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The spider community in the litter of a coppiced chestnut woodland (Forêt de Montmorency, Val d'Oise, France)

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Introduction

Spider communities have received increasing attention in the last 25 years, but ecological analyses are scarce and quantitative studies are to be desired (Turnbull, 1973). Gabbutt (1956), Turnbull (1960) and Duffey (1962) were perhaps the first arachnologists who published quantitative works on spider communities. Duffey, for example, working in a grassland habitat, collected samples by means of metal quadrats (1/16 m^2), sampling points being distributed at random in the study area. Quadrat sampling was also used by Huhta (1965, 1971) in various forests in Finland, and by Polish ecologists in different meadows (e.g. Breymeyer, 1969). In tropical countries such methods were developed in a West African savannah ecosystem by Y. & D. Gillon (1967a) and preliminary data were obtained concerning spiders (Y. & D. Gillon, 1967b; Blandin, 1971, 1974).

Russell-Smith & Swann (1972) and Jocqué (1973) pointed out that little attention has been paid to woodland spider communities in Europe. As no such work has previously been done in France, we thought it was of interest to study a spider community from a quantitative point of view, in order to determine its specific structure and its spatio-temporal characteristics. The chestnut forest of Montmorency (about 20km NW of Paris) was chosen and the work was done in the "Reserve de Bois-Corbon" with the permission of the "Office National des Forêts".

The complete work, with a population dynamics study of *Macrargus rufus* Wider, was the subject of a 3rd Cycle Doctorate Thesis (Christophe, 1974). In the present paper we report only the main results concerning the spider community.

Study area

The work was done between October 1971 and January 1973 in a 50ha reserve in which no visitors are allowed. The average altitude is 175m. In the region the mean annual temperature is 11.1°C and the mean annual rainfall 585mm. Some general characteristics of climate are presented in Table 1.

The canopy consists of *Castanea sativa* Mill. with some *Betula verrucosa* Ehrh.; it was last coppiced about 25-30 years ago. The shrub layer comprises only young *C. sativa,* and there is almost no ground vegetation.

In the study area the litter shows three distinct layers, which are easiest to characterize in winter:

1) the L layer, formed by the leaves which fell during the previous autumn;
2) the F layer, which consists of partly decomposed leaves;
3) the H layer, which consists of amorphous humus.

Following Heatwole's classification of litter (1961), the chestnut litter is of the "bent type" included in his first group; the leaves of the L layer are folded, with large spaces between them.

	J	F	M	A	M	J	J	A	S	O	N	D
Temp. °C max.	5.9	7.2	12.0	15.6	19.4	22.6	24.4	24.0	21.1	15.6	9.9	6.6
Temp. °C min.	0.4	0.8	2.8	5.4	8.6	11.7	13.7	13.5	11.3	7.3	4.0	1.6
Rainfall (mm)	54	43	32	38	52	50	55	62	51	49	50	49

Table 1: Monthly means of maximum and minimum temperatures and monthly means of rainfall (data from Météorologie Nationale, Station du Bourget, 1931-1960).

		1971							1972							1973
	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J
Hand-collecting																
routine samples	10	4	4	4	4	4	4	4	4	4	4	4	4	–	–	–
additional samples		3	20	4	20	8	4	–	20	8	4	–	20	5	–	10
Samples controlled by Berlese-Tullgren	–	–	–	–	–	–	–	4	8	12	8	4	9	–	–	–
Direct Berlese-Tullgren extraction	–	–	–	–	–	–	–	–	–	–	–	–	–	5	–	10

Table 2: Monthly numbers of samples and collecting methods.

Methods*

In the reserve a uniform area with regular topography and homogeneous vegetation was chosen and divided into 95 squares of 100 m^2. For each series of n samples, n 100 m^2 squares were selected at random and the definitive sampling points were chosen in well characterized litter at always a minimal distance (50cm) from any tree. At each point, a 0.25m^2 surface was limited by a 50 x 50cm metal frame, inside which spiders were hand-collected; 4 samples took at least 5 hours.

