Bull.Br.arachnol.Soc. (1978) 4 (5), 197-203

The life-history of *Achaearanea lunata* (Cl.) in Denmark, with a note on *Theridion varians* Hahn (Araneae: Theridiidae)

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Introduction

In a previous paper the life-history types found among the spiders of the Danish beech-forest Hestehaven, Eastern Jutland were presented (Toft, 1976). Detailed descriptions of life-history patterns were given for single representatives of the main developmental types, whereas other species were only grouped according to these types. However, assignation of a species to a certain life-history pattern is only a very crude characterization, and more detailed knowledge is required for a full appreciation of life-history variation in a spider community. The present paper should contribute towards this. Furthermore, an attempt is made to understand the performance of the species in the beech-wood habitat by comparison with other spider species of the same habitat as well as with related species of other habitats.

Material and Methods

Data for the phenological description of *Achaearanea lunata* (Cl.) and *Theridion varians* Hahn were obtained from a standard sampling programme, aimed at a general survey of the phenology of spiders in the beech-wood. It comprised the following five sampling methods: quadrat sampling of litter, pitfall traps, sweep-net samples from ground vegetation, beating young beech trees with clubs, and arboreal photoeclectors (for futher details, see Toft (1976) and references therein). In presenting these data I have followed the standard type of diagram used in the earlier paper, even though not all sampling methods may be appropriate for these particular species. For example, neither of the species treated here were caught in pitfall traps (Figs. 1 and 4), but this may be considered as additional information.

For *A. lunata* information on reproduction was gathered separately by collecting nests in different parts of the beech stand throughout the breeding season. The hibernating population was studied in a nearby spruce stand, as the hibernation cocoons, to be described, could be found in great abundance there.

Achaearanea lunata (Cl.)

Distribution

The seasonal and vertical distribution of each instar and sex of *A. lunata* is shown in Fig. 1, where two years' collections are condensed into a single-year diagram. The separation of instars was made by measuring the length of tibia I. For each instar and sex, catches are indicated separately for the five sampling methods used, as explained in the legend. It is observed that adults and juveniles of instars IV and III are taken predominantly in the canopy layer. The species makes its web close to tree-trunks, usually suspended in the angle between the trunk and a large branch. The small juveniles (instars I and II) are also commonly taken by sweeping ground vegetation, thus showing a wider habitat range. This phenomenon, which seems to be a common feature among canopy spiders, probably reflects a more universal occurrence of suitable web-sites for small spiders than for large ones.

A. lunata is not restricted to deciduous forests; in fact, the greatest densities are found in young, dense and dark spruce plantations.

Phenology

Figure 1 suggests that adults are found in the months June-August. However, this is not the true adult period, but is a result of a reduction of sampling activity in the canopy during the autumn. The period of egg-laying extends into the second half of September (heavy bar above the diagram), and nests with females guarding small young have been observed well into November. The full period of the adults is therefore June-November. A very small number of adults may also be found hibernating (Table 1).

After leaving the nest of the mother (in August-November) the spiderlings disperse in the wood, before hibernation. Only a few individuals go through a moult before the winter, and Table 1 shows that 1.6-7.7% of the hibernating population are in instar II. In May of the following spring activity is resumed and development is rather fast. However, the end point of this line of development is rather obscure, as the subadults occupy the whole of the warm season.

As demonstrated later, the species hibernates in two distinct age-groups, viz. instar I in the first winter and instar IV (subadults) in the second winter. It is therefore concluded that the subadults from May and early June have hibernated in this instar, moulting into adults in June, whereas subadults from July-August belong to the following generation.

