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Life cycle patterns in Wisconsin spiders

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Abstract: Five life cycle patterns in spiders are described and examples given. The most common pattern, maturation and mating in spring and early summer, is elaborated with a detailed description of the seasonal development of *Philodromus cespitum*. The four other patterns are exemplified by the following southeastern Wisconsin species: *Argiope trifasciata*--fall mating, *Centromerus sylvaticus*--winter mating, *Trochosa terricola*--two mating seasons, and *Pholcus phalangioides*--year round mating.

Introduction

Life cycle information may be one of the most elementary steps for analysis of the ecological relationships of an organism, but in the case of spiders this basic information is often lacking. One reason for this paucity of information is that there is a high degree of variability among spiders of the same species in the field at any one time, making interpretation of the life cycle difficult. Spiders of the same age, offspring of the same female, may differ from each other by a number of instars in their development to maturity. For example, in a rearing study which provided uniform environmental conditions, three siblings did molt to maturity on the same day (100 days after emergence from the egg sac), but one was in the sixth instar, one was in the seventh, and the third was in the eighth (Kaston 1970).

Studies to describe spider life cycles include several approaches. One has been to delineate life cycle patterns based on laboratory studies of representative species from a number of spider families, and then to create an overall summary that groups a regional fauna into several life cycle pattern categories (Schaefer 1977). Others, for example Toft (1975), emphasize that while such summaries may be useful in a descriptive way, the influences of local climate and habitat conditions are so strong that species-specific field studies are required to reveal the actual complexities of spider life cycles.

Dondale (1961) showed that the life cycles of spiders can be reconstructed by analysis of size groups based on measurements of the width of the carapace. Measurements of the strongly sclerotized parts of the body, such as the carapace, provide the best index of body size because they are less variable than a character such as total body length, which includes the abdomen. The abdomen expands and contracts according to the amount of food in the gut and, for female spiders, according to the stage in the process of egg maturation and release.

Because all growth in the strongly sclerotized parts occurs at the time of molting, these parts provide good indices of body size. Dondale determined the variability in measurements of six linear characters in newly hatched and adult individuals of five spider species and found carapace width to be generally the least variable. Carapace width as a tool for evaluating the development of spiders in the field was further tested by Hagstrum (1971) who found that mean carapace width showed a linear relationship to instar for 14 species in eight spider families.

Philodromus cespitum was chosen as the subject for my intensive study because preliminary collecting had revealed that samples of 20 or more individuals could readily be obtained by sweep netting. This brown and cream-colored species is a member of the family Philodromidae, spiders which do not build webs but hunt down their prey. However, they are rather short-sighted hunters, failing to react until prey is within 3 to 5 mm (Putman 1967). Like their crab spider relatives, philodromids have the first two legs held out to the side and turned so that the morphologically dorsal surface is posterior. Prey is generally caught with these legs but the philodromids are more active hunters than the ambush-adapted crab spiders. Philodromids have the four pairs of legs about equal in length, each leg possessing small brushes of hair as well as a tuft near the claw, giving the spider gripping power for a more active hunting style of moving about on precipitous surfaces and capturing prey.

Here a detailed life cycle pattern is determined for one spider, *Philodromus cespitum*, based on a field study of a Wisconsin population. A season-long program of sweep netting resulted in samples which allowed the reconstruction of this spider's life cycle based on comparative analysis of measurements of the specimens collected. The life cycle information from this population is used as an example of the most common of the five patterns from the summary scheme delineated by Schaefer (1977). Schaefer's four other life cycle categories are briefly described using species collected at the University of Wisconsin-Milwaukee Field Station or elsewhere in southeastern Wisconsin.

Methods

An intensive study of the life cycle of the holarctic philodromid spider *Philodromus cespitum* was made following Dondale's methodology (Jass 1979). A sampling program of removal sweep netting was carried out from June through September 1978 at an unmowed area of parkland along the Milwaukee River in Milwaukee County where vegetation was dominated by grasses with some forbs intermixed. Scattered sparsely at the site were large sugar maples (*Acer saccharum*). This is typical *Philodromus cespitum* habitat (Putman 1967).

Each sample of 150 sweeps was emptied into a plastic bag and poisoned with ethyl acetate. All spiders were removed from the sample and placed in 70% ethanol. Under the microscope, preserved spiders were measured across the widest part of the carapace to the nearest 0.1 mm. Each specimen was also assigned to one of three categories: male, female or immature. Mature males have swollen pedipalps. Mature females have a hard plate, the epigynum, on the ventral surface of the abdomen. Immatures lack swollen pedipalps and epigyna.