After a 10 sample trial in October 1971, it was decided to do a routine series of 4 samples each month until October 1972 (always by the two same collectors). Additional samples were done for various purposes (Table 2). In particular, series of 20 samples were done in December 1971, February, June and October 1972 in order to study the horizontal distribution of the spider community, with the help of other collectors (statistical analysis of the results has shown that in October 1972 there were significant differences between the collecting efficiency of different teams, and the results of only 11 samples were kept).

The efficiency of hand-collecting was first checked from May to October 1972, when juveniles of small size were abundant; the litter, after hand-sorting, was kept in plastic bags and, back in the laboratory, was put in "Berlese-Tullgren" funnels, with light as heat source, in order to extract the spiders which had escaped the eye. Using the ratio:

$$\frac{\text{number of spiders extracted in funnels after hand-sorting}}{\text{total number of spiders hand-sorted and extracted}}$$

on the results from 45 samples, it was shown that on average 12% of adult spiders and 22% of juveniles escaped the eye (standard deviation 16% in each case); assuming that the funnels probably did not extract 100% of the spiders, these values are minimum estimations of error in the hand-collecting method.

We also compared hand-collecting with direct extraction for winter samples (November 1972 and January 1973), when adult and subadult spiders are dominant. The results are given in Table 3, and were tested with the non-parametric Mann-Whitney U-test. The U value at the 5% level of significance for two series of 15 samples is 64, the difference between the

	Hand-collecting	Berlese-Tullgren extraction	Calculated values of U-statistic (Mann-Whitney U-test)
Number of samples	15	15	
Number of adult spiders	145	186	64
Number of juveniles	36	127	28

Table 3: Comparison of hand-collected samples with directly extracted samples (November 1972 and January 1973).

* A detailed discussion of sampling programme and methods is given by Christophe (1974).

two series being significant if the calculated U is equal to or less than this level value. Thus it appears that extraction gave significantly higher estimates of spider densities than hand-collecting, especially for juveniles, but also for adult spiders.

Nevertheless, if results are studied at species level, it appears that species living in the L layer can be collected efficiently by hand, unless they are very small. This is the case for example with the winter adults of *Macrargus rufus* and *Microneta viaria.* On the contrary, species living in the F layer such as *Centromerus aequalis,* or in the H layer, like *Hahnia helveola,* are collected better by extraction (Table 4).

Lastly, the possibility must be mentioned that dry-funnel extraction could give overestimated numbers because of "hatching effect" if there are cocoons in the litter. If that is the case then quantitative results would be better considered as relative values for a number of species rather than giving absolute measures of density.

Taxonomic structure of the community

For determinations the following works were used: Simon (1914-1937), Locket & Millidge (1951-1953), Locket, Millidge & Merrett (1974) and Wiehle (1956-1960). Forty-seven different species

	Hand-collecting	Funnel extraction
Macrargus rufus	25	23
Microneta viaria	28	20
Centromerus aequalis	4	46
Hahnia helveola	0	14

Table 4: Comparison of hand-collecting with direct funnel extraction. Total numbers of adults of species from different litter layers (10 samples by each method – January 1973).

