

Data points for a study of population dynamics of an Orb-Weaving spider (*Larinioides cornutus*, Araneae, Araneidae)

par
Frédéric Ysnel

Summary: Series of samples have been carried out all over a year in a mesophilous heathland of the west of France. Spiders collected were classified according to the developmental stages. From knowledge on the phenology of the different instars, the developmental patterns of the species have been worked out. *Larinioides cornutus* belongs to the stenochronous species of spring and summer; the survival curve of the population is closely connected to the type III of Deevey. Besides this, laboratory experiments showed that ovarian maturation or embryogenesis are controlled by photoperiod.

1. INTRODUCTION

The orb-weaving spider *Larinioides cornutus* is widely spread in Septentrional Europe (BONNET 1959). In the west of France, we always observe it on higher vegetation of natural wet areas (mesophilous or hygrophilous heathlands, wet grasslands, salt meadows, mixed forest plots, rush-beds...). In Switzerland, this species also show high densities in some agrocoenoses (NYFFELER 1982). However, the knowledge concerning the biological cycle, the fecundity and the species' survival still remain scattered. In a Polish grassland, KAJAK (1965) shows that the highest densities of adults occur in spring; in summer, juvenile instars are highly represented and the medium-sized individuals are the most numerous in autumn. In Germany, KITCHNER (1965) points out that adults and immatures of different size groups spend winter in a state of quiescence. In a cereal field of Switzerland, NYFFELER (1982) shows that the abundance of the population is maximal in spring and at the beginning of summer. Under laboratory conditions, BONNET (1927) notices that one female can lay up to ten times.

No study have been done on the population dynamics. Our former works concerning the development of the species in the laboratory have defined criteria of discrimination of the different postembryonic instars. These new data allow us to follow the demographic evolution and to study the life cycle of a population of the west of France.

2. METHOD

All over the year series of samples have been carried out in a mesophilous heathland of an edge-pond (étang de l'Abbaye, Paimpont, France) in the areas where spiders show the highest densities (consisting mainly of *Juncus effusus* and *molinia coerulea*). At twilight, all the spiders leave their retreats and build their webs. Therefore the successive samplings (from units of 20 m²) take place at nightfall by hand collecting with a torch provided with a red screen. The juveniles of *Larinioides cornutus* are easily recognizable by the characteristic pattern of their carapace. All the spiders collected are classified according to the different stages of development by using patterns of posterior and anterior sides of leg trichobothria (YSNEL 1988). The subadult males and females are respectively characterized by the swell of the tarsi of pedipalps and by the rough shape of the epigyne. The parallel evolution of the number of egg sacs and of the number of females per unit of surface is followed on six different plots (total surface = 150 m²) by marking and counting the cocoons during all the egg-laying period. In the mean time, some more data points concerning the species' fecundity are obtained from the breeding of adult females taken from the spot during different seasons (group I: females collected on 15/12 /1990; group II: females collected on 7/03/1990; group III: females collected on July 1991). Females collected at the end of winter (group II) are divided into two groups and reared under two different light-dark cycles (group IIa, long days: 16 hr light/8 hr dark; group IIb, short days: 8 hr dark/16 hr light). The two groups were kept at 27°C and reared under the same feeding regimen. When the spiders of the third group are caught with their laying, or when they lay less than 48 hours past their capture, we are searching to give an account between the size of the females (length of tibia PIV) and the number of eggs per cocoons.

3. RESULTS AND DISCUSSION

In the case of Argiopidae, the first free-living instar is called J2 (CANARD 1987). For the population studied, it exists from 5 to 8 immatures instars and from 1 to 4 adult stages (figure 1, tableau I).

adult instars	VII	VIII	IX	X
males	31.2%	59.2%	9.4%	0%
females	35.1%	58.8%	4.6%	1.5%

Tab. I - Distribution of males and females per instars.

