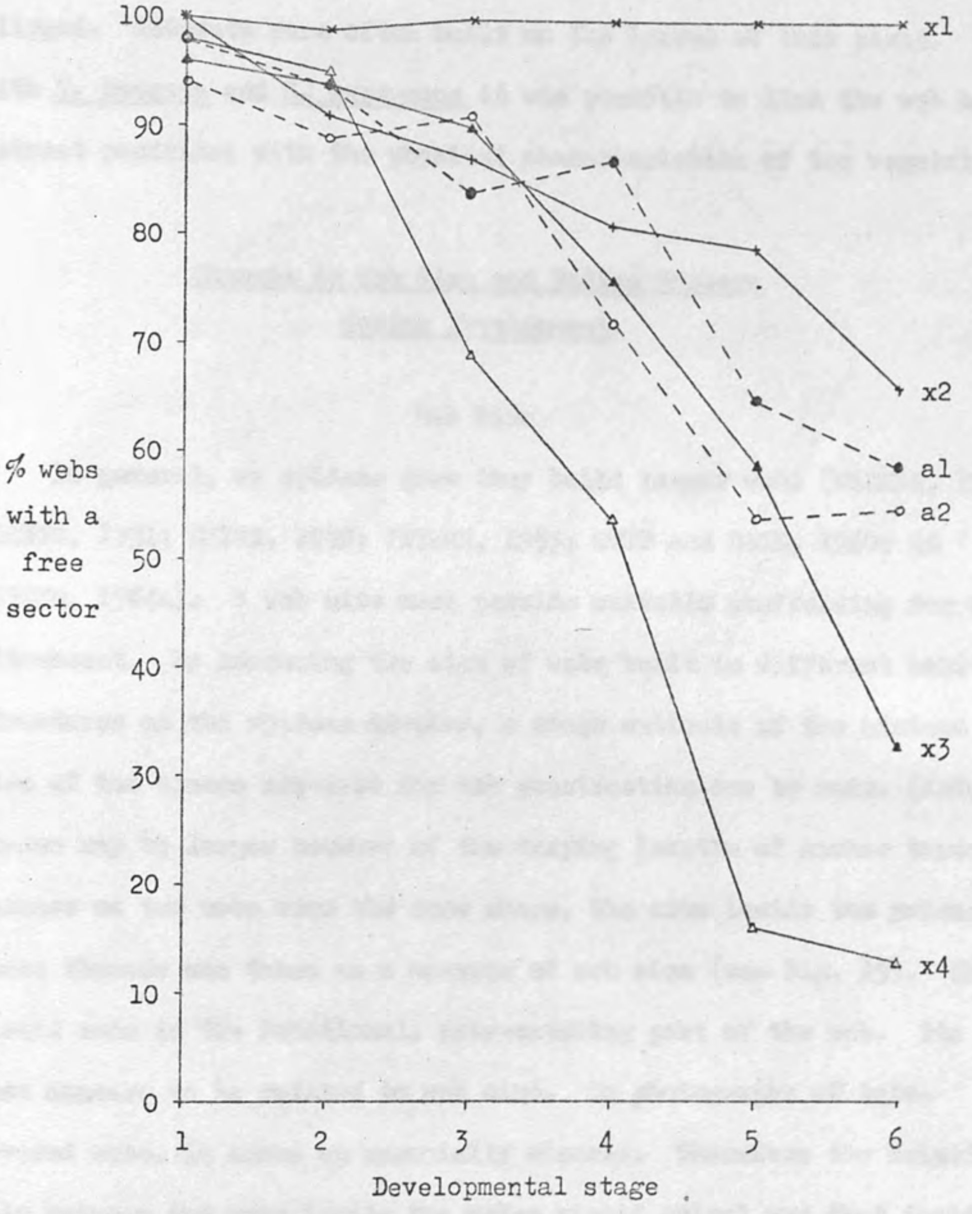
Material and Method

Six well-populated sites, four x-notata and two atrica, were classified as to habitat type (see Results). A hundred webs were selected at random for each type and spider developmental stage, and the percentage noted which possessed a complete free sector. Early first nymph webs without retreats and signal threads were not included.

Results

The results show (Fig. 14) that as the season progressed and the spiders developed, the percentage of free sector webs decreased to varying degrees on different vegetation. This indicates that the angle of the signal thread to the web increased progressively during this time. On the almost two-dimensional railings, this was impossible and the webs remained sectorial. Several factors seemed to influence the siting of the web and retreat, and some have been mentioned previously. As the spiders grew, they built larger webs and therefore needed more space in which to do so. Retreats increased in size and required more substantial supports for attachment. Rigidity of supports was important too. On the slow-growing, dense Taxus baccata hedge, stage one retreats were typically built between leaves growing on the small terminal shoots, with the webs constructed below, many at right angles to the hedge. Most were sectorial. Hedge growth seemed not to keep pace with spider growth, the spiders moving further into the foliage to build their larger retreats where the twigs forked. Most of the webs were built parallel to the hedge,

Fig. 14. Percentage webs with a completely free sector at different developmental stages and on different types of support



Species	Code	Type of support
x-notata	x1 x2 x3 x4	Iron railings Crataegus monogyna, clipped in October Crataegus monogyna, clipped three times a year Taxus baccata, clipped in October
atrica	a1 a2	Ulex europaeus Crataegus monogyna, clipped in October

n = 100 for each reading

the anchor threads being attached to the terminal shoots. *Ulex europaeus* tended to be less dense, more rigid and to grow somewhat more quickly. *Crataegus monogyna* grew very quickly, the density and rigidity of the twigs being dependent on how regularly the hedge was clipped. Retreats were often built on the leaves of this plant. As with *T. baccata* and *U. europaeus* it was possible to link the web and retreat positions with the physical characteristics of the vegetation.

Changes in Web Size and Radius Numbers during Development.

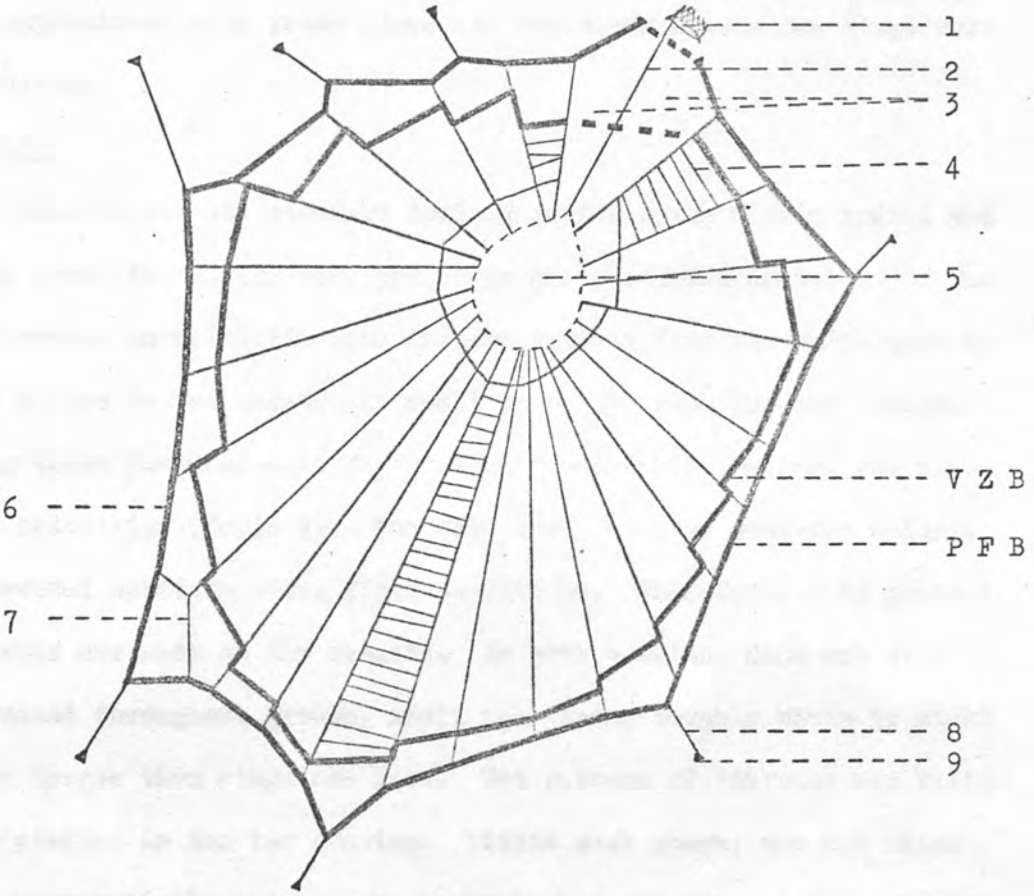
Web Size

In general, as spiders grow they build larger webs (WIEHLE, 1927; KOENIG, 1951; MAYER, 1952; PETERS, 1953; WITT and BAUM, 1960; LE GUELTE, 1964a). A web site must provide suitable scaffolding for web attachment. By measuring the size of webs built in different habitat structures as the spiders develop, a rough estimate of the minimum size of the spaces required for web construction can be made. (Actual spaces may be larger because of the varying lengths of anchor threads). Because no two webs were the same shape, the area inside the primary frame threads was taken as a measure of web size (see Fig. 15). The viscid zone is the functional, prey-catching part of the web. Its size appears to be related to web size. On photographs of talc-covered webs, it shows up especially clearly. Therefore the relationship between the area inside the outer viscid spiral and that inside the primary frame threads was investigated as a possible tool for assessing web size.

Material and Method

From the web photographs mentioned earlier, thirty, showing all frame threads clearly, were selected for each developmental stage.

Fig. 15. Area boundaries in a typical web



V Z B	Viscid zone boundary
P F B	Primary frame boundary
1	Retreat entrance
2	Signal thread
3	Free sector
4	Viscid thread
5	Hub
6	Primary frame thread
7	Secondary frame thread
8	Anchor thread
9	Anchor thread attachment

The areas inside the primary frame and outer viscid spiral (Fig. 15) were measured with a planimeter and the results used to calculate a factor for the relationship of frame area to outer viscid spiral area. The outer viscid spiral area was measured on a further seventy webs at each stage, and using the multiplication factors from above, the approximate mean frame areas for one hundred webs per stage were calculated.

Results

Mean values and standard deviations for outer viscid spiral and frame areas for thirty webs per stage are presented in Table 8. The differences in multiplication factors derived from the means must in part be due to the relatively small number of webs for each stage. Using these factors, mean frame areas for one hundred webs per stage were calculated (Table 9). The webs were built by numerous spiders in several habitats under field conditions. Therefore, only general comments are made on the results. In both species, mean web size increased throughout growth, adult webs being roughly seven to eight times larger than stage one webs. The pattern of increase was basically similar in the two species. Within each stage, the web sizes were very variable and as webs commonly had one or more long anchor threads, site dimensions were even more variable. Never-the-less, results show that larger spiders build larger webs and sufficiently large spaces are required in which to do so. A habitat must provide at least minimum-sized spaces for all spider stages if the spiders are to complete their life cycles within it.

No measure has yet been developed to characterize the irregular shape of a web (WITT et al, 1968). However, one may compare the dimensions of the space filled by the web with those of the sides of a rectangle of minimum width into which the web can be placed. For both species, the dimensions were mainly in the ratio of from 1:1 to 2:1 with the larger dimension tending towards the vertical.

Table 8. Outer viscid spiral and frame areas of field webs built by spiders at all stages of development.

Species	Spider stage	No. of webs	a Area inside outer viscid spiral in cm.^{2}		b Area inside frame in cm.^{2}		Multiplication factor b/a
			$\bar{x}$	s.d.	$\bar{x}$	s.d.	
<u>x-notata</u>	1	30	17.1	6.8	23.8	11.2	1.39
	2	30	32.5	13.9	45.0	17.9	1.38
	3	30	44.8	18.1	62.5	18.8	1.40
	4	30	75.2	27.8	97.9	33.6	1.30
	5	30	97.9	34.8	128.8	45.5	1.32
	6	30	128.6	52.5	181.4	66.7	1.41
<u>atrica</u>	1	30	22.5	8.2	28.4	10.0	1.26
	2	30	38.7	12.1	52.1	14.5	1.35
	3	30	51.0	16.2	68.3	17.2	1.34
	4	30	72.7	27.1	95.4	32.1	1.31
	5	30	117.6	34.8	151.1	43.4	1.28
	6	30	123.4	49.3	163.7	32.2	1.33

Table 9. Frame areas, derived from outer viscid spiral areas, of webs built by spiders at all stages of development.

Species	Spider stage	No. of webs	c Area inside outer viscid spiral in cm.^{2}		d Multiplication factor	Area inside frame in cm.^{2} c x d
			$\bar{x}$	s.d.		
<u>x-notata</u>	1	100	16.6	7.0	1.39	23.1
	2	100	31.8	13.8	1.38	43.9
	3	100	46.4	18.3	1.40	65.0
	4	100	80.6	30.0	1.30	104.8
	5	100	100.2	39.8	1.32	132.3
	6	100	138.5	57.1	1.41	195.3
<u>atrica</u>	1	100	20.6	8.0	1.26	26.0
	2	100	37.0	14.0	1.35	50.0
	3	100	54.3	16.2	1.34	72.8
	4	100	76.7	26.4	1.31	100.5
	5	100	129.8	36.2	1.28	166.1
	6	100	134.2	52.6	1.33	178.5

Number of Radii

Adult atrica webs are said to contain more radii than x-notata (BRISTOWE, 1941; KASTON, 1948). For atrica, the number is usually over 40 (BRISTOWE, 1941). WIEHLE (1929, 1931) noted 38-54 (mean = 46, n = 10) in mid-July and 33-37 at the end of August. Figures for x-notata are more variable. They include 14-34 but usually 25-30 (WIEHLE, 1927, 1931); 20-41 (TILQUIN, 1942); 21-31 (mean = 25)(KOENIG, 1951); 20-60 (mean = 42.5, n = 104)(WITT, 1955) and 21-56 (mean = 36, n = 430) for all stages except adults (LE GUELTE, 1964). Such variation called for further study.

Material and Method

From various habitats, a total of two hundred webs for each spider stage were selected at random, and the radii counted. The signal thread was not included. Tertiary radii were included if at least four viscid spirals were attached to them.

Results

The mean number of radii did not remain constant throughout development (see Table 10)

Table 10. Radius numbers of field webs throughout spider development.

Species	Spider stage	No. of webs	No. of radii		
			Range	Mean	s.d.
x-notata	1	200	14-38	27.1	4.9
	2	200	15-51	29.1	6.0
	3	200	16-44	32.8	5.5
	4	200	19-50	32.9	6.4
	5	200	15-50	30.9	5.5
	6	200	11-41	30.2	5.1
atrica	1	200	20-46	33.7	4.7
	2	200	21-55	37.7	5.9
	3	200	25-58	43.1	5.9
	4	200	23-58	39.2	5.9
	5	200	23-53	35.6	5.3
	6	200	19-45	31.8	5.4

For *x-notata*, the mean increased from 27.1 in stage one to 32.9 in stage four, then decreased to 30.2 in stage six. For *atrica*, the increase was greater, from 33.7 to 43.1 with the peak at stage three, and then an even larger decrease to 31.8 in stage six. In spite of the large range for each stage, "t" tests show that *atrica* webs have significantly more radii than *x-notata* webs at equivalent stages ($P < 0.001$ for stages one to five, and < 0.01 for stage six.) Mean values for laboratory *x-notata* webs are given by LE GUELTE (1966b). Allowing that the developmental stage was accurately known and that the females matured at stage five, the above results compare quite favourably with them. The *atrica* mean values help to confirm those of WIEHLE (1929) whose mid-July figures were probably for stage three or four spiders. Those at the end of August were for adult females.

That radius numbers decrease in later stage webs may be explained by a change in the body weight to leg length relationship, although this was not examined. WITT and BAUM (1960) demonstrated this in *Araneus diadematus* and LE GUELTE (1966b) found that the number of radii decreased before and increased after egg-laying in adult *x-notata*.

Radius numbers alone are of little value in identifying the stage or species of single individuals. However, they could be useful when natural groups of spiders are considered, for mixed populations are uncommon and neighbouring spiders tend to be at about the same stage of development.

Effect of Web Size on the Number of Radii

Several factors are known to affect radius numbers. They include spider age (WIEHLE, 1927; KOENIG, 1951; WITT and BAUM, 1960), body weight (MAYER, 1952; CHRISTIANSEN et al, 1962; LE GUELTE, 1966b) and leg number (PETERS, 1936; LE GUELTE, 1965; REED et al, 1965). Web size is an additional factor. In several species, including *x-notata* (MAYER, 1952; LE GUELTE, 1966b), large adult webs have been shown to contain more radii than small ones. This effect of web size on radius numbers was investigated for early and late developmental stages in both species.

Material and Method

The outer viscid spiral areas of numerous stage two and five webs were converted into approximate outer frame areas as described earlier. For each stage, the areas were placed in arbitrary groups of increasing area value, and the mean number of radii calculated for each group.

Results

These are presented in Table 11.

Table 11. Variation in the number of radii with web size for two developmental stages

Spider stage	Outer frame area in cm.^{2}	*x-notata*		*atrica*	
		No. of webs	Mean radii	No. of webs	Mean radii
2	20 - 40	45	30.8	28	33.0
	40 - 60	34	33.9	42	36.5
	60 - 80	13	36.5	13	39.7
5	40 - 80	10	27.3	-	-
	80 - 120	26	29.7	9	31.8
	120 - 160	19	32.3	25	34.4
	160 - 200	17	35.5	26	37.6
	200 - 240	11	35.2	21	39.8

For both species and stages, the mean number of radii, with one minor exception, increased with web size. This may help to explain the large variation in radius numbers in laboratory and field observations quoted by different authors. MAYER (1952) and LE GUELTE (1964a) have shown that longer radii have smaller angles between them, hence larger webs have more radii. The relationship is not constant throughout development or there would be an increase in the mean number of radii from stage one to adulthood. That there is a decrease in the later developmental stages has been demonstrated earlier.

CHAPTER V

ENVIRONMENTAL FACTORS - PREFERENCES

Microclimate has been shown to influence the siting of spider webs (see INTRODUCTION). This may be reflected in different environmental factor preferences and tolerances, which can be tested in the laboratory. It is with preferences that this section is concerned. Humidity (SAVORY, 1930; CLOUDSLEY-THOMPSON, 1957; LAGERSPETZ and JÄYNAS, 1959; CHERRETT, 1964; ENDERS, 1972), temperature (NØRGAARD, 1951; CLOUDSLEY-THOMPSON, 1957; ALMQUIST, 1971) and light (CLOUDSLEY-THOMPSON, 1957; CHERRETT, 1964; ENDERS, 1972) preferences have been demonstrated in gradient and/or choice chamber experiments for various web and non-web spiders.

HUMIDITY

Humidity is important in that it interacts with temperature to influence evaporative water loss (CHEW, 1961). The only comparative work on humidity preferences in the two Zygiella species is that of SAVORY (1930). Using simple humidity gradient apparatus, SAVORY found that at ordinary temperatures, atrica preferred high relative humidities and was positively hygrotropic (-tactic), while x-notata showed the opposite preference and was negatively hygrotropic (-tactic). (Of interest, x-notata reversed its choice below 5°C). It was suggested that this explains why atrica "almost invariably" spins webs on shrubs and bushes where humidity is higher than on walls, sheds and houses, the usual sites for x-notata webs. Habitat choice differences are not so clear-cut as this, and therefore humidity preferences have been re-examined in gradient and choice chamber experiments. Adult females were used because of their length of life and ease of identification from field collections.

Humidity Gradient Experiments

Material and Method

The apparatus consisted of a glass tube 46cm. long and 2.5cm. in diameter which could be closed at both ends by rubber bungs. To give a theoretical humidity gradient from approximately 100% R.H. to 0% R.H., distilled water in a small container with a filter paper wick was placed at one end and granular calcium chloride at the other. They were separated from the remainder of the tube by two vertical partitions of nylon gauze, stretched across tightly fitting polythene rings, leaving a 36cm. long chamber in which the spiders could move freely. The spiders were introduced into the middle of the chamber via a 1cm. diameter hole normally closed with a rubber bung. The adult females used had been collected from outside, kept under laboratory conditions for at least three days prior to the experiment and liberally fed on Drosophila during this period. The apparatus was set up in darkness at constant temperature and left for three hours for the humidity gradient to be established. Five spiders of one or other species were introduced into the apparatus, left overnight and their positions noted after eighteen hours. The spiders were removed, the tube cleared of threads and the experiment repeated using fresh animals. In all, 30 animals of each species were tested at 20°C. and 5°C. The humidities were checked using a "Model 91 Y.S.I." dew point hygrometer. All readings were above 93% R.H. at the moist end, below 13% R.H. at the dry end and from 45% to 53% R.H. in the middle.

Results

The spiders tended to come to rest at or near the ends of the apparatus, or in the middle 4 cms. because of the relative ease in attaching threads round the entrance. Therefore, their positions were classed only as "dry," "moist" or "middle." End and other effects which, if not recognised, may lead to incorrect interpretations of preference experiments are discussed by MACFADYEN (1963).

Table 12. Gross positions of adult females in humidity gradients (theoretically 0% - 100% R.H.) at 20°C. and 5°C.

Temperature	Species	No. of spiders	% spiders in different gradient positions		
			Dry	Middle	Moist
20°C.	*x-notata*	30	80.0	10.0	10.0
	atrica	30	70.0	10.0	20.0
5°C.	*x-notata*	30	66.6	13.4	20.0
	atrica	30	66.6	16.7	16.7

Chi-squared tests on the results (Table 12) indicate that *x-notata* and *atrica* at 20°C. and 5°C. both prefer the drier half of the humidity gradient ($P < 0.001$ for *x-notata* at 20°C.; $P < 0.01$ for *x-notata* at 5°C. and *atrica* at 20°C. and 5°C.) In control experiments without a gradient, spiders showed no significant preference for a particular half, although end effects were apparent.

The results for *x-notata* at 20°C. agree with those of SAVORY (1930) but those for *x-notata* at 5°C. and *atrica* at 20°C. do not. This is not easy to explain, but differences in physiological states may be important here (AGRELL, 1947). In the above experiments, the spiders were in the gradient apparatus for a much longer time. They were prevented from reaching the water, as *atrica* especially will drink readily in the laboratory. They were tested in groups of five in order to stimulate locomotory activity. Spiders avoid one another, therefore their grouping in the gradient apparatus is significant. Spiders left in the apparatus for a further twenty-four hours showed little change in behaviour. ENDERS (1972) found that several other Argiopids in humidity gradients reversed their choice from dry to moist conditions after twenty-four hours.

Humidity Choice Chamber Experiments

Material and Method

Humidity preferences at 20°C. were examined more closely using choice chambers (GUNN and KENNEDY, 1936). Each chamber consisted of a rectangular perspex box with a tightly fitting transparent lid. The box was divided horizontally by a perforated zinc sheet on which the spiders could walk, and vertically by a central partition extending upwards from the base to the zinc floor and downwards from the lid to within 0.7cm. of the floor, allowing free passage beneath it. The upper partition was modified in shape to form a wide-angled "V" in cross-section. This dissuaded the naturally climbing spiders from coming to rest within 1cm. of the mid-line. Each upper compartment measured 12.0 x 12.0 x 2.4cm. Animals could be introduced into each compartment via separate holes in the lid, normally closed with stoppers. Into the lower compartments were placed petri dishes containing granulated calcium chloride, distilled water or saturated salt solutions to control relative humidities in the compartments above (see Table 13).