Family Amaurobiidae
Amaurobius similis (Bl.)
Family Dictynidae
Dictyna or *Heterodictyna* sp. juv.
Lathys humilis (Bl.)
1 unidentified juv.
Family Clubionidae
Clubiona terrestris Westr.
C. compta C.L.Koch
Family Anyphaenidae
Anyphaena accentuata (Walck.)
Family Thomisidae
Xysticus sp. (1 subadult ♂)
Family Salticidae
Neon reticulatus (Bl.)
Unidentified juv.
Family Lycosidae
Pardosa lugubris (Walck.)
P. hortensis (Thor.)
Trochosa terricola Thor.
Family Agelenidae
Coelotes terrestris (Wider)
Cicurina cicur (Fabr.)
Hahnia montana (Bl.)
H. helveola Simon
Family Mimetidae
Ero sp. (1 subadult ♀)
Family Theridiidae
Enoplognatha ovata (Cl.)
Robertus lividus (Bl.)
Family Nesticidae
Nesticus cellulanus (Cl.)
Family Tetragnathidae
Pachygnatha degeeri Sund.
Meta merianae (Scop.)
Family Araneidae
Cyclosa sp. (1 juv.)
Family Linyphiidae
Walckenaera acuminata Bl.
W. cucullata (C.L.Koch)
W. corniculans (O.P.-C.)
Tapinocyba praecox (O.P.-C.)
Micrargus herbigradus (Bl.)
Diplocephalus picinus (Bl.)
Meioneta rurestris (C.L.Koch)
Microneta viaria (Bl.)
Centromerus sylvaticus (Bl.)
C. dilutus (O.P.-C.)
C. aequalis (Westr.)
C. serratus (O.P.-C.)
Oreonetides abnormis (Bl.)
Macrargus rufus (Wider)
Bathyphantes gracilis (Bl.)
Tapinopa longidens (Wider)
Lepthyphantes tenuis (Bl.)
L. zimmermanni Bertk.
L. flavipes (Bl.)
L. pallidus (O.P.-C.)
Lepthyphantes sp. unidentified (2♂)
Linyphia sp.

Table 5: List of species collected in quadrat samples (following check-list of Locket, Millidge & Merrett, 1974).

were caught in the quadrat samples; some species were represented only by juveniles, and six of them could not be fully identified, as was also the case with two linyphiid species although they were represented by adult specimens (Table 5).

The Linyphiidae were the most important family, with almost 49% of the species. This dominance is even more important if the relative frequency of specimens collected is considered; the average relative frequency of linyphiids for the year November 1971 to October 1972 was 80.2%, the lowest monthly value 63.6% (April), and the highest 94.0% (May). The only other family of any importance was the Agelenidae, with 8.5% of the species and an average relative frequency of specimens of 10.9%.

Comparisons concerning abundance of the various species are difficult, as densities are measured with variable efficiency according to the spider's size and habitat in the litter layers. In order to give an idea of abundance of the species, we have considered the maximum adult densities observed and the annual average densities, calculated for the November 1971 – October 1972 period (Table 6). Only about 19% of the species have a maximum density of two or more ind./m^2; the most abundant species are five linyphiids and two agelenids; it is possible that the densities of *Hahnia montana* and *H. helveola* are underestimated, as they live in the H layer where they are rather difficult to collect; this is true also for *Centromerus aequalis*, living in the F layer, and for *Diplocephalus picinus*, because of its small size. Nevertheless, *Macrargus rufus* and *Microneta viaria* are almost certainly the two species reaching the highest densities.

Species	Maximum adult density (ind./m^2)	Average annual density (ind./m^2)
Macrargus rufus	23.1	8.9
Microneta viaria	14.9	8.2
Hahnia helveola	7.0	2.2
Centromerus aequalis	2.5	1.3
Diplocephalus picinus	6.5	1.2
Hahnia montana	3.0	0.9
Lepthyphantes zimmermanni	3.5	0.8
Neon reticulatus	2.0	0.6
Walckenaera corniculans	1.1	0.3
W. cucullata	1.0	0.2
Oreonetides abnormis	1.0	0.2
Centromerus serratus	1.0	0.2
Micrargus herbigradus	1.0	0.2
Tapinopa longidens	2.0	0.2
Pardosa lugubris	1.5	0.2

Table 6: Ranking of the 15 commonest species in order of abundance of adults. Annual average densities calculated for the period November 1971 – October 1972, from results of hand-collected samples only.

Species	L layer	F+H layers	Results of Wilcoxon test
Macrargus rufus	16	8	–
Microneta viaria	15	5	+
Diplocephalus picinus	11	0	+
Centromerus aequalis	11	35	+
Hahnia helveola	0	35	+

Table 7: Distribution of some species between the litter layers (10 samples, 0.25m^2; 23-24 January 1973). Results of Wilcoxon matched-pair test; + = observed difference is significant (at 95% level), – = not significant.