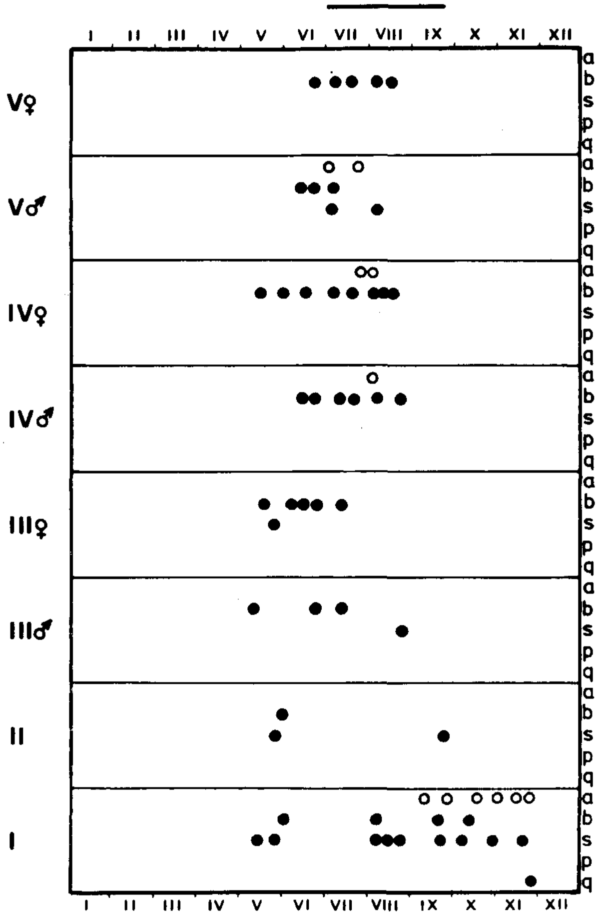

Fig. 1: Phenology of *Achaearanea lunata* (Cl.)
Roman numbers in left column indicate instars; letters in right column define the catches of the five sampling methods used: a – arboreal photo-eclectors (traps attached to tree-trunks), b – beating of young beech trees with large clubs, s – sweep-net samples from herbaceous vegetation, p – pitfall traps, q – quadrat samples of litter. Open circles – presence of instar in catches by activity-measuring methods (traps); closed circles – presence of instar catches by semi-quantitative methods. Heavy bar above the diagram: egg-laying period. I-XII: January-December. All data from the period July 1969 – August 1971 have been grouped together into a single-year diagram.

This means that *A. lunata* belongs to the group of biennial summer-breeders, hibernating twice as juveniles. It shares this type of life-history with the majority of beech-canopy spiders (Toft, 1976).

The hibernation cocoon

A. lunata spends the winter in a special kind of construction, a hibernation cocoon, suspended by means of a few silken threads a few millimetres from the bark surface of the tree trunk, usually under a knob or small branch. It consists of a sphere of tough silk, just large enough for the spider with its legs drawn in. On the outside the cocoon is covered with small pieces of bark or lichens from the immediate surroundings and even bud-scales and spruce-needles may be incorporated. It is thus well camouflaged on the tree trunks, whether they be beech, oak, birch, spruce or fir, on all of which I have found it.

The time of hibernation

By the end of August the subadults disappear from the collections (Fig. 1). In fact, the first animals have already gone into their hibernation cocoons in the first half of August. In the autumn of 1970, I followed the course of entering the hibernation cocoons. In a small spruce stand close to the beech wood research site, I selected ten trees, which were searched at regular dates for hibernation cocoons (Table 1a).

At every visit all cocoons found from ground level up to two metres height were removed, and the animals identified to instar and sex. The table shows that by 1 September almost all of the subadults were in the hibernation cocoons, explaining their total disappearance from the collections (Fig. 1). The pattern is very different for instar I. As previously pointed out, there are young leaving the nest from August to November. Before hibernation, they must first build up some reserves for the winter. For this age-group the last part of September and October is therefore the main period of entering the hibernation cocoons.

The late-winter inspection of the same trees produced only two first instars. This may indicate that offspring from very late cocoons do not survive.

Age-structure of hibernating population

In November 1969, 50 trees of the above-mentioned spruce stand were searched for hibernation cocoons and the population age-structure determined (Table 1b). The total autumn collection from 1970 may serve the same purpose. Though there are small differences between the two succeeding years, especially in the proportion of instars II and III, the main pattern is very similar: *A. lunata* hibernates in two distinct age-groups, instars I and IV, thus supporting the pattern of development described earlier.

Aerial dispersal

A. lunata was caught in flight on two occasions, both in May 1971, in a farm garden a few hundred metres from the wood. This indicates that the species has a period of aerial dispersal in the early spring. In both cases the flying animals were instar III females.

