Are two cohorts responsible for the bimodal life-history pattern in the wolf spider *Pardosa agrestis* in Hungary?

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Summary

Pardosa agrestis (Araneae, Lycosidae) is the dominant wolf spider in many Hungarian agricultural habitats and other disturbed areas. We have started to decipher its success in occupying these human-influenced habitats by examining the seasonal dynamics and life history of the species. Data from nine localities in the country, collected by pitfall trapping and suction sampling over three years, were gathered for all life stages and standardized for sampling effort and method. The seasonal dynamics curves revealed an unusually long reproductive period. Catches of females showed two distinct peaks in May and August, with peaks of males being concurrent. Each adult peak was preceded by a peak of subadults. Spiderlings were caught from early June until October. Overwintering occurred in juvenile and subadult stages: we found no adults overwintering. All stages having a bimodal phenology has not been reported in related species. We have formulated two hypotheses about the life history of *P. agrestis*: the first proposes that the two peaks indicate two generations; the second suggests that two cohorts might be responsible for the peaks. Both scenarios might be slightly altered if females produce more than one brood. The two cohort hypothesis includes the possibility that some level of isolation exists between the two cohorts of the field population.

Introduction

Wolf spider species of the genus *Pardosa* show a typical stenochronous life cycle, adults reproducing in the spring and different instars of the juvenile stage overwintering (Schaefer, 1977). The life cycle is typically one year long (Tretzel, 1954; Vlijm *et al*., 1963; Merrett, 1968) in Western and Central Europe, but at more Northern latitudes it can be extended to two (Edgar, 1972; Stepczak, 1975) or three (Workman, 1979) years, with no change in the season of the reproductive period.

In Hungary one *Pardosa* species, *P. agrestis*, has received special attention, because it can be regarded as the most dominant surface-active spider in every agricultural or human-influenced habitat (Samu *et al*., 1996; Tóth *et al*., 1996). A large amount of data has been collected on this species by the authors over three years, from numerous localities, as part of a nationwide survey on the spider diversity in agro-ecosystems. Examining the individual datasets of the adult specimens, it was obvious that the phenology of *P. agrestis* was different from the typical *Pardosa* life cycle, but we were unable to draw direct conclusions about its exact pattern. In the present study, to obtain a more complete picture of the life cycle of *P. agrestis*, we merged data from the different sites and attempted to work out methods which would allow us to incorporate data on different stages

Site	Crop	Method	Year	Non-*agrestis* (%)
Julianna-major 1	alfalfa	pitfall	1993	1.2
Julianna-major 1	spring barley	pitfall	1993	0.7
Kartal	winter wheat	pitfall	1993	5.0
Felsõnána	alfalfa	pitfall	1993	2.4
Felsõnána	alfalfa	pitfall	1994	6.4
Julianna-major 2	alfalfa	suction	1994	0.0
Romhány	alfalfa	suction	1994	0.0
Szombathely	winter wheat	pitfall	1994	1.0
Kisdorog	alfalfa	suction	1995	0.0
Kisdorog	alfalfa	pitfall	1995	5.3
Rétság	winter wheat	suction	1995	0.0
Romhány	alfalfa	suction	1995	0.0
Julianna-major 1	alfalfa	pitfall	1995	0.5
Julianna-major 1	alfalfa	suction	1995	11.5
Julianna-major 1	winter wheat	pitfall	1995	0.4
Julianna-major 1	winter wheat	suction	1995	11.4
Páty	alfalfa	suction	1995	0.0

Table 1: Sampling sessions involved in the analysis, and percentage of adult *Pardosa* spp. non-*agrestis*.

and different sampling methods into the same graphical analysis.

Material and methods

Sampling procedures

Material was collected by pitfall traps and a hand-held suction sampler. Pitfalls were plastic cups of 72 mm upper diameter, containing 50% ethylene glycol solution and a few drops of detergent. They were emptied at approximately ten-day intervals. Traps were open during the field season, but they were closed during the winter (December–March). Suction sampling was carried out in the field at similar intervals and over the same period by a hand-held device with a 0.01 m² suction nozzle as described by Samu & Sárospataki (1995) and Samu *et al.* (1997). Ten applications of the suction device in a transect gave one sampling unit (0.1 m²).

Spiders were collected in two crop types: alfalfa and cereals. There were over 20 sites in the country where these crops (one or both) were sampled between 1993 and 1995. We regarded a sampling session as the unit for our study. One sampling session was a unique combination of site, crop, method and year. Each sampling session provided a data set.