Spatial structure

Vertical distribution

In order to study stratification, 10 samples were collected in January 1973, the litter being more complex in winter, with an important L layer. For each sample the L layer was gathered separately, but the F and H layers were collected together, as there is no precise limit between them. Dry funnels were used for extraction of the spiders.

The results suggested that spiders were less abundant in the L layer, 46 juveniles and 51 adults being collected there, compared with 53 juveniles and 74 adults in the F+H layers. However the Wilcoxon matched-pair test revealed no significant differences, but it did show significant differences for certain species (Table 7). Adults of *Microneta viaria* and subadults of *Diplocephalus picinus* are more abundant in the L layer, *Centromerus aequalis* and *Hahnia helveola* in the F and H layers. More adults of *Macrargus rufus* were collected in the L layer than in the F and H layers, but the difference is not significant; however, *M. rufus* individuals live only in the L layer, where they have their webs; but when disturbed, they may fall down into the lower layers, this behaviour probably explaining why a number of individuals are collected in the F layer. On the contrary, individuals of *M. viaria* and *D. picinus* remain motionless on their webs when disturbed.

Horizontal distribution

At four times in the year large series of samples were collected. For (i) all spiders collected, (ii) *Macrargus rufus,* (iii) *Microneta viaria*, a dispersion index was calculated, $\frac{s^2}{x}$, where x is the average density and s^2 the corresponding variance (Table 8). A χ^2 test allows us to test whether the observed distribution agrees with a random distribution ($\chi^2 = \frac{s^2}{x}(n-1)$, n being the number of samples in a series (Southwood, 1966; Elliott, 1971).

The test shows that spiders are not distributed at random, but form clumps from place to place (contagious distribution); this is often the case for spider communities (von Broen & Moritz, 1963; Cherrett, 1964; Huhta, 1971). Nevertheless it is not always true for *Macrargus rufus* and *Microneta viaria,* which are possibly sometimes distributed at random. Considering *M. rufus*, subadults and adults show a random distribution in autumn and winter, but juveniles present a contagious one in June, some time after the hatching period. This shows that the dispersion of juveniles is progressive and that horizontal distribution would have to be studied from a dynamic point of view.

Temporal structure

Seasonal variations of the community

Fig. 1 shows the variations during a year of the monthly average density of the spider community with and without *Macrargus rufus.* From October to February this density decreases, winter values being about 50 spiders/m^2; a period of increase begins in March, with a burst in May, density reaching more than 150 spiders/m^2. This rapid augmentation is due to *M. rufus*, but the other species also show an increasing density after February. Figs. 2, 3 and 4 show details concerning adults and juveniles; they emphasize the dominating importance of *M. rufus.*

Of interest are the seasonal variations in the sex-ratio (Fig. 5). At all times there are more females than males, the average sex-ratio (from November 1971 to October 1972) being 0.33 (3 females to 1 male). Huhta (1965) obtained nearly the same value in his study (3.3:1). Such results suggest that females live longer than males.

Biological cycles

As previously discussed, quantitative results are significant for some species only. Nevertheless, for other species, regular sampling provides accurate

Dates	4 Dec 1971			26 Feb 1972			17 June 1972			12-13 Oct 1972		
No. of samples	20			20			20			11		
Random distribution when:	$\frac{s^2}{x} < 1.59$			$\frac{s^2}{x} < 1.59$			$\frac{s^2}{x} < 1.59$			$\frac{s^2}{x} < 1.88$		
	x	s^2	$\frac{s^2}{x}$	x	s^2	$\frac{s^2}{x}$	x	s^2	$\frac{s^2}{x}$	x	s^2	$\frac{s^2}{x}$
All spiders	8.45	20.79	2.46	8.35	18.56	2.22	28.2	123.01	4.36	18.09	48.09	2.66
M. rufus	4.35	6.98	1.60	1.95	1.31	0.67	17.6	54.99	3.12	4.55	3.28	0.72
M. viaria	1.85	2.13	1.15	2.90	5.15	1.78	1.4	1.73	1.23	5.18	9.16	1.77

Table 8: Horizontal distribution of spiders in the litter (0.25m^2 samples, hand-collecting)

phenological data in spite of imprecise measurements of density.