Reproduction

Information about the course of egg-laying was obtained by regular collecting of nests throughout the summer and autumn of 1970 (Fig. 2). *A. lunata* becomes adult at the beginning of June and, by the end of the month, most females have produced their first egg-cocoon. The second is made during the first third of July, and the third cocoon follows soon after. According to Fig. 2, about 50% of the females make only three cocoons, while 30-40%, with some delay in time, also make a fourth. Five and even six cocoons were observed in single cases.

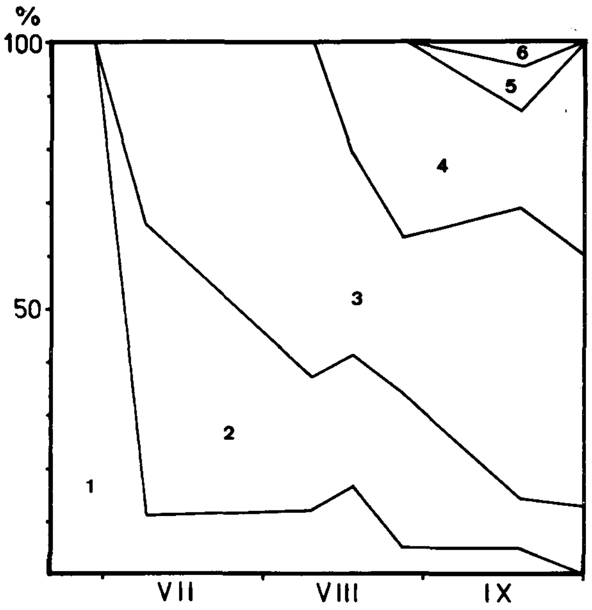

Fig. 2: Changes in the percentage of nests with different egg-cocoon numbers in *Achaearanea lunata* during the egg-laying period, 1970. Figures indicate number of cocoons per nest.

		Instar							
		I	II	III♂	III♀	IV♂	IV♀	V♂	V♀
(a)	17-8-1970		2	1	1	4	11		
	1-9-1970	1	4	4	2	10	15		
	15-9-1970	2	1		1	3	3		
	30-9-1970	22	1		1		1		
	31-10-1970	21	1	1			2		
	29-3-1971	2							
	Total	48	9	6	5	17	32		
	%	41.0	7.7	5.1	4.3	14.5	26.8		
(b)	25-11-1969	226	7	1	20	51	111		2
	%	53.0	1.6	0.2	4.7	12.0	26.0		0.4

Table 1: (a) Age structure of *Achaearanea lunata* in hibernation cocoons, collected from the same ten spruce trees during the autumn, 1970.
(b) Age-structure of hibernating population of *A. lunata* in winter, 1969/70 (total from 50 trees).

Figure 2 may not be fully correct. For example, during the whole period of reproduction there are a fair number of nests with only one or two cocoons. Nests may, for one reason or other, be destroyed, and the females must then produce a new one, that will never contain high cocoon-numbers. Regular inspection of marked nests showed nest destruction to be quite a frequent event. It is thus possible that a larger proportion of females actually make four cocoons.

The sequence of the cocoons can be determined by the stage of development of their contents at the time of collecting. On this basis the number of eggs per cocoon was counted with the following results (mean ± 1 S.D.):

First cocoon: 109.0 ± 29.9 (N = 60)
Second cocoon: 76.9 ± 33.8 (N = 65)
Third cocoon: 61.1 ± 29.9 (N = 55)
Fourth cocoon: 61.8 ± 32.9 (N = 25)
Fifth cocoon: 44.3 ± 32.7 (N = 4)

As most females make 3-4 cocoons, the number of eggs produced per average female will be in the range of 250-300. This is an extremely high number for a spider of its size (2.5-3 mm), at least within this ecosystem; in other species studied during the same investigation the range was 20-100 eggs per female (Toft, 1976).