During the identification, non-adult spiders were classified into three groups: spiderlings—the instar which leaves the cocoon; subadults—the instar before the adult stage; and juveniles—all other instars falling between the previous two categories. To study the phenology of a spider species in non-adult stages we need to have a reliable identification of these juvenile stages. However, in *Pardosa* it was only possible to generic level. Fortunately, in the fields sampled, a dominance of *P. agrestis* was the norm, and other species, such as *P. palustri*s, *P. lugubris* and *P. hortensis,* were present in variable, but usually low, numbers. To have a reliable, but still probabilistic, abundance estimate of the juvenile stages in *P. agrestis*, we included in the analysis only those sampling sessions where the abundance of adult *P. agrestis* was over 85% of all adult *Pardosa* individuals. Although it is possible that adult specimens of the non-*agrestis* species were collected with a lower efficiency as adults (e.g. due to stage-determined micro-habitat preference), and therefore their presence as juveniles was underestimated, given the available biological information (Loksa, 1972; Hänggi *et al.*, 1995), we regarded this possibility as negligible. Consequently, we made the approximation that in these sampling sessions all *Pardosa* juveniles were *P. agresti*s. The sampling sessions are listed in Table 1.

Data analysis

The analysis was separate for each life stage distinguished. First, at this point treating the

methods separately, average catches per sampling unit (1 pitfall or 0.1 m^2 suction sample) and per ten-day interval (decades) were calculated adding data from all sampling sessions. Next, we combined the results of the two methods by transforming pitfall trap catches so that they would be on the same scale as suction catches. To avoid altering the temporal pattern in the data, this was achieved by multiplying the pitfall trap results for each decade P_{ij} (where i stands for the decades, and j represents life stages) by a stage-specific constant factor, f_j, which was obtained as:

$$f_j = S_{.j}/P_{.j}$$

where $S_{.j}$ is the mean catch by suction sampling for stage j for the whole period, and $P_{.j}$ is the same measure for pitfall traps (Table 2). Pitfall trap data transformed in this way for each stage had the same mean catch over the study period as that of the suction sampling. Having brought the data sets to the same scale, they were added, yielding the raw time series. These were finally smoothed by the two-point moving median method. The phenological graphs were finally re-tested against raw data. No contradictions were found, and it was confirmed that no new pattern was added by the superposition. *P. agrestis* populations were synchronous at the different localities within the ten-day precision of the study. In fact, all patterns revealed by the graphs could be traced back in the single raw datasets.

Results and discussion

There were 17 sampling sessions (Table 1) where *P. agrestis* had an overwhelming dominance of adults, and thus provided data for the present analysis. Of the 5017 animals caught, 547 were spiderlings, 1130 juveniles, 123 subadults, 832 females and 2385 males.

For wolf spiders it is known that not only do the various sampling methods differ from each other in their efficiency, but also that each varies in its efficiency in collecting the various life stages (Samu & Sárospataki, 1995; Sunderland *et al*., 1995; Samu *et al*., 1997). For the calibration of these methods, i.e. the establishment of exact stage- and method-specific efficiencies, a problem is knowing the absolute densities of the animals in the field. There have been recent attempts to estimate wolf spider densities by mark-recapture methods (Dinter, 1995; Samu & Kiss, 1997). In other spiders, comparisons with absolute methods have been made in order to assess suction sampling efficiency (Sunderland & Topping, 1993). Absolute densities are still difficult to estimate, especially for juveniles. From the frequencies of the life stages caught we know that the two methods used are somewhat complementary. Suction sampling is the most efficient for juveniles, whereas pitfall traps are good at collecting adults, particularly males (Samu *et al*., 1996). Since one or the other method provides a good picture of some stages and a poor picture of others, we believe that the combination of their results was essential for the exploration of the full life cycle.

The phenological graphs obtained for the various stages are shown in Figure 1. As it follows from the data manipulation procedure, each graph shows the abundance changes as recorded by the linear combination of the two methods. The scales resulting from the transformation are arbitrary, and if we have to attach any explanation, then they can be said to reflect the catching probabilities of the different stages by suction sampling (N.B. juveniles are caught in the highest numbers, subadults in the smallest).

The picture emerging from the phenological graphs partly corresponded with the typical life history pattern of the genus *Pardosa* reported by numerous authors (Tretzel, 1954; Vlijm &

Method (No. of sampling units)	Spiderling	Juvenile	Subadult	Female	Male
Suction sampling (420)	0.15	1.77	0.06	0.11	0.07
Pitfall trapping (638)	0.77	0.63	0.11	1.21	3.23
Scaling factor f_j	0.20	2.78	0.55	0.09	0.02