Adult females of both species were collected in quantity from outside. They were kept and liberally fed for a minimum of five days under normal laboratory conditions before being used in experiments. In one series of experiments at 20°C., groups of ten spiders were given a choice between 100% R.H. and the other relative humidities mentioned in Table 13. In a second series, the choice was between 0% R.H. and the other humidities. In a third series, following the results of the first two, preferences between different relative humidities near the drier end of the scale were investigated. In each case the choice chambers were set up for some hours before the spiders were placed in them. The positions were noted after sixteen hours in darkness. The intensity of reaction was calculated as the excess percentage of animals in the favoured zone (GUNN and COSWAY, 1938). Relative humidities were checked in each compartment 3cm. from the partition, using the "Y.S.I." hygrometer. No value differed from the theoretical one by more than 4% and in most cases by no more than 2%.

Table 13. Production of relative humidities in the laboratory

Compound	Form	Theoretical % R.H. at 20°C.
Distilled water	Liquid	100
KCl	Saturated solution	85*
NaCl	" "	76*
$Ca(NO_3)_2.4H_2O$	" "	56*
$MgCl_2.6H_2O$	" "	33*
$LiCl.H_2O$	" "	13*
$CaCl_2$	Granulated	0

* WINSTON and BATES, 1960.

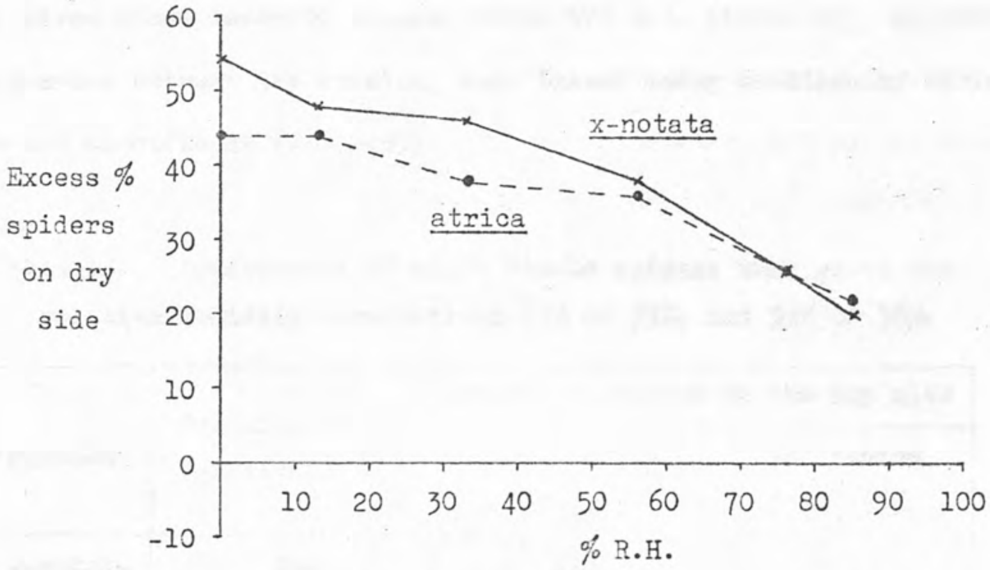
All the saturated salt solutions are satisfactory for this purpose (O'BRIEN, 1948).

Results

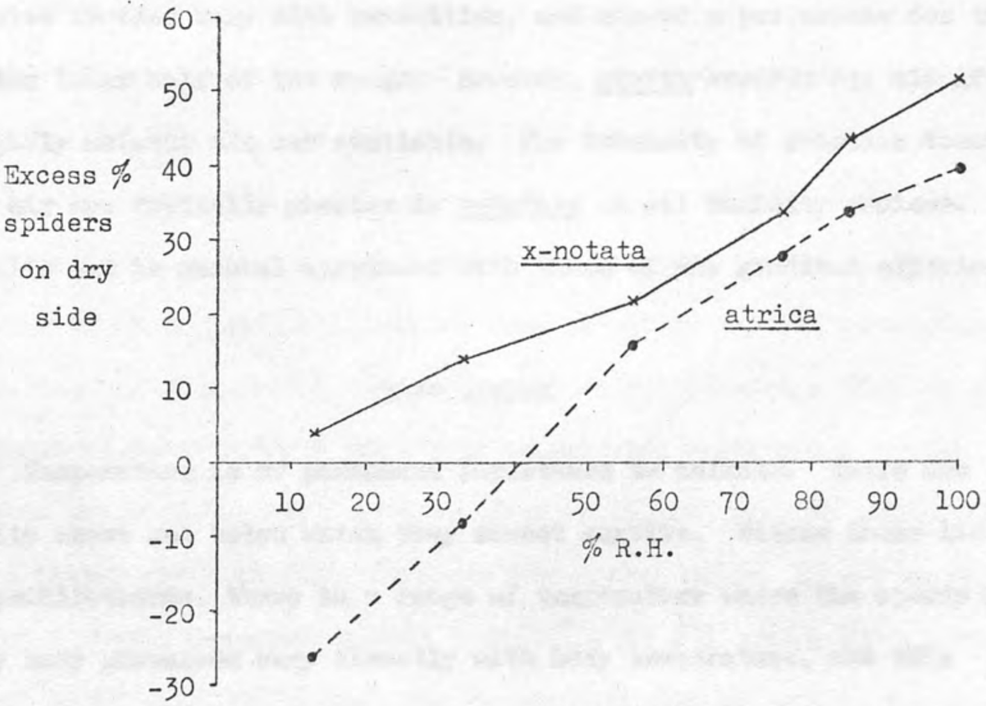
When given choices between 100% and lower relative humidities (Fig. 16a), chi-squared tests show that significantly more spiders of both species chose the drier conditions ($P < 0.05$). This was especially marked where humidity differences were very large ($P < 0.001$).

Fig. 16. Humidity preferences of adult female spiders at 20°C.

(a) Choice between 100 % R.H. and other R.H. values given in Table 13.
(n = 100 spiders for each reading)



(b) Choice between 0 % R.H. and other R.H. values given in Table 13.
(n = 100 spiders for each reading)



With choices between 0% and higher relative humidities (Fig. 16b), more *x-notata* again chose the drier conditions, significantly more when the alternative relative humidities were from 56% ($P < 0.05$) to 100% ($P < 0.001$). Unlike *x-notata*, *atrica* preferred the higher humidity ($P < 0.05$) when presented with a 0% : 13% R.H. choice. However, when given other humidity choices below 57% R.H. (Table 14), apparent differences between the species, when tested using contingency tables, were not significant ($P > 0.05$).

Table 14. Preferences of adult female spiders when given the relative humidity alternatives 13% or 33%, and 33% or 56%.

Species	No. of spiders for each choice	Excess % spiders on the dry side	
		R.H. choice 13% : 33%	R.H. choice 33% : 56%
x-notata	150	8.0	13.3
atrica	150	-9.3	8.0

Under the experimental conditions, adult female spiders of both species avoided very high humidities, and showed a preference for those in the lower half of the range. However, *atrica* avoided dry air if slightly moister air was available. The intensity of reaction towards dry air was typically greater in *x-notata* at all humidity choices. The results are in general agreement with those of the gradient experiments.

TEMPERATURE

Temperature is of paramount importance to animals. There are limits above and below which they cannot survive. Within those limits, in poikilotherms, there is a range of temperature where the speeds of many body processes vary directly with body temperature, and this affects such activities as growth and reproduction. Outside it, sublethal and lethal effects begin (FRAENKEL and GUNN, 1961). The influence of temperature on evaporation rate has been mentioned. Literature on the biological effects of temperature on terrestrial arthropod distribution is included in a review by CLOUDSLEY-THOMPSON (1962). Many animals aggregate in regions of favourable temperature if given the opportunity (FRAENKEL and GUNN, 1961). Temperature preferences at constant relative humidity were investigated for first nymph spiders using a temperature gradient apparatus, and for adult females using choice chambers.

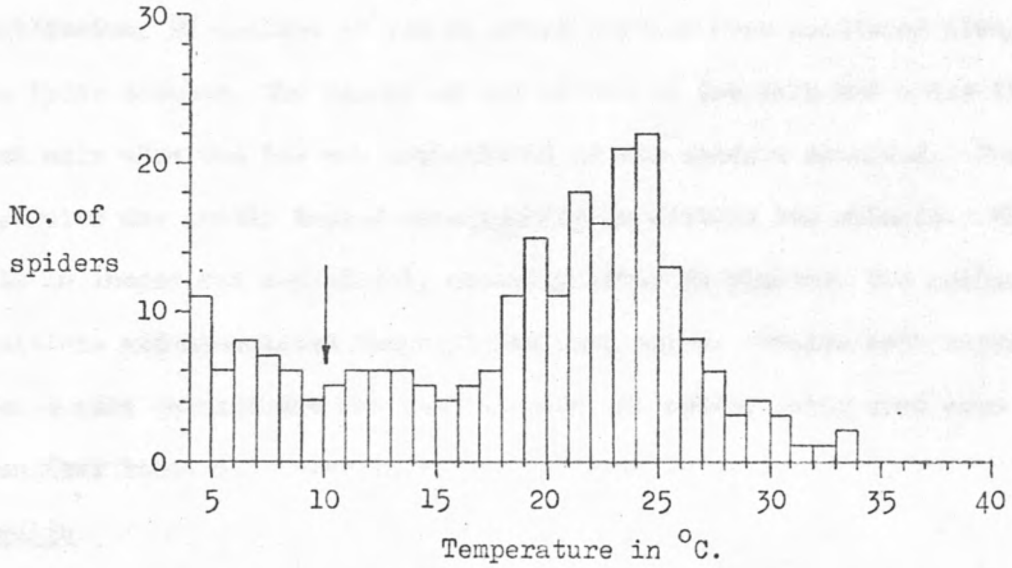
Temperature Gradient Experiments

Material and Method

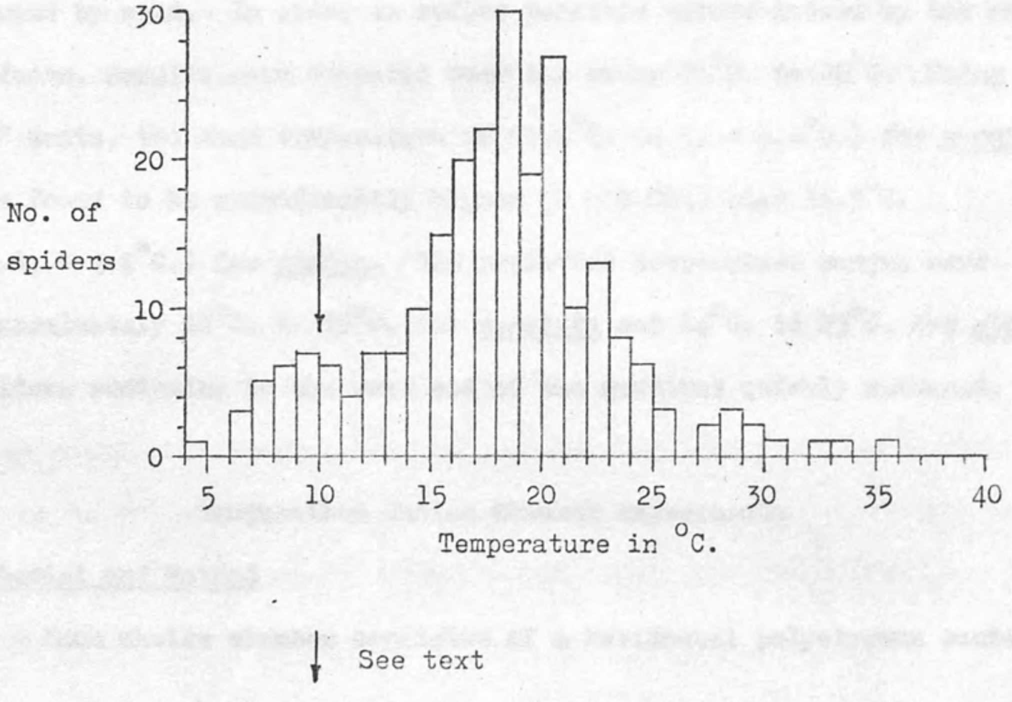
The apparatus was a slightly modified version of that used by WIGGLESWORTH (1941). An inner zinc trough 44.0 x 1.5 x 2.5cm. deep was supported inside a larger one 50.0 x 4.0 x 4.0cm. such that the tops were level; sand saturated with water was placed between them. The inner one was divided into upper and lower chambers by a horizontal perforated zinc strip covered with fine nylon gauze. In the smaller lower chamber were placed several boats containing a saturated solution of $MgCl_2.6H_2O$ to give a theoretical relative humidity of about 34% throughout the temperature range $0^{\circ}C.$ - $40^{\circ}C.$ (Normally a humidity gradient is associated with a temperature gradient). The upper chamber in which the spiders were placed was roofed with microscope slides. One end of the apparatus was heated with a "Photax Dishwarmer, Model 2," and the other cooled with melting ice placed between the troughs. By judicious placing of foam plastic insulation and a filter paper overflow to drain off excess water, it was possible to get a steady temperature fall from $40^{\circ}C.$ to $4^{\circ}C.$ along the apparatus. As WIGGLESWORTH found, the temperature inside, and in the sand

Fig. 17. Distribution of first nymph spiders in a temperature gradient

(a) *x-notata*



(b) *atrica*



immediately outside the test chamber were the same and thus the temperature in the chamber could be indirectly measured at any point along it.

First nymph laboratory spiders were used for these experiments in sufficient numbers to give a clear indication of preference over the whole temperature range. After allowing the apparatus to come to equilibrium, 20 spiders of one or other species were scattered along the inner chamber, the apparatus was placed in the dark and a dim light used only when the ice was replenished or the spiders observed. The apparatus was gently tapped occasionally to disturb the animals. When this no longer had any effect, normally after 90 minutes, the spider positions and associated temperatures were noted. Twelve such experiments were carried out for each species, no spider being used more than four times and never in successive experiments.

Results

The distributions of the two species in the temperature gradients are indicated in Figs. 17a and b. While atrica avoided the lowest temperatures, reacting especially strongly to the cold metal, x-notata did not. The larger numbers in the region of 4°C. were due to an apparatus end effect, and not to temperature choice or immobility caused by cold. In order to reduce possible errors caused by the end effects, results were compared over the range 10°C. to 40°C. Using "t" tests, the mean temperature of 21.4°C. (s.d. = 5.0°C.) for x-notata was found to be significantly higher ($P < 0.001$) than 18.9°C. (s.d. = 4.2°C.) for atrica. The preferred temperature ranges were approximately 18°C. to 26°C. for x-notata and 14°C. to 23°C. for atrica. Spiders venturing to the warm end of the gradient quickly returned.

Temperature Choice Chamber Experiments

Material and Method

Each choice chamber consisted of a horizontal polystyrene container of inside length 6cm. and diameter 3cm., with tightly fitting rubber discs forming the effective ends. The container was divided into upper and lower chambers by a horizontal foam plastic partition. The lower chamber was itself divided into two by a vertical wooden partition to prevent horizontal air flow, and into each half was placed a small container of saturated $MgCl_2.6H_2O$ solution to maintain the relative humidity at about 34%. A spider placed in the upper chamber could move freely within it.

Temperature differences between the two halves of the choice chambers were maintained as follows. A removable vertical perspex partition completely divided into half an insulated glass tank measuring 22 x 22 x 35cm. Sixteen choice chambers were pushed through holes in the partition and firmly gripped about their midlines. The tank was filled with water to cover the choice chambers, and the water was heated by separate aquarium heaters in each half of the tank. Each heater had its own adjustable thermostat and the water was stirred by bubbling air through it. By placing the tank at a constant temperature below that of the temperature choices being tested, differences of several degrees could be maintained between the two halves of the choice chambers. Temperatures were measured directly using a "Telemax M-type" electrical thermometer with a $1mm.^3$ sensor probe. Except at points within 1cm. of the mid-line, the temperatures of the chambers and surrounding water were similar.

Adult female spiders collected from the field at least five days beforehand were placed individually in the choice chambers and kept in darkness overnight for a period of sixteen hours. Their positions were then noted, those within 1cm. of the mid-line being classed as "middle." Based on the results of the gradient experiments, five different temperature alternatives were investigated, using the same 120 spiders for each one.

Results

The choices of spiders presented with different temperature alternatives are given in Table 15.

Table 15. Distribution of adult female spiders in temperature choice chambers

Temperature alternatives	Number of spiders at each temperature		"Middle" excluded, excess % spiders at the higher alternative temperature	
	x-notata	*atrica*	*x-notata*	*atrica*
14°C.	49	43	3.0	11.3
Middle	19	23		
19°C.	52	54		
17°C.	34	45	27.7	7.2
Middle	26	23		
21°C.	60	52		
19°C.	41	52	18.8	-10.6
Middle	19	26		
24°C.	60	42		
20°C.	53	64	-3.9	-30.6
Middle	18	22		
26°C.	49	34		
22°C.	56	74	-7.7	-46.5
Middle	16	19		
27°C.	48	27		

Comparing the two species, the results were significantly different for 19°C./24°C. ($P < 0.05$) and 22°C./27°C. ($P < 0.01$), and were almost so for 20°C./26°C. ($P < 0.1$). More *atrica* chose 19°C. than 24°C., the opposite of *x-notata*. Significantly more *atrica* than *x-notata* chose 22°C. compared with 27°C., and to a lesser extent 20°C. compared with 26°C. The results suggest that the preferred temperature range was in the region of 20°C. to 26°C. for *x-notata*, and 17°C. to 22°C. for *atrica*, although *x-notata* generally reacted less positively to temperature differences. These figures were in the same order as those obtained for first nymphs in the temperature gradient experiments.

LIGHT

Light often acts as a token stimulus for more important factors including humidity and temperature (FRAENKEL and GUNN, 1961). It is also the chief environmental clue with which diurnal rhythms of activity are synchronized (CLOUDSLEY-THOMPSON, 1962). It is of interest that while young Zygiellae emerging from the cocoon are photopositive (McCOOK, 1889; LE GUELTE, 1964a), x-notata adult females at least are photonegative (LE GUELTE, 1964a). Phototactic responses at different stages of development were investigated to see at what stage this change in behaviour occurs. Preliminary experiments suggested that at least the adult female reaction to light could alter under certain circumstances, and this was further investigated using choice chambers. Finally, using a microaktograph, the patterns of locomotory activity in adult female spiders in confined spaces were investigated, and the relationship between such activity, the time of day and the presence or absence of light noted. This has bearing on gradient and choice chamber experiments which depend on the animal moving around within the apparatus.

Phototaxis throughout Spider Development

Material and Method

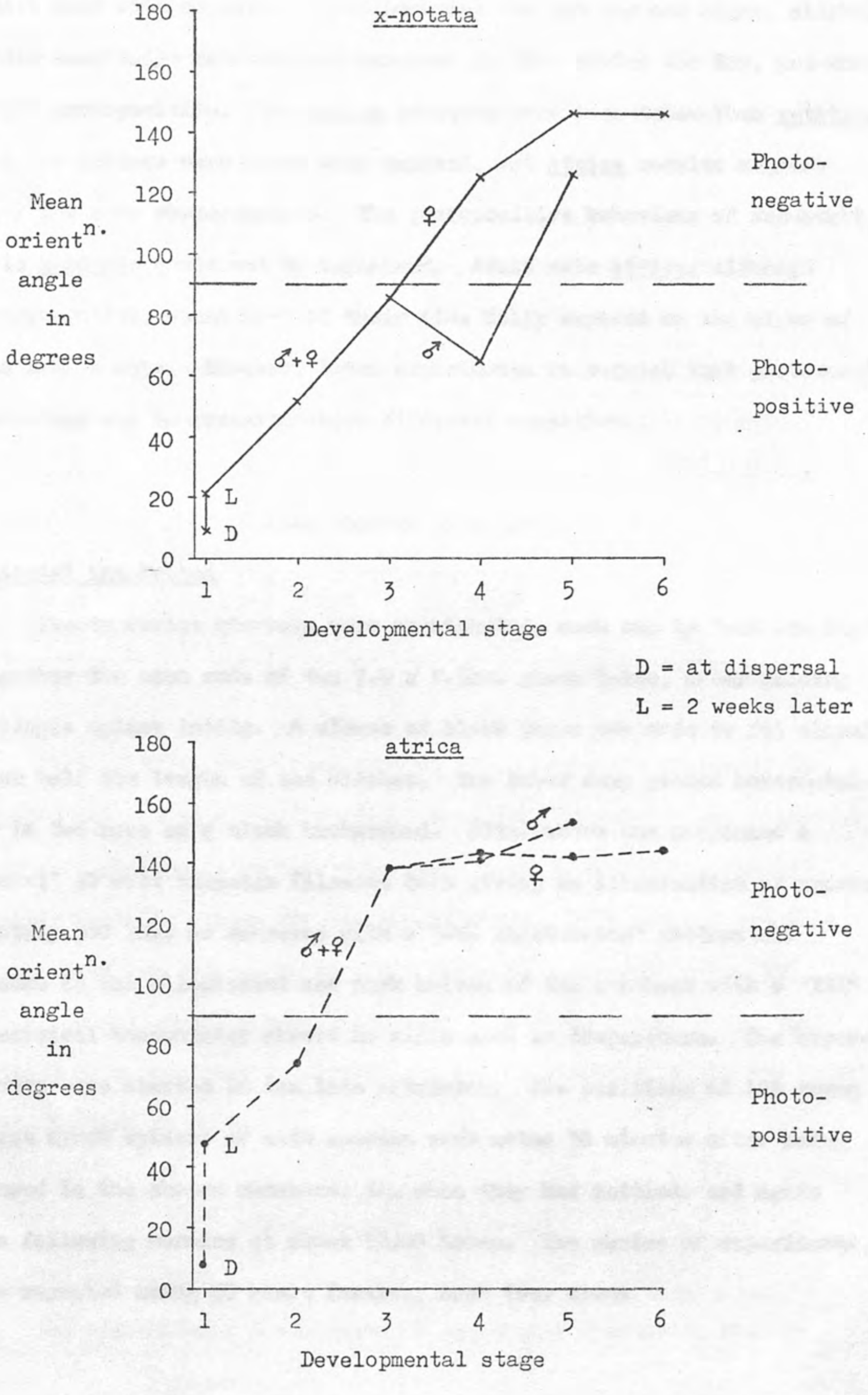
This experiment, designed to demonstrate how the angle of orientation to a light source changed during spider development, was carried out in a darkened room. An inverted 40 watt "Sunshine Opal Candle Lamp" bulb, shielded by a sleeve except for the bottom centimetre, acted as a bench-high light source of 1cm. diameter. It was supported just above the base of the inner of two glass troughs. Water between the troughs formed an effective heat shield as demonstrated by mercury thermometers placed at different distances from the light. The apparatus was placed on white paper and outlined in pencil. Laboratory-reared spiders had been kept in daylight for several hours before the experiment began. Each one, supported on its own thread was gently lowered onto a pencil mark "O," 10cms. from the outer trough and 18.5cms. from a point "L," immediately below the centre of the light source. The tension on the thread was relaxed and the spider's path traced with a following pencil, after two trial runs. Tracings were made for forty different spiders at each stage of development, first nymphs being tested both at cocoon emergence and fourteen days later. Most of the paths were curved, forming either a spiral towards or away from the light source. The orientation angle to the light was obtained as follows. A tangent to the curved path was drawn at a point "A," 10cms. along the path from the origin "O," as measured with a map measurer. The angle between the tangent in the direction of locomotion and the line joining "A" to the point "L" was measured. The orientation angle was less than 90° for photopositive animals and greater than 90° for photonegative ones (FRAENKEL and GUNN, 1961).

Results

The way in which the mean orientation angles altered as the spiders developed is shown in Fig. 18. There was no sudden change from strongly photopositive to strongly photonegative behaviour. It occurred over five stages in x-notata and three in atrica. Changes during stage one were very noticeable, atrica first nymphs especially being strongly photopositive when they emerged from the cocoon, but much less so a fortnight later. The trend was continued in older spiders as reflected in the wide range of orientation angles for each stage. An interesting species difference was the photopositive behaviour of sub-adult male x-notata and the photonegative behaviour of sub-adult male atrica.