As in many species of spiders, there is a decrease in the number of eggs in successive cocoons. However, the number of eggs in the fourth cocoon is identical with the number observed in the third. As shown in Fig. 2 the time spent in producing the fourth cocoon is much longer than for the first three. Apparently,

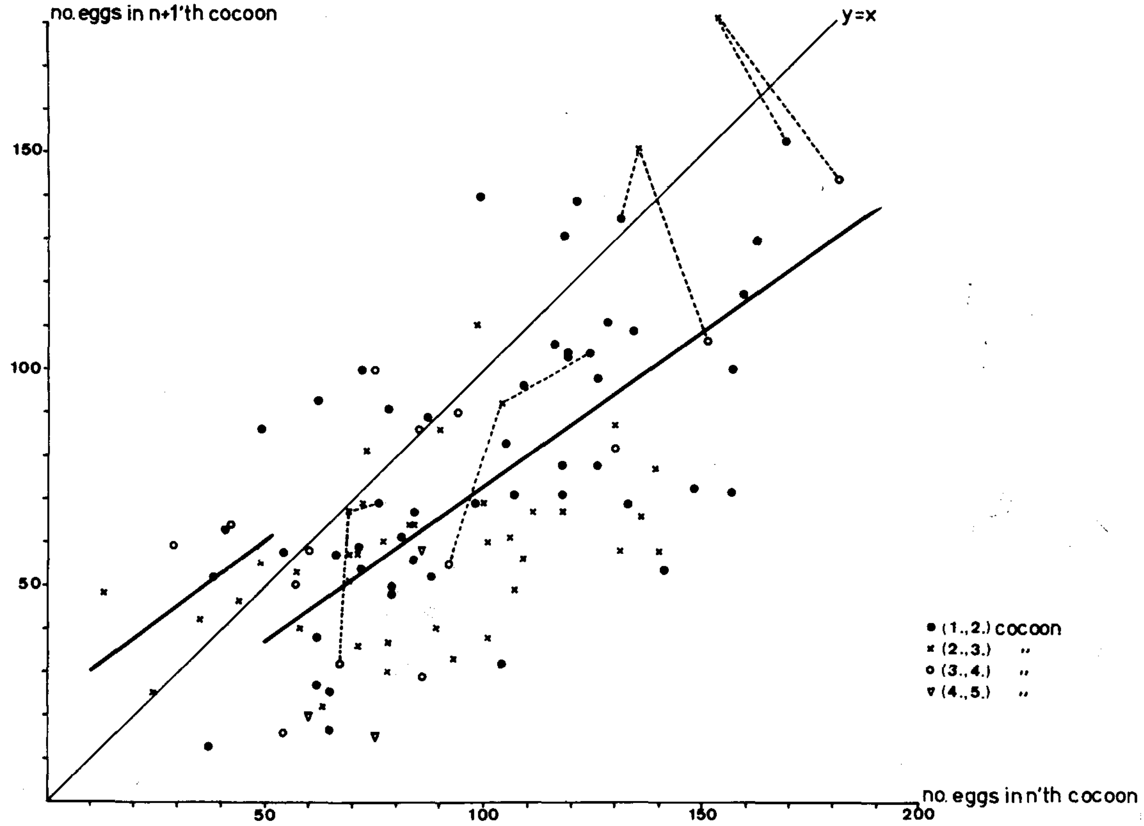

Fig. 3: Relationship between the number of eggs in an egg-cocoon and that of the following cocoon in females of *Achaearanea lunata*. Dashed lines connect values of successive cocoons in four individual females. Regression lines for all data are shown for x < 50 and x > 50 separately (heavy lines).

the spider is able to increase the number of eggs in a clutch by spending more time producing it.

Furthermore, as indicated by the very large standard deviations, the egg-producing capacity of individual females varies widely. This is further analysed in Fig. 3. Here the number of eggs in the second cocoon is plotted against the number of eggs in the first cocoon, that of the third cocoon against the second, and so forth. Linear regression coefficients have been calculated for each set of data (except 4th-5th cocoon) and they are all highly significant. This means that if a female produces a large (or small) number of eggs in her first cocoon, she will also have a large (or small) number in the following ones.

Four nests were found in which it was possible to count the contents of all of the first four cocoons. In Fig. 3 the values for each of these nests have been connected by dashed lines. By chance they are distributed over most of the range, and they neatly confirm the general relationship. The total number of eggs in the four cocoons for each female was 244, 375, 524 and 647.