Results

Results are summarized in Figure 1 which graphs the frequency of individuals by their carapace width measurements for June, July and August. The means for carapace widths of all individuals increased from 1.43 to 1.60 millimeters between the June and July samples ($t = 5.04$, $df = 276$, $P < 0.00001$, SAS Institute 1985).

Immature *Philodromus cespitum* accounted for almost half (76 of a total of 172) of the mid June captures but less than 10% (10 of a total of 106) of early July sampling. This and the increase in mean carapace widths between June and July support a life cycle picture of many young in the population in the spring and early summer, molting to maturity by early July.

Besides information about the season of maturation, the data in Figure 1 can be used to show whether *Philodromus cespitum* is an annual or biennial species in southeastern Wisconsin. Among the species whose life histories Dondale analyzed by his method of size grouping based on carapace width measurements, there were two basic frequency distribution patterns. One was a bimodal frequency distribution. Species which require two years to reach maturity have a single generation added annually to the population in the North Temperate Zone (Dondale 1961), and have two generations in the field during most of the year, resulting in bimodality of graphed size measurements. The other, simpler developmental pattern was unimodal, showing a single generation of individuals of both sexes. From this difference, Dondale concluded that unimodal species were annual in their development, with bimodal species being biennial, having an approximately two-year life span.

Dondale (1961) showed that a spring-maturing spider that was biennial would have a strongly bimodal frequency distribution for June measurements, with two large, separated peaks indicating the presence of two subgroups (yearlings and two year olds) within the overwintered population. The frequency distribution pattern of June measurements for the Wisconsin population studied (Fig. 1) corresponds most closely to the pattern for species displaying a unimodal distribution, leading to the conclusion that in southeastern Wisconsin this species is annual in its development.

To briefly contrast the life cycle picture of *Philodromus cespitum* with a spider in which the season for maturation and mating is late summer and fall rather than spring and early summer, Figure 2 presents data on the month of collection for the orb weaver *Argiope trifasciata*. Data from southeastern Wisconsin specimens in the Milwaukee Public Museum collection show that over 96% of the mature males and females were collected in August or later, the majority having September collecting dates.

Discussion

The seasonal development for *Philodromus cespitum* fits that reported for spring-maturing annual species elsewhere (Dondale 1961, Putman 1967). The adults mature and mate in spring or early summer and the eggs are laid soon after. The adults subsequently die off. After leaving the egg sac, the young spiderlings undergo 3-4 molts (there is some variability) the rest of that season, before overwintering in a state of little or no growth. In spring the overwintered individuals grow at a relatively rapid rate and complete the final molts to maturity by early summer.

The developmental time for spider populations is normally shorter in more southerly parts of a species' range. Although Dondale found *Philodromus* *cespitum* to be biennial in Nova Scotia, Putman (1967) found it to be annual in the Niagara Peninsula of Canada. The more southerly, annual, life cycle is the pattern *P. cespitum* follows in southeastern Wisconsin.

Lacking sampling programs of equal intensity to the one for *Philodromus cespitum*, we can nevertheless note some interesting examples of the various life cycle patterns from among specimens collected at the University of Wisconsin-Milwaukee Field Station and elsewhere in southeastern Wisconsin. Schaefer (1977) delineated five different life cycle patterns among spiders in the Schleswig-Holstein area of northern Germany (Table 1).

