Life histories of eight Danish wetland spiders

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The life-history patterns of eight spider species from stands of *Typha* and *Sparganium* in a small lake at Aarhus, Denmark, are worked out. Six of the species have annual cycles, of these *Gnathonarium dentatum* (Wider) and *Pachygnatha clercki* Sund. complete development in their first season, while *Hypomma bituberculatum* (Wider), *H. fulvum* Bös., *Microlinyphia impigra* (O. P.-C.), and *Tetragnatha striata* L. K. hibernate mainly as subadults. *Clubiona phragmitis* C. L. K. has a biennial cycle, hibernating first as juveniles, then as adults. *Pirata piraticus* (Cl.) is mixed annual and biennial in both cases only juveniles hibernate. All species breed in spring and summer.

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Introduction

In a recent paper Duffey (1978) lists a number of ecological characteristics that should be investigated for any species of spiders as they seem important for a general understanding of the life strategies within the group. The intention was to provide a framework to which researchers in different areas might contribute so that, eventually, the data may be compiled to create a more coherent picture of spider ecology. The present study contributes some of the life history data demanded for on eight species commonly encountered in wetland vegetation in Denmark.

This approach, however, more or less neglects the spiders' adaptations to the ecosystem in which they are elements. Elsewhere (Toft, 1976, 1978) I have shown that the spider species of different habitats show some striking patterns in a number of life-history characteristics that must be understood in the light of the phenological patterns of the lower trophic levels. The species treated here comprise all the abundant spiders of a particular wetland habitat, so the results may also allow more general statements on this spider community.

Study area and methods

Spiders were collected at a small lake at Toveshøj, Brabrand, just west of Aarhus. The lake forms the bottom of a depression and is surrounded on all sides by fields. Only a narrow belt of natural lake vegetation is developed, especially at the east and west ends. Most intensive sampling was done in the outermost part of this vegetation, which at high water levels was covered by water at the base. Particularly, stands of *Typha latifolia* L. and *Sparganium ramosum* Huds. were searched and, with lower water levels, also the dead plant material below. Both plant species mentioned have hollow leaf sheaths, which are seeked out by many spiders.

The collections are strictly qualitative as the animals were taken by simple hand collecting or, for most of the samples, by help of a suction apparatus. This has the advantage that even the smallest juveniles can be taken with ease.

The material has been treated following the scheme developed in a previous paper (Toft, 1976): Where possible juveniles have been determined to instar by measuring the length of tibia of the first leg (tibia I); in larger instars sexes have been distinguished by the swelling of the palpal tarsus in the male; the period of reaching adulthood in species with more or less overlapping generations was assessed by recording newly moulted (soft) adults; breeding periods and egg numbers have been determined by dissection of adult females, the degree of development of their gonads being assigned to either of four subjectively defined phases: 1.

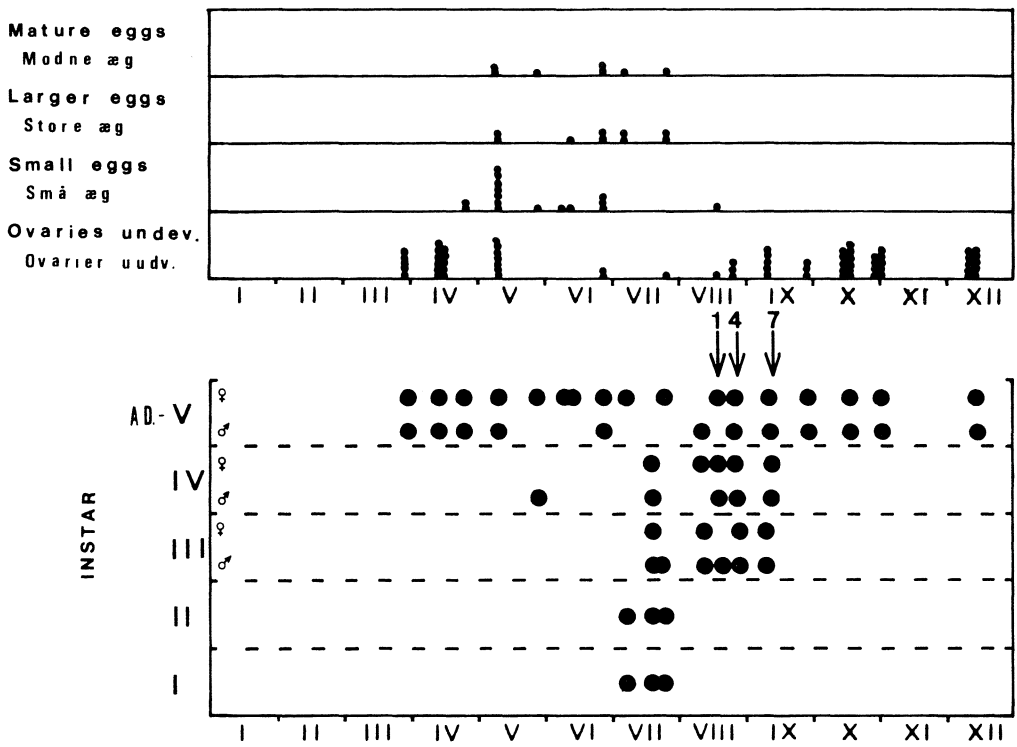


Fig. 1. *Gnathonarium dentatum.* Upper diagram: Gonad condition of adult females. Each dot denotes an observation. Lower diagram: Phenology of instars and sexes. Dots indicate occurrence, irrespective of numbers. Arrows = occurrence of "soft" (newly moulted) adults in numbers indicated above.

ovaries undeveloped, 2. ovaries with small eggs, 3. ovaries with larger eggs, 4. ovaries with mature eggs. The eggs are assumed to be deposited shortly after becoming mature. Further data on reproduction was gathered by collecting egg-cocoons in the field. The batch of simultaneously developing eggs is termed a clutch, to be distinguished from the contents of an egg-cocoon.