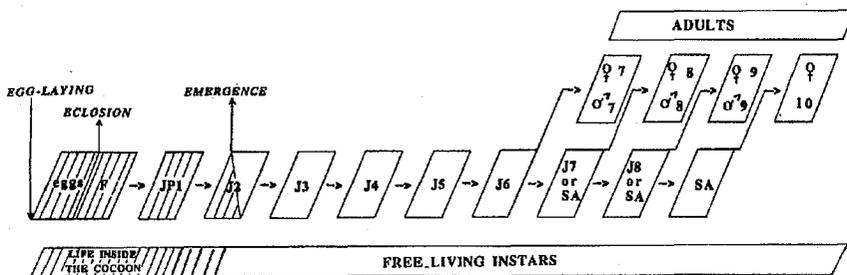


Fig. 1 - Development of *Larinioides cornutus* under natural conditions (west of France). (F: foetal instar; JP1: prejuvenile instar; J: juvenile instar, SA: subadult; >: moult)

3.1 Number of developmental stages and sexual ratio

Subadults from both sex appear during the 5 th juvenile moult and reach adulthood at stage 7 (31.2% of males and 35.1% of females collected). Roughly 60% of the spiders (males and females) undergo another moult and reach maturity at stage 8. A low proportion of individuals (9.4% of males and 4.6% of females) reach adult stage on the seventh free-living moult (adult 9). Only 2 females (1.5%) reach maturity at stage 10. These variations of the number of postembryonic instars are probably linked with the variations of the environmental conditions throughout the life cycle; they correspond to the variations observed for spiders reared from eggs to adults under different conditions of temperature and feeding regimens (YSNEL 1988; 1990). Adult males do not built webs any more, become wanderers and fastly disappeared after mating; therefore they probably are underestimated in the samples. Supposing that the duration of intermoult period and the mortality are the very same for the subadults of both sex, we can estimate the sex ratio of the population by using the sex ratio of subadults (table IV). Concerning *Larinioides cornutus*, a non-migrant species, the sex ratio (52 subadult females for 46 subadult males) is nearly 1.

In analysing the distribution of the counted group per instars for the successive samples, we can follow the demographic evolution of the population (figure 2). From the end of spring to the beginning of autumn, the first free-living instars (II,III) become visible and their density increase in summer. The first spiderlings emerging from the

3.2 Demographic evolution

Egg sacs laid from the end of spring to the beginning of summer (cohort C1) reach at least the instar V as early as september, and reach the subadult or adult instars at the beginning of winter (instars VI, VII, VIII). The first free-living instars which appear later in the year (end of summer) form another cohort (C1'); the individuals of the cohort C1' are still immatures in autumn (instars II,III, IV). The latest point of recruitment of young is up in autumn. All the stages of development are settled at the beginning of winter. Low temperatures in winter can stop the postembryonic development, namely for *Larinioides cornutus*; in this case, the spiders enter in quiescence (KIRCHNER 1965). At the end of winter, the structure of the population is only different because of the winter mortality and the development can go on. In spring 1989, all the spiders of the cohort C1 reach the adult stages and can mate. The ones of the cohort C1' become adult at the beginning of summer and they may be confounded with the surviving adults of the cohorts C1. Although the subadult and adult males are very numerous during the captures at the end of summer, they are not very well represented in autumn. So we may suppose that males can mate in autumn (the males

becoming at that time potential preys for the females and so fastly disappear). The cohort C-1 includes adult or subadult spiders which were born at the end of spring 1987. The density of adults is more important in 1989 than in 1988.

So it produces an important variation of the number of spiderlings between the two successive generations.

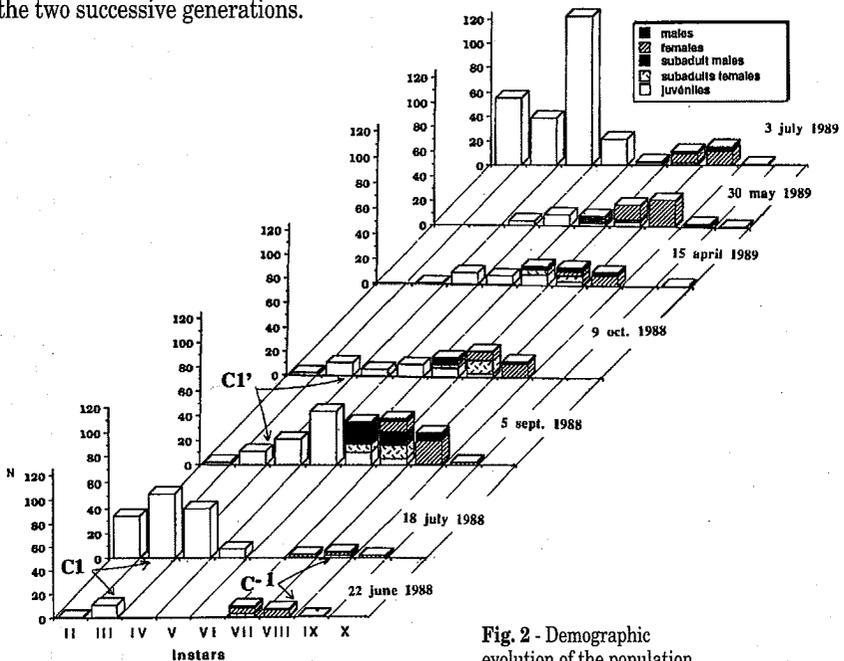


Fig. 2 - Demographic evolution of the population.