Table 2: *Pardosa agrestis* mean catches per sampling unit by the two different sampling methods and scaling factors to scale all catches to that of suction samples.
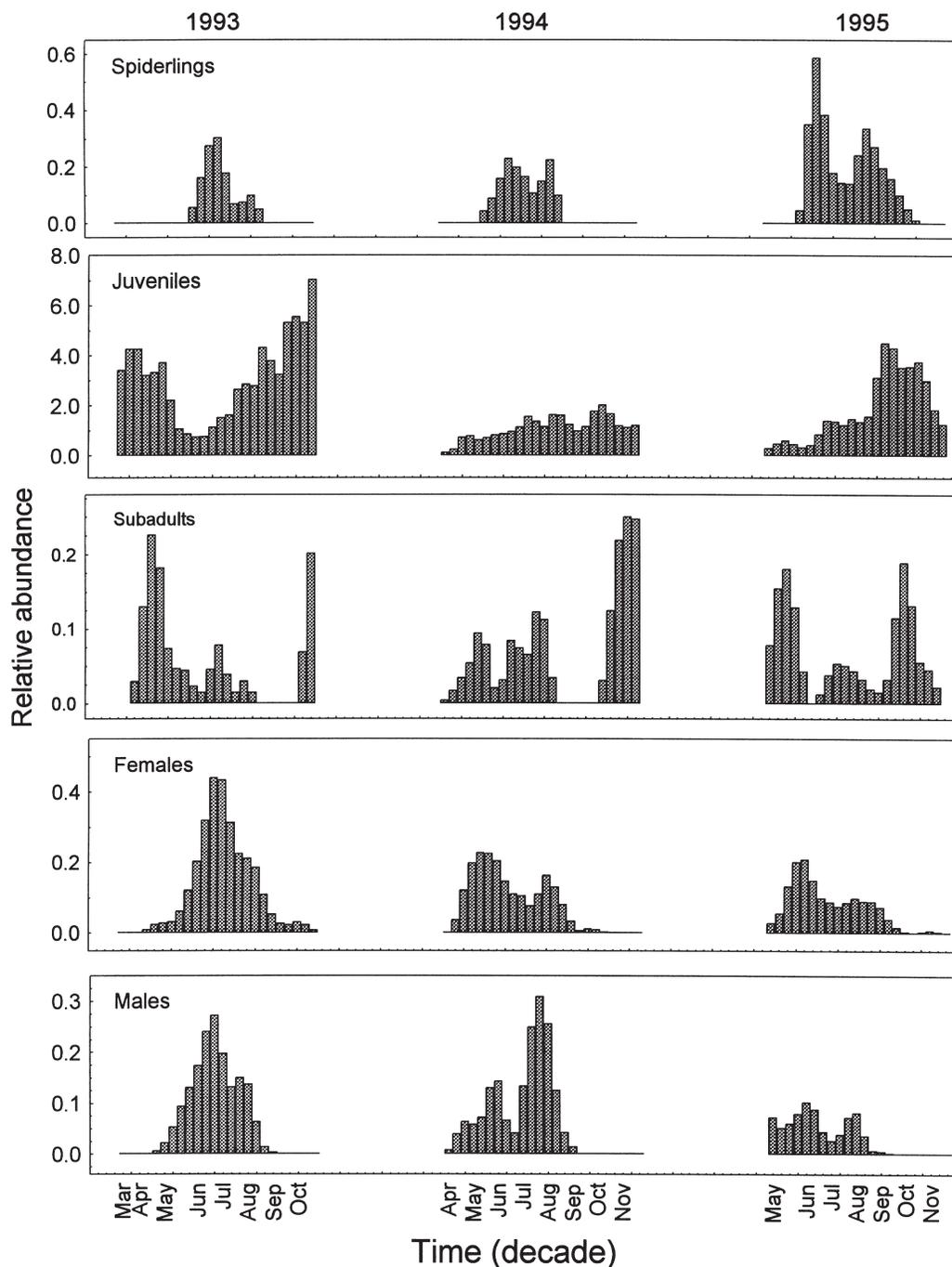
Fig. 1: Phenology of different stages of *Pardosa agrestis* in different Hungarian arable lands, 1993–95. Relative abundance is standardized to 0.1 m² suction samples. Zero level horizontal lines indicate zero catches, gaps show periods when pitfalls were not in operation. See text for details on standardization and definition of stages.

Kessler-Geschiere, 1967; Merrett, 1968; Schaefer, 1972; Workman, 1979; Steinberger, 1990; Groppali *et al.*, 1995). The population that emerged after winter consisted mostly of juveniles and a few subadults. Subadults had an early peak in April. Females and males appeared not too long after, in late April and May, and peak densities were reached by June. This was the season of mating and cocoon formation. Spiderlings emerged from mid-June, but their peak density was reached in July. If the *P. agrestis* life cycle had followed the pattern described for the majority of congeneric species, then all males should have died by July. Females might have produced a second cocoon, but also die by August, and juveniles from the June and July cocoons should develop by next spring. This scenario has in fact been reported for *P. agrestis* by Tretzel (1954). However, the Hungarian populations showed a different pattern in all three years studied. In late July and early August, subadults showed a second peak, which was followed by a second peak of adults in August. This second peak was very weak for adults in 1993. This might have been due to sampling bias; in that year data were obtained by pitfalls, and most of them originated from cereals, where, except for Julianna-major, sampling ceased after harvest in July. The occurrence of a second generation of spiderlings in late August and September proved that this second adult cohort actually reproduced. A third peak of subadults in late autumn can be explained by the first cohort reaching that stage by then.