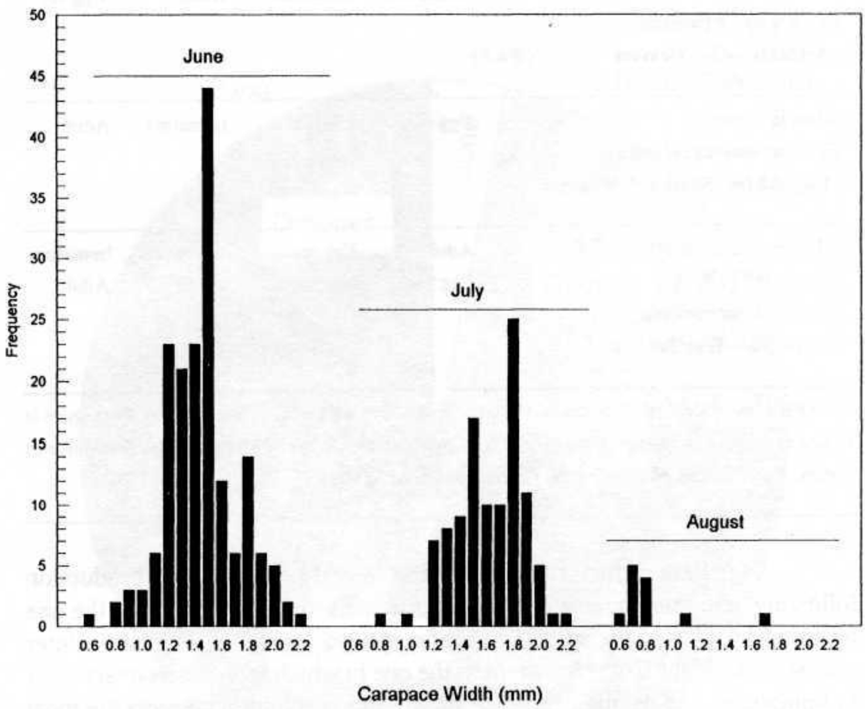

Figure 1. Frequency of carapace width measurements, to the nearest 0.1 mm, for all individuals sampled in June, July, and August from a population of *Philodromus cespitum* (n=290).

Table 1. Phases of seasonal development of spiders for life cycle pattern categories established by Schaefer (1977), and examples from southeastern Wisconsin species.

LIFE CYCLE PATTERN	SPRING	SUMMER	FALL	WINTER
1. Mate in spring Eg. *Philodromus cespitum*, Philodromidae--Philodromid Spiders	Adult	Egg sac	Immature	Immature
2. Mate in fall Eg. *Argiope trifasciata*, Araneidae--Orb Weavers	Immature	Immature	Adult	Egg sac
3. Mate in winter Eg. *Centromerus sylvaticus*, Linyphiidae--Sheet-web Weavers	Egg sac	Immature	Immature	Adult
4. Mate in spring (most)	Adult	Egg sac	Immature	Immature
Mate in fall (a few) Eg. *Trochosa terricola*, Lycosidae--Wolf Spiders	Egg sac	Immature	Adult	Adult

5. VARIOUS--Individuals follow one of the patterns above but because they live long lives, there is no one synchronous pattern in the population, and individuals in any phase may be found in any season. Eg. *Pholcus phalangioides*, Pholcidae--Cellar Spiders

A pattern of maturing and mating in early summer, egg production following, and immatures emerging later in the summer and fall was the one followed by 45% of the spiders Schaefer studied. His focus was the winter season, so he identified this pattern as the one in which individuals overwinter as immatures. As detailed above, *Philodromus cespitum* represents the most common pattern, that of maturation and mating in spring and early summer.

By contrast, the category which Schaefer found to have the smallest number of member species was that in which spiders overwinter in the egg sac, either as eggs or as recently hatched immatures, after a fall season of maturation and mating. The banded garden spider *Argiope trifasciata* is a large-bodied orb weaver whose web is found among grasses and weeds in sunny fields. A thickened zigzag of extra silk called the stabilimentum transects the hub of the web where the female spider resides, males usually being found at the web peripheries. The fully mature female collected September 11, 1978 at the UW-M Field Station is typical of southeastern Wisconsin specimens in the Milwaukee Public Museum collection, in that over 60% of the mature males and females were collected in September (Fig. 2). By the end of September after the fall mating, most females of this species will have produced a large egg sac swathed in protective silk and placed in the vegetation near the web site. Shortly after the first frost, all adults die leaving only the egg sac to survive the winter.