It was not always possible to link laboratory phototactic behaviour with that observed in the field. Young stage one spiders certainly moved towards light, and this aided dispersion. Web-building during

Fig. 18. Mean orientation angles to light from first nymphs to adults



daylight hours was less common in older spiders, and the latter were more reluctant to come onto the web during the day. Their retreats were often less exposed. However, although many young first nymphs built webs with no retreats and occupied the hub day and night, slightly older ones built retreats and remained in them during the day, yet were still photopositive. The atrica retreats were less dense than x-notata and the spiders were often very exposed, yet atrica results suggest they are more photonegative. The photopositive behaviour of sub-adult male x-notata could not be explained. Adult male atrica, although photonegative, spent most of their time fully exposed on the edges of the female webs. However, later experiments do suggest that phototactic behaviour may be reversed under different conditions.

Choice Chamber Experiments

Material and Method

Twenty choice chambers were constructed, each one by "sellotaping" together the open ends of two 7.0 x 2.5cm. glass tubes, after placing a single spider inside. A sleeve of black paper was made to fit closely over half the length of the chamber. The tubes were placed horizontally in two rows on a black background. 60cm. above was suspended a "pearl" 40 watt tungsten filament bulb giving an illumination of approximately 380 lux, as measured with a "EEL Lightmaster" photometer. Checks in the illuminated and dark halves of the chambers with a "YSI" electrical thermometer showed no difference in temperature. The experiments were started in the late afternoon. The positions of 100 young first nymph spiders of each species were noted 30 minutes after being placed in the choice chambers, ie. when they had settled, and again the following morning at about 10.00 hours. The series of experiments was repeated using 50 adult females, each four times.

Results

Following the phototactic experiments, not unexpectedly, x-notata and atrica first nymphs were strongly photopositive ($P < 0.001$), both after 30 minutes and 15 hours (Table 16). Also as expected, adult females were strongly photonegative ($P < 0.001$) after 30 minutes, but $14\frac{1}{2}$ hours later there had been a very significant change ($P < 0.001$) and they had become photopositive ($P < 0.05$).

Table 16. Preferences of first nymphs and adult females in light/dark choice chambers

Stage	Species	No. of spiders	Excess % spiders in the light	
			After ½ hr. in the evenings	After 15 hrs. overnight
First nymphs	x-notata atrica	100 100	92% 96%	88% 96%
Adult females	x-notata atrica	200 200	-74% -79%	26% 17%

ENDERS (1972) noted that several other Argiopids preferred the illuminated end of a light gradient when left overnight, and suggested that such photopositive behaviour would tend to direct the spider towards suitable spaces for web construction. This seems a possible explanation for the change in adult Zygiella behaviour, since the spiders would normally have built webs some three hours before the fifteen hours had passed. Inside the choice chambers, there was insufficient space to do so.

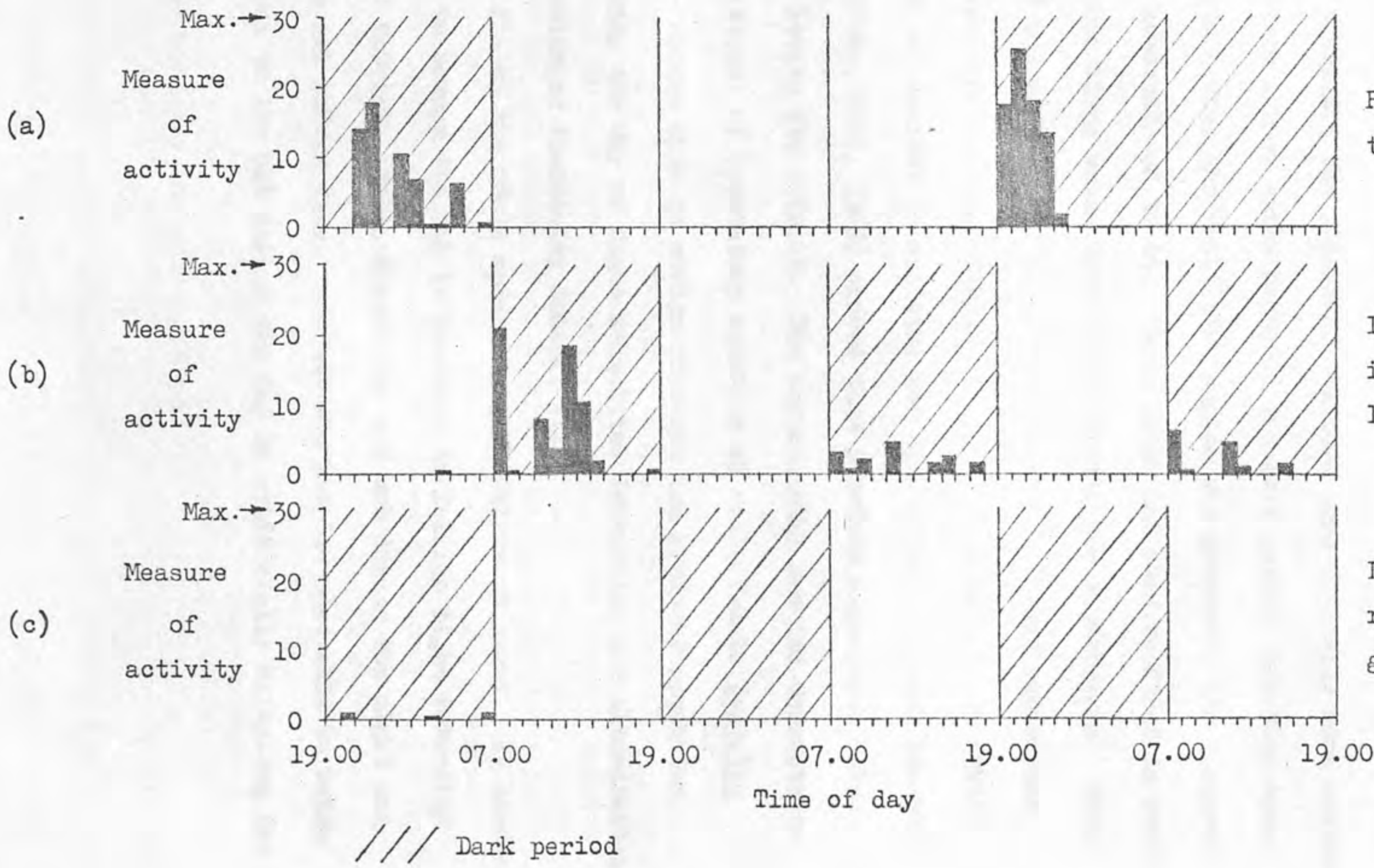
Microaktograph Experiments

Material and Method

The microaktograph consisted of an elongated activity chamber pivoted such that it tipped when the animal inside moved from one half to the other. These movements were recorded by an electrical pen recorder. The activity chamber, measuring 12.0 x 1.2 x 1.2cm., was constructed of thin, transparent, semi-rigid plastic. In order to pivot the chamber without preventing free passage within it, the middle portion of an entomological pin, sharpened at both ends, was bent into the form of a "V". The chamber was cradled in the "V" and firmly attached to the pin. The ends of the pin were freely supported in vertical slots in a specially constructed frame which restricted the angle of tip to about 7° to minimise the effect of geonegative behaviour. A photoelectric cell, shielded from other than a thin pencil of low intensity light from a variable intensity lamp, was in circuit with a 6 volt dry battery, switch, suitable resistance and a "Servoscribe Is" pen recorder. A vane attached to the chamber above the fulcrum interrupted the light when one particular end of the chamber was down, and the recorder pen moved rapidly across the paper in one or other direction each time the chamber tipped. With the recorder speed set at 30mm./hour, the degree of spider activity per hour was judged by the number of millimetres of paper covered with ink. The activity apparatus was housed in a "Griffin" cooled incubator at a temperature of 18°C., and light provided by an 8 watt "Atlas Double Life Warm White" fluorescent tube controlled by a time switch.

The spiders used were adult laboratory females, some of which had been kept throughout development in containers large enough for web-making and others in 7.0 x 2.5cm. tubes. All had spent at least three weeks prior to the experiments at 20°C. under twelve hours illumination (from 7.00 to 19.00 hours) and twelve hours darkness. Individual spiders were placed in the activity chamber at 19.00 hours and subjected to different combinations of illumination and darkness in units of twelve hours over periods of three days. No spider was used more than

Fig. 19. Activity patterns of three adult atrica females in different 12 hour light/dark regimes during a 72 hour period



Restriction of activity to dark periods.

Immediate accommodation in activity pattern to light/dark reversal.

Little activity following restriction in a small glass tube since hatching.

once.

Results

Spiders of both species were found to have very similar patterns of locomotory activity when subjected to the same experimental conditions. The patterns changed when the conditions were altered, as illustrated by the atrica examples in Fig. 19. In general, locomotion was almost completely confined to the dark periods, switching off the light often providing the stimulus. Spiders were typically more active during the first six or seven hours of the dark period, but even then only in bursts. When the dark/light regime was reversed, the spiders immediately accommodated to it. Those which had been confined in small tubes all their lives moved very little during the experiments. REED et al (1970) and WITT et al (1972) have pointed out that experience may modify behaviour through habituation and learning. SZLEP (1964) demonstrated habituation in spiders, and BAYS (1962) apparent learning. LE GUELTE (1966c, 1967, 1969) showed that previous experience helped x-notata to locate its retreat. The experimental results demonstrate the basic patterns of locomotory activity of adult female Zygiella in confined spaces such as choice chambers and gradient apparatus. Darkness during the day or night stimulates locomotion and illumination and prior prolonged inactivity inhibit it.

In the field, the adult spider is more active at night. It leaves its retreat to occupy the hub in response to falling light intensity (MARPLES and MARPLES, 1971), clears its old web during the night and builds a new web before dawn. MARPLES and MARPLES were able to bring indoor spiders to the hub during the day by artificially darkening the room.

CHAPTER VI

ENVIRONMENTAL FACTORS AND STARVATION - TOLERANCES

Various climatic factors which influence the choice of web site are undoubtedly closely linked to the physiological needs and tolerances of spiders (TURNBULL, 1973). Temperature and relative humidity preference differences between x-notata and atrica have already been demonstrated, and tolerance differences to such factors might also be expected. Tolerances to temperature extremes, evaporative water loss and starvation are investigated here.

TEMPERATURE

Spiders are very resistant to high temperatures (HOLM, 1950). However, the extent to which spiders can tolerate sub-zero temperatures and also the rate of cooling may be as ecologically important as thermal death-points (DUFFEY, 1962b). Regarding Zygiella, SAVORY (1928) suggested that x-notata does not require a higher temperature than atrica but may be able to withstand greater variation. Both species commonly overwinter in the egg stage. Some adult female x-notata successfully overwinter (WIEHLE, 1929; BRISTOWE, 1941), but not atrica (NIELSEN, 1932; BRISTOWE, 1941). In this study, the upper paralysis temperatures of both species are investigated. For dune spiders, ALMQUIST (1970) found this to be about 1°C. lower than the thermal death-point which was more difficult to fix. The effects of sub-zero temperatures on adult females and eggs are also examined.

Upper Paralysis Temperature

Material and Method

Adult female spiders were pre-adapted over seven days to a moisture-laden atmosphere at 20°C. Eleven 7.0 x 2.5cm. glass tubes were weighted with lead shot and a little water added to each to keep the atmosphere moist. A closely fitting foam plastic bung, on which the spider could walk, was inserted above the water. Five similar-sized spiders of each species were placed one to a tube, and the tubes closed with rubber bungs. The temperature in the spider compartments was read to the nearest 0.5°C. on a 50°C. mercury thermometer pushed through the bung of the remaining tube. The supported tubes were almost immersed in an electrically heated water bath and the temperature raised at about 0.4°C. per minute, commencing at 25°C. Upper thermal paralysis was denoted by lack of movement, retraction of legs and non-production of drag-line silk, followed by recovery. The experiment was repeated twice more with fresh spiders.

Results

For the fifteen spiders of each species tested, the mean x-notata upper paralysis temperature was 45°C. (s.d. = 0.8°C.), significantly higher ($P < 0.001$) than the equivalent atrica temperature of 43.6°C. (s.d. = 0.9°C.). Thus, x-notata has both a higher temperature preferendum and upper paralysis temperature than atrica. For comparison, NØRGAARD's (1951) values for the paralysis temperatures of two Lycosid spiders inhabiting a Sphagnum bog were 35°C. and 43°C., and these were reflected in their temperature preferences. ALMQUIST (1970) found that the upper temperatures for fifteen non-Argiopid dune-living species varied from 37.4°C. to 46.4°C. However, there was no correlation between the temperatures preferred and those tolerated. The upper paralysis temperature for Lycosa carolinensis, a desert species, was approximately 48°C. (MOEUR and ERIKSEN, 1972), and that for Aphonopelma, a tarantula, was 43°C. (SEYMOUR and VINEGAR, 1973). The value for x-notata especially is high when compared with these mainly ground-living species. Other Argiopid values were not available for comparison.

The Length of Life of Adult Females kept at -2°C.

Material and Method

Adult females were collected from the field in mid-November. They were kept in individual tubes at 10°C. for seven days and liberally fed. Twenty of each species were then placed above saturated $MgCl_2.6H_2O$ solution (R.H. = 34%) at -2°C. and a similar number at 10°C. as controls. The spiders were no longer fed. The numbers alive each day were noted. It was found necessary to warm the -2°C. tubes a few degrees each time to distinguish living spiders, there being little or no spider movement at -2°C.

Results

Adult female x-notata survived for much longer at -2°C. than atrica, eighteen days compared with five days for 50% survival (Table 17).

Table 17. Mortality of adult female spiders at -2°C.

Temperature	Species	No. of spiders	No. of days before 50% and 100% mortality	
			50% mortality	100% mortality
-2°C.	x-notata	20	18	32
	atrica	20	5	14
10°C.	x-notata	20	>32	>32
	atrica	20	>32	>32

As only 10% x-notata and 25% atrica had died after 32 days at 10°C., it seems that lack of food was not responsible for death at the lower temperature. The results tend to confirm field observations regarding Zygiella survival during the late autumn and winter months.

Viability of Eggs kept at -2°C.

Material and Method

Eggs laid outside in December were collected at the end of that month and two hundred apparently fertile ones for each species were selected at random for this experiment. One hundred of each were placed above saturated $MgCl_2.6H_2O$ at 20°C., and the percentage noted which hatched. Another one hundred eggs were similarly placed at -2°C. (the lowest available temperature). Twenty were randomly selected at the end of every four weeks, placed at 20°C. and the percentage which hatched again noted. Over periods of up to twenty weeks at -2°C. it was possible to calculate the percentage of eggs which remained viable.

Results

Comparing the percentage of eggs which hatched after increasing periods at -2°C. (Table 18), no significant differences were found between the species.

Table 18. Percentage of eggs hatching at 20°C. after varying periods at -2°C.

Species	Percentage of eggs hatching after periods at -2°C.					
	0 days	28 days	56 days	84 days	112 days	140 days
x-notata	97	75	60	65	50	55
atrica	89	75	50	70	60	50

For each species, n = 100 at 0 days
n = 20 at 28 to 140 days

For both, even after twenty weeks, at least 50% of eggs remained viable. Eggs of both species could withstand sub-zero temperatures of this order far better than adult females, and this was especially marked in *atrica*. At what phase in the life cycles this increased ability is lost has not been examined, but one might assume that at least larval and first nymph spiders are quite resistant to sub-zero temperatures, for both species may over-winter in these stages in addition to the egg stage.

EVAPORATION OF WATER

Argiopids are very resistant to desiccation (NEMENZ, 1954; DUFFEY, 1962b). In both *Zygiella* species in dry air the rate of evaporation below the critical temperature is low (DAVIES and EDNEY, 1952). They suggested that the critical temperature is between 34°C and 36°C for *atrica* and somewhat higher for *x-notata*, and that the rate of weight loss thereafter increases much more rapidly in *atrica* than *x-notata*. Because of the importance of these findings, the evaporation rates have been studied in detail.

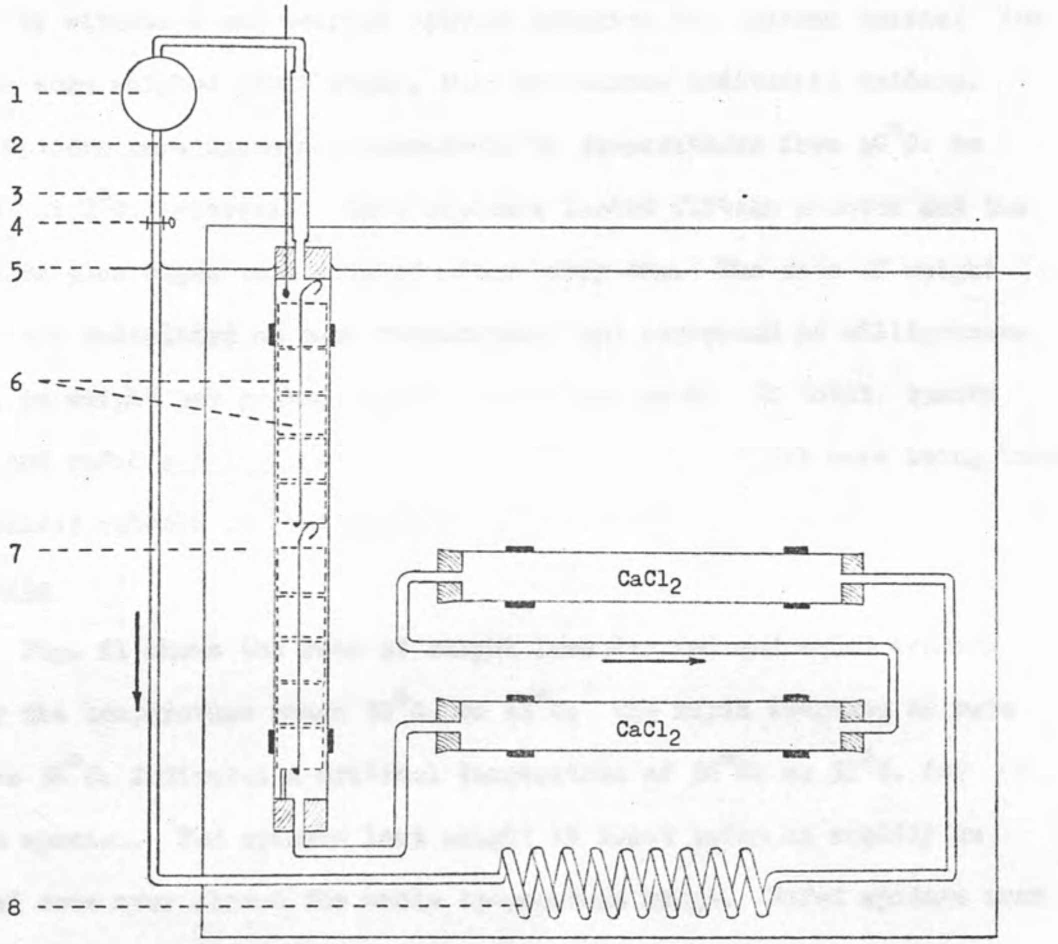
Evaporation Rates in Dry Air at Different Temperatures

Material and Method

In the following experiments involving the measurement of spider weight loss in dry air at different temperatures, decrease in weight was taken as a measure of water lost by evaporation. No spiders defaecated during the experiments, although "vomiting" was occasionally noted in spiders in other circumstances when exposed to lethal high temperatures. Half the adult females collected for the experiments were liberally fed on *Drosophila* and used within one day of collection; the others were not fed and were used ten days after collection.

The apparatus used (Fig. 20) was a modified version of that described by EDNEY (1951). Modifications included non-corrosive wire gauze spider cages, a flow-meter to measure air flow, and horizontal

Fig. 20. Apparatus for measuring the rate of evaporation from spiders under controlled temperature and humidity conditions



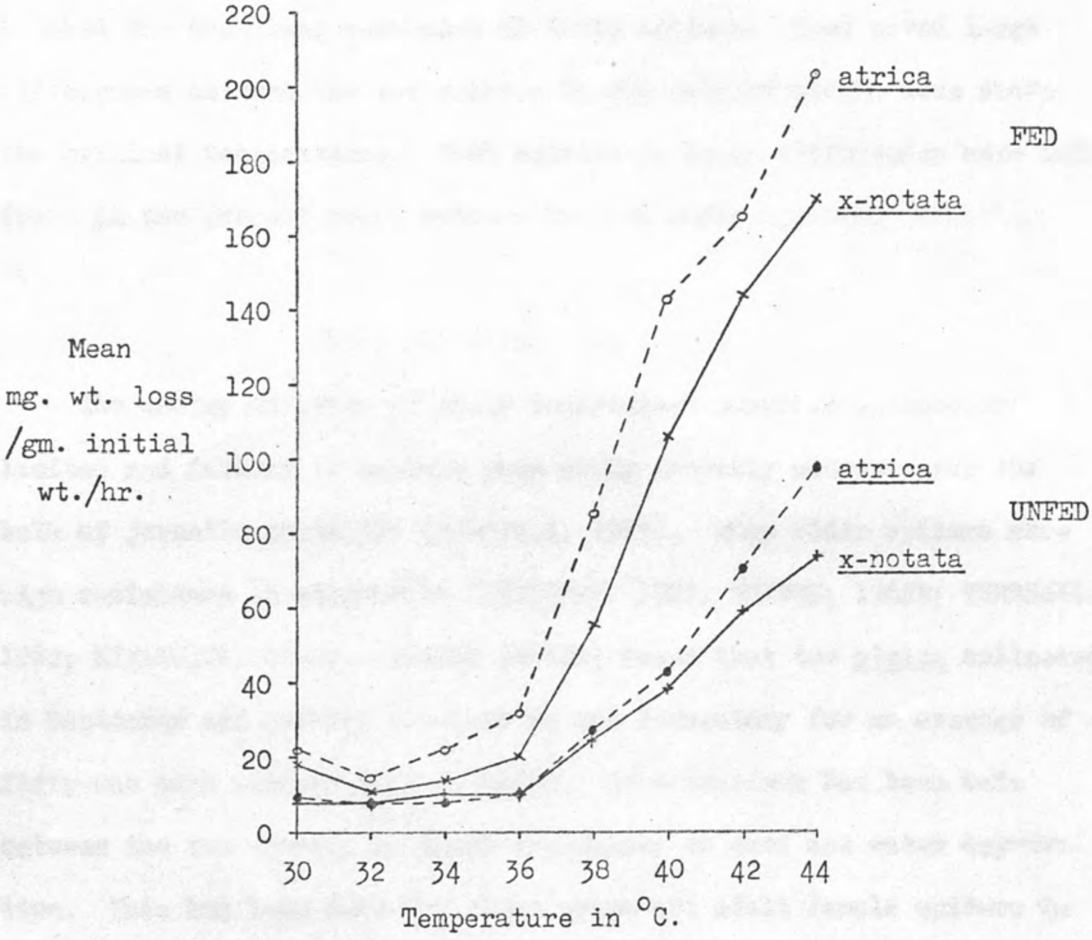
1 = Air pump
2 = Thermometer
3 = Flow-meter
4 = Screw clip to control air flow
5 = Water level of water bath
6 = Wire gauze cages containing experimental animals
7 = Board
8 = Copper coil

instead of vertical calcium chloride tubes to prevent clogging. Air was pumped round the apparatus at about one litre per minute. It was warmed by almost total immersion of the apparatus in a controlled temperature water bath and dried by passing through granular calcium chloride. The spider cages were in two groups of five and could be rapidly withdrawn and weighed without damaging the spiders inside. Ten cages were weighed first empty, then containing individual spiders. The spiders were exposed successively to temperatures from 30°C. to 44°C. at 2°C. intervals. Each exposure lasted fifteen minutes and the spiders plus cages were weighed after every one. The rate of weight loss was calculated at each temperature, and expressed as milligrammes loss in weight per gramme initial weight per hour. In total, twenty fed and unfed x-notata and atrica were compared, initial care being taken to select spiders of similar size and weight.