In some of the species the tibial measurement did not allow a safe instar determination, either because of overlap or because the number of instars is variable. It has therefore been necessary to present the data for the species differently.

In the two years, 1975 and 1976, the locality was visited 24 times. Except for January and February collections were made all months of the year. In the figures, however, the data are presented in one-year diagrams.

Results

1. *Gnathonarium dentatum* (Wider) (Linyphiidae)

This is the smallest (2–3 mm) spider treated in this study, and it is exceedingly common in the vegetation of lakes and rivers. The phenology is depicted in Fig. 1. Adults are found all year round, but the breeding period is restricted to the months of May, June and July; in all other months the females have undeveloped ovaries. The small young appear in midsummer. The very restricted period of juveniles signifies a fast development; already in mid-August the first new adults appear, and by mid-September the whole new generation has reached maturity. In this stage it hibernates. Only a single specimen, a subadult male taken in late May, departs from this picture. A very low proportion of the population may thus hibernate as juveniles, but in both circumstances the cycle is

strictly annual. Though not fully conclusive the dissection data indicate that females develop two egg-clutches, the first one in May and the second in late June to July. From the dissections egg-numbers were counted with the following results (mean ± one standard deviation).

First clutch: 26.5 ± 2.6 (n = 6)
Second clutch: 29.6 ± 10.5 (n = 11)

Two early egg-cocoons contained 20 and 23 eggs, a late one 25 eggs.

Few comparative data exist in the literature. However, the diagram of Palmgren (1976, Fig. 32) indicates a similar life-cycle in Finland.

2. *Hypomma bituberculatum* (Wider) and *Hypomma fulvum* Bös. (Linyphiidae)

These two species must be treated together as I have not been able to distinguish the juveniles. The adults are very similar in appearance and of approximately the same size, but *H. bituberculatum* is by far the most abundant. However, the very clear phenological pattern of the juveniles, though the species are mixed, and the identical adult periods (Fig. 2) indicate that they are phenologically similar. The main adult period covers the months May to July, and egg-laying takes place in June and July. First instar juveniles appear from July, and by August–September they have reached the subadult stage (instar IV). They hibernate in this stage, and start growing again in late April. A few adult females of both species, however, hibernate as adults; these specimens must have become adult already in autumn. As with the previous species, the cycle is strictly annual.

Egg-sacs are deposited protected in leaf sheaths and the females sit guard on them. The

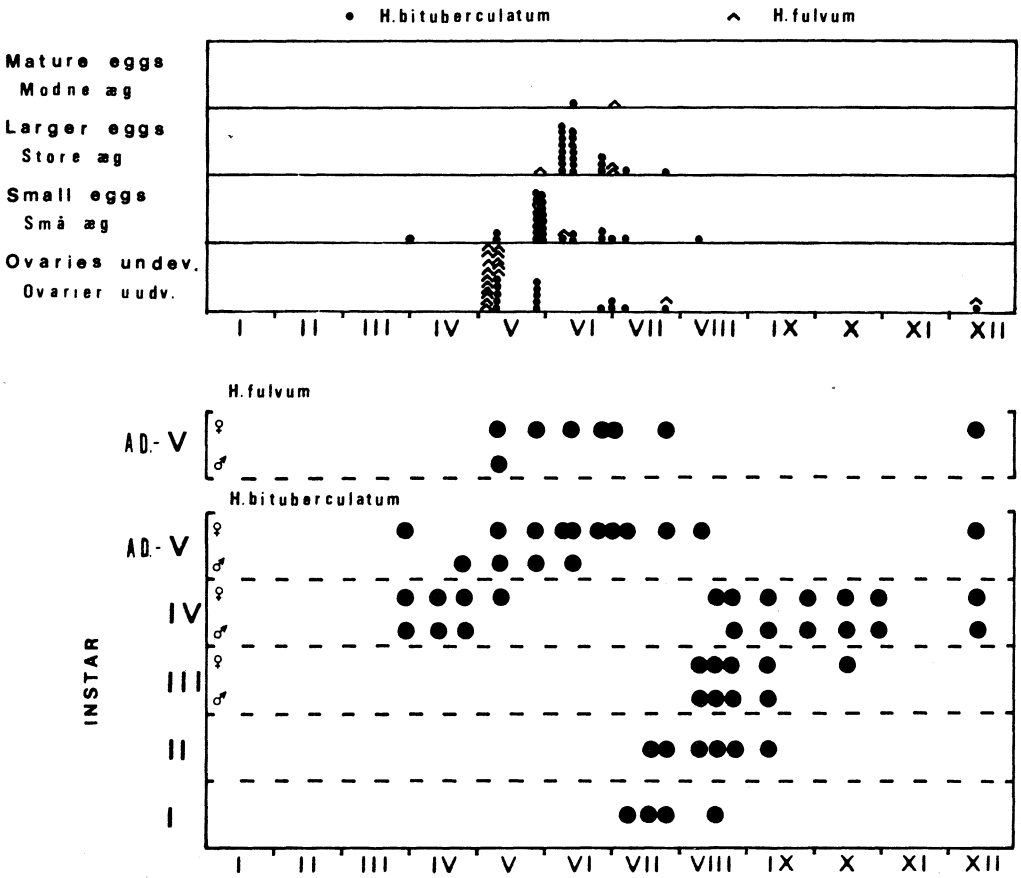


Fig. 2. *Hypomma bituberculatum* og *H. fulvum*. Upper diagram: Gonad condition of adult females. Lower diagram: Phenology of instars and sexes. Explanation as in Fig. 1. In the juvenile data the species are mixed.