3.3 Adult longevity

During those two successive years, the decreasing number of females between the two populations sampled at the end of spring and at the beginning of summer shows that the females adult in autumn (and overwintering in quiescence) die at the end of the following spring. They may live from seven to eighth months. The females adult at the beginning of summer (overwintering as immatures) will live two months and disappear at the end of summer. So it probably explains the decreasing number of females between the samples done in september 1988 and october 1988. Some of the males adult in autumn probably mate at this time and die so they don't live more than one month; the other ones mate next spring and in that case, they can live up to six months. The males reaching the adult instars in spring and in summer can mate right now and their longevity (one month) must be the same than the one of the males mating in autumn.

3.4 Data on fecundity

3.4.1 Fertility of overwintering females and effect of photoperiod on fecundity

All the females collected in winter (group I) and reared under long days at different temperature conditions (from 15°C to 27°C) have laid viable cocoons which prove the existence of a mating period just before winter. Females collected at the end of winter (groups IIa, IIb) show different rates of reproduction (table II). Under short photophases the average number of cocoons per females is significantly inferior (Wilcoxon-Mann-Whitney test, $P < 0.001$). On the other hand, the number of non hatched cocoons is significantly lower under long days (X^2 test, $P < 0.001$)

	Ni	Nc	total egg-sacs	E.G./F	Nh	longevity of females (days)
long days (IIa)	21	19 (90%)	116	6.1	38 (32.7%)	84.2 ± 36.05
short days (IIb)	20	15 (75%)	59	3.9	38 (64.4%)	42.7 ± 35.1

Tab. II - Summary of results concerning the rearing experiments of females of group II. (Ni: initial number of females; Nc: number of females producing egg sacs; E.G./F: average number of egg sac per female; Nh: non-hatched cocoons)

Moreover we observe that the average longevity of females of group II a is significantly higher than those of females of group IIb (Wilcoxon-Mann-Whitney test, $P < 0.002$).

The short photophases inhibit the reproductive possibilities of *Larinioides cornutus*. As mentioned before concerning the others species (YSNEL & CANARD 1990) they are

likely to act on the activity of neurosecretory cells which control, in *L. cornutus*, the ovarian maturation (lack of cocoons or decrease of the number of cocoons), the egg-fertilization or the embryogenesis (sterile eggs production). The lowest longevity of females bred under short photophases could prove that short days disturb the running of the hormonal system of individuals after the ending of quiescence

3.4.2 Number of cocoons per females and number of eggs per cocoons

The parallel evolution of the number of new cocoons and of females picked up on the six plots shows that the egg-laying period spreads out from the end of spring until the beginning of autumn (table III). The number of cocoons is more important in may and july. Among all the retreats recorded, 77% contain one cocoon, 20% two cocoons and only one contains three cocoons; 30.8% are infested with Diptera (Chloropidae) or Hymenoptera (Cryptinae) (Rollard 1987).

	april	may	june	july	aug.	sept.	oct.	nov.
number of egg sacs	0	12	0	14	5	5	1	0
number of females	/	22	21	17	19	14	12	/

Tab. III - Number of egg sacs and females collected on the six diferent plots.

Because short photophases inhibit reproduction in autumn, we will suppose that all the cocoons collected are laid by the females of cohort C-1. The average number of cocoons per females must be evaluated by taking the proportion of new females (F) appeared on the six plots studied throughout the egg-laying period into consideration. If we assume that the rate of mortality is low during the last moult, we can estimate F for two successive samples by refeering to the demographical evolution of subadult and adult individuals during the reproductive period such as: $F = N_{sa\ t} / N_{ad\ t+1}$

(N_{sad} = number of subadults females at time t; $N_{ad\ t+1}$ = number of adult females at times t+1)

The values of N_{sa} and N_{ad} used are reported on table IV

	22 /VI/88	18 /VII/88	5 /IX/88	9 /X/88	15 /IV/89	30 /VI/89	3 /VII/89
subadult females	3	3	19	14	8	4	1
females	11	6	31	18	12	35	19
subadult males	0	0	29	7	4	5	1

Tab. IV - Number of subadults of both sex and number of females collected in each sample.