Results

Fig. 21 shows the rate of weight loss for fed and unfed spiders over the temperature range 30°C. to 44°C. The rapid increase in rate above 36°C. indicates a critical temperature of 36°C. or 37°C. for both species. Fed spiders lost weight at least twice as rapidly as unfed ones over almost the whole temperature range. Unfed spiders were initially partly dehydrated and therefore would have less available water to lose. Whether fed or not, atrica lost weight at a greater rate above 36°C. than x-notata, but in general, differences in rates seemed to depend more on the physiological state of the spiders than on the species. That the weight loss in fed spiders was higher at 30°C. than 32°C. might be explained by their activity when first placed in the apparatus. Otherwise, spiders were generally inactive during the experiment. Book lung spiracles are opened widely in moving spiders but are almost closed in quiescent ones (ROBINSON and PAIM, 1969). That relatively little water loss occurs from the book lungs in

Fig. 21. The rate of weight loss with increasing temperature of fed and unfed spiders



n = 20 for each reading

quiescent spiders has been demonstrated by PALMGREN (1939), DAVIES and EDNEY (1952) and NEMENZ (1954). With the book lung spiracles permanently open, water loss may be increased by 50% to 100% (DAVIES and EDNEY, 1952; CLOUDSLEY-THOMPSON, 1957). The difference in the critical temperatures of the two species was smaller than that noted by DAVIES and EDNEY (1952). Direct comparison of the rate of weight loss in the two investigations cannot be made, for DAVIES and EDNEY used different units, temperatures and field spiders at each temperature, and also blocked the book lung spiracles of these spiders. They noted large differences between the two species in the rate of weight loss above the critical temperatures. Such relatively large differences were only found in the present study between fed and unfed spiders.

FOOD AND WATER DEPRIVATION

The energy reserves of newly independent juvenile spiders are limited and failure to capture prey early probably accounts for the bulk of juvenile mortality (TURNBULL, 1973). Many older spiders show high resistance to starvation (BRISTOWE, 1929; DUFFEY, 1962b; TURNBULL, 1962; MIYASHITA, 1968). DUFFEY (1962b) found that two atrica collected in September and October survived in the laboratory for an average of fifty-one days without food or water. No comparison has been made between the two species in their tolerances to food and water deprivation. This has been done for first nymph and adult female spiders in this study.

Survival Time of Unfed First Nymph Spiders
at Different Temperatures

Material and Method

Immediately after the moult from larvae to first nymphs, twenty laboratory-raised spiders were placed in individual tubes inside large screw-top jars at each of the following temperatures, viz. 10°, 15°, 20° and 25°C. The relative humidities were maintained at about 34% with saturated $MgCl_2.6H_2O$ solution. The survival time of each spider was noted. Death was recognised as for upper thermal paralysis by lack of movement, leg contraction and non-production of dragline silk, but there was no subsequent recovery.

Results

In both species, the mean survival time decreased with rising temperature (Table 19), possibly as a result of increased metabolic and evaporation rates.

Table 19. The survival time of first nymphs without food or water, at constant humidity but different temperatures

Temperature	Species	No. of spiders	Survival time in days	
			mean	s.d.
10°C.	x-notata	20	91.0	38.3
	atrica	20	72.9	22.4
15°C.	x-notata	20	50.7	16.3
	atrica	20	45.4	9.5
20°C.	x-notata	20	44.4	13.6
	atrica	20	31.0	7.6
25°C.	x-notata	20	37.8	8.7
	atrica	20	23.7	5.5

Evaporation is very restricted in spiders at low temperatures (EDNEY, 1952). Increase in metabolic rate with temperature has been demonstrated in spiders and other poikilotherms (NEWELL, 1966; ANDERSON, 1970; MOEUR and ERIKSEN, 1972; SEYMOUR and VINEGAR, 1973), although the Q_{10} value was found to be generally low. At all temperatures tested, x-notata lived longer than atrica, significantly so ($P < 0.001$) at

20°C. (43.2% longer) and 25°C. (59.5% longer). Before leaving the egg cocoon, young spiders of some species feed on unhatched eggs (JUBERTHIE, 1954; PECK and WHITCOMB, 1970). This was not evident in Zygiella. Spiders leaving the cocoon still have substantial yolk in their abdomen (TURNBULL, 1973). Whether x-notata yolk reserves are greater than atrica at this time is not known, but comparison of the mean diameter of ten x-notata eggs from each of twenty cocoons ($\bar{x}$ = 1.035mm., s.d. = 0.075mm., n = 200) with that of a similar number of atrica eggs ($\bar{x}$ = 0.970mm., s.d. = 0.035mm., n = 200) shows that x-notata eggs are larger ($P < 0.001$).

Survival Time and Weight Loss of Unfed Adult Female Spiders at Constant Temperature and Relative Humidity

Material and Method

Adult female spiders were collected from the field in late September. They were kept at 20°C. and 34% R.H., each in a 7.0 x 2.5cm. glass tube with a foam plastic stopper. They were liberally fed on Drosophila. After seven days, each was weighed to the nearest 0.5mg. Twenty of each were no longer fed; ten were fed to act as controls. Individuals were weighed every two days and the day they died.

Results

These are given for the unfed spiders in Table 20. The mean survival period of 41.9 days for x-notata was significantly greater ($P < 0.01$) than the 31.7 days for atrica. Although x-notata lost relatively more weight before death than atrica (47.9% compared with 42.7%), the percentage loss per day was less (1.14% compared with 1.35%). WITT (1963) found that one of three Argiopid species (quite possibly x-notata) was still capable of building webs when 49% of the body weight had been lost. The lethal percentage weight losses of both x-notata and atrica are high compared with the 20% to 31% for various non-Argiopids (PALMGREN, 1939; PALMEN and SUOMALAINEN, 1945; CLOUDSLEY-THOMPSON, 1957; LAGERSPETZ and JÄYNÄS, 1959).

Table 20. The number of days survival and percentage weight loss of unfed adult female spiders

Species	No. of spiders	No. of days survival		% loss in weight before death	
		mean	s.d.	mean	s.d.
x-notata	20	41.9	10.8	47.9	9.7
atrica	20	31.7	10.8	42.7	8.7

Spiders break down body tissues during food deprivation (WITT et al, 1968). Many Zygiellae under investigation undoubtedly contained eggs. Observation showed that a spider may lose up to half its weight when egg-laying, and therefore some of the weight lost during starvation may have been due to egg breakdown. During the starvation period, the rate of weight loss was not constant, but decreased with time. This emphasizes again the importance of selecting spiders in the same physiological state for comparative experiments.

CHAPTER VII

TEMPERATURE AND RELATIVE HUMIDITY IN THE FIELD

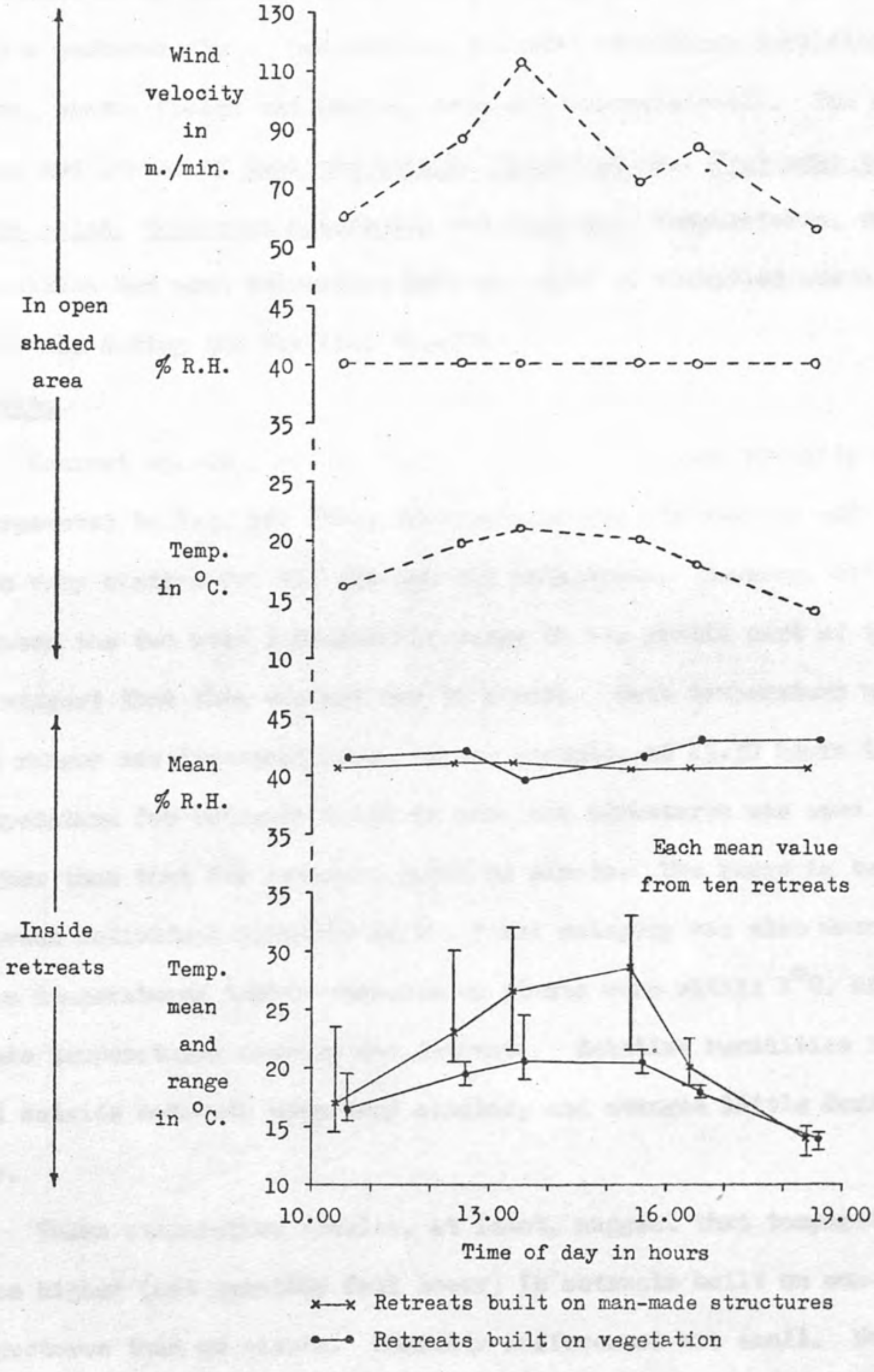
Laboratory experiments have indicated differences between *x-notata* and *atrica* in their temperature and relative humidity preferences and tolerances. These differences might be related to the climatic conditions found at permanent web sites, bearing in mind that microclimates experienced by spiders may be very different from the prevailing macroclimates (see reviews by CLOUDSLEY-THOMPSON, 1962 and TURNBULL, 1973). It has been shown that *atrica* typically builds webs on vegetation whereas *x-notata* often selects man-made structures. SAVORY (1928) suggested that humidity changes and exposure to winds must be more severe, and daily temperature extremes less severe on bushes than on the sides of houses. BRISTOWE (1939) pointed out that compact foliage or dense vegetation provides shelter from wind and prevents both temperature and humidity extremes. DAVIES and EDNEY (1952) suggested that temperatures rise higher and humidities fall lower in buildings than hedgerows, although they acknowledged the lack of precise information.

Zygiella spends daylight hours in the retreat. During the summer and autumn of 1972 and 1973, field measurements were made of temperatures and relative humidities inside occupied retreats in various habitats. Of the many recordings made, three examples are presented here. On a warm October day in a suburban garden, conditions were compared inside *x-notata* retreats built on man-made structures and on plants. For comparison, recordings were made on a day with similar weather conditions in *atrica* retreats built on *Ulex europaeus*. Finally, temperatures and relative humidities were measured during a very hot summer day in x-notata retreats constructed on iron railings. The values illustrate especially the high temperatures which spiders encounter on such structures in these conditions. Retreats were chosen within a restricted height range of 1.3 - 1.8 metres, for height above the ground is one of many factors known to influence air temperature (KROGERUS, 1932; GEIGER, 1961; NØRGAARD, 1951; LAKE, 1956; MACFADYEN, 1963).

Measurement of Temperature and Relative Humidity in the Field

Temperatures in the retreats were recorded to the nearest 0.5°C. using a portable 'M type Telemax 1050' electrical thermometer, with a 1mm.^{3} sensor probe pushed through the rear retreat exit to within three millimetres of the spider. Relative humidities were measured to the nearest five per cent using cobalt thiocyanate paper and comparing with colour standards from a 'Lovibond' humidity test kit by Tintometer Ltd., Salisbury, England (SOLOMON, 1957). A 5mm. x 4mm. strip of paper was placed in the retreat above and behind the spider, left for an hour, then stored in liquid paraffin until comparison could be made. In each experiment, temperatures and relative humidities were measured at suitable time intervals during daylight hours both in the retreats and in a neighbouring shaded open area 1.5 metres above the ground, for comparison. Wind velocities were measured at the same spot with a 'Low speed, 1000 ft. (305m.)/min. maximum, Type LS2' air meter by Baird and Tatlock Ltd., the meter being exposed for one minute per reading. This gave an indication of wind conditions at intervals throughout the day, but not necessarily those experienced by spiders inside their retreats.

Fig. 22. Microclimatic conditions inside and outside x-notata retreats constructed on man-made structures and vegetation in a suburban garden at Greenford, Middx. - 5th October 1972



Microclimatic Conditions in x-notata Retreats in a Suburban Garden, Greenford, Middx.

Material and Method

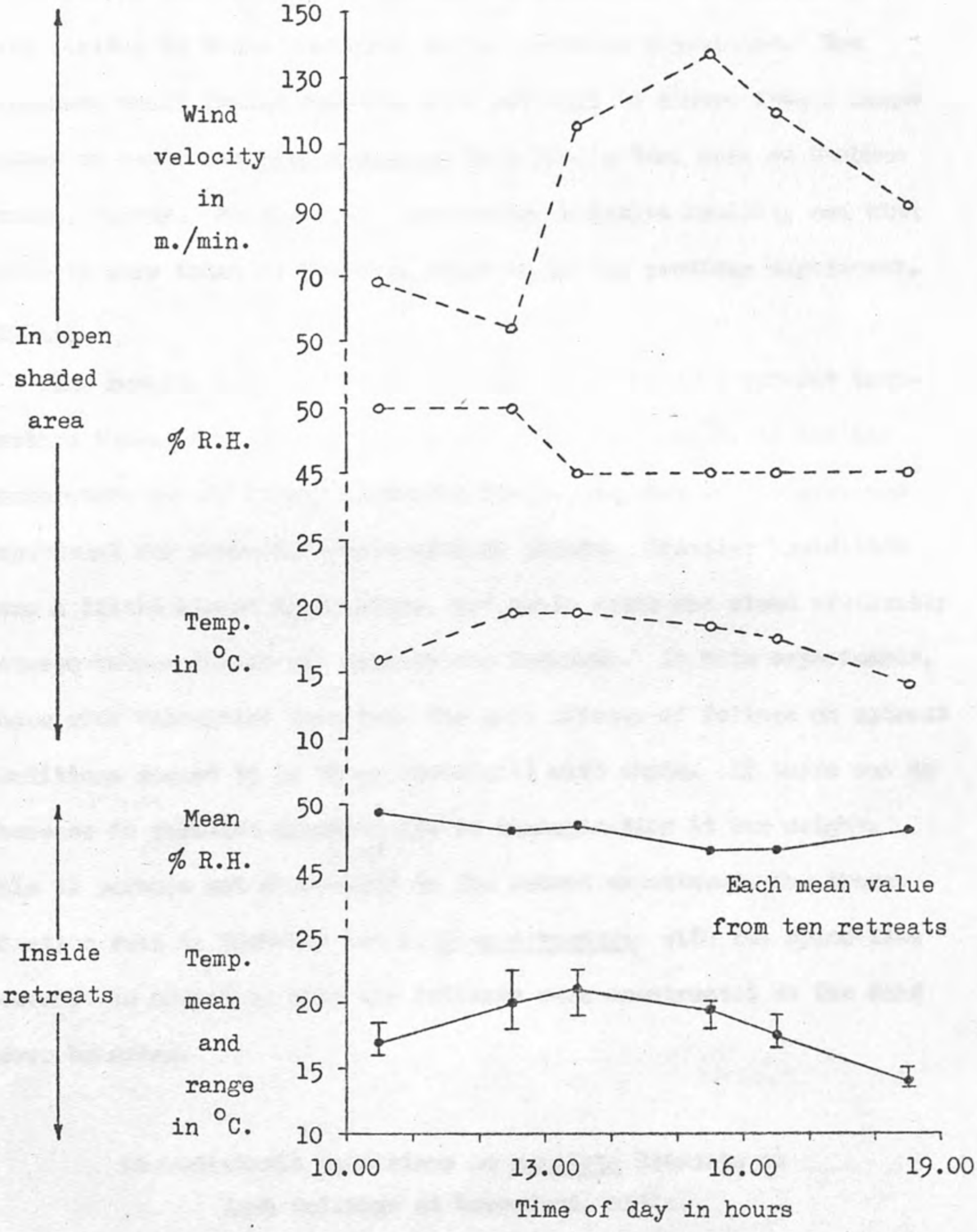
On 5th. October 1972, a fine day with an east to north-east breeze, twenty permanent, adult female retreats were selected from a number of different sites in a sheltered, south-facing garden, and each marked with a numbered flag. Ten were on man-made structures including shed eaves, window frames and wooden, iron and concrete posts. Ten were on twigs and leaves of *Lonicera nitida*, *Ligustrum* sp., *Crataegus monogyna*, *Picea abies*, *Cupressus macrocarpa* and *Rosa* sp. Temperatures, relative humidities and wind velocities were measured as described above at intervals during the day (see Results).

Results

Retreat measurements of temperature and relative humidity are represented in Fig. 22. Mean temperatures for mid-morning and evening were very similar for the two habitat categories. However, differences between the two were sufficiently large in the middle part of the day to suggest that this was not due to chance. Both temperature means and ranges are important here. As an example, at 15.30 hours the mean temperature for retreats built on man-made structures was some 8°C. higher than that for retreats built on plants. The range in temperature between individual retreats in the first category was also much greater. Mean temperatures inside retreats on plants were within 1°C. of the shade temperatures outside the retreats. Relative humidities inside and outside retreats were very similar, and changed little during the day.

These comparative results, at least, suggest that temperatures rise higher (and possibly fall lower) in retreats built on man-made structures than on plants. Humidity differences are small. Many factors affect air temperature and humidity, and therefore these

Fig. 23. Microclimatic conditions inside and outside *atrica* retreats constructed on *Ulex europaeus* at Chobham Common, Surrey - 3rd October 1972



conclusions should be extended to other situations with caution.

Microclimatic Conditions in atrica Retreats built on Ulex europaeus at Chobham Common, Surrey

Material and Method

October 3rd. 1972 was a day with general weather conditions very similar to those mentioned in the previous experiment. Ten permanent adult female retreats were selected at random from a large number on scattered Ulex europaeus in a 50m. x 30m. area on Chobham Common, Surrey. Readings of temperature, relative humidity and wind velocity were taken at the same times as in the previous experiment.

Results

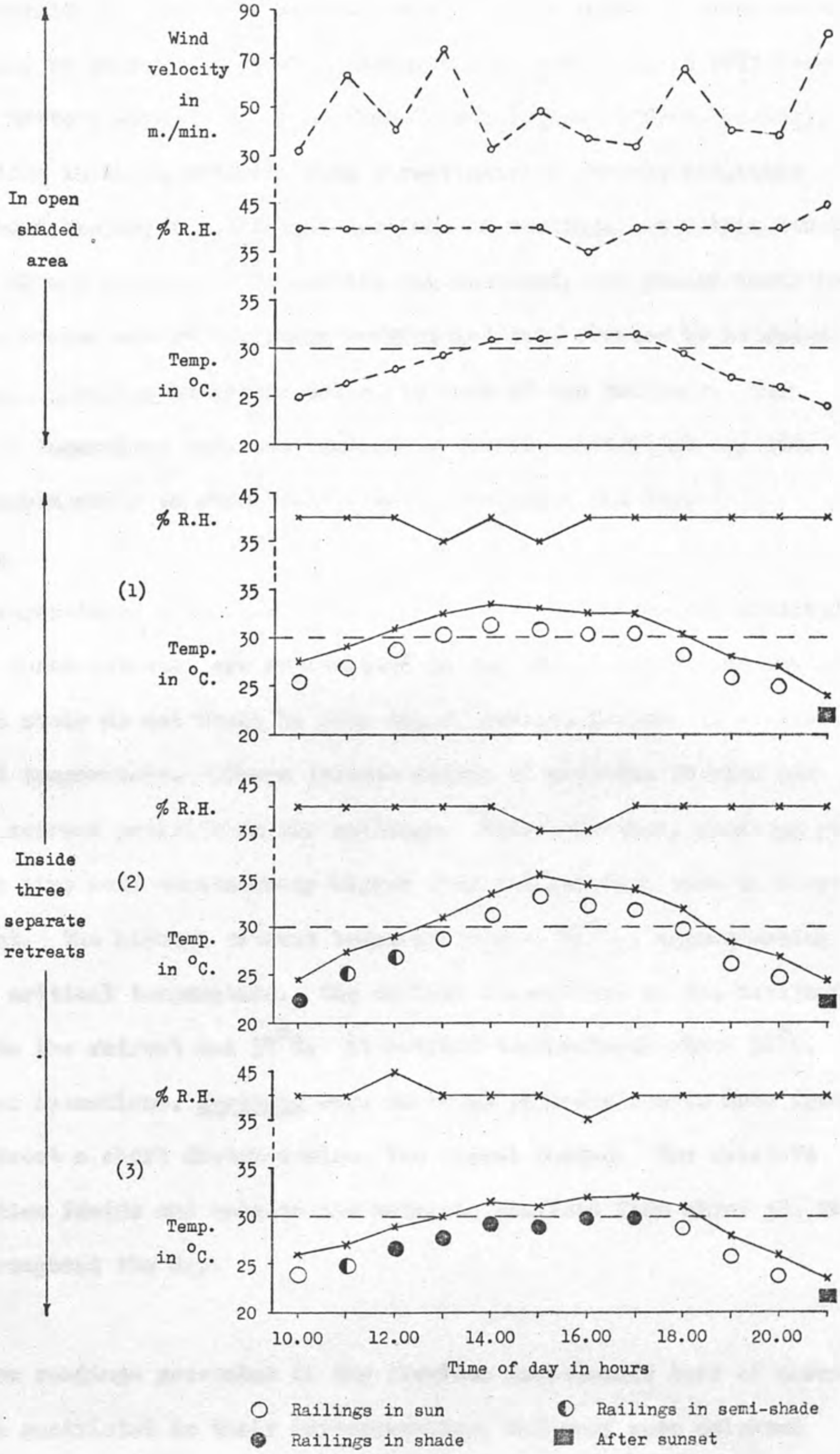
The results are represented in Fig. 23. The mean retreat temperature throughout the day was in general within 1.5°C. of the air temperature in the shade, a similar finding to that of the previous experiment for retreats constructed on plants. Relative humidities were a little higher than before, but again there was close similarity between values inside and outside the retreats. In both experiments, where wind velocities were low, the main effects of foliage on retreat conditions seemed to be those associated with shade. If there was an increase in relative humidity due to transpiration it was slight. This is perhaps not unexpected in the second experiment, for transpiration rate is probably low in Ulex europaeus with its spine-like leaves. In addition, half the retreats were constructed on the dead lower branches.