It is evident, however, that the true relationship is not a simple linear one. Notice, for example, that for abscissa values below 50 nearly all points are above the y = x line, whereas the opposite is true for abscissa values above 50. Therefore, regression lines have been calculated separately (and are shown in Fig. 3):

$$x < 50: y = 0.76 x + 22.47 \; (r = 0.4239, \text{n.s.})$$
$$x > 50: y = 0.71 x + 2.19 \; (r = 0.6460, p < 0.001)$$

Whether the lines are actually parallel, as the formulae indicate, cannot be proved because the data for the lower end of the scale are too scanty. The following comments should therefore be regarded as tentative.

As suggested above the fall in egg-numbers might be counteracted by spending more time in producing the clutch. The upward shift of the regression line for low egg-numbers, supports this view, and extends it to apply to every cocoon number. The general inference is therefore that whenever egg-numbers tend to be too small (below 50), some physiological mechanism sets in, raising the egg-number (perhaps with a constant value of about 20), by increasing the period of egg-development.

Theridion varians Hahn

The phenological data on *T. varians* are shown in Fig. 4. It is immediately seen to correspond very closely to the pattern of *A. lunata* (Fig. 1). The only noticeable differences are, that in *T. varians* a larger proportion goes through the first moult before hibernating for the first time and in the subadults the succeeding generations are more clearly separated. A significant similarity is that the early disappearance of subadults in the autumn (early September) is repeated in this species. I have no information about how *T. varians* hibernates, but the pattern suggests that they are hidden away, either in a hibernation cocoon, or otherwise out of reach of standard collecting methods.

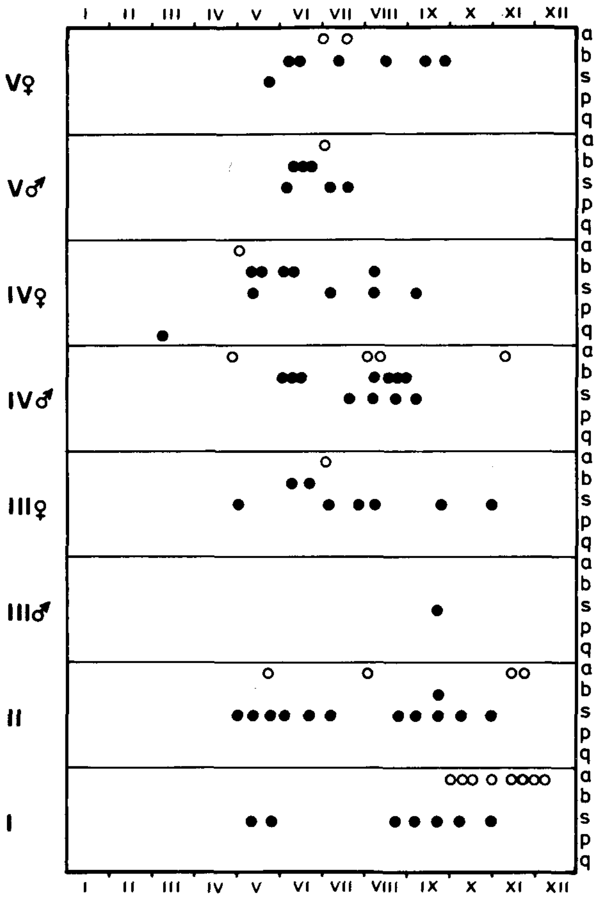

Fig. 4: Phenology of *Theridion varians* Hahn. Explanation as in Fig. 1.

Very few data were collected on the reproduction of *T. varians.* However, the species is known to make a fairly large number of egg-cocoons (3-5), deposited below a leaf, and the females guard the eggs until they hatch and the young have dispersed. There is no nest-building, however, as in *A. lunata.* A second and a third egg-cocoon produced by the same female both contained 26 eggs.