For some species, adults are present in winter; males disappear in February, while hatching is just beginning, the offspring reaching the adult instar in autumn. This is the case for *Macrargus rufus* (Fig. 6) and *Microneta viaria* (Fig. 7), as well as for *Hahnia helveola* and *Centromerus aequalis.*

For other species, like *Diplocephalus picinus* (Fig. 8), the adults are present in spring and summer, and there are only subadults or juveniles in winter. This is also the case for *Oreonetides abnormis, Lepthyphantes zimmermanni, Neon reticulatus, Dictyna* sp., *Enoplognatha ovata* and *Nesticus cellulanus.* No adults of the last three species were found in the

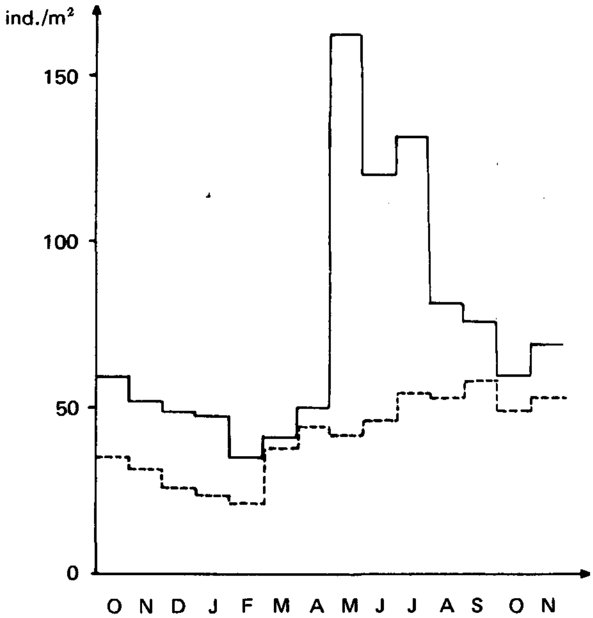

Fig. 1: Monthly average density of the spider community. Solid line: with *Macrargus rufus;* dashed line: without *M. rufus.*

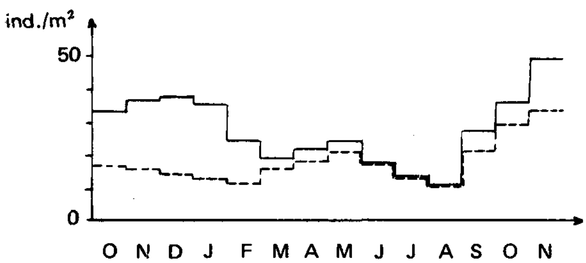

Fig. 2: Monthly average density of adults. Solid line: with *Macrargus rufus;* dashed line: without *M. rufus.*

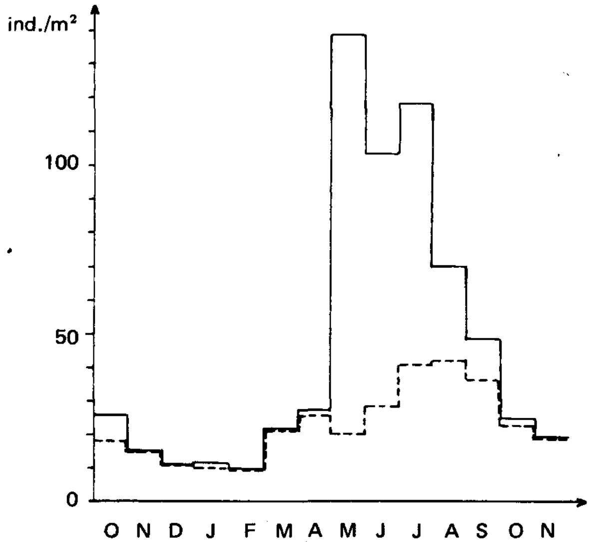

Fig. 3: Monthly average density of juveniles. Solid line: with *Macrargus rufus;* dashed line: without *M. rufus.*