Microclimatic Conditions in x-notata Retreats on Iron Railings at Greenford, Middx.

Material and Method

A large population of x-notata inhabited an east/west stretch

Fig. 24. Microclimatic conditions inside and outside _x-notata_ retreats constructed on iron railings at Greenford, Middx. - 14th August 1973



of dark green iron railings at Greenford. The railings formed the boundary between a road and adjoining fields. The retreats built on the underside of the upper horizontal bar of the railings were protected laterally by downward projecting flanges. On 14th. August 1973 (one of the hottest days of the year from Meteorological Office records), conditions in three retreats were investigated at hourly intervals throughout the day on different sections of railings but within twenty metres of one another. One section was unshaded, one shaded until noon and one shaded except for early morning and late evening by adjacent Crataegus monogyna bushes on the south side of the railings. The retreats themselves were not exposed to direct sunlight at any time. There was a south to south-west breeze throughout the day.

Results

Temperatures and relative humidities measured at hourly intervals in the three retreats are represented in Fig. 24. Whether the railings were in shade or not would be only one of several factors to influence retreat temperature. Others include degree of exposure to wind and actual retreat position on the railings. Never-the-less, readings at any one time were consistently higher when the railings were in direct sunlight. The highest retreat temperature was 35½°C., approximating to the critical temperature. The surface temperature of the railings close to the retreat was 37°C. At retreat temperatures above 36°C. in other situations, x-notata were observed on occasions to move from the retreat a short distance along the signal thread. The relative humidities inside and outside the retreats remained from about 35% to 45% throughout the day.

The readings presented in the previous experiments must of necessity be restricted in their interpretation, but they were selected from numerous others to illustrate specific points. The three particular habitat sites were chosen because one or other species was very common at each of them, and therefore conditions in general presumably suited at least that particular species. In August 1972, forty female atrica were placed on a section of the iron railings at Greenford which had been cleared of x-notata. None could be found one week later. In the same month, fifty male and female atrica were placed in the suburban garden at Greenford, mainly on Cupressus macrocarpa and Picea abies previously cleared of x-notata. All had disappeared by the middle of October, except for one found under shed eaves in November. No young atrica were noted the following year. In an attempt to preserve the atrica population at Chobham Common, and because x-notata had been found at sites elsewhere apparently similar to Chobham, no experimental x-notata were introduced onto the Common.

CHAPTER VIII

FACTORS AFFECTING DEVELOPMENT

The literature review has indicated that the life cycles of x-notata and atrica are basically similar. However, the times quoted for cocoon emergence, attainment of maturity, mating and so on suggest that the cycles are not identical, and this could be significant in ecological isolation, habitat selection and degree of interspecific competition in mixed populations.

When studying spider life cycles, the following points are important. Males tend to moult fewer times than females (BONNET, 1930; LEVY, 1970) and smaller species fewer times than larger ones (BONNET, 1935; LEVY, 1970). When raised under apparently similar conditions, spiders from the same cocoon may differ in the number of nymphal stages (BONNET, 1930) or grow at different rates (WITT et al, 1968). Important extrinsic factors which have been shown to modify spider development are temperature, humidity and feeding rate. Growth rate increases with temperature (BONNET, 1926), and with both temperature and humidity (BROWNING, 1941; JONES, 1941; PECK and WHITCOMB, 1970). Length of life decreases as the temperature increases (ALLEE et al, 1949; DONDALE, 1961). Growth rate increases with higher feeding rate and the animals are larger and die earlier (BONNET, 1930; TURNBULL, 1962; and for x-notata, WITT, 1956; LE GUELTE, 1963, 1966b). At lower feeding rates, the number of nymphal stages is increased in some species (BONNET, 1930, DEEVEY, 1949; MIYASHITA, 1968), but not in Agelenopsis potteri Bl. (TURNBULL, 1965). Tables in LE GUELTE (1966b) suggest that in x-notata, the number decreases. No such values are available for atrica.

The ratio of males to females reaching maturity depends on the feeding rate (FLORIS, 1936; MONTEROSSO and FLORIS, 1936; BONNET, 1938).

In this study, the effects of temperature and humidity on egg development, and temperature and light on emergence of first nymphs from cocoons (a very photopositive stage) have been investigated. So too have the effects of temperature on all other developmental stages, and of different feeding rates on the nymphal and adult stages.

FACTORS AFFECTING EGG DEVELOPMENT

Observation has shown that both species may pass the winter in the egg, larval or first nymphal stages. Temperature, and to a lesser extent humidity, are known to affect the rate of development of spiders, and their effect on egg development in *Zygiella* are investigated here.

Effect of Temperature on Egg Development

Material and Method

For each species, thirty newly-laid fertile eggs were selected from each of five cocoons. Five eggs from each cocoon were placed in darkness at 10°C., 15°C., 20°C., 25°C., 27½°C. and 30°C. The relative humidity was controlled at about 33% at all temperatures by placing the tubes above saturated $MgCl_2 . 6H_2O$ solution in screw-topped jars (WINSTON and BATES, 1960). The percentage hatching and the development times were noted. Hatching was taken as completed when the spider was free from the egg membranes except for attachment at the spinnerets.

Results

Eggs of neither species survived at 30°C. (Table 21). At 27½°C., nearly half the *x-notata* eggs hatched, but no *atrica* eggs. As the temperature decreased from 25°C. to 15°C., the percentage hatching in both species increased, the higher temperatures favouring *x-notata*. At 15°C. and 10°C., more *atrica* hatched. The mean incubation period increased with falling temperature most markedly at 10°C. At all temperatures below 27½°C., the period was longer in atrica than x-notata. However, the percentage difference in length between the species decreased from 52% at 25°C. to 38% at 20°C., 20% at 15°C. and 12% at 10°C.

Table 21. Length of incubation period and percentage of eggs hatching at constant humidity (33% R.H.) but different temperatures

Temp. in °C.	x-notata eggs				atrica eggs			
	No. of eggs	Incubation period in days		% hatching	No. of eggs	Incubation period in days		% hatching
		mean	range			mean	range	
30	25	-	-	-	25	-	-	-
27½	25	10.5	10-11	44	25	-	-	-
25	25	11.5	11-12	60	25	17.5	17-19	48
20	25	14.5	14-15	76	25	20.0	19-22	72
15	25	25.5	25-27	80	25	30.5	29-33	88
10	25	72.5	65-79	76	25	81.0	76-95	88

Results indicate that prior cooling is not required before eggs will hatch, and also that there is no diapause.

Effect of Humidity on Egg Development

Material and Method

The previous experiment was repeated, but at constant temperature (20°C.) and different relative humidities, viz. 13%, 33%, 56% and 85%. The latter were controlled by saturated salt solutions (WINSTON and BATES, 1960). The length of the incubation period and the percentage of eggs hatching were again noted.

Results

These are presented in Table 22.

Table 22. Length of incubation period and percentage of eggs hatching at constant temperature (20°C.) but different relative humidities

% Relative humidity	*x-notata* eggs			*atrica* eggs		
	No. of eggs	Incubation period in days	% hatching	No. of eggs	Incubation period in days	% hatching
85	25	14-15	92	25	19-21	80
56	25	14-15	92	25	19-21	88
33	25	14-15	76	25	19-22	72
13	25	15-16	60	25	21-23	40

The main effect of relative humidity on the length of incubation appeared to be at the lowest value tested, that of 13% R.H. Compared with 33% R.H., for example, the incubation period increased by approximately one day (7%) in *x-notata* and two days (10%) in *atrica*. Fewer eggs hatched in drier air. Only two-thirds as many *x-notata*, and half as many *atrica* hatched at 13% R.H. as at 85% R.H. It seems unlikely that such low values as 13% R.H. would commonly occur inside *Zygiella* cocoons.

FACTORS AFFECTING LARVAL DEVELOPMENT

The larval stage immediately follows the egg stage and is completed within the cocoon. It lasts only about four days at 20°C., too short a time for there to be measurable differences at different relative humidities. However, an investigation into the effect of temperature on larval development time is described below.

Effect of Temperature on Larval Development

Material and Method

Numerous eggs were kept at 20°C. and 33% R.H. Groups of twenty larvae hatching from the eggs were placed at 10°C., 15°C., 20°C. and 25°C., and at 33% R.H. The duration of the larval stage was noted at each temperature.

Results

As in the case of eggs, larvae developed more slowly as the temperature decreased from 25°C. to 10°C. (Table 23).

Table 23. Length of the larval stage at constant humidity (33% R.H.) but different temperatures

Temperature	*x-notata*			*atrica*		
	No. of larvae	Length of larval stage in days		No. of larvae	Length of larval stage in days	
		mean	range		mean	range
25°C.	20	3.5	3 - 4	20	3.5	3 - 4
20°C.	20	4.5	4 - 5	20	4.5	4 - 5
15°C.	20	6.5	6 - 7	20	6.5	6 - 7
10°C.	20	25.5	23 - 29	20	26.0	23 - 28

The greatest change was from 15°C. to 10°C., development taking about four times as long. Unlike eggs, there was no significant difference between the species in larval development time at any of the four temperatures investigated.

There were no mortalities during the experiment. As no food was given, the larvae were probably utilizing yolk reserves in their bodies.

FACTORS AFFECTING THE EMERGENCE OF FIRST NYMPHS FROM COCOONS

Zygiella first nymphs emerge from the cocoons in April or May. Some nymphs have spent part of the previous autumn and all the winter inside the cocoon. Increasing temperature and day length in spring might well be factors stimulating cocoon emergence.

Effect of Temperature on Emergence

Material and Method

Egg cocoons were carefully collected from outside in autumn. They were lightly glued to the foam plastic stoppers of small glass tubes. The tubes were placed in darkness at 20°C. and 33% R.H. Five days after egg cases could be discerned through the cocoon walls ie. approximately at the time of moulting from larvae to first nymphs, eight cocoons of each species were placed at 10°C., 15°C. and 20°C., again in darkness and 33% R.H. The total number of spiders emerging from each cocoon per day and any which finally failed to emerge were noted.

Results

Table 24. The mean emergence time and percentage emergence of first nymphs from cocoons placed in darkness at 33% R.H. but different temperatures

Species	Temp.	No. of cocoons	Total spiders in cocoons	% spiders emerging	E_{50} for each cocoon in days	Mean E_{50} in days
x-notata	20°C.	8	321	89	23, 22, 24, 27, 19, 20, 26, 17.	22
	15°C.	8	258	91	28, 24, 40, 49, 44, 32, 27, 50.	37
	10°C.	8	249	76	68, 63, 87, 75, 62, 63, -, -.	70
atrica	20°C.	8	259	93	19, 21, 17, 15, 12, 25, 8, 22.	17
	15°C.	8	254	91	37, 26, 45, 31, 43, 55, 38, -.	39
	10°C.	8	232	75	64, 70, 73, 89, 77, 82, -, -.	76

Differences in temperature greatly affected emergence time, the mean E_{50} value approximately doubling for each 5°C. drop in temperature between 20°C. and 10°C. (Table 24). At each temperature, there was a large variation in the cocoon E_{50} values. Once emergence from a cocoon began, it took many days for completion. In five cocoons, of which four were at 10°C., less than half the spiders actually emerged. The average period from the beginning to completion of emergence for x-notata and atrica respectively was 19 and 17 days at 20°C., 29 and 28 days at 15°C., and 38 days for both at 10°C. The over-all results show close similarity between the species.

LE GUELTE (1962) found that x-notata at 20°C. emerged before those at 17°C., indicating again the importance of temperature. No mention was made of any extended period taken for completion of emergence, which in the field may only take a few hours. Observation suggests that fluctuating temperatures are important. Spiders do not eat their way out of the cocoon. By mass movement of the spiders inside, the cocoon wall stretches and finally parts. Fluctuating temperatures seem to stimulate activity to a greater extent than steady temperatures, even relatively high ones. ENDERS (1972) suggested that before spiderlings leave their cocoons, a form of diapause may have to be broken, but this is not confirmed in the above experiments.

Effect of Light on Emergence

Material and Method

The previous experiment carried out at 15°C. and 33% R.H. in darkness was repeated under a constant diffuse illumination of about 350 lux. The number of spiders emerging per day was noted as before.

Results

Although emerging spiders are very photopositive, the mean E_{50} values at 15°C. for cocoons in the light (Table 25) are slightly

Table 25. The mean emergence time and percentage emergence of first nymphs from cocoons placed in light at 33% R.H. and 15°C.

Species	Temp.	No. of cocoons	Total spiders in cocoons	% spiders emerging	E_{50} for each cocoon in days	Mean E_{50} in days
x-notata	15°C.	8	234	86	32, 35, 43, 51, 39, 49, 45, 31.	41
atrica	15°C.	8	254	84	43, 26, 50, 30, 49, 62, 45, -.	44

higher than for those in the dark. Constant illumination does not stimulate emergence, but *Zygiella* first nymphs when they do emerge move towards the light (McCOOK, 1890).

Humidity seems to play little or no part in stimulating emergence in *Zygiella*, unlike *Epeira (Mangora) gibborosa* which only emerges if the relative humidity is above 90% (WEESE, 1924).

FACTORS AFFECTING DEVELOPMENT OF NYMPHAL AND ADULT STAGES

Reference has been made to the influence of different feeding rates and temperatures on development in some spiders. These factors are investigated in both *Zygiella* species.

The Effects of Different Feeding Rates and Temperatures on Development

Material and Method

Groups of *x-notata* and *atrica* spiders were reared at one of two different feeding rates. "Poorly fed" groups were given female wild-type *Drosophila melangaster* at the rates of one twice a week for nymphal stages one and two, one plus two for stages three and four, and two twice a week for stages five and six. "Moderately fed" groups were given *Drosophila* at the rates of three twice a week for stages one and two, four twice a week for stages three and four, and five twice a week for stages five and six. Dead flies were removed at each feed. All spiders were watered twice weekly by moistening the foam plastic bungs of the 7.0 x 2.5cm. glass tubes in which they were individually kept. Throughout, they were subjected to alternate twelve hours light (about 325 lux) and darkness, and to a constant temperature of 25°C., 20°C. or 10°C. 15°C. was not available. For each spider note was made of the number of stages, length of each stage and the sex.

The number of stages was also noted for two "well fed" groups at 20°C. which were given excess Drosophila. Spider size was compared in moderately fed and poorly fed groups by reference to tibia I length.

Results

The experimental results provided information on various aspects of the development of spiders raised under controlled conditions of feeding and temperature.

(A) Developmental stage at which maturity is reached

Results show (Table 26) that at 25°C. the majority of x-notata and atrica males and females in all groups matured at stage five.

Table 26. The effect of feeding rate and temperature on the stage at which x-notata and atrica mature

Species	Sex	Feeding rate	No. of spiders		% spiders reaching maturity at developmental stage 4, 5 or 6					
			25°C.	20°C.	25°C.			20°C.		
					4	5	6	4	5	6
x-notata	M	W.F.	-	20	-	-	-	20	70	10
		M.F.	19	22	-	95	5	50	50	-
		P.F.	17	19	-	100	-	74	26	-
	F	W.F.	-	14	-	-	-	-	43	57
		M.F.	18	16	-	67	33	19	69	12
		P.F.	18	19	-	100	-	42	42	16
atrica	M	W.F.	-	17	-	-	-	-	100	-
		M.F.	12	16	-	100	-	12	88	-
		P.F.	10	15	-	100	-	13	87	-
	F	W.F.	-	15	-	-	-	7	60	33
		M.F.	18	20	-	100	-	20	80	-
		P.F.	11	19	9	91	-	26	74	-

(W.F. = well fed)
Degree of feeding (M.F. = moderately fed) see text for details.
(P.F. = poorly fed)

This was also true for atrica at 20°C. but not for x-notata, where feeding rate greatly influenced the stage at which the spiders matured. From the 25°C. and 20°C. results only, the trend, evident in both species but more pronounced in x-notata, was for spiders to mature at an earlier stage at 20°C. and low feeding rate, and at a later stage at 25°C. and high feeding rate. No spiders reached maturity at 10°C. They were very inactive and Drosophila were seldom captured. At the higher temperatures, Drosophila usually were captured. This illustrates that the amount of food supplied and that actually consumed are not necessarily correlated.

That less well fed spiders of both species tend to reach maturity at an earlier stage is in general agreement with the x-notata results of LE GUELTE (1966b), although he appeared not to find spiders maturing as early as stage four.

(B) Length of developmental stages at different feeding rates and temperatures

Of the moderately fed and poorly fed spiders at 25°C. and 20°C., the majority in most groups matured at stage five. The mean lengths of the developmental stages for these spiders are included in Table 27. Also included are values for spiders at 10°C., none of which reached maturity. In the latter spiders, development was very slow, with most stages taking over one hundred days. Different feeding rates seemed to have little effect on the length of a stage, probably because the spiders were almost too inactive to catch Drosophila. The survival powers were greater in x-notata than atrica.

At both 25°C. and 20°C., there was little difference between the species in their rates of development when spiders raised at the same feeding rate were compared. However, within a species, at different feeding rates, better fed spiders matured more quickly, for example, in two-thirds of the time at 25°C. Development was faster at 25°C.

Table 27. Length of developmental stages at different feeding rates and temperatures

Temp.	Sex	Species	Feeding rate	Length of developmental stage in days															Mean no. of days to reach maturity
				Stage 1			Stage 2			Stage 3			Stage 4			Stage 5			
				$\bar{x}$	s.d.	n	$\bar{x}$	s.d.	n	$\bar{x}$	s.d.	n	$\bar{x}$	s.d.	n	$\bar{x}$	s.d.	n	
25°C.	M	x-notata	M.F.	23	2.7	19	12	1.5	19	14	2.4	19	18	2.4	18	71	34.2	16	67
			P.F.	24	1.3	18	14	2.3	18	30	9.1	18	34	6.8	17	83	26.7	16	102
		atrica	M.F.	22	3.6	16	13	1.6	16	15	2.6	16	20	2.3	12	13	5.9	5	70
			P.F.	28	6.5	15	17	5.5	15	25	6.4	15	34	5.8	10	10	4.2	2	104
	F	x-notata	M.F.	23	2.2	12	13	2.7	12	15	2.4	12	28	6.4	12	103	40.2	10	79
			P.F.	25	3.5	18	18	6.1	18	31	9.2	18	54	20.7	18	84	41.6	18	128
		atrica	M.F.	23	4.1	18	13	1.7	18	17	6.1	18	21	4.5	18	62	23.5	14	74
			P.F.	30	5.1	10	19	9.3	10	31	6.9	10	42	15.6	10	27	13.2	3	122
20°C.	M	x-notata	M.F.	47	4.0	11	15	3.1	11	17	3.2	11	20	2.0	11	99	40.5	10	99
			P.F.	49	6.0	5	18	4.5	5	28	9.2	5	38	14.0	5	92	32.1	5	133
		atrica	M.F.	53	4.4	14	14	3.2	14	17	4.1	14	22	5.0	14	29	19.4	14	106
			P.F.	51	4.3	14	14	2.3	14	19	4.5	14	34	5.9	13	40	25.0	12	118
	F	x-notata	M.F.	47	3.7	11	14	2.4	11	19	3.2	11	24	4.0	11	124	76.0	10	104
			P.F.	48	3.2	8	19	3.9	8	27	6.1	8	63	16.6	8	85	73.6	7	157
		atrica	M.F.	54	4.4	16	14	2.8	16	17	3.3	16	23	3.8	16	103	48.0	16	108
			P.F.	48	5.0	14	18	3.9	14	25	5.9	14	39	11.3	14	90	45.2	14	130
10°C.	M and F	x-notata	M.F.	133	52.4	32	110	38.2	17	93	11.3	6	110	-	1	4	-	1	-
			P.F.	99	57.2	38	141	41.1	24	115	29.6	17	65	-	1				-
		atrica	M.F.	164	43.8	12	114	26.5	7	132	-	1							-
			P.F.	118	49.2	23	119	15.9	5										

M.F. = moderately fed, P.F. = poorly fed.

than 20°C., mainly because of a much shorter first nymphal stage. Why this was so was not absolutely clear, but at 25°C. first nymphs built webs earlier. Later nymphal stages were able to capture flies trapped in drag-line silk, there being insufficient space to build webs. Except for poorly fed female *atrica* at 20°C., the adult *atrica* did not live for as long as their *x-notata* counterparts. In males at least, this may be partly because they refused to eat. In the field, on several occasions, mature *atrica* males were seen to take insects from the female webs on which they were residing.

These general findings agree with those cited by other authors for other spiders already mentioned at the beginning of the chapter.

(C) Temperature, feeding rate and the percentage of spiders reaching maturity

The percentage of spiders reaching maturity varied greatly with temperature and feeding rate. From groups of forty moderately fed and poorly fed first nymphs at 10°C., none reached maturity or even the final moult. Table 28 shows the results for spiders raised at 20°C. and 25°C. Because of the rather high mortality of *atrica* first nymphs at 25°C., first nymphs in all groups which died were replaced to ensure that forty successfully moulted to stage two. Except for the *atrica* groups at 25°C., 80.0% to 92.5% of spiders in all others reached maturity. At 25°C., only 41.3% and 14.6% of the moderately fed and poorly fed *atrica* groups respectively reached the adult stage. Death occurred both during and between moults, but especially during the final moult. 80.0% of the poorly fed sub-adult *atrica* males and 54.5% females died at this time. The females were unable to extract their legs, and the males had great difficulty with their very long pedipalps. It would seem that the exuvial fluid evaporated before the appendages could be fully withdrawn. This has been reported in other species (WHITCOMB, 1967; HORNER and STARKS, 1972).

Table 28. The effect of temperature and feeding rate on the percentage of spiders reaching maturity

Temp.	Species	Feeding rate	No. of first nymphs	No. reaching final moult			No. reaching adult stage			% reaching final moult	% reaching adult stage	% sub-adults dying during final moult	
				M.	F.	Total	M.	F.	Total			M.	F.
25°C.	x-notata	M.F.	40	18	18	36	17	15	32	90.0	80.0	5.6	16.7
		P.F.	41	17	18	35	16	18	34	85.4	82.9	5.9	-
	atrica	M.F.	46	12	18	30	5	14	19	65.2	41.3	58.3	22.2
		P.F.	48	10	11	21	2	5	7	43.7	14.6	80.0	54.5
20°C.	x-notata	M.F.	40	22	16	38	21	16	37	95.0	92.5	4.5	-
		P.F.	40	19	19	38	18	18	36	95.0	90.0	5.3	5.3
	atrica	M.F.	40	16	20	36	16	20	36	90.0	90.0	-	-
		P.F.	41	15	19	34	14	19	33	82.8	80.5	6.7	-

M.F. = moderately fed. M. = male.
P.F. = poorly fed. F. = female.

Feeding rate did not greatly influence the proportion of males to females reaching maturity at either of the two temperatures.

(D) Feeding rate and spider size

Tibia I length was used in the assessment of spider size. The species were compared at each of the two feeding rates, "moderately fed" and "poorly fed". The effect of feeding rate on spider size in each species separately was also investigated. Little difference was observed in spiders raised at 25°C. and 20°C., and the results were combined. Not all spiders were measured in early developmental stages. In later ones, because of mortalities, results in some cases were boosted by measurements taken of spiders in "reserve" groups. At all stages, where selection for measurement was necessary, it was randomly made.

At the higher feeding rate, <u>x-notata</u> tibia I length was significantly greater (at the 5% level) than <u>atrica</u> at all developmental stages (Table 29a). Differences were highly significant ($P < 0.001$) in sub-adults and adults. There was a roughly parallel situation at the lower feeding rate (Table 29b). Tibia I lengths, together with other measurements such as carapace width and body length and weight taken during this study indicated that in these particular experimental conditions at least, <u>x-notata</u> males and females were larger than their <u>atrica</u> counterparts.