Moreover we will suppose that the proportions of females appeared between may and the beginning of summer are the same for the years 1988 and 1989. The lack of individuals of stage 6 as early as july 1988 shows that the females of the previous generation (cohort C-1) have disappeared in october 1988. The number of females appeared on the six plots studied must be: $22 + (4/19) (21) + (3/6) (17) + (3/31)(19) = 37$ females. 37 cocoons have been collected; on the average, females lay one egg sac.

There is a good correlation ($r = 0,78$) between the size (x) of the females of group III and the number of eggs per cocoons (Y) ($Y = 143,07x - 112,05$). As, on an average, spiders lay only one egg sac, we will use this relation to estimate the number of eggs laid per females in natural conditions.

3.5 Survival curves

The analysis of the demographic evolution per developmental stages throughout the year allows to characterize three cohorts in the population (table V). The individuals of cohort C1 are issued from the egg sacs laid by the females in May and June 1988; we estimate the number of females living in May 1988 basing on the rate of survival of females (42.8%) between may and june 1989 (that is to say a total of 26+11 females for May and June 1988). Because of the middle size of the females in June 1988 ($x = 1.95 \text{ mm} + 0.5$) we can estimate the number of eggs from which the individuals of cohort C1 come from. The individuals of the cohort C1' are issued from the cocoons laid by the females in july 1988, and according to the proportion of subadults females living in july, from those laid by half of all the females of august (so a total of 6+15= 21 females). The number of eggs laid is estimated from the middle size ($x = 1.98 \text{ mm} + 0.2$) of the females.

instars	II	III	IV	V	VI	VII	VIII	IX	X
	C1					C-1			
22 june 1988	1	11	0	0	0	9	7	1	0
18 july 1988	34	51	10	7	0	3	5	2	0
5 sept. 1988	2	11	21	44	35	38	26	2	0
9 oct. 1988	C1'	2	11	6	10	17	22	13	0
15 april 1989	0	1	12	9	15	14	11	0	1
30 may 1989	0	0	4	9	8	18	22	3	1
3 july 1989	39	122	21	3	11	15	1	0	0

Tab. V - Number of individuals per cohort (years 1988-1989)

The survival curves (figure 3) established from these estimations are closely connected to the type III of DEEVEY (1948).

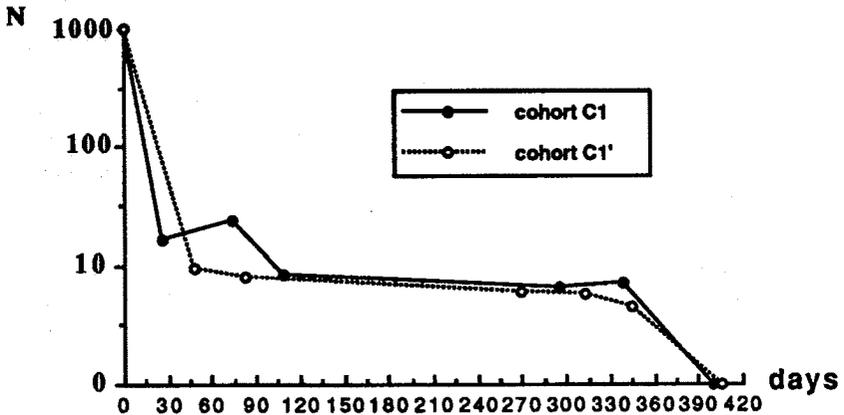


Fig. 3 - Survival curves for the two cohorts (years 1988-1989).

4. CONCLUSION

Taking place among the orb-weaving species, *Larinioides cornutus* belongs to the stenochronous species of spring and summer (YSNEL & CANARD 1986); sexual activity takes place from spring to autumn but the egg-laying period is confined to summer (figure 4). The egg-laying cycles are under the control of regulating mechanisms; the short photophases induce ovarian diapauses which reject the coming out of laying in good conditions. Studying the individuals of a same population, we can establish that the duration of the life cycle (from 6 months to one year), the adults longevity (from one to six months), and the overwintering instars (immatures or adults in a state of quiescence) vary and depend on sex of individuals and on the moment where the first free-living instars appear. Up to that point, the exact studies about the survival curves of the spiders concerned mainly the wanderers spiders (BLANDIN & CELERIER 1986); with regard to the orb-weaving spider *Larinioides cornutus*, the demographic analysis allow to assimilate the variations of numbers of spiders per cohort as a survival curve of type III, with a very high rate of mortality at the beginning of the development, connected to the high proportion (30.8%) of parasitized cocoons, then a low and constant rate of mortality for the end of the development. The seasonal regulation of the egg-laying cycles may imply that the rate of reproduction stay the same from a generation to another for the females of the same size; the variations of number of adults studied for both successive generations may be more dependant on the winter mortality during the postembryonic development.