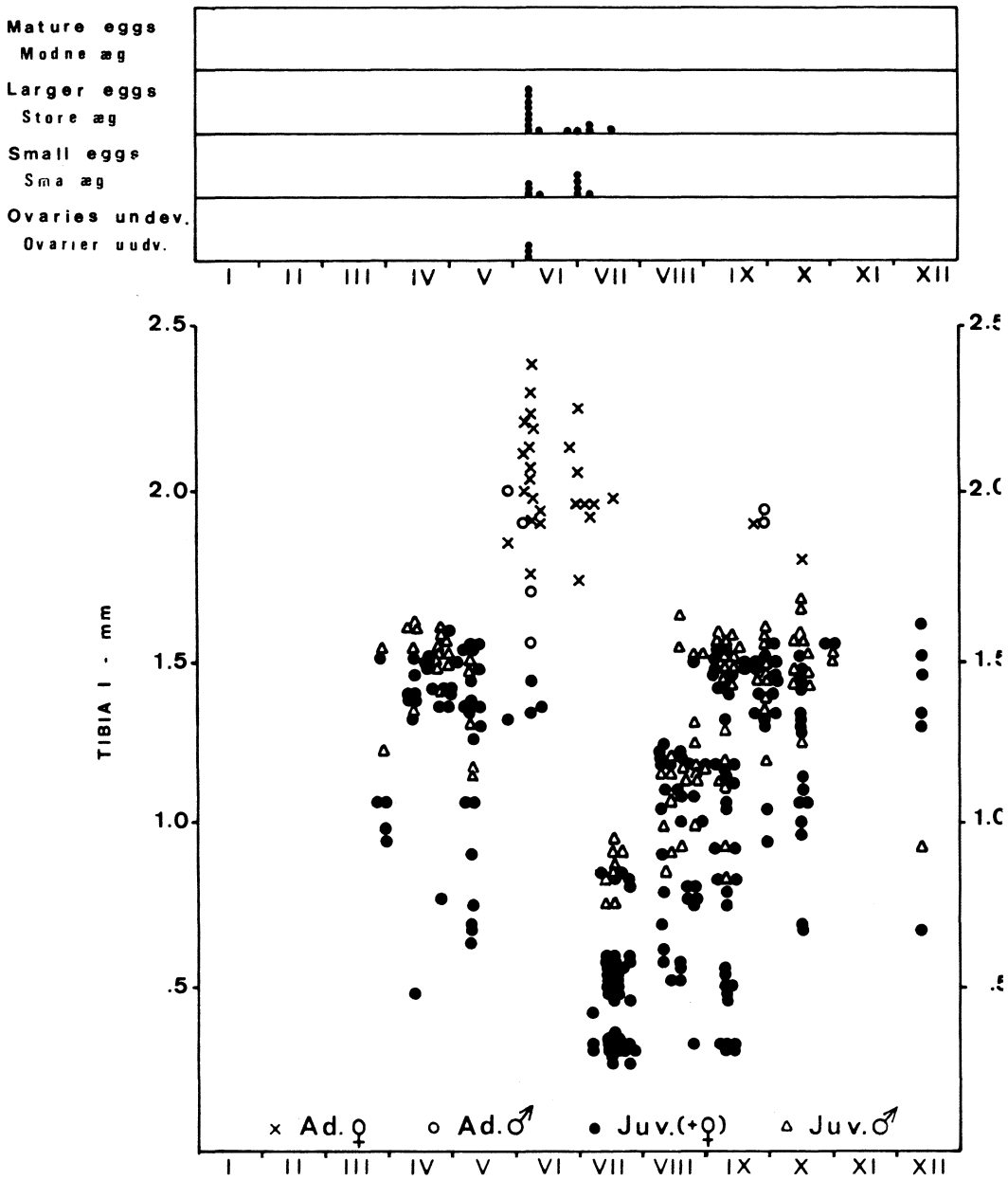


Fig. 3. *Microlinyphia impigra.* Upper diagram: Gonad condition of adult females. Explanation as in Fig. 1. Lower diagram: Seasonal occurrence of every individual according to size (length of tibia I).

females of *H. bituberculatum* may go through one or two cycles of ovarian development: In June females contain 47.1 ± 9.4 eggs (n = 13), in July two females contained 21 and 22 eggs. However, in the cocoons egg-numbers varied between 24 and 37; the first clutch developed must therefore at least in some females be divided in two cocoons. This is verified by a single observation of a female guarding two cocoons spun together, containing 24 and 32 eggs, respectively. For *H. fulvum* only data for June are available (27.3 ± 2.9 eggs per female (n

= 8)). It is noted that there is a striking difference in the reproductive capacity of the two species. This may perhaps be referred to the different habitat relations of the species. *H. fulvum* is rather stenotopic, occurring in wetland situations only, whereas *H. bituberculatum* is also very abundant in sand dunes. According to Palmgren (1976) the life cycle of *H. biturberculatum* is similar in Finland.

3. *Microlinyphia impigra* (O. P.-C.) (Linyphiidae)

The main life-cycle of this species (Fig. 3) is very similar to that of the two *Hypomma* species. It becomes mature by the end of May, and the adults survive for about two months. The small juveniles appear at the beginning of July; they reach the subadult stage, in which they hibernate, by September. A small proportion spends the winter in some smaller instar. Some adult specimens may also be found in autumn. As no large juveniles have been taken in summer, it is considered that these have become adult already in their first autumn.

Eggs are laid in June–July, in one or two cocoons. Clutch size: 81.4 ± 14.3 (n = 7).

4. *Tetragnatha striata* L. K. (Tetragnathidae)

Though the data are incomplete, they are sufficient to ascribe to this species a cycle similar to the previous species (Fig. 4): it is annual, with adults in summer and hibernation as subadults.