Comparing separately the <u>x-notata</u> and <u>atrica</u> results in Tables 29a and 29b, feeding rate had a large effect on spider size. No significant difference was apparent at stages one (as expected) or two, but from three onwards in both species, moderately fed spiders were significantly larger ($P < 0.001$). Of interest, the mean sizes of field spiders (Appendices 1 and 2) were broadly equivalent to a feeding rate between the two experimental rates, except for field sub-adult and adult male <u>atrica</u> which were much larger. Possibly, the new cuticle hardened in

Table 29. Comparison of tibia I length in *x-notata* and *atrica* throughout their development

(a) Moderately fed spiders

Nymphal stage	Species	Sex	No. of spiders	Length of tibia I in mm.		Comparison of mean tibia I length using t-test	
				$\bar{x}$	s.d.	t	P
1	*x-notata*	M & F	30	0.385	0.033	2.279	<0.05
	atrica	M & F	30	0.367	0.028		
2	*x-notata*	M & F	28	0.643	0.045	2.213	<0.05
	atrica	M & F	26	0.615	0.049		
3	*x-notata*	M & F	25	1.000	0.095	2.658	<0.025
	atrica	M & F	26	0.996	0.076		
4	*x-notata*	M	26	1.863	0.183	6.300	<0.001
	atrica	M	23	1.543	0.172		
	x-notata	F	20	1.608	0.129	7.323	<0.001
	atrica	F	17	1.347	0.086		
adult	*x-notata*	M	26	2.913	0.168	13.469	<0.001
	atrica	M	21	2.329	0.129		
	x-notata	F	28	2.061	0.175	4.088	<0.001
	atrica	F	32	1.897	0.129		

(b) Poorly fed spiders

Nymphal stage	Species	Sex	No. of spiders	Length of tibia I in mm.		Comparison of mean tibia I length using t-test	
				$\bar{x}$	s.d.	t	P
1	*x-notata*	M & F	30	0.382	0.034	1.691	>0.05
	atrica	M & F	30	0.368	0.030		
2	*x-notata*	M & F	28	0.625	0.046	1.118	>0.10
	atrica	M & F	26	0.610	0.051		
3	*x-notata*	M & F	18	0.942	0.084	0.973	>0.10
	atrica	M & F	26	0.917	0.084		
4	*x-notata*	M	24	1.556	0.126	7.784	<0.001
	atrica	M	18	1.283	0.101		
	x-notata	F	28	1.382	0.078	5.013	<0.001
	atrica	F	18	1.242	0.100		
adult	*x-notata*	M	19	2.426	0.169	7.089	<0.001
	atrica	M	17	2.012	0.180		
	x-notata	F	14	1.813	0.120	3.003	<0.01
	atrica	F	19	1.682	0.129		

laboratory conditions before expansion of the leg segments had been fully completed. Female field spiders of both species typically matured one stage later than laboratory spiders. Differences in quantity (and quality) of food probably explain in part why leg length in adult female x-notata, for example, varied greatly in works of different authors (SIMON, 1874; PETERS, 1951; FRANK, 1957; LE GUELTE, 1964; LE GUELTE, 1966b). As indicated earlier, different feeding rates certainly result in different sized spiders in other species.

CHAPTER IX

COMPARATIVE LIFE CYCLES IN THE FIELD

Literature quoted in the INTRODUCTION seems to point to temporal differences between equivalent phases of x-notata and atrica life cycles. However, these works from authors in several countries are mainly non-comparative and the information sparse. It was therefore decided to compare life cycles in the field and this was done over two consecutive cycles from the latter part of 1971 to early 1974. Because of the very few mixed or adjacent populations which were discovered, the relatively small number of atrica in them and the difficulty in separating the species in the early nymphal stages, the study was carried out on two large, single-species populations.

Each year, the investigation followed the same pattern. Note was made of when the egg cocoons appeared, the average number of eggs per cocoon, the stage of development inside the cocoons in the middle of January after egg-laying was completed, and the degree of cocoon parasitism at that time. After the emergence of first nymph spiders in spring, their rates of development were followed through the season. Changes in spider numbers were investigated during the second cycle to discover when spider losses occurred. Finally, courtship and mating behaviour were closely studied.

STUDY SITES

Mention has been made in earlier chapters of the selected x-notata and atrica sites. They were particularly suitable because of the large number of spiders at each, a necessary pre-requisite in this type of study.

The *x-notata* site was at Greenford, Middlesex (Map ref. TQ134836). A large population (several hundreds in early summer) lived on dark green iron railings bordering the A40 trunk road where it crossed the Grand Union Canal. The railings were approximately 780 metres long and 1.6 metres high. Very few other spiders lived permanently on the railings except for a small population of *Araneus sclopetarius* Cl. next to the canal bridge. The structure of the railings was of interest. The 2.0 cm. square vertical bars protruded through and were supported 12.0 cm. apart by upper and lower horizontal bars. The horizontal bars had downward projecting flanges, and were ┌─┐-shaped in cross-section. Typically, retreats were built in the flange angles of the upper bar with the webs below. The height and shape of the upper bar and the distance between the vertical bars made possible the building of retreats and webs throughout the life cycle. Sections of railings were selected for the study of egg cocoons, stages of spider development and spider numbers throughout the season. Details are given later.

The *atrica* site was at Chobham Common, Surrey, a large open undulating area of about six and a half square kilometres lying in the ten kilometre square SU96 of the National Grid. MURPHY and MURPHY (1973) describe the area as mostly covered with *Calluna vulgaris* L. (ling), *Erica cinerea* L. (bell heather), *E. tetralix* L. (cross-leaved heather) and such coarse grasses as *Molinia caerulea* L. These authors found *atrica* to be fairly common on *Pinus sylvestris* L. but no mention was made of its frequent presence on *Ulex europaeus* L. It was more commonly found on this plant near or at the tops of the undulations. Members of the Thomisidae and Theridiidae especially, together with *Araneus diadematus* Cl. as the other main Argiopid, were found in similar situations. Suitable areas of *U. europaeus*, of which more details appear later, were selected for the different parts of the study outlined above.

Period of Egg-Laying and Number of Cocoons per Spider

In both species each clutch of eggs is laid close to the retreat and enclosed in a silken cocoon, the outer threads of which are pale golden brown. Observation suggested that cocoons adjacent to a particular retreat were constructed by the same spider.

Material and Method

From late summer 1971 onwards and again in 1972, on a well-populated section of railings, note was made when and where *x-notata* cocoons appeared in order to discover the period of egg-laying and the number of cocoons adult female spiders constructed.

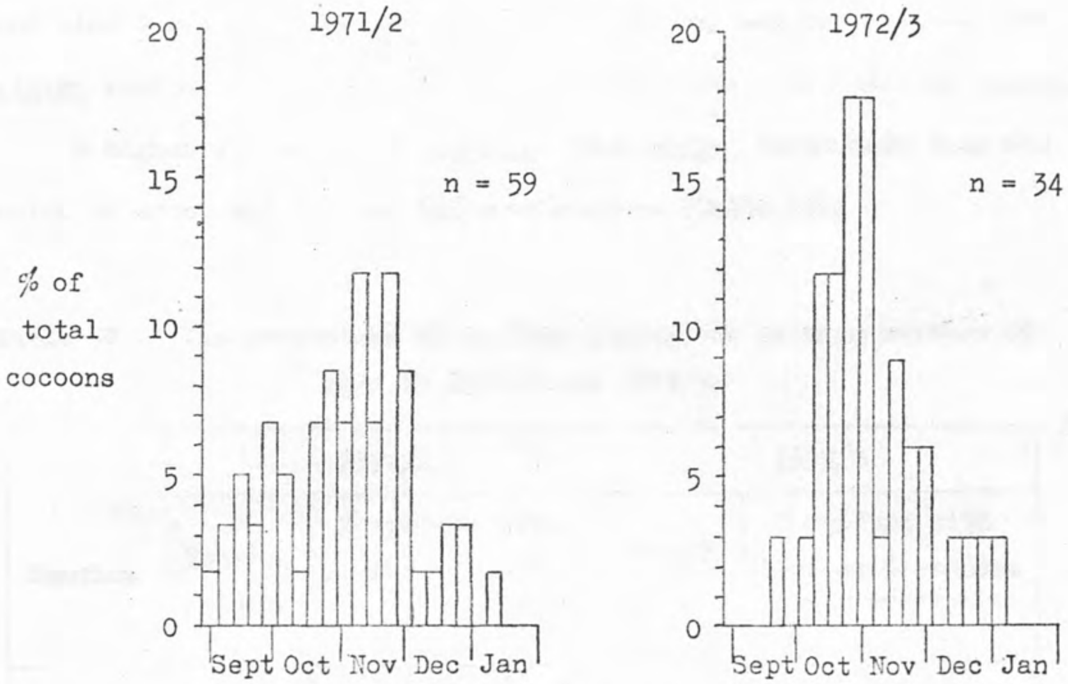
A parallel investigation was carried out on *atrica* cocoons but this was more difficult because of the nature of *Ulex europaeus* on which the spiders lived. A populated area of *U. europaeus* was chosen which consisted of small individual clumps, none more than 1.9 metres high. A plan of the area was made and cocoons plotted weekly as they appeared. Each cocoon position was marked on the plant with a twist of plastic-covered wire. The operation was tedious, but positions of webs and retreats helped in the location of cocoons. Unlike *x-notata* on the railings, some *atrica* cocoons on *U. europaeus* were doubtless undiscovered.

Results

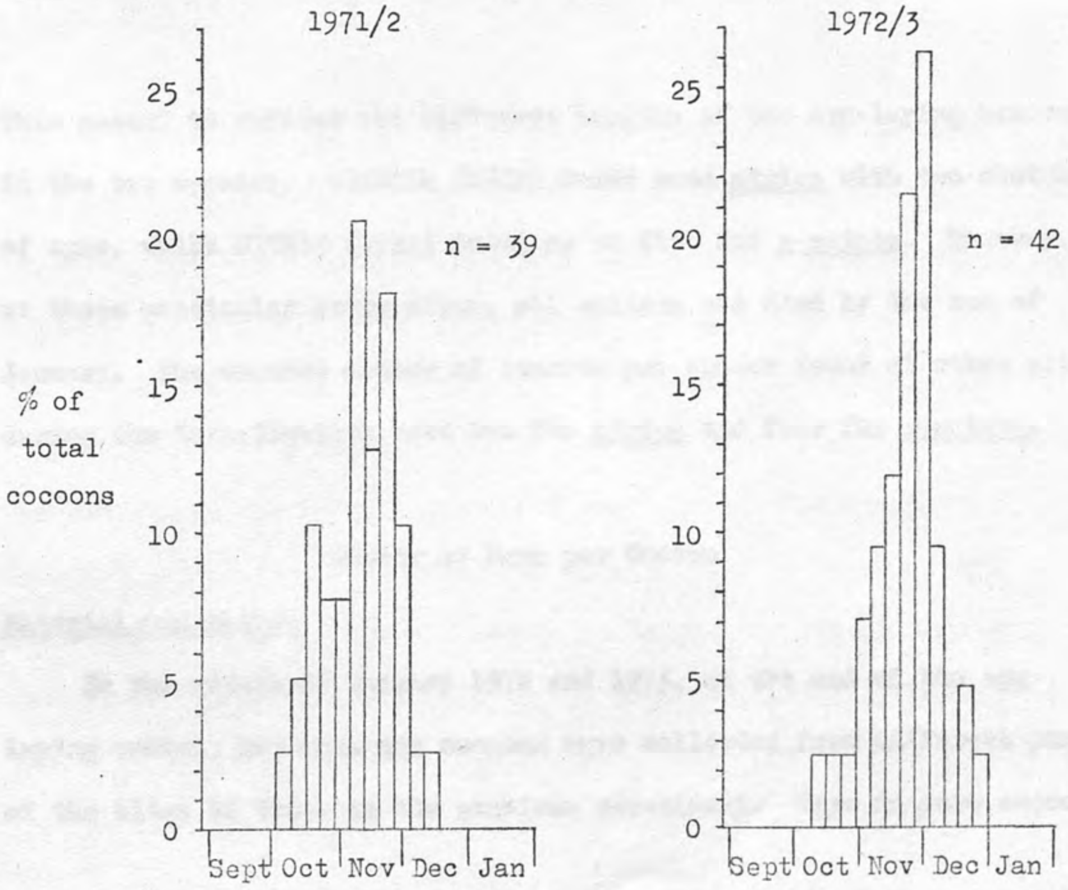
The appearance of egg cocoons in the two seasons is shown in histogram form in Fig. 25. Each weekly number is expressed as a percentage of the total cocoons for the season. The species totals are not strictly comparable. In both seasons, egg-laying began earlier and finished later in *x-notata* than *atrica*. For example, in 1971/2

Fig. 25. Weekly appearance of egg cocoons in 1971/2 and 1972/3

x-notata



atrica



x-notata was laying from late August to early January, whereas the *atrica* egg-laying period was from early October to mid-December. The period also started later in 1972/3, probably because early development was slow during the previous cold and windy May and early June. The *atrica* peak of egg-laying was almost three weeks after that of *x-notata*.

A higher proportion of *x-notata* than *atrica* layed more than one batch of eggs, but one was the most common, (Table 30).

Table 30. The percentage of spiders laying one or more batches of eggs in 1971/2 and 1972/3

	1971/2				1972/3			
Species	Total spiders	% spiders with 1, 2 or 3 cocoons			Total spiders	% spiders with 1, 2 or 3 cocoons		
		1	2	3		1	2	3
x-notata	50	84	14	2	29	83	17	-
atrica	39	100	-	-	40	95	5	-

This seemed to reflect the different lengths of the egg-laying season in the two species. NIELSEN (1932) found some *atrica* with two clutches of eggs, while WIEHLE (1931) noted up to five for *x-notata*. However, at these particular study sites, all spiders had died by the end of January. The maximum number of cocoons per spider found at other sites during the investigation were two for *atrica* and four for *x-notata*.

Number of Eggs per Cocoon

Material and Method

In the middle of January 1972 and 1973, at the end of the egg-laying period, numerous egg cocoons were collected from different parts of the sites to those in the previous experiment. Eggs in some cocoons had hatched. Some cocoons had been parasitised by ichneumon flies. However, the parasitic grubs left egg membranes behind and therefore it was possible to calculate the number of eggs originally laid in each cocoon.

Results

The mean numbers of eggs in x-notata cocoons in 1971/2 and 1972/3 were almost identical, 38.7 and 38.3 respectively, (Table 31).

Table 31. Mean number of eggs laid in x-notata and atrica cocoons collected in mid-January 1972 and 1973

Species	Date cocoons collected	No. of cocoons	Total eggs laid	Eggs laid per cocoon		
				$\bar{x}$	s.d.	range
x-notata	16-1-72	80	3097	38.7	11.0	23-68
	17-1-73	55	2104	38.3	11.5	18-63
atrica	17-1-72	70	3187	45.5	16.1	19-91
	18-1-73	75	2705	36.1	13.2	12-83

The mean number of eggs in atrica cocoons was significantly greater ($P < 0.001$) in 1971/2 than in 1972/3, 45.5 compared with 36.1. However, combining the total 1971/2 and 1972/3 figures for x-notata and atrica separately, then comparing their means of 38.5 and 40.6 eggs per cocoon respectively indicated no significant difference between the species ($P > 0.1$). The two species seem not to have been directly compared in the literature regarding egg numbers per cocoon. For x-notata, BRISTOWE (1939) gives an average of 30 eggs from 10 batches, and NIELSEN (1932) 54 eggs from 8 batches. Ranges for atrica eggs vary from 80-90 (BLACKWALL, 1864) to 17-103 (NIELSEN, 1932). The high numbers have been confirmed in this study.

In some species, the first batch of eggs is the largest and subsequent ones contain progressively fewer eggs (BRISTOWE, 1958; COOKE, 1965a; EMERIT, 1965; MIKULSKA and JACUNSKI, 1968; TURNBULL, 1973). No particular pattern was found in either *Zygiella* species, thus confirming the *x-notata* findings of LE GUELTE (1966b).

Stage of Development inside Cocoons Collected in Mid-January 1972 and 1973

Material and Method

The coldest weather of the year is expected in January and February in Great Britain. Analysis of cocoons collected in mid-January 1972 and 1973 gave an indication of the developmental stages which pass through this period. Only cocoons containing living stages were included.

Results

In mid-January 1972, eggs had hatched in over half the *x-notata* cocoons, and in almost 43% the first nymphal stage had been reached (Table 32).

Table 32. Developmental stages of spiders inside cocoons collected in mid-January 1972 and 1973

Species	Date cocoons collected	Total cocoons	% cocoons containing different developmental stages				
			Eggs	Eggs + larvae	Larvae	Larvae + first nymphs	First nymphs
x-notata	16-1-72	75	42.7	4.0	10.6	-	42.7
	17-1-73	55	92.8	-	3.6	-	3.6
atrica	17-1-72	61	100.0	-	-	-	-
	18-1-73	74	100.0	-	-	-	-

In 1973, eggs had hatched in only about 7% of the cocoons, and in only half of these had the first nymphal stage been reached. It may be recalled that egg-laying began earlier in the 1971/2 season

(Fig. 25). No eggs had hatched in any of the *atrica* cocoons in either year. It would seem that factors such as the time of laying, mildness or otherwise of the weather after laying and the shorter incubation period in *x-notata* determine which developmental stages overwinter in the cocoon. These results show that *x-notata* at least does not strictly belong to the group of spiders, proposed by MILLOT (1949) and JUBERTHIE (1958), which overwinter in the egg stage.

Degree of Parasitism of Cocoons by Ichneumon Fly Larvae

There are many parasites of both spiders and spider eggs (BRISTOWE, 1941; EASON et al, 1967; EVANS, 1969 and ASKEW, 1971). These authors plus NIELSEN (1923, 1928, 1929, 1932) and HORSTMANN (1970) mention Hymenopterous ichneumon flies as some of the more important parasites. Ichneumon larvae found in egg cocoons are commonly classed as egg parasites although they may well be termed egg predators. Such larvae were found in *Zygiella* cocoons during this study. No other egg parasites were observed.

Material and Method

Some of the cocoons collected in mid-January contained ichneumon larvae. These were fed on spider eggs in the laboratory and identified when adult.

Results

The parasitic larvae were identified as *Tromatobia oculatoria* Fab. and *Ocymorus similis* Gmel., known parasites of both *Zygiella* species. Of the two parasites, *T. oculatoria* was by far the most common (Table 33). In other circumstances, BRISTOWE (1941) and EVANS (1969) found *O. similis* to be as common as *T. oculatoria*. The degree of parasitism was much greater in 1971/2 than 1972/3. In 1971/2, approximately 16% *x-notata* and 26% *atrica* cocoons were parasitised.

Table 33. Ichneumonidae parasitising *x-notata* and *atrica* egg cocoons in mid-January 1972 and 1973

Species	Date	Total cocoons	% cocoons parasitised	No. of parasitic larvae per cocoon	Parasite
x-notata	16-1-72	80	16.3	1 x 6 p. 6 x 1 4 x 2 2 x 3	*O. similis* *T. oculatoria* " "
	17-1-73	55	-	-	-
atrica	17-1-72	70	25.7	10 x 1 p. 6 x 2 2 x 3	*T. oculatoria* " "
	18-1-73	75	5.3	1 x 1 p. 2 x 2 1 x 5	" " "

In about half, all the eggs had been destroyed. Observation showed that *T. oculatoria* larvae frequently consumed all the eggs before they themselves pupated, a fact noted by NIELSEN (1923).

Other than *Zygiella*, *Araneus diadematus* Cl. is a host for *O. similis* (BRISTOWE, 1941). *T. oculatoria* has several other hosts including *A. diadematus*, *A. cucurbitinus* Cl. and *Cyclosa conica* Pall. (NIELSEN, 1923; BRISTOWE, 1941).

Rate of Spider Development through the 1972/3 and 1973/4 Seasons

Material and Method

On sections of iron railings and patches of *Ulex europaeus*, a maximum of fifty *x-notata* and fifty *atrica* respectively were selected at random each week during the 1972/3 and 1973/4 seasons. The stage of development was ascertained from tibia I length, as described in

Table 34. Stage, gender and number of field spiders collected weekly throughout 1972/3

				May					June				July					August				September					October				November				December					January		
	Stage	Sex	Adult	29	6	13	20	27	3	10	17	24	1	8	15	22	29	5	12	19	26	2	9	16	23	30	7	14	21	28	4	11	18	25	2	9	16	23	30	6	13	20
x-notata	1	M&F	-	23	50	48	44	47	37	12	3	1																														
	2	M&F	-			2	6	3	13	38	47	29	16	6	1																											
	3	M&F	-									20	34	38	27	22	3																									
	4	M	-											2	13	11	19	15	2																							
		F	-											4	9	14	28	26	9	3	1																					
	5	M	A															2	8	11	6	12	9	6	8	2	2															
			-																																							
		F	A																	1		1		2		1	2	2	2	2	2	3	2	2	3	2	3	1	1			2
			-													3		7	31	19	12	12	7	6	3	5			1	2		3										
	6	M	A																																							
			-																																							
		F	A																	16	31	25	34	36	39	42	46	48	47	46	48	44	48	48	47	48	47	38	33	22	18	3
			-																																							
atrica	1	M&F	-				7	50	50	50	49	46	7	2	2																											
	2	M&F	-								1	4	43	47	29	19	6	2																								
	3	M&F	-											1	19	31	32	10	11	4	2		2																			
	4	M	-														6	21	15	17	17	15	22	11	11	1			2													
		F	-														6	16	24	15	10	15	2		3			1	1													
	5	M	A																			3	2	8	5	17	16	20	19	12	7	9	3		2							
			-																																							
		F	A															1		6	11	7	7	12	8	9	11	8	7	16	17	11	20	22	20	7	3	2				
			-																	8	10	7	13	13	11	14	10	4	6	5	9	8	2	2								
	6	M	A																																							
			-																																							
		F	A																			3	2	6	12	9	13	17	15	17	17	22	25	26	28	14	3		3		1	
			-																																							

Table 35. Stage, gender and number of field spiders collected weekly throughout 1973/4

				May					June					July				August				September					October				November				December					January		
	Stage	Sex	Adult	28	5	12	19	26	2	9	16	23	30	7	14	21	28	4	11	18	25	1	8	15	22	29	6	13	20	27	3	10	17	24	1	8	15	22	29	5	12	19
x-notata	1	M&F	-		28	50	46	29	23	17																																
	2	M&F	-				4	21	27	31	43	44	23	4	2	2																										
	3	M&F	-							2	7	6	27	40	34	8	10																									
	4	M	-											3	5	5	12	3																								
		F	-											3	5	18	9	13	6																							
	5	M	A														2	9	11	13	10	6	2	3	3	1																
			-															2																								
		F	A																																							
			-												4	15	17	21	25	4	6	13	3	2																		
	6	M	A																	1			1																			
			-																																							
		F	A													2		2	8	32	34	31	44	45	47	49	50	50	50	50	50	50	50	50	50	50	34	21	23	12		
			-																																							
atrica	1	M&F	-				50	50	46	35	21	2							1																							
	2	M&F	-						4	15	29	48	44	15																												
	3	M&F	-										6	35	50	21	22	8																								
	4	M	-													20	20	22	33	19	20	13	5																			
		F	-													9	8	10	7	18	4																					
	5	M	A																			10	13	19	22	17	19	14	7	2	3											
			-																																							
		F	A																		2	2		1	1	3			2	2	2	2	3	1	2	1	3					
			-															10	9	13	18	16	9	6	8	10	4	2	5		3											
	6	M	A																																							
			-																																							
		F	A																		6	9	23	24	19	20	27	34	36	46	42	48	39	24	18	11	6	2	1			
			-																																							

Chapter II. Mature females were recognised by the epigynes and males by the palps. For observation of young spiders it was often only necessary to entice them to the web hub. Older spiders removed from their webs for closer examination were replaced as far as possible.