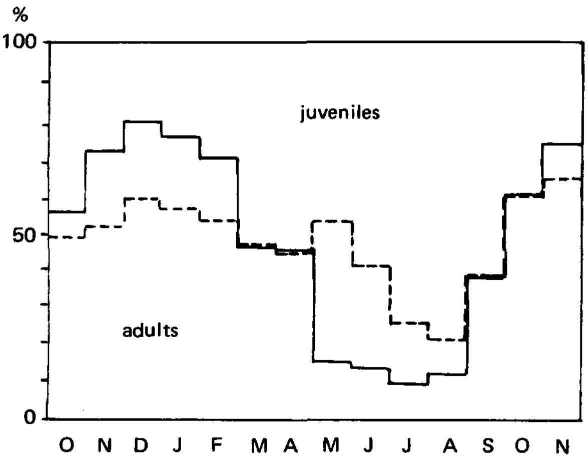

Fig. 4: Monthly average percentages of adults and juveniles. Solid line: with *Macrargus rufus;* dashed line: without *M. rufus.*

litter; they may live in the arboreal stratum where some adults were collected.

Fig. 9 shows the periods of presence for males of some linyphiid species, for which sampling data are consistent; the two types of biological cycle are clearly illustrated. Most of the species we observed in the litter have a one-year biological cycle, but some of them probably have a two-year cycle. This appears to be the case for *Coelotes terrestris* and *Cicurina cicur,* but details are lacking as our sampling method was not well adapted to these species.

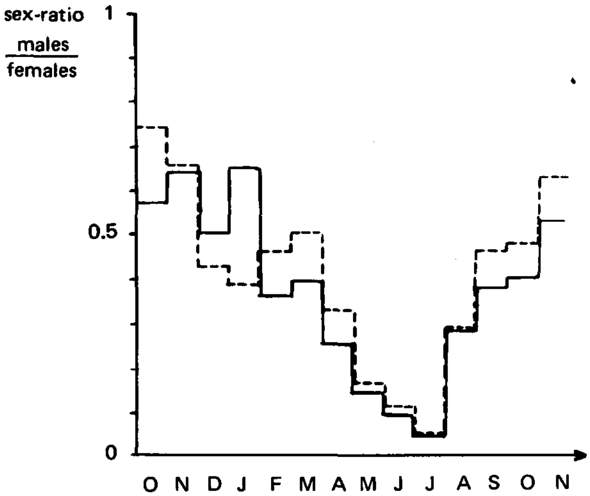

Fig. 5: Monthly average sex-ratio. Solid line: with *Macrargus rufus;* dashed line: without *M. rufus.*

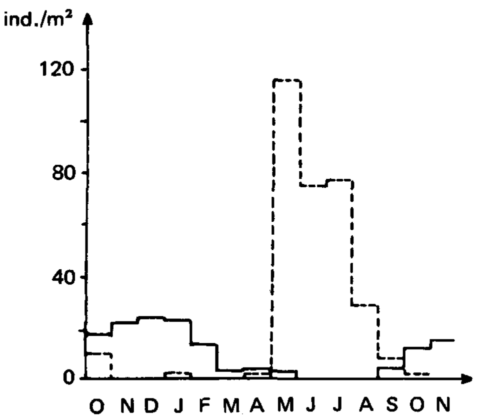

Fig. 6: Monthly average density of *Macrargus rufus.* Solid line: adults; dashed line: juveniles.

Conclusions

The average density of the spiders collected by hand from November 1971 to October 1972 is 74.8 individuals/m^2; this is a minimum estimate, considering the efficiency of the hand-collecting method. Spider densities observed by other authors in forest litter vary from less than 50 ind./m^2 to more than 200 ind./m^2 (van der Drift, 1951; Gabbutt, 1956; Turnbull, 1960; Huhta, 1971). Accurate ecological data would be necessary in order to interpret such differences.