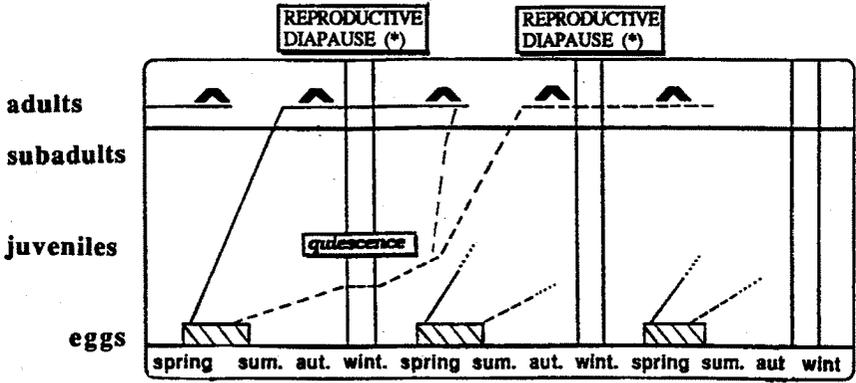


Fig. 4 - Life-history patterns of *Larinioides cornutus* in the west France.

REFERENCES

- BONNET, P.- (1927). Etude et considérations sur la fécondité chez les Aranéides. *Mém. Soc. Zool. Fr.*, 28 (3): 1-47.
- BONNET, P.- (1959). Bibliographia araneorum (II): 1-5058.
- BLANDIN, P. & CELERIER, M.L. - (1986). L'étude des stratégies démographiques chez les Araignées. *Mém. Soc. r. belge Ent.* (33) : 1-14.
- CANARD, A.- (1987). Analyse nouvelle du développement postembryonnaire des Araignées. *Rev. Arachnol.* 7(3):91-98.
- DÉEVEY, E. - (1947). Life tables for natural populations of animals. *Quat. Rev. Biol.*, 22: 283-314.
- KAJAK, A.- (1965). An analysis of food relations between the spiders - *Araneus cornutus* Clerk and *Araneus quadratus* Clerk - and their prey in meadows. *Ekologia Polska - Seria A, (XIII)*. 32: 717-763. Warszawa.
- KIRCHNER, W.- (1965). Wie überwintert die Schilfradspinne *Araneus cornutus* ? *Natur and museum*, 95 (4). Frankfurt a M., 1. 4.: 163-170.
- NYFFELER, M. - (1982). Field studies on the ecological role of spiders as insect predators in agrosystem. *D. Sc. Thesis, Swiss fed. Inst. Technol., Zürich, Aku-Photodruck*. 174 pp.
- ROLLARD, C. - (1987). La biocénose associée aux Aranéides en landes armoricaines. Etude des relations Insectes-Araignées. *Thèse de Doctorat de l'Université de Rennes-I*, 292 pp.
- YSNEL, F. - (1988). Caractérisation des stades de développement de *Larinioides cornutus* (Clerk, 1757) (Araneae, Argiopidae) par la trichobothriotaxie.- *XI Eur. Arachnol. Colloq., Techn. Univ. Berlin, Dokumentation Kongresse u. Tagungen*. 38:72-78.
- YSNEL, F. - (1990). Energy consumption of *Larinioides cornutus* (Araneae, Araneidae) during postembryonic development under different temperature conditions. *XI International Congress of Arachnology, Turku. Acta Zool. Fennica*. 190: 409-414.
- YSNEL, F. & CANARD, A. - (1986). Réflexions sur les cycles vitaux des Araignées européennes, l'exemple des espèces à toiles géométriques. *Mém. Soc. r. belge Ent.* (33): 213-222.
- YSNEL, F. & CANARD, A. - (1990). Régulations saisonnières des cycles biologiques des Araignées européennes. *Colloque "Régulation des cycles saisonniers chez les Invertébrés" - Dourdan, France. Ed. INRA (52): 73-78.*

Frédéric Ysnel

Laboratoire de Zoologie et d'Ecophysiologie, Université de RENNES I
Av. du Général Leclerc, F-35042 RENNES