Results

The numbers, stages and sex of the spiders collected at weekly intervals during 1972/3 and 1973/4 are included in Tables 34 and 35. Emergence in x-notata began at the end of April in 1972 and in early May in 1973, approximately three and two weeks respectively before atrica. However, May and the first part of June 1972 were cold and windy, and this appeared to slow down early development. In both years, adult x-notata were first noted at the beginning of August and adult atrica about a month later. Adult females of both species which had matured at stage five were more common in 1972/3 than in the following season, when they typically matured at stage six. The mating period lasted from August to mid-September for x-notata and from September to late October or early November for atrica. As adult female x-notata were still found at the beginning of January and atrica were not, the egg-laying period for x-notata was several weeks longer, as demonstrated earlier in the chapter. This would give a female x-notata more time in which to lay a second or third batch of eggs, at least at these two sites. Although some x-notata females under shed eaves successfully overwintered, none on the railings survived, presumably because of exposure to low temperatures during the winter.

Variation in Spider Numbers through the Season

This part of the study was designed to investigate how the number of spiders varied through the season on a restricted part of the iron railings for x-notata and Ulex europaeus for atrica. Except for adult males, only those spiders which had constructed a retreat or web were included.

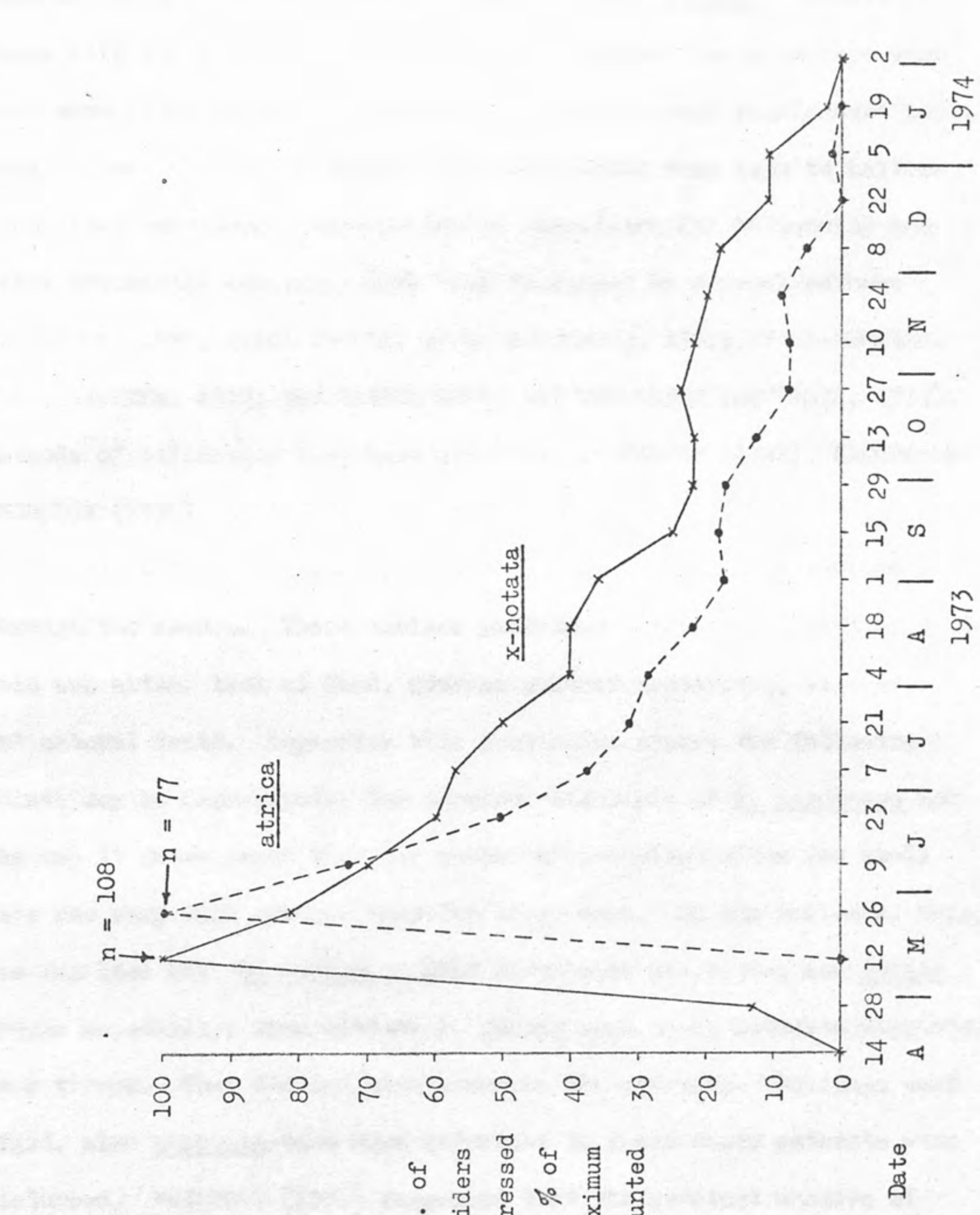
Material and Method

In March 1973, *x-notata* cocoons were counted on a section of iron railings. Cocoons within ten metres of the section were removed. Similarly, *atrica* cocoons were counted on two small isolated patches of *U. europaeus*. At fortnightly intervals throughout the 1973/4 season the numbers of spiders were ascertained at these sites. No attempt was much to prevent spiders moving onto or from the sites. Counting was made easier on the railings than on *U. europaeus*, but talc puffed onto the webs helped in locating the spiders, and counts were not made when conditions prevented web building. As only the presence of spiders was required, the minimum disturbance was made, especially important in the case of *atrica* which easily vacated their retreats. Adult males do not build orb-webs. Male *atrica* were normally found at the edges of the female webs, and although male *x-notata* often were not, the structure of the railings enabled them to be located.

Results

The greatest number of spiders counted at one time was 108 *x-notata* and 77 *atrica*. Other counts throughout the season were expressed as percentages of these numbers (Fig. 26). Emergence from cocoons began at the end of April for *x-notata* and in the third week of May for *atrica*. Numbers reached a peak within two weeks in both cases, then rapidly decreased such that *atrica* numbers had been halved as early as the third week in June and *x-notata* by the third week of July. They continued to decrease, somewhat less rapidly, until the high mortality rate of adult male *x-notata* in September and *atrica* in October. There followed some stabilization until December when numbers dropped again quite sharply. Although *x-notata* appeared better able to withstand cold weather, neither species overwintered in the adult stage.

Fig. 26. Spider numbers throughout the 1973/4 season



There were originally twenty-one x-notata and ten atrica cocoons found at the sites. Allowing for infertile and parasitised eggs, perhaps an average of thirty spiders emerged from each cocoon, giving very approximate totals of 630 x-notata and 300 atrica. Comparing these with the maximum counts above indicates that many spiders were lost soon after emergence, ballooning playing a very significant part. Thirteen out of fifteen spiders from one cocoon were seen to balloon soon after emergence. Reasons and/or conditions for ballooning and other aeronautic behaviour have been discussed by several authors (BRISTOWE, 1929, 1939; DUFFEY, 1956; SOUTHWOOD, 1962; WYNNE-EDWARDS, 1962; RICHTER, 1970; VAN VALEN, 1971; VAN WINGERDEN and VUGTS, 1974). Methods of ballooning have been described by KASTON (1948), CLOUDSLEY-THOMPSON (1958) and TURNBULL (1973).

Many factors undoubtedly contribute to a decrease in numbers through the season. These include predation, parasitism, lack of suitable web sites, lack of food, adverse weather conditions, migration and natural death. Regarding this particular study, the following points may be emphasized. The physical structure of U. europaeus and the way it grows meant that the number of potential sites for small webs was very much greater than for large webs. On the railings, this was far less so. U. europaeus main stems were not rigid, and atrica nymphs especially, when disturbed, jumped from their retreats supported on a thread. They did not always regain the retreats. Railings were rigid, also x-notata were more reluctant to leave their retreats when disturbed. BRISTOWE (1941) suggested that the greatest enemies of spiders were other spiders. That many spider species including atrica inhabited U. europaeus, and that x-notata was almost the only species living on the railings have been mentioned previously. Difficulty in pinpointing spiders on U. europaeus applied more to young ones and therefore does not explain why atrica numbers dropped more sharply than x-notata and a lower percentage apparently reached maturity. The overall results may not indicate real differences between the species but reflect differences in characteristics of the sites themselves.

Sexual Behaviour

Brief descriptions of courtship and mating in x-notata have been given by WALCKENAER (1842), LOCKET (1926), BRISTOWE (1929a) and WIEHLE, (1931), and in atrica by BRISTOWE (1929a) and WIEHLE (1931). These last two authors quoted from more detailed descriptions by GERHARDT (1924, 1926) for atrica and x-notata respectively. In the present study, the two species have been closely compared at all stages.

Material and Method

Information was gathered both in the field and from mixed male and female groups in glass tanks in the laboratory. Each 35 x 22 x 22 cm. tank containing four mature females and six mature males, was large enough for the females to construct normal webs. Close observations and notes were made during behaviour sequences and on these are based the following descriptions.

Results

Courtship and mating in both species occurred on the female webs, although the males often laid down a special mating thread, as described later. Before mating, each male charged its palps with semen. On one occasion only for each species was this seen to take place just prior to courtship, suggesting that it usually occurred earlier.

(A) Sperm induction

Differences between the species in sperm induction may be partly attributable to differences in palp lengths. In each case, the spider constructed a short horizontal thread and then hung on it ventral side uppermost. In x-notata, the abdomen was held near the thread and abdominal contractions followed. The spider moved slightly backwards and applied a palp probably to the unseen semen on the thread. The process was repeated, first the pumping action, then application of the second palp. The spider moved away within twenty seconds. In atrica, while hanging on the thread, the palpal tarsi were alternately moved from a position some distance in front of the chelicerae to the region of the sternum and held there for two or three seconds. These actions were soon accompanied by up and down pumping movements of the abdomen, then again without them. The whole action lasted three minutes, followed by a rest of three minutes. The spider moved away, then stopped and applied the palps in turn to the mouth. It marked time with the palps twice a second before moving off with the tarsi held a little in front of the chelicerae.

(B) Courtship and mating.

This behaviour was observed during the day and at night, in both species.

When a male x-notata came into contact with female silk, it approached the female retreat either along a retreat anchor thread or more usually via the web and web hub. Often plucking movements were made with legs one and two, the left first and the right second plucking almost together, then the right first and left second, alternating about once per second. The female sometimes did not seem to react, or made plucking movements on the signal thread. If at the hub it returned to the retreat, dropped from the web on a thread, or approached the male in an agitated manner. Unless actually chased off, and this was not observed, the male quickly constructed a mating thread in one of several ways. Such threads were spun from a retreat anchor thread to scaffolding, from the hub to scaffolding or to a radius bounding the free sector or a neighbouring one. In one instance, the male cleared part of the upper web and constructed a mating thread similar to a new radius. Returning part way along the thread, the male enticed the female onto it by plucking as before, by rapid vibrations of the first legs then the second legs, or seemingly making little movement. Usually within a few seconds, the female moved onto the thread with plucking movements. As the spiders almost touched, the male moved slightly backwards and the female presented as follows. The thread was gripped by the third pair of legs in the region of the epigyne. The other legs were spread widely and the spider hung head downwards in a quiescent manner with its ventral surface facing the male. The male moved forward frantically stroking the female with its front legs and alternately plucking the thread close to the female epigyne with its second legs. The male lunged with one palp towards the epigyne. Insertion was accomplished immediately, after a number of lunges (up to twenty) or was unsuccessful. Only during insertion was the male quiescent. Whether successful or not, typically the other palp was applied to the mouthparts before lunges with it were commenced. When the male rested, the female moved away but was often enticed or came back onto the same mating thread, or another constructed by the male. Actual attempts at mating lasted from one to thirty minutes and palpal insertions numbered from nil to twenty. Each insertion took from one to over twenty seconds, the higher the number of insertions, the less time each one lasted. One male successfully mated with the same female on two occasions one hour apart. Both males and females were seen to mate with more than one partner.

During the autumn, single or less commonly two male atrica were found on the edge of the female web, usually some distance from the retreat. They were either on their own thread attached to the web frame, on a web anchor thread or on a frame thread. Most were quiescent although on a few occasions males were seen to feed on insects trapped on the web. Courtship often began by stretching the legs, applying the tarsi of the palps and legs one and two to the mouthparts, and rubbing the palps together and against the chelicerae. There followed a "loosening up" of the first three pairs of legs. The legs on one side were rotated in unison in a wheel-like motion for one second (three rotations per second) and after a short pause, repeated with the other three legs. This continued for two or three minutes. The male then began plucking the thread it was on with legs one and two as in x-notata, first quietly, then more firmly. This lasted from a few minutes to over an hour. Sometimes there was an intervening rest period followed by the tarsi being applied to the mouthparts and wheel motion of the legs before plucking recommenced. Plucking usually ended with the female moving from the retreat or hub and approaching the male while violently shaking the web. This often frightened the male which quickly moved away or dropped on a thread. Occasionally, the male stood its ground so that the two spiders met on the thread with their ventral surfaces uppermost. There was frantic interplay of legs one and two, and this seemed very near to fighting. The interplay lasted from a few seconds to two or three minutes, the male apparently stroking the female's front legs and parts of the body. After applying a palpal tarsus to the mouthparts, the male lunged at the female epigyne with this palp, and in doing so the long palp passed horizontally above the female's mouth. When insertion was successful, the female was seen to be holding the palp in its chelicerae at the distal end of the femur. It was released after a few seconds as the palp was withdrawn and the spiders sprang apart. Both spiders were only quiescent during insertion. Many lunges were unsuccessful. After a maximum of two insertions, the second with the other palp, the male was chased away and the female returned to its retreat. On a few occasions, the male later resumed plucking, but either gave up or was chased away by the female.

The above descriptions are in basic agreement with those of GERHARDT (1924, 1926), but contain details not mentioned by this author. The wheel motion of the legs by male atrica in early courtship, and the grasping in the female chelicerae of the male *atrica* palp during insertion are examples. As described, observed differences between the species in courtship and mating behaviour are numerous and may be summarized as follows.

x-notata	*atrica*
The male does not take up residence on the edge of the female web.	The male takes up residence on the edge of the female web.
The male constructs a mating thread.	The male may use a web frame thread as a mating thread.
From the beginning of courtship to attempted mating is usually quite short, perhaps one to two minutes.	Courtship is often quite long. Wheel motion of the legs followed by thread plucking may last an hour or more.
The female may take the lead during courtship.	The male takes the lead during courtship.
The female is not usually aggressive. It "presents" and is quiescent during male lunges.	The female appears aggressive. It does not "present" and is only quiescent during palpal insertion.
During mating, the female hangs downwards and the male partly downwards facing the female.	During mating, both hang ventral side uppermost, facing one another.
The female does not grip the male palp in its chelicerae during insertion.	The female grips the male palp in its chelicerae during insertion.
There may be a series of one or two palpal insertions over as much as half an hour.	The maximum number of palpal insertions appears to be two, and renewed courtship is unsuccessful.
Courtship normally ends in at least attempted mating.	Courtship frequently ends in the female chasing away the male without any attempted mating.

CHAPTER X

DISCUSSION

In this investigation, it has been confirmed that *x-notata* and *atrica*, so similar morphologically, especially in the early nymphal stages, are distinct species which do not interbreed. In other families, copulation has been observed between different species of *Eresus*, Eresidae (GERHARDT, 1928), *Dolomedes*, Pisauridae (BONNET, 1933) and *Salticus*, Salticidae (LOCKET, 1939). Two *Lycosa*, Lycosidae species have mated and produced fertile eggs in the laboratory (LOCKET and MILLIDGE, 1951). However, neither *x-notata* nor *atrica* males responded sexually towards females of the other species in the laboratory, and differences in courtship and mating probably preclude such behaviour. Normal courtship is elicited by contact with adult female silk. The tarsal organs described by DAHL (1883) are chemosensitive (BLUMENTHAL, 1935; FOELIX, 1970a), as are probably other blunt-tipped hairs on the legs and palps (FOELIX, 1970b). Sex pheromones associated with drag-line silk have been demonstrated in *Pardosa* (VLIJM and RICHTER, 1966; RICHTER, STOLTING and VLIJM, 1971), and contact sex pheromones in four other Lycosid spiders, three being species-specific (HEGDEKAR and DONDALE, 1969). Such stimuli are probably the prime releasers of male courtship behaviour in many families, including the Argiopidae (Araneidae) (PLATNICK, 1971). In *Zygiella*, the presence of an orb-web is not essential for the initiation of courtship behaviour.

Of various positions adopted by male and female spiders during copulation (MONTGOMERY, 1903), five basic types, with variations, have been recognised by GERHARDT (1924, 1926). GERHARDT included both *x-notata* and *atrica* in his type I position. It is possible that the *x-notata* evolved from the *atrica* position. After approaching the male on the mating thread prior to copulation, the female *x-notata* partly releases the thread to hang head downwards, as distinct from *atrica* which does not. Male *x-notata* are certainly less vulnerable to attack from the female just before and during copulation. The evolution of sexual behaviour in spiders is discussed by MONTGOMERY (1903), ALEXANDER and EWER (1957) and PLATNICK (1971).

A short literature review of the types of habitat selected by the two species is presented, and the information augmented by observations made during this study. Mixed populations do occasionally occur, primarily on vegetation. However, *atrica* is typically found on plants distant from human habitation, and *x-notata* on houses, sheds etc. and often on neighbouring shrubs and bushes. Some of the latter spiders migrate from man-made structures, generally as ballooning first nymphs. By marking mature female spiders (with a spot of paint on the carapace) it was found that this migration was partly reversed in late autumn, especially from deciduous plants. Correlation between the distributions of some spider and plant species has been demonstrated by CHEW (1961), SCHICK (1965), POLENEC (1967) and RIECHERT and REEDER (1972). However, gross differences between *x-notata* and *atrica* in plant preference are not indicated, and both are commonly found on *Ulex europaeus* and *Crataegus monogyna*, for example. Differences seem to be linked more with where the plants are situated than with the actual species.

As stated in CHAPTER I, a suitable web site must provide scaffolding for the retreat and web, microclimatic conditions suited to the physiological needs of the spider, and an adequate food supply. Various authors have investigated factors which influence the siting of webs in different spiders. Their conclusions are summarised by

ENDERS (1972). McCOOK (1889) suggested that spiders find sites by chance but SAVORY (1930) considered that physical conditions determine precisely where webs are located. TILQUIN (1942) agreed with SAVORY, emphasizing the importance of tropisms (taxes). TURNBULL (1964) found that web sites were vacated unless adequate prey was captured. CHERRETT (1964) suggested that prey was not particularly important, but was able to show a link between web position and light and humidity preferences as demonstrated in the laboratory. However, ENDERS (1972) concluded that light and low humidity preferences in laboratory experiments could not be deciding factors in site selection. EBERHARD (1971, 1972) and ENDERS (1972) noted that windy sites were not chosen. Several authors, including DUFFEY (1962b, 1966) and ENDERS (1972, 1973) stressed the importance of habitat structure in web site selection. These findings show that many factors, not all of equal importance, influence where webs are built. The investigation of such factors in x-notata and atrica formed part of this study.

Except for young first nymphs which do not build retreats, spiders of both species build them before the webs. Surprisingly, there seems to be little or no investigation of the potential web site before retreat construction. At least on structures where mixed populations are found, retreat positions indicate that x-notata and atrica select sites in a similar way. Throughout development, both show a tendency to climb, and in all but the youngest spiders, after climbing, to settle in holes, crevices etc. which seemingly provide contact stimuli from more than one direction. Often within a few minutes of settling, spiders commence retreat construction. In animals, low thigmotactic behaviour (remaining in crevices) is almost always associated with negative phototaxis (FRAENKEL and GUNN, 1961). Most middle and late stage spiders are negatively phototactic in strong light, but adult females and probably younger stages reverse this behaviour when confined in small spaces overnight. The change in behaviour may well be important in guiding the spider to open places where the web itself can be built.

Both species build webs daily, typically just before sunrise, a time of temperature minimum (SPRONK, 1935). Based mainly on laboratory studies, factors which may cause a decrease in the frequency of web-building include wind and bright light (EBERHARD, 1971), heavy feeding (WIEHLE, 1927; KOENIG, 1951; WOLFF and HEMPEL, 1951), even temperature and brevity of daylight (WITT, 1956), rising or high temperatures (SPRONK, 1935) and moulting (WITT et al, 1968). However, it was noticed several times in the field that webs almost covered in small insect prey were replaced the next and subsequent days. Also, spiders moulting only a few hours after building webs renewed them the following morning. When adverse weather eg. strong winds or rain, prevented web-building before dawn, it often took place later when conditions improved, although less commonly as the day progressed.

Under controlled laboratory conditions, <u>x-notata</u> and <u>atrica</u> tend to build webs which transect the incident light rays. Field webs commonly lie parallel to the faces of dense hedges, shrubs and bushes on which they are built. Often the retreat is not in the plane of the web, but lies deeper in the foliage. The spider moves outwards from the retreat to construct the web. Here, phototactic responses certainly play a part. On other structures, for example railings or window frames, the direction in which the web faces and the relative positions of retreat and web are largely governed by the structural characteristics of the scaffolding. Both species build their webs in the same manner, and this has been described in detail elsewhere.

Except for the smaller amount of silk used by <u>atrica</u> in retreat construction, the larger number of radii in *atrica* webs and one or two other minor differences, the close similarity in the webs of the two species has been demonstrated. They are alike in basic design, approximately vertical, with the retreat typically above the level of the hub. The free sector, characteristic of the genus, is not as common as the literature generally states. Its presence or absence is linked with the position of the retreat relative to the web plane. As might be expected, larger spiders built larger webs, but at equivalent stages of development, mean web size was similar in the two species. In mixed populations, no significant difference was observed in the height of webs, either between the instars or the species. ENDERS (1972) noted that web height increased with instar in *Argiope aurantia*. Also, young *A. aurantia* webs were nearer the ground than those of *A. trifasciata*, although there was no such difference in adult webs.

It was noted that *atrica* field webs deteriorated more quickly than *x-notata* webs on hot, still and warm, windy days. The reasons for this are not known. However, it is known that temperature and humidity can have a great effect on thread elasticity (DE WILDE, 1945). Also, older webs are more susceptible to wind damage than newly spun ones (POINTING, 1965), presumably because threads become fatigued. Thin threads fatigue more quickly than thicker ones, losing their elasticity or strength from over-extension or drying out (EBERHARD, 1971). Spiders can control the thickness of the web frame and radial threads produced from the ampullate glands (WILSON, 1962a, b, 1969), and also the viscid thread (CHRISTIANSEN et al, 1962). The function of the different silk glands and the chemistry and properties of the silks in Argiopids (mainly *Araneus diadematus*) are discussed by LUCAS (1964), PEAKALL (1964, 1969), WITT et al (1968) and ANDERSON*(1970). LANGER (1969) describes the effect of external forces on spider webs.

Differences between *x-notata* and *atrica* webs in their ability to withstand damage may therefore be as a result of differences in thickness of comparable threads, in the chemistry and properties of equivalent silks or in web gross structure. Investigation is required on this point. The web differences could enable *x-notata* to inhabit warmer, drier situations than *atrica*.

There are physical conditions which spiders cannot tolerate, and within the tolerance limits are conditions which spiders prefer. Temperature and humidity (in that it interacts with temperature, wind velocity etc. to influence evaporation rate) are two important physical factors referred to previously. Regarding preferences, these may differ in the same species depending on hunger, sex, stage of life cycle, season, acclimatization to non-optimal conditions and so on (MACFADYEN, 1963). However, first nymph spiders used in the temperature gradient experiments were of the same age, and had been reared in similar conditions in the laboratory. Adult females of both species in the temperature choice chamber experiments were collected from neighbouring field populations at the same time, and kept in the laboratory for several days before experimentation. Adult females in humidity experiments were treated similarly. The temperature experiments suggest that both first nymph and adult female *x-notata* in dry air prefer temperatures 3°C. to 4°C. higher than *atrica*. Humidity experiments indicate that at 20°C. (and to a lesser extent at 5°C.), adult females of both species avoid moist air and actually prefer relatively dry air, especially *x-notata*. Together, the experiments suggest that *x-notata* prefers somewhat drier, warmer conditions than *atrica*.