Discussion

In Denmark most theridiid spiders of above-ground layers have one-year cycles. In the beechwood studied this was found for *Anelosimus vittatus* (C.L.K.), *Theridion mystaceum* L.K., *T. pallens* Bl. (in this species a small part of the population has a two-year cycle) and *Enoplognatha ovata* (Cl.) (Toft, 1976). *A. lunata* and *T. varians* were the only biennial theridiids. Apart from the cycle-length they differ from the other species mentioned in other aspects of their life-history: their breeding period is very long (3 months, at least in *A. lunata*), and they make a larger number of cocoons; the subadults hibernate very early in the autumn, whereas the other theridiids are caught until snowfall. Another point, related to the cycle-length, is the very short period of growth: in *A. lunata*, growth is restricted to 3½-4 months (May-August), in *T. varians* this is probably 4-4½ months (May to mid-September).

Both climatic and biological factors must be considered to influence the cycle-length. Based on laboratory breeding Juberthie (1954) concluded that in southern France *A. lunata* and *T. varians* have two generations per year, one developing in spring/summer and one in autumn/winter. As both species are biennial in Denmark, the conclusion is obvious that in some area of mid-Europe they must have annual cycles.

Both genera, *Achaearanea* and *Theridion* have annual and biennial representatives in Denmark. The climate of different habitats may be part of the reason, as species of open areas all seem to be annual. But this is probably not the whole explanation. The variation in life-history patterns of spiders within a particular habitat is much smaller than between different habitats (the different layers of the forest, for example), not only as regards cycle-length but also seasonal periodicity (Toft, 1976). Thus the seasonal occurrence and activity of prey insects probably influence cycle-length.

Finally, care of offspring may be of importance. Hirschberg (1969) describes three stages in the evolution of brood care in theridiid spiders: (1) no feeding of the young in the nest, (2) the young are offered some of the prey caught by the mother, and (3) the young are fed digested food from the mouth of the mother in the early stages, and later they cooperate in prey-capture. *A. lunata* is stated to belong to the first group, and the young leave the nest in the first instar, and are unable to develop further in the autumn months. In *A. riparia* (Bl.) and *Theridion sisyphium* (Cl.), belonging to the second and third group respectively, the young moult a number of times before leaving the nest. They are thus well ahead by the time they start an independent life.

The stage at which the spiderlings of these species leave the nest may vary within the species. However, some measure of the effect of brood-care on the rate of development may be obtained simply by recording the largest stage still to be found in the nests. The three species mentioned above are ideal for this comparison as they have identical breeding periods (end of June, July and August). Table 2 summarizes the points I wish to make: the young of *A. lunata,* with the least developed type of brood-care, leave the nest early, hibernate in a very early instar, and take two years to complete their life-cycle. In *A. riparia*, with more elaborate brood-care, the young moult twice while in the nest and here the cycle is completed in one year. *T. sisyphium*, with the most highly developed type of brood-care, reaches even further in development; it may hibernate as a subadult (Kirchner & Kullmann, 1975), and the cycle takes one year.

The hibernation cocoon of *A. lunata* described in this paper may be an adaptation specifically evolved

	Brood-care group of Hirschberg (1969)	Largest instar in nest	Cycle-length (years)
Achaearanea lunata	1	1	2
Achaearanea riparia	2	3	1
Theridion sisyphium	3	4	1

Table 2: Comparison of the largest instar found in the nest and cycle-length with the degree of brood-care in three theridiid spiders in Denmark.

to meet the conditions prevailing in the northernmost ranges of its distribution. Populations in southern Europe, producing a second generation during the winter months, could hardly exhibit this phenomenon. The observation of Locket (1975) is particularly interesting in this connection. He found that in the closely related *A. simulans* (Thor.), specimens from Poland make a similar hibernation cocoon, whereas British specimens do not. The difference in mean January temperatures of Poland and southern England is about 8°C (Poland −3°C, southern England +5°C, Wallén, 1970). Only future studies can reveal whether such a difference also exists in *A. lunata*, and if it shows any relationship to the changing cycle-length.

A. riparia (Bl.) may sometimes spend the winter in a similar cocoon (Nørgaard, 1956). According to Nørgaard this is not obligatory, and the hibernation cocoon merely seems to be a modification of the nest, which in this species is made by spiders of all stages. In *A. lunata* the juveniles build no nest in their webs, so here the hibernation cocoon is an independent construction, though the two products may, of course, be evolutionarily related.

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