The bluish egg-cocoons are deposited openly exposed on leaves. The very short period in which they can be found (June only), signifies that only a single cocoon is made. Egg-numbers are: 71.6 ± 15.6 (n = 11). From Germany Wiehle (1963) states that *T. striata* becomes adult already in the first autumn. He also gives egg-numbers far lower than those reported here (about 30). Information from Finland (Palmgren, 1974) agrees with my results.

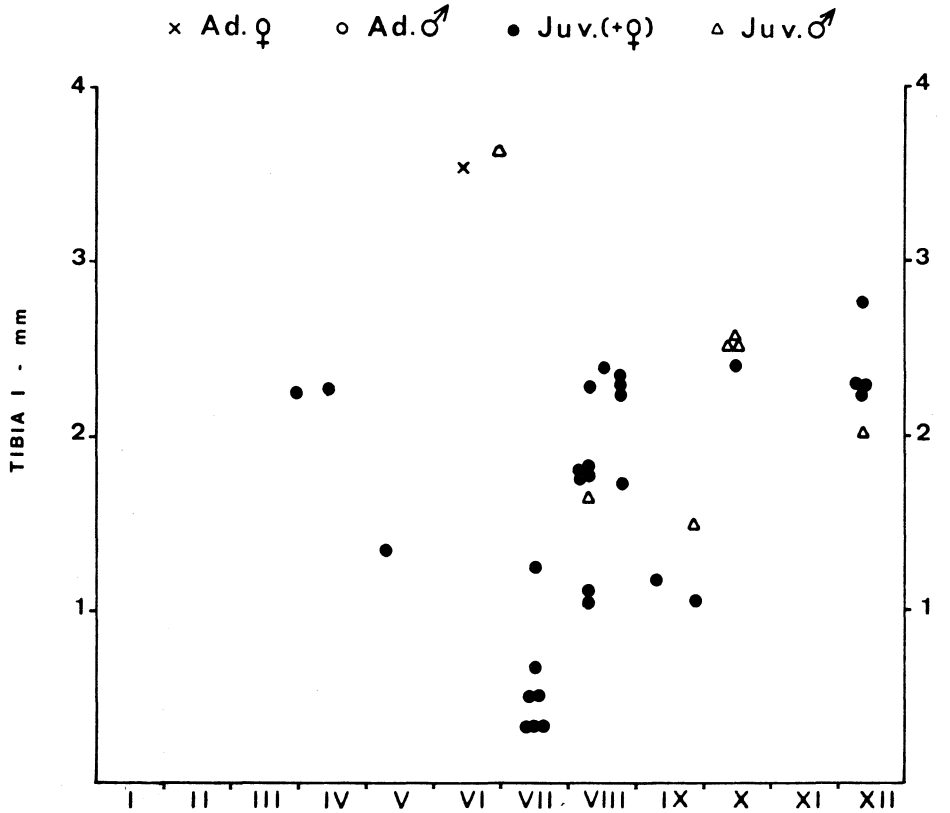


Fig. 4. *Tetragnatha striata.* Seasonal occurrence of every individual according to size (tibia I).

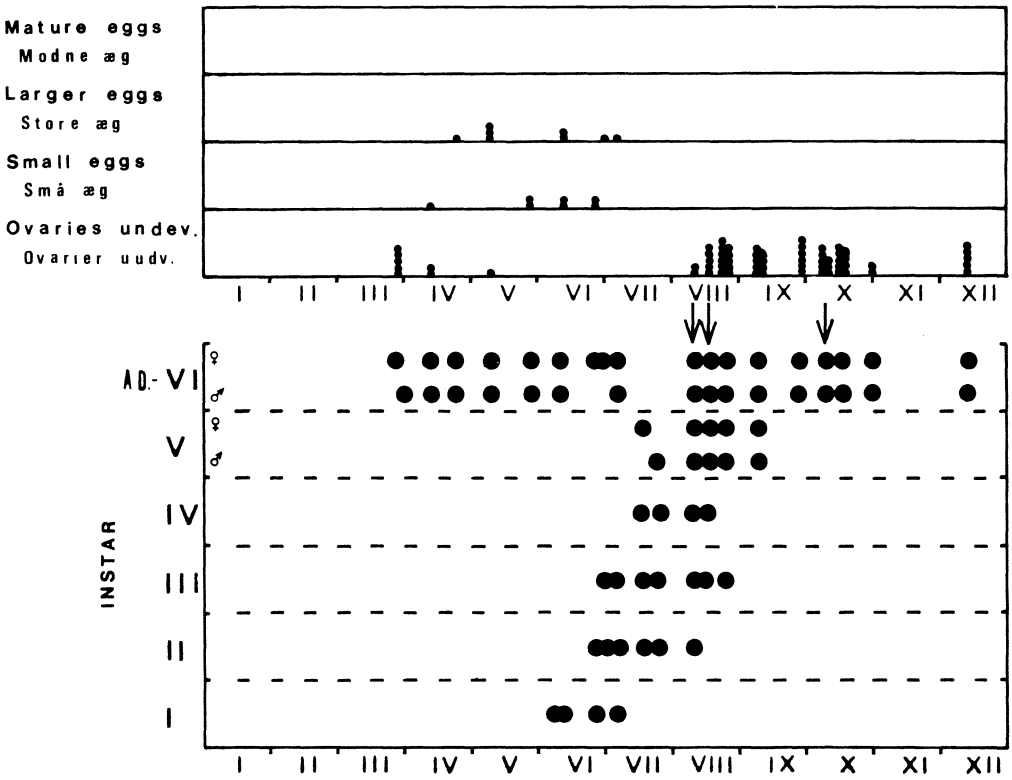


Fig. 5. *Pachygnatha clercki.* Upper diagram: Gonad condition of adult females. Lower diagram: Phenology of instars and sexes. Explanation as in Fig. 1.