Our study has indicated the importance of Linyphiidae in the spider community of the Montmorency Forest litter; almost 50% of the species collected belong to this family. In other forests similar percentages have been observed: 48.2% in an oak wood

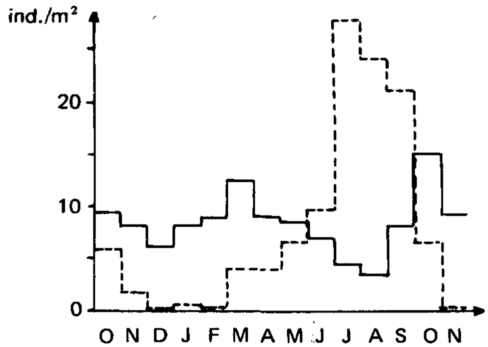

Fig. 7: Monthly average density of *Microneta viaria.* Solid line: adults; dashed line: juveniles.

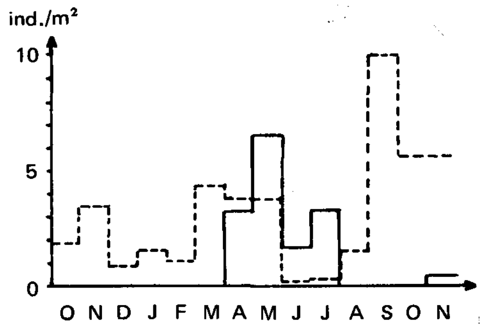

Fig. 8: Monthly average density of *Diplocephalus picinus.* Solid line: adults; dashed line: juveniles.

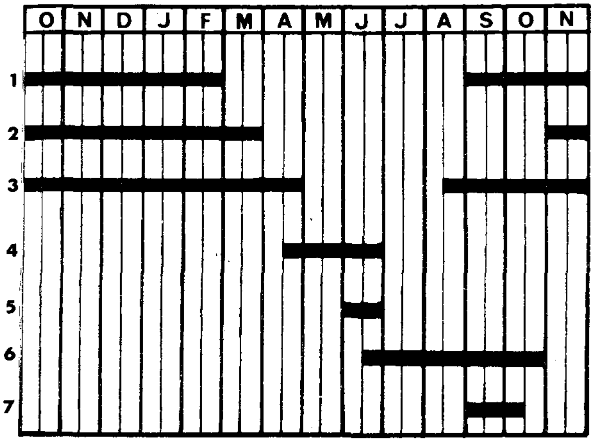

Fig. 9: Presence periods of males of some Linyphiidae: 1 *Macrargus rufus;* 2 *Centromerus aequalis;* 3 *Microneta viaria;* 4 *Diplocephalus picinus;* 5 *Oreonetides abnormis;* 6 *Lepthyphantes zimmermanni;* 7 *Walckenaera corniculans.*

in England (Gabbutt, 1956); 51% in Finnish forests (Huhta, 1971); a greater percentage (68%) was found in a coppiced chestnut woodland in southern England (Russell-Smith & Swann, 1972); in Belgium Jocqué (1973) found 52.4% in a beech wood and 66.7% in an adjacent coppiced woodland (Querco-betuletum). In our study, the dominance of Linyphiidae appears to be even greater when considering the specimens collected; 80.2% of them are linyphiids (average value for a year).

Figs. 1-4 emphasize the importance of *Macrargus rufus* in the community. This dominant species (46.3% of our 3,121 hand-collected specimens) appears to be common in many European woodland areas (Buche, 1966; Huhta, 1965, 1971; Jocqué, 1973; Polenec, 1962, 1964; Russell-Smith & Swann, 1972; van der Drift, 1951; von Broen & Moritz, 1963). Therefore it was of interest to develop a detailed study of this species, which is a characteristic example of a dominant family in many spider communities of forest litter. The results we obtained on the population dynamics and production of *M. rufus* will be published in another paper.

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