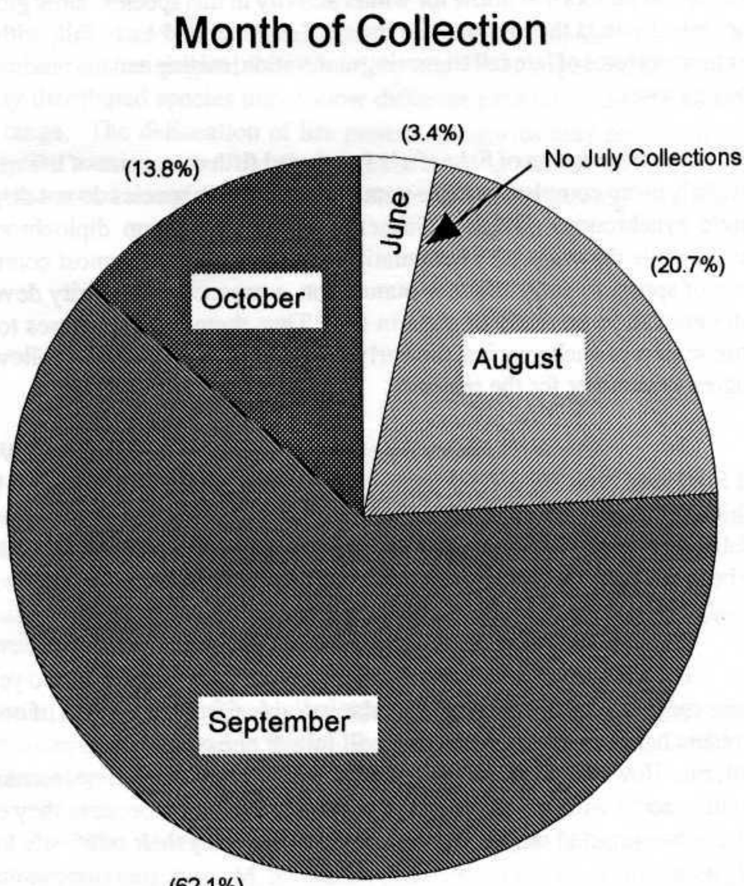

Figure 2. Month of collection, from June through October, for mature females and males of the fall maturing orb weaver *Argiope trifasciata* (n=29).

Only slightly larger was the group of spiders spending winter in the adult stage and using that season for maturation and mating. Examples given by Schaefer for spiders of the winter maturing and mating category are all linyphiids, members of the sheet-web weaver family. Although they are by far the commonest spiders of the North Temperate Zone, sheet-web weavers are often overlooked because of the small size (2-3 mm in body length) of most species. A mature male of the linyphiid *Centromerus sylvaticus* (determined by Dr.J.Kaspar) was collected October 2, 1987 in the leaf litter of the upland hardwood forest of the UW-M Field Station. Schaefer (1977) identified the physiological factors that allow for winter activity in this species: slow growth of the immatures at the high temperatures of summer and early fall, with the lower temperatures of late fall triggering maturation, mating and the production of the egg sac.

The description of Schaefer's fourth and fifth categories of life cycles are slightly more complex because populations of these species do not display a single synchronous pattern. Schaefer termed one group diplochronous because, while the majority of population members follow the most common pattern of spring to early summer maturation, a precocious minority develop rapidly enough to be ready to mate in fall. Thus there are two phases to the mating season of such species, the early fall for a minority and the following spring/early summer for the majority.

The wolf spider *Trochosa terricola*, collected at the UW-M Field Station in both the upland hardwood and bog forests, is a species which exhibits the pattern of having mature individuals in the population both in spring and fall (Aitchison 1980), Schaefer's diplochronous category. Mature individuals have been collected in Wisconsin as early as May 2nd but also as late as October 2nd.

The fifth group is influenced chiefly by the long lives (over two years) of these species. If we look at a particular individual in a population of one of the spiders belonging to this group, it will follow one of the single phase type of patterns. However, if we look at the whole population at one time, some will be mature, some will be in the egg sac and some immature, because they each will have been started on this cycle at different times by their relatively long-lived parents.

Pholcus phalangioides is a Wisconsin species that has a longevity close to that of Schaefer's final category of species with life spans of two years and longer. It is frequently found in damp areas of buildings and is so adapted to that habitat that it may be called a synanthrope, meaning a species we are more likely to find in domestic rather than natural habitats. Known as the long-bodied cellar spider, this spider belongs to a family frequently found in caves. Cave dwellers and synanthropes share the trait of living in habitats which provide shelter from the seasonal fluctuations of our climate. *Pholcus phalangioides* seems able to produce an egg sac at any time of year. The sac is not swathed in a lot of extra silk and is carried in the jaws of the female until the young are ready to emerge. This species was collected in March in the Field Station building.

As Toft (1975) and others have emphasized, spider life cycles are influenced by phenological factors and the context of a specific environment. Widely distributed species may follow different patterns in different parts of their range. The delineation of life pattern categories may provide a useful descriptive summary, but detailed species-specific studies are necessary to reveal the actual complexities of spider life cycles in real ecological situations.

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