5. *Pachygnatha clercki* Sund. (Tetragnathidae)

In this species the life-history pattern (Fig. 5) is similar to that of *Gnathonarium dentatum* (Fig. 1): The whole development takes only about two months, so the new generation of adults appears already in August. There is no reproductive activity in autumn, and only adults hibernate. Eggs are laid in May–June (–July); one or two clutches are developed. Clutch size: 56.7 ± 9.1 (n = 7). According to Schaefer (1976) up to four egg-cocoons are made with a total of 58.9 eggs (sum of average values); the clutches are thus split up in more cocoons.

Pachygnatha listeri Sund. was found to have an identical life-cycle (Toft, 1976). According to Palmgren (1974, Fig. 28) all three North-European species are similar in their developmental pattern.

6. *Pirata piraticus* (Cl.) (Lycosidae)

The cycle (Fig. 6) is mainly annual: Adults are found in spring and summer only; females carrying egg-sacs have been taken from June to August. The young disperse from their mother from July; many of them reach the subadult stage by September, though any juvenile size group may hibernate. A rather large number is found as smaller juveniles during the whole breeding season; this part of the population must have hibernated for the first time in an early instar, and they will hibernate once again as subadults. In this species, therefore, two developmental lines can be distinguished, one annual, the other biennial.

Females seem to develop one or (in some) two clutches. The first egg-sacs contain 66.5 ± 13.6 (n = 17) eggs, second egg-sacs 27.5 ± 11.4 (n = 4) eggs.

These results agree very well with those obtained by Schaefer (1974) from Northern Germany.

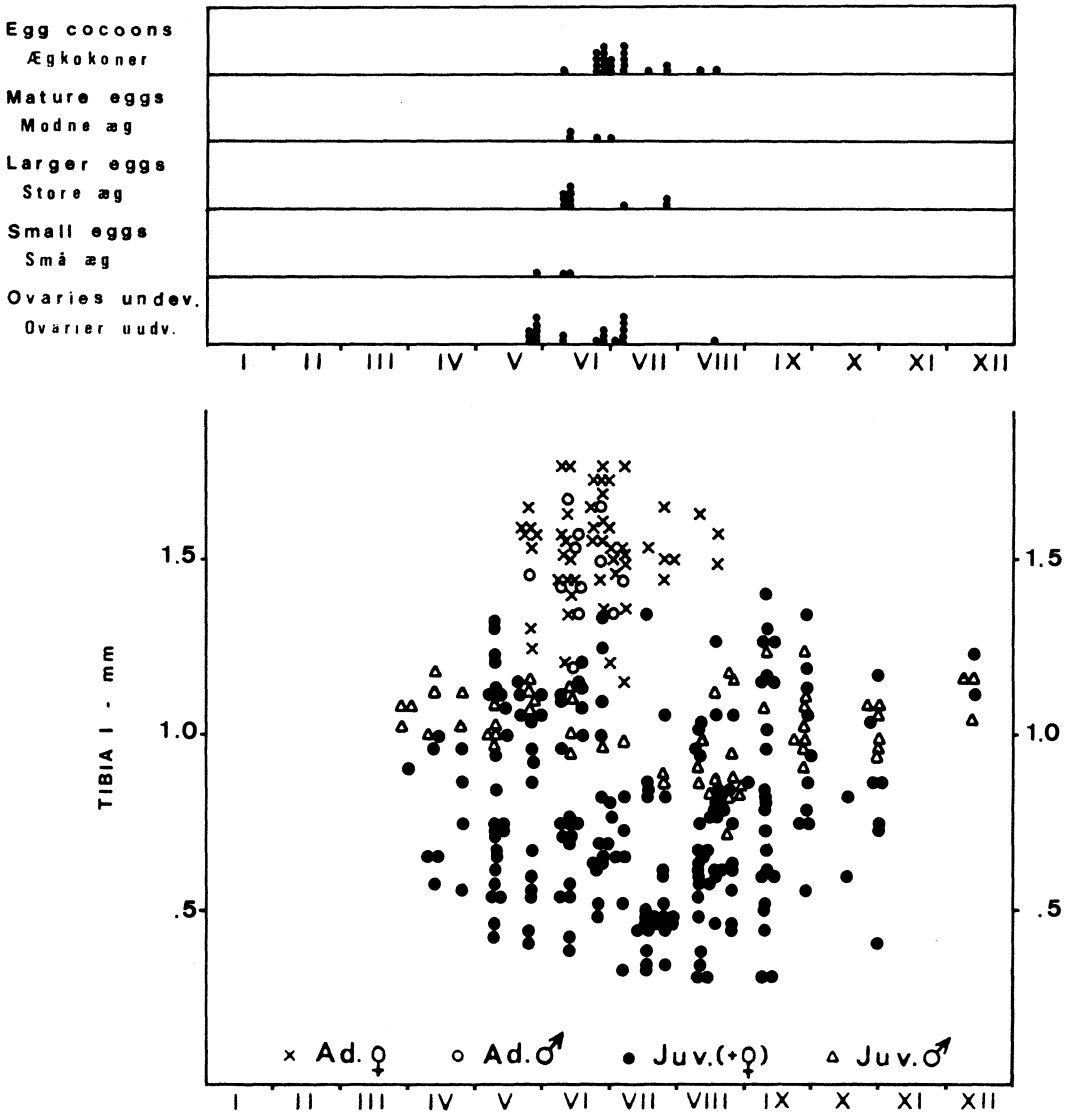
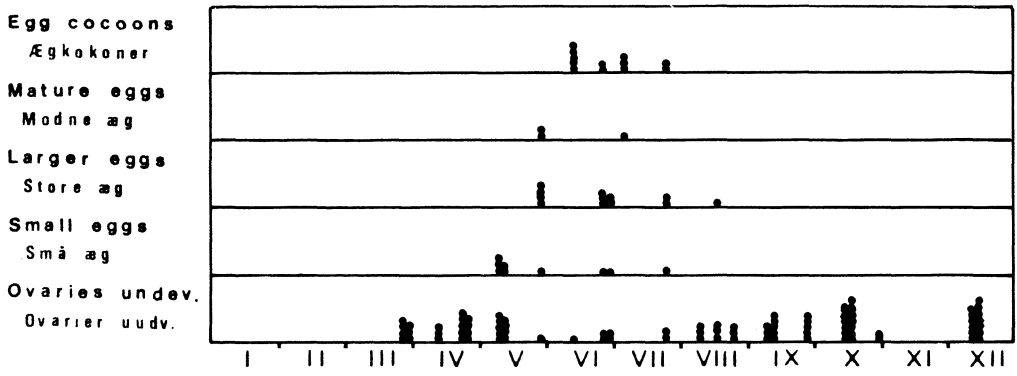