Adult female *x-notata* in the laboratory can withstand prolonged periods at -2°C. much better than *atrica*, and this confirms field observations that *atrica* are more susceptible to cold weather. The *x-notata* mean upper paralysis temperature of 45°C. is $1\frac{1}{2}$°C. higher than *atrica*, presumably giving *x-notata* an advantage at these high temperatures. The upper paralysis temperature is not affected by acclimatization (SEYMOUR and VINEGAR, 1973).

Spiders are adapted to a terrestrial mode of life. They reduce water loss by excreting 73% - 87% waste nitrogen in the form of guanine, which is more insoluble than uric acid (ANDERSON, 1966). Spiders are similar to insects in that the cuticle has an outer waterproofing waxy layer (SEWELL, 1955; CLOUDSLEY-THOMPSON, 1957; LOCKWOOD, 1963). There is a critical temperature associated with this type of cuticle above which there is a rapid increase in the rate of water loss. This is probably because the ordered wax layer is disrupted and the molecules become randomly orientated (LOCKWOOD, 1963). The critical temperatures of both *x-notata* and *atrica* are about 36°C. Above 36°C., the rate of weight loss increases rapidly, but more so in *atrica*. At 44°C., it is from 20% to 30% higher than in *x-notata*.

Both species are very resistant to desiccation, *x-notata* to a greater degree than *atrica*. The difference between them is especially marked at higher temperatures. Even at 20°C., *x-notata* first nymphs at 34% R.H. and without food and water lived for an average of 44 days, 43% longer than *atrica*. Adult females lived for an average of 42 days, 32% longer than *atrica*. These results suggest that *x-notata* is better able to withstand warmer drier conditions than *atrica*. From temperature and humidity readings taken in spiders' retreats in the field, it seems that upper temperature extremes especially are more likely to be encountered in *x-notata* retreats. Water lost from the body is replaced either by water in the food or by drinking. No water is taken up through the body surface (NEMENZ, 1954). MILLOT and FONTAINE (1937) divided spiders into two groups, those with body contents less than 70% water having no need to drink. Lycosids are able to drink soil capillary water (PARRY, 1954), but field-layer spiders only drink if there is rain or mist, unless they move down to the ground (DUFFEY, 1962b). McCOOK (1893) noted that young Zygiellae could take water droplets off the web and carry them in their chelicerae. This was not noted in the field during this study. In the laboratory, it was quite common to see atrica drinking but unusual to see x-notata, except when very dehydrated.

Attention has been drawn to the high mortality rate of atrica raised at 25°C. compared with x-notata, and also with both species raised at 20°C. The rate is especially high in males during the final moult. Probably the moulting fluid evaporates before the appendages, particularly the long palps, can be extracted. Whether the process of moulting normally takes longer in atrica, or the properties of the moulting fluids are different in the two species remains to be investigated. Moulting in spiders, as in many arthropods, seems to be controlled by ecdysterone (KRISHNAKUMARAN and SCHNEIDERMAN, 1968). Observation shows that it may occur at any time of the day, and is not confined to cooler, humid periods. In warm drying conditions, atrica will have difficulty in completing its life cycle. This could be an important factor preventing atrica from occupying those sites favoured by x-notata, where temperatures may reach between 30°C. and 40°C. in the retreats. Even x-notata on a few occasions were seen to vacate their retreats and move a little way along the signal thread where the temperature was a few degrees lower. PARRY (1951) and CLOUDSLEY-THOMPSON (1962) discuss factors controlling body temperature in terrestrial arthropods. LEVI (1967) suggests that a tendency towards silver colour will help to reduce body temperature, and in general, atrica is more silver in colour than x-notata.

Feeding experiments at temperatures where spiders are able to catch prey indicate that the length of each developmental stage is greater at low rates of feeding than at high rates. However, in x-notata especially, spiders at low feeding rates tend to mature at an earlier stage, and this might enable them to complete their life cycle even when food is scarce. It has been pointed out that several authors working with other species have found an increase in the number of stages, while TURNBULL (1965) noted no difference in Agelenopsis potteri. After hatching, the length of development in the two species is approximately the same for spiders raised in similar conditions. However, atrica are smaller than x-notata, and poorly fed spiders smaller than well fed ones. This may be important in that within a family, the number of eggs increases with the size of the mother (PETERSON 1950), and also better fed spiders lay larger batches of eggs (BONNET, 1933a, 1935a; BRISTOWE, 1939).

Both Zygiella species are very resistant to starvation, as mentioned earlier. In the field, there was no evidence to suggest that the two species differ in their food preferences. No insect prey was seen to be rejected with distaste, as reported by BRISTOWE (1941), although the reaction to insects striking the web was very variable. In some cases, the spiders attacked the prey immediately, while at other times, they did not leave their retreats. TURNBULL (1960a, 1973) refers to similar behaviour in other spiders, pointing out that differences in the physiological state of the spider may help to explain this inconsistent behaviour. In general, spiders are very sensitive to objects entering their webs and can distinguish between prey and young spiders (TRETZEL, 1961) or artifacts (PARRY, 1965). However, satiated spiders sometimes reject normally acceptable prey (BRISTOWE, 1941), and spiders close to moulting may refuse food (MIYASHITA, 1968a).

In the laboratory, TURNBULL (1964) found that Achaearanea tepidariorum moved its web from sites yielding insufficient prey to others yielding ample prey. DABROWSKA-PROT (1960) and LUCZAK (1963) noted that an increase in insects near vegetation was associated with an increase in shade and humidity. LEWIS (1969) found that flying insects tend to be concentrated behind windbreaks. Webs built on iron railings sheltered by bushes, for example, would be subject to less wind damage and also be in a favoured position for trapping insects. Although wind is probably the primary factor, in the laboratory at least, spiders are stimulated to build webs by the presence of flying insects. It may be that such insects are detected by vibrations generated either in threads attached to the retreat or in the air. Web spiders have lyriform organs on the legs sensitive to web vibrations (PRINGLE, 1955; LIESENFELD, 1956, 1961; WALCOTT, 1969), and trichobothria sensitive to airborne sounds (FRINGS and FRINGS, 1966; GÖRNER and ANDREWS, 1969). EISNER et al (1964) and EISNER (1965) observed that several types of flying insect including Lepidoptera often escape from webs. TURNBULL (1960a), KAJAK (1965) and ROBINSON and ROBINSON (1970) found that prey caught in webs was not the same as that available, judged by samples taken using sweep nets and other similar means. Observation of prey in Zygiella webs and the way the spiders reacted to it did not suggest any gross differences in the feeding behaviour of the two species.

Reasons have been given for studying the life cycles in two separate one-species populations instead of in mixed populations. From laboratory work, the lengths of the individual developmental stages in the two species, raised under the same conditions, are very similar. An exception is the egg stage, where development is more rapid in x-notata, especially at higher temperatures. As a result, it seems likely that in mixed populations, x-notata emerges from egg cocoons earlier than atrica, giving it an advantage in web site selection. Comparing the two separate populations, x-notata certainly emerged before *atrica*, and this also occurred at other "typical" *x-notata* and *atrica* sites. Maturity was reached and mating took place earlier in *x-notata*, resulting in a longer egg-laying period. Although there was no significant difference between the species in the number of eggs laid per batch, more batches were laid by *x-notata*. Sperm was stored in the female for several weeks at least, and this has been noted in other species (WILD, 1957; COOKE, 1966). BONNET (1927, 1935b) found no evidence for parthenogenesis in several spider species, and this present work supports that view, although WASOWSKA (1971) describes parthenogenesis in *Theotima feminina* (Ochyroceratidae).

Evidence from both field and laboratory indicates that *x-notata* can tolerate and actually prefers warmer, drier conditions than *atrica*. Moreover, the later developmental stages are more resistant to low temperatures than *atrica*, and all stages tested survived for longer periods without food or water. These and other facts discovered during this research and brought out in discussion indicate that *x-notata* is more adaptable, and this may explain its wider and more varied distribution.

Examples have been cited where *atrica* placed on structures cleared of *x-notata* either moved away or did not survive. A specific case where over a period of four years, *x-notata* encroached upon and almost took over an *atrica* site indicates that *x-notata* can probably survive in most habitats occupied by *atrica*. Other observations support this theory. Continued urbanization will see the advance of *x-notata* into areas inhabited by *atrica*, and it is likely that *atrica* will be further restricted in its distribution as a result.

Both species were first reported in North America a little less than a century ago, almost certainly imported from Europe (GERTSCH, 1964). Of the two, *x-notata* has spread much more rapidly, down both the east and west coasts. On the west coast especially, it is common on shrubs, trees, rock cliffs and dirt banks along streams, in addition to the more usual domestic situations. This illustrates the dispersal powers and the adaptability of this species.

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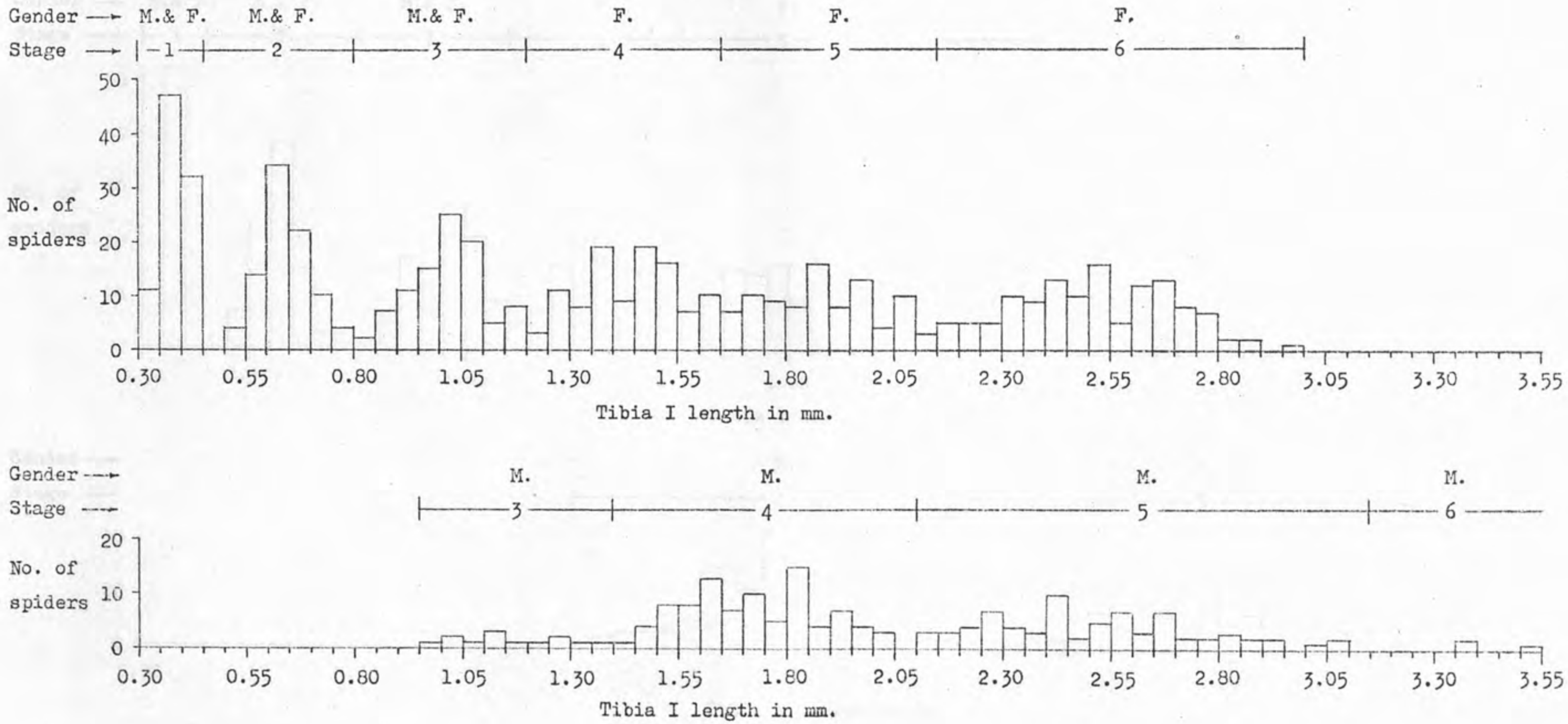
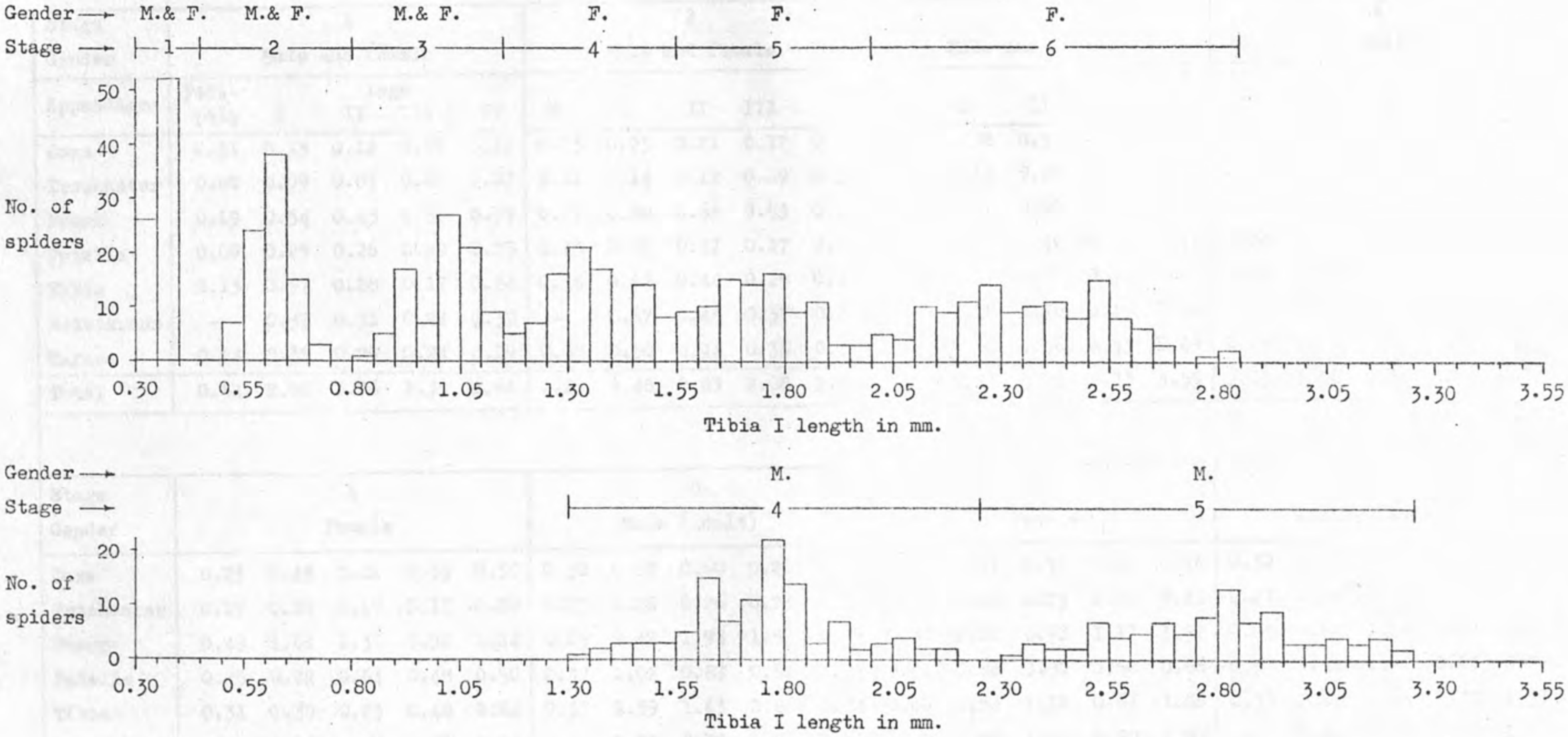
Appendix 1

Length of x-notata tibia I and stage limits from samples taken at Greenford, Middx. during 1971



Appendix 2

Length of <u>atrica</u> tibia I and stage limits from samples taken at Chobham, Surrey during 1971



Appendix 3. Field spiders - Mean appendage segment lengths in millimetres

x-notata

Stage	1					2					3					4				
Gender	Male and female					Male and female					Male and female					Male				
Appendages	Pedi-palp	Legs I	II	III	IV	P	I	II	III	IV	P	I	II	III	IV	P	I	II	III	IV
Coxa	0.11	0.13	0.12	0.09	0.12	0.15	0.25	0.21	0.17	0.20	0.19	0.38	0.34	0.28	0.30	0.23	0.51	0.43	0.35	0.39
Trochanter	0.08	0.09	0.07	0.06	0.07	0.11	0.14	0.12	0.09	0.11	0.15	0.18	0.16	0.13	0.16	0.19	0.22	0.20	0.17	0.20
Femur	0.19	0.54	0.43	0.35	0.39	0.27	0.88	0.66	0.53	0.63	0.38	1.26	0.99	0.68	0.96	0.47	1.80	1.39	0.94	1.30
Patella	0.09	0.29	0.26	0.20	0.25	0.13	0.42	0.37	0.27	0.34	0.20	0.58	0.48	0.35	0.41	0.24	0.77	0.62	0.49	0.50
Tibia	0.13	0.37	0.28	0.17	0.24	0.18	0.62	0.44	0.29	0.41	0.23	1.07	0.67	0.37	0.65	0.26	1.73	1.12	0.60	0.83
Metatarsus	-	0.37	0.31	0.24	0.30	-	0.67	0.45	0.37	0.43	-	1.18	0.76	0.49	0.62	-	2.07	1.32	0.70	0.92
Tarsus	0.24	0.35	0.29	0.24	0.29	0.37	0.50	0.44	0.36	0.41	0.54	0.60	0.56	0.43	0.49	0.64	0.76	0.66	0.52	0.57
Total	0.84	2.14	1.76	1.35	1.66	1.21	3.48	2.69	2.08	2.53	1.69	5.25	3.96	2.73	3.59	2.03	7.86	5.74	3.77	4.71
Stage	4					5					5					6				
Gender	Female					Male (adult)					Female					Female (adult)				
Coxa	0.23	0.49	0.42	0.35	0.39	0.30	0.69	0.60	0.48	0.52	0.27	0.61	0.53	0.44	0.46	0.32	0.76	0.68	0.52	0.56
Trochanter	0.19	0.21	0.19	0.17	0.20	0.25	0.28	0.26	0.23	0.26	0.23	0.24	0.23	0.20	0.23	0.27	0.28	0.27	0.24	0.27
Femur	0.48	1.64	1.37	0.92	1.24	0.65	2.49	1.93	1.35	1.79	0.61	2.02	1.70	1.17	1.52	0.85	2.68	2.25	1.47	2.01
Patella	0.25	0.72	0.64	0.48	0.50	0.32	1.02	0.87	0.64	0.76	0.31	0.88	0.80	0.56	0.66	0.37	1.14	1.00	0.66	0.86
Tibia	0.31	1.39	0.83	0.48	0.82	0.37	2.59	1.63	0.86	1.23	0.40	1.84	1.18	0.67	1.08	0.55	2.47	1.64	0.79	1.37
Metatarsus	-	1.56	1.12	0.65	0.84	-	3.00	2.02	1.06	1.41	-	1.98	1.50	0.80	1.09	-	2.84	1.90	1.04	1.52
Tarsus	0.63	0.71	0.64	0.52	0.55	0.76	1.03	0.84	0.60	0.69	0.73	0.88	0.72	0.53	0.60	0.85	1.08	0.83	0.56	0.65
Total	2.09	6.72	5.21	3.57	4.54	2.65	11.10	8.15	5.22	6.66	2.55	8.45	6.66	4.37	5.64	3.21	11.25	8.57	5.28	7.24

Appendix 3. - Continued

atrica

Stage	1					2					3					4				
Gender	Male and female					Male and female					Male and female					Male				
		Legs																		
Appendages	Pedi-palp	I	II	III	IV	P	I	II	III	IV	P	I	II	III	IV	P	I	II	III	IV
Coxa	0.09	0.14	0.12	0.09	0.12	0.12	0.25	0.21	0.16	0.20	0.15	0.38	0.33	0.26	0.29	0.23	0.52	0.45	0.37	0.40
Trochanter	0.07	0.09	0.07	0.05	0.07	0.09	0.14	0.12	0.09	0.12	0.12	0.18	0.16	0.14	0.16	0.21	0.23	0.21	0.16	0.21
Femur	0.20	0.54	0.43	0.32	0.37	0.29	0.86	0.62	0.51	0.61	0.39	1.22	0.96	0.67	0.94	0.99	1.95	1.52	1.02	1.48
Patella	0.12	0.27	0.25	0.19	0.23	0.17	0.40	0.36	0.27	0.32	0.21	0.58	0.48	0.34	0.41	0.43	0.76	0.64	0.47	0.57
Tibia	0.16	0.36	0.29	0.19	0.25	0.21	0.61	0.43	0.28	0.39	0.27	0.99	0.62	0.37	0.62	0.53	1.71	1.14	0.58	0.87
Metatarsus	-	0.36	0.30	0.23	0.30	-	0.67	0.46	0.34	0.43	-	1.02	0.72	0.46	0.66	-	1.93	1.31	0.70	1.06
Tarsus	0.26	0.35	0.28	0.23	0.28	0.35	0.50	0.42	0.34	0.39	0.45	0.58	0.54	0.41	0.46	0.81	0.79	0.65	0.49	0.56
Total	0.90	2.11	1.74	1.30	1.62	1.23	3.43	2.62	1.99	2.46	1.59	4.95	3.81	2.65	3.54	3.20	7.89	5.92	3.79	5.15

Stage	4					5					5					6				
Gender	Female					Male (adult)					Female					Female (adult)				
Coxa	0.19	0.51	0.43	0.35	0.38	0.37	0.78	0.71	0.49	0.53	0.24	0.62	0.53	0.42	0.46	0.32	0.76	0.67	0.48	0.53
Trochanter	0.16	0.22	0.20	0.16	0.20	0.35	0.29	0.25	0.20	0.24	0.20	0.26	0.23	0.18	0.22	0.27	0.30	0.26	0.21	0.25
Femur	0.53	1.56	1.36	0.91	1.19	1.73	2.98	2.33	1.48	2.06	0.64	1.94	1.68	1.14	1.54	0.91	2.62	2.03	1.48	1.93
Patella	0.27	0.73	0.61	0.44	0.54	0.75	1.01	0.86	0.61	0.76	0.35	0.89	0.77	0.55	0.68	0.42	1.09	0.89	0.65	0.80
Tibia	0.36	1.36	0.92	0.53	0.84	1.12	2.79	1.88	0.88	1.41	0.43	1.75	1.16	0.65	1.04	0.56	2.32	1.48	0.81	1.26
Metatarsus	-	1.57	1.04	0.60	0.91	-	3.19	2.37	1.27	1.78	-	1.96	1.37	0.78	1.12	-	2.64	1.84	1.02	1.54
Tarsus	0.60	0.72	0.63	0.47	0.54	0.83	1.03	0.82	0.62	0.69	0.71	0.86	0.71	0.53	0.61	0.85	0.94	0.81	0.61	0.68
Total	2.11	6.67	5.19	3.46	4.60	5.15	12.07	9.22	5.55	7.47	2.57	8.28	6.45	4.25	5.67	3.33	10.67	7.98	5.26	6.99