To find a functional explanation for the phenological pattern observed, we propose two possible life history scenarios. These can be regarded as alternative hypotheses that we already have some evidence for or against, and which can be further tested in future studies.

Two generations hypothesis. A second generation, originating from females of the June peak, finished development by August. Thus *P. agrestis* had two generations per year. Heydemann (1960) suggested that adults of *P. purbeckensis* observed in September and October can belong to a second generation. Almquist (1969) gave a similar explanation for the occurrence of male *P. nigriceps* specimens observed in August. The test for the existence of a second generation would be the exact knowledge of developmental times in nature. We have no such information available for *P. agresti*s. It is known that *Pardosa* species, depending on size, need seven to nine moults to reach adulthood from the spiderling stage (Edgar, 1972; Van Dyke & Lowrie, 1975). The length of the instars may vary between 10 to 31 days in *P. ramulosa*, and the average time needed to reach maturation is 117 days (Van Dyke & Lowrie, 1975). Edgar (1972) gave the length of the subadult stage to be a minimum of 15 days at 22 °C for *P. lugubri*s. Almquist (1969) found that *P. nigriceps* spiderlings needed 4 months to reach subadult stage. In our opinion, these developmental periods make it improbable that *P. agrestis* could produce a second generation in little more than two months, but careful checking will be necessary.

Two cohorts hypothesis. The phenology curves are created by two cohorts of *P. agresti*s. The two peaks in the spiderling, subadult and adult stages indicate the mass emergence of these stages. Juveniles do not show these peaks, because they represent a mixed category (by the present definition) and therefore animals from both cohorts are included. Since adult peaks are quite distinct, it is possible that animals from the early and the late cohorts have the same generation time (one year) and, as a consequence, they exist side-by-side in time, but might not actually mix. This involves some degree of isolation of the two cohorts. Depending on this degree, the coexistence of two sibling species cannot be excluded. This could be tested by detailed morphometric studies and mating experiments.

Modulating factors. Further factors might modify the simple life history patterns outlined in the hypotheses. Multiple brood production has been reported in a number of *Pardosa* species (*P. amentata*: Vlijm *et al.*, 1963; Richter, 1970; *P. lugubri*s: Edgar, 1972; *P. prativaga*: Workman, 1979). Although we have no such data at present, the formation of a second (or further) cocoon by *P. agrestis* females cannot be excluded. The production of a second brood might alter the phenology curves in a number of ways: (1) spiderlings emerging from a second cocoon will cause a second peak, or add to existing peaks; (2) females which show different activity during the different phases of their reproductive cycle (Vlijm & Dijkstra, 1966) might be more trappable at certain times, and

might cause peak catches; (3) if the two-cohorts hypothesis is correct, then females which produce a second brood might decrease or eliminate reproductive isolation between the cohorts; (4) fast-developing individuals from the second brood might catch up with those from the first one, and thus part of the population may have a generation time shorter than one year.

To test the presence of multiple brood production in field populations of *P. agrestis*, the state of the ovaries should be assessed by the dissection of trapped material. This would reveal the time necessary to produce a second egg sac, so that we would be able to see whether it is as long as the time lag between two peaks or shorter and, therefore, if this phenomenon exists, whether it plays a role only within one peak/cohort.

Conclusions

The relatively large data set that we combined from various agricultural areas in Hungary revealed a bimodal phenology of *P. agrestis* in all three years examined. This phenological pattern is different from the basic pattern reported for congeneric species, although a number of reports on the phenology of *Pardosa* species indicate that there is a large degree of flexibility of the life histories in this group, even within species. Examining the phenology curves, we suggest that the underlying life histories could be basically of two kinds. One possibility is that the two peaks represent two generations of the species in one year. The second hypothesis proposes that the peaks are caused by two cohorts, each having a full year life cycle. One way to choose between these possibilities would be further experimentation on developmental times necessary to reach maturity. A further factor, the production of a second brood by at least a portion of the females, can modulate the two basic scenarios. The generation originating from the second egg sac can be a bridge between the cohorts, and may decrease isolation between them. We must emphasise that even if we have proposals about the underlying life histories that cause bimodal phenologies in *P. agrestis*, the most difficult task for any future investigation will be to find out what evolutionary forces maintain the distinctness of these peaks.

Acknowledgements

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