Fig. 6. *Pirata piraticus.* Upper diagram: Gonad condition of adult females. Lower diagram: Seasonal occurrence of every individual according to size (tibia I).

7. *Clubiona phragmitis* C. L. K. (Clubionidae)

Contrary to all other species of this study, *C. phragmitis* seemingly has a pure two-year cycle. Fig. 7 shows the rather confusing phenological pattern, illustrating an even occurrence of all size classes all year round. However, females develop eggs in June–July only. The resulting juveniles first appear in mid-July, but spiderlings continue to disperse from the nests for about three months. Early juveniles seem to grow with some speed, and they may reach in-

Fig. 7. *Clubiona phragmitis.* Upper diagram: Gonad condition of adult females. Lower diagram: Seasonal occurrence of every individual according to size (tibia I). Dashed lines approximately delimit separate generations. Further explanation in Fig. 1.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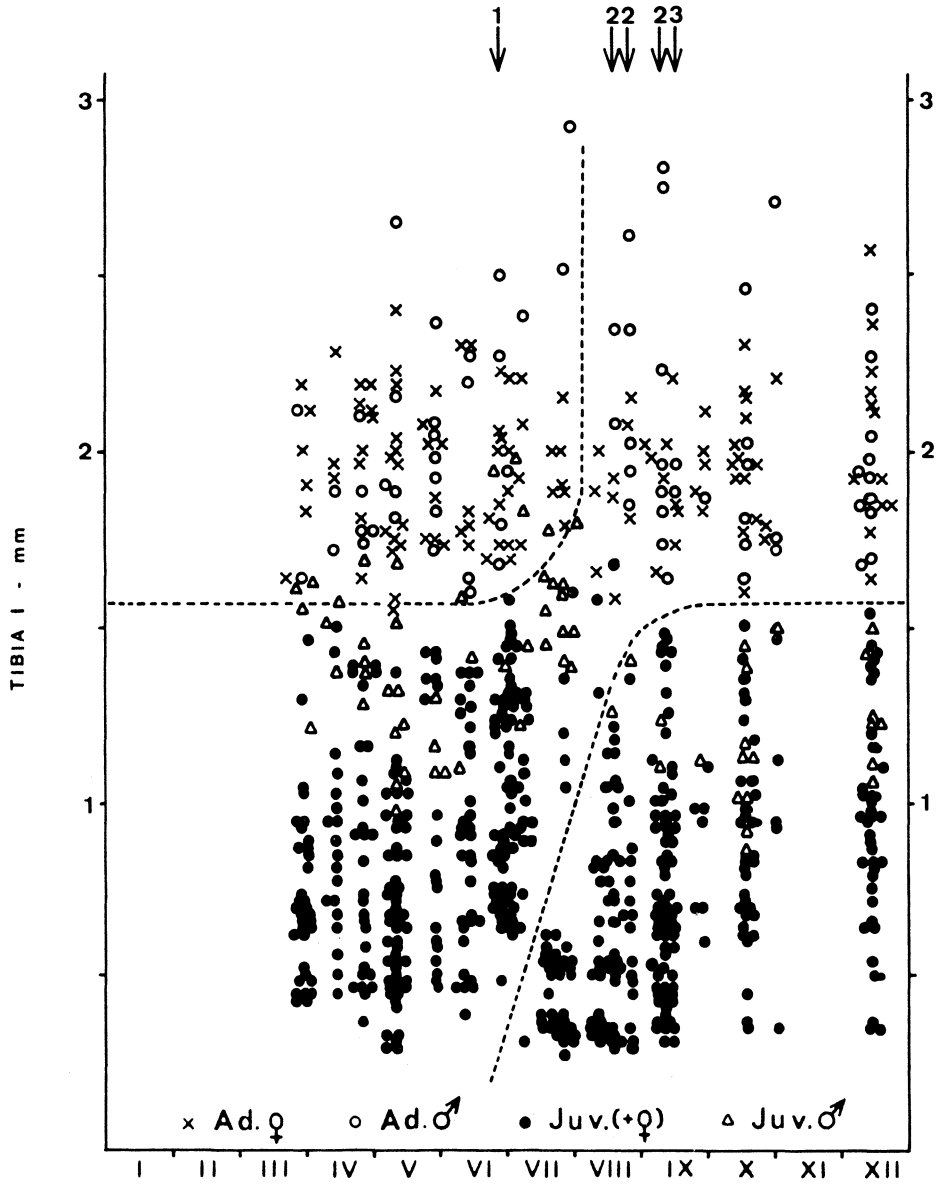
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star IV or so before hibernation (Schaefer (1976) states five (males) or six (females) instars for the whole cycle). Later juveniles grow extremely slowly, if at all. Thus, the first winter is spent in nearly all juvenile instars. In spring growth seemingly is not resumed until mid-June, but then proceeds rather fast, and all become adult during August and September. According to Schaefer (1976) copulation may take place in autumn, but there is no development of eggs until the following spring.

As outlined above the growth period is extremely short in this species, about three months (June–August). This is caused by a very high lower temperature limit for growth: 10–12°C (Schaefer, 1976).

One or two clutches are developed, in June and July. In June females contain 145.6 ± 20.3 (n = 7) eggs, in July 93.3 ± 37.4 (n = 3) eggs. Egg-cocoons collected in both months contain 122.6 ± 30.1 (n = 12) eggs. There is a significant positive correlation between egg-numbers in the cocoon and the length of tibia I of the female ($y = 2.09 x - 88.8$, $r = 0.87$ with $p < 0.001$, $n = 12$); thus differences in body size explain much of the great variation in reproductive capacity within the species. Applying this regression to tibia-measurements of all (cocoonless) females captured during the whole study period, a mean cocoon size of 122.9 ± 21.8 (n = 109) eggs is obtained. This is identical with the cocoon size observed. The egg-numbers given here are far higher than those reported by Schaefer (1976): 30–60 (mean 45.2) eggs!

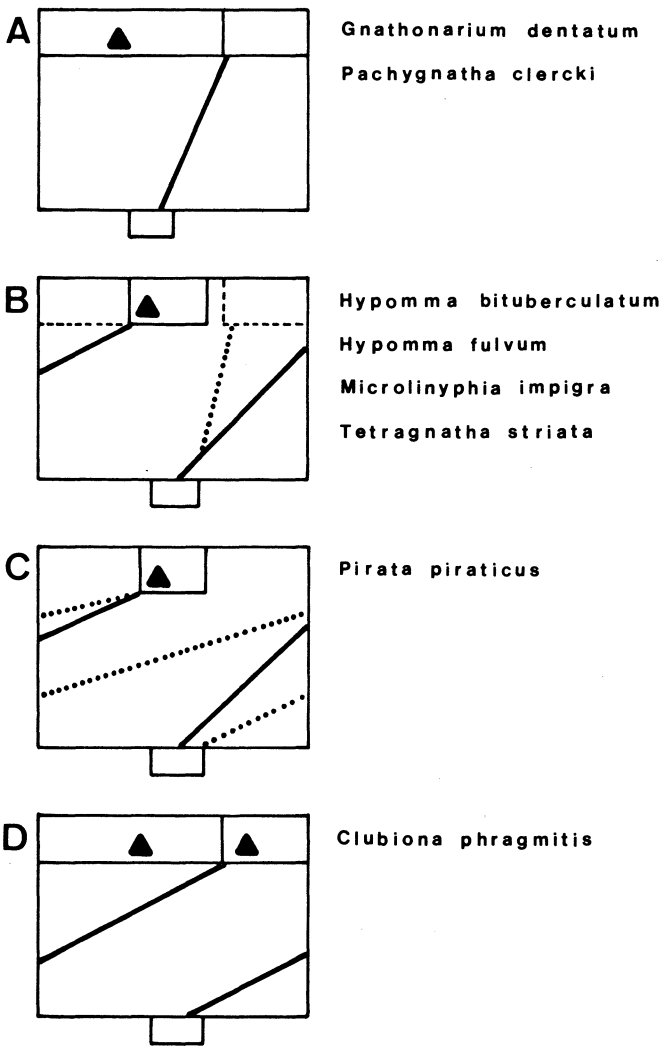

Fig. 8. Schematic representation of the life-history types of the eight lake-side spiders investigated. Explanation of the diagrams: rectangle in upper part = adult period; triangle = time of copulation; rectangle below = egg-laying period; heavy line inside = main path of juvenile growth; dotted line = secondary path of juvenile growth. The diagrams cover events during one calendar year.

Discussion

The life-history types met with in this study are summarized schematically in Fig. 8. Six species have pure annual cycles (types A–B), one species is biennial (D) and one is intermediate (C). Thus, in the habitat considered there is a predominance of annual spiders. Even more striking, however, is the restriction of breeding periods to spring and early summer, in spite of the fact that three species become adult already in autumn. Compared to the situation in beech-woods (Toft, 1976) these lake-side spiders resemble those of the herb-layer with respect to cycle length (annuals predominate), and those of the canopy with respect to the concentration of breeding periods. This interspecific synchronization probably stems from the vegetational composition of the habitats. As with the beech canopy they are composed of rather pure stands of single plant species with restricted periods of above-ground growth to which, in the first place, herbivorous insects must adapt. Spiders, in turn, must adapt to the seasonality of their prey insects (cf. Toft, 1976).

It is quite uncertain what determines, whether a habitat is inhabited by annual or biennial species; average temperature conditions may be important, as well as the general level of insect activity, especially outside periods of peak activity. More different kinds of habitats should be investigated before detailed hypotheses can be formulated.

The peculiar size distribution of *Clubiona phragmitis* deserves comment. One of the ways that closely related spider species are belived to coexist in the same habitat is by differing in body size. Now, *C. phragmitis* occupies nearly all sizes possible for these kinds of spiders under Danish conditions, and it does so for the whole year. It may therefore not be accidental that it is practically the only species of the clubionid/gnaphosid guild in its habitat. Only one relative, *Clubiona stagnatilis* Kulcz. turned up regularly in the collections, but in small numbers only, and they may be stray animals from neighbouring habitats. Also, the very great scatter of adult body sizes (Fig. 7) may have resulted from the lack of competitors. For comparison, in the three coexisting species of *Clubiona* from a beech-wood every size group was phenologically clearly restricted (Toft, 1978, fig. 1–3).

Acknowledgement

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Sammendrag

Livscyklus hos otte edderkoppe-arter fra vådområder.

På grundlag af regelmæssige indsamlinger af edderkopper ved en lille sø beliggende ved Toveshøj, Brabrand, beskrives livscyklus hos 8 arter, der alle er almindeligt forekommende i søbredsvegetation o. l. i Danmark. Indsamlingerne strakte sig over to år, 1975–76, og foregik hovedsagelig i vegetation af Dunhammer og Pindsvineknop ved hjælp af en sugeflaske; fangsterne er således rent kvalitative.

Materialet er behandlet efter følgende fremgangsmåde: Udover artsbestemmelsen er ungerne, hvor det har været muligt, fordelt på udviklingsstadier (instar) ved måling af tibia på første benpar (tibia I); hos større unger er hanner udskilt på deres opsvulmede palpetarsus; for arter med overlappende generationer er fremkomsten af en ny generation indiceret af forekomsten af 'bløde' individer, der netop har gennemgået det sidste hudskifte og endnu ikke er fuldt udfarvede; æglægningsperioder og ægtal er bestemt ved dissektion af adulte hunner, dels ved indsamling af ægkokoner i felten. Ved dissektionerne er ovariernes udviklingstilstand henført til én af følgende fire faser: 1. ovarier uudviklede, 2. ovarier med små æg, 3. ovarier med store æg, 4. ovarier med modne æg.

Gnathonarium dentatum (Wider) (Fig. 1): Hele udviklingen foregår i løbet af en enkelt sæson, fra juli til september; overvintringen finder således sted i det adulte stadium. To kuld æg udvikles i maj–juli.

En identisk udviklingstype findes hos *Pachygnatha clercki* Sund. (Fig. 5).

Hypomma biturberculatum (Wider) og *H. fulvum* Bös. har ligeledes 1-årig cyklus, men af en noget anden type (Fig. 2). Forplantningen foregår om foråret, og i løbet af sommeren og efteråret vokser ungerne op til det subadulte stadium, i hvilket de overvintrer. Voksenstadiet nås tidligt om foråret. Denne udviklingstype er fundet hos to arter mere, *Microlinyphia impigra* (O. P.-C.) (Fig. 3) og *Tetragnatha striata* L. K. (Fig. 4). For alle fire arter gælder dog, at en meget lille del af populationerne udvikler sig som de to førstomtalte arter, og derfor i sjældne tilfælde kan findes adulte om efteråret/vinteren.

Hos *Pirata piraticus* (Cl.) (Fig. 6) har hovedparten af populationen ligeledes denne udviklingstype. En betragtelig del er dog noget langsommere i udviklingen; de overvintrer to gange som unger, og har således en 2-årig cyklus.

En givetvis ren 2-årig cyklus findes hos *Clubiona phragmitis* C. L. K. (Fig. 7). Efter at have overvintret første gang i et (hvilket som helst) ungestadium, når de adultstadiet det følgende efterår. De overvintrer således anden gang som voksne, inden forplantningen det følgende forår.

De otte arter omfatter alle dominerende edderkopper i den pågældende vegetationstype. Det er derfor muligt på grundlag af disse arter at udtale sig mere generelt om edderkoppefaunaen her. En skematisk oversigt over de fundne livscyklustyper findes i Fig. 8. 6 ud af 8 arter har rent 1-årig cyklus, én art er 2-årig, mens én art er blandet 1- og 2-årig. Ved sammenligning med forholdene i en dansk bøgeskov opfører søbredsfaunaen sig med hensyn til udviklingshastighed mest som urtevegetationens edderkopper, idet der også her blev fundet overvægt af 1-årige arter, mens krone- og førnfaunaen hovedsagelig bestod af 2-årige arter. Et andet interessant træk findes i fordelingen af æglægningsperioderne. Som det fremgår af Fig. 8 har alle otte arter forplantning i månederne maj–juli. På dette punkt opfører søbredsedderkopperne sig mest som bøgeskovens kronefauna, hvor en koncentration af forplantningen i sommermånederne kunne påvises.

To arter af *Ectobius* (Dictyoptera: Blatellidae) fundet indendørs ved Jyllands vestkyst.

Under et sommerhusophold i klitområderne ved Ringkøbing Fjord, august 1977, blev to arter af kakkerlakker, *Ectobius lapponicus* (L.) og *E. panzeri* (Steph.), fundet levende i sommerhuset. *E. lapponicus* er i forvejen kendt som beboer af huse. Den synanthrope levevis er hyppigere i de nordlige dele af artens udbredelsesområde og Winding & Mourier (1971: Statens Skadedyrslaboratoriums Årsberetning 1970, p. 11–15) meddeler, at *E. lapponicus* allerede har forårsaget nogen skade indendørs her i landet. Det var derfor ikke overraskende, at finde denne art i sommerhusets badeværelse. Arten blev derimod ikke fundet udendørs på klitvegetationen. Kun voksne individer blev fundet som typisk for august måned.

Mere interesant var fundet af *E. panzeri* i sommerhuset. Denne art blev hyppigt fanget med ketsjer og i Moericke-fælder på den rige vegetation mellem klitrækkerne. Dens parasit, *Brachygaster minuta* (Hymenoptera, Evaniidae) fløj også i fælderne. Det må derfor antages, at der eksisterer en stabil population af *E. panzeri* i klitområderne ved den jydske vestkyst. Sommerhuset, hvor arten blev fundet, er bygget med yderdøre i niveau med det omgivende terræn. Den oprindelige vegetation når stadig husets mure, således at kakkerlakkerne har let ved at komme ind i huset. Indendørs opfører *E. panzeri* sig på samme måde som *E. lapponicus* og foretrækker ligesom denne art fugtige steder. (Oversat af red. En afhandling på tysk om samme emne og med mere udførlig litteraturgennemgang er af forfatteren publiceret i Ent.Mitt.Zool. Mus. Hamburg 6, nr. 104).

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