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RELATIONS BETWEEN WANDERING SPIDERS  
AND OTHER EPIGEIC PREDATORY *ARTHROPODA*\*

The results of research on the predatory epigeic macrofauna of eight habitats in the Kampinos National Park near Warsaw are presented in this study. The first part of the study is devoted to an analysis of communities of wandering spiders, giving variations in their penetration during the season and during the day. The second part of the study is concerned with the relations between spiders and other groups of epigeic predatory *Arthropoda*. It was found that these relations are competitive in type. In the spring the wandering spiders are the earliest of all predators to appear on the surface of the soil. In forest habitats they exhibit a tendency to seasonal alternation with *Carabidae*. They also exhibit differences in the time of their occurrence, dividing the season between the group of large and medium body-sized species. During the day they usually alternate with *Opiliones* and *Carabidae*. The fewer the ants present on meadow stations, on the other hand, the more intensively the spiders occupy these stations.

Contents

- I. Conditions under which material was collected
  1. Study area and stations
  2. Weather conditions
  3. Methods
- II. Arachnofauna in the study areas
  1. Systematic remarks and elements of biology
  2. Description of the spider communities in different habitats
  3. Seasonal variations in penetration by the spiders
- III. Spiders and other predatory *Arthropoda*
  1. Preliminary remarks
  2. Daily cycles of penetration by predatory *Arthropoda*
  3. Variations in penetration during the season and in the two study years
- IV. Summary of results

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Wandering spiders form one of the abundant groups of predatory *Arthropoda* penetrating the surface of the soil. Only *Formicidae* and certain *Coleoptera* are similarly numerous and also (although not exclusively, like spiders) predatory in Poland in this habitat; *Opilionidae* and *Chilopoda* are far less frequently encountered on the surface of the soil<sup>1</sup>.

The present study is composed of two parts, in the first of which there is a discussion of the wandering spiders of different habitats. The second part is concerned with relations between spiders and the predatory *Arthropoda* mentioned above which co-occur with them. It is well known from the data on the biology and ecology of all these predators that they occupy similar ecological niches and play a similar part in biocenoses.

Factors determining the occurrence of wandering spiders have been fairly extensively discussed in literature. In many studies devoted to them (chiefly *Lycosidae*) Petruszewicz (1933, 1933a, 1935a, 1938) gives a detailed description of the places in which they occur, suggesting a high degree of habitat selection in many species. Tretzel (1952-3) created a comprehensive nomenclature in order to give a concise description of the habitat requirements of many species. Knülle (1951, 1952, 1953, 1954), Mikulska (1950, 1955), Nørgaard (1951), Prószyński (1961), Duffey (1962, 1962a, 1963) analyse the effects of different factors on the occurrence of spiders, and discuss the larger or smaller parts of the habitat in which they can be found, connecting this with a fastidious selection of habitats by these organisms. On the other hand Tretzel (1952-3) conducted an interesting experiment forming evidence of the great habitat tolerance of wandering spiders. On the basis of aut-ecological data and an established range of reactions to two main factors only - humidity and light, he defines theoretically the qualitative composition of spider communities for different habitats. Comparison of the theoretically envisaged communities and those found in nature showed that they were very similar, almost identical. If therefore it is possible to envisage the composition of a larger combination of species according to two main factors, then this proves, after Tretzel (1952-3), that different species are not closely connected either with the whole habitat complex or with the large number of small side factors. Similar suggestions are made by H.D. Barnes and B. Barnes (1955).

In the present investigations the author was interested primarily in the conditions of the biotic habitat determining the level of occurrence of the spiders. These conditions have been taken into consideration in a few arachnological studies - amongst which may be mentioned in the first place that by Tretzel (1952-3, 1955a) already referred to, then the study by Heydemann (1960, 1960a) and Kuenzler (1958), and of Polish studies that by Łuczak (1953, 1954, 1963) and by Kajak (1965). In addition some

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<sup>1</sup>According to data given by Forsslund (1945) (after Vité 1953) spiders form about 30% of the macrofauna of the litter in 200-year old Swedish forests.



faunistic studies make incidental reference to biotic factors as among those conditioning the abundance of species (Buchar and Zdarek 1960).

In papers on the whole of epigeic invertebrate fauna spiders have been dealt with by Pillai (1922), Pfetten (1925), Forsslund (1943) (after Vité 1953), then Balogh and Loksa (1948), Van Der Drift (1951, 1959), Thiele (1956), Krogerus (1960), Kaczmarek (1963) and a few others. In the majority of cases these are descriptions of the spider communities found – in addition to other *Arthropoda* – in defined habitats.

From the point of view of a considered opinion as to the significance of dependence on biotic factors it is particularly the studies by Balogh and Loksa (1948) and Kaczmarek (1963) which are of interest here.

Balogh and Loksa (1948) in their investigations of epigeic *Arthropoda* divide the spiders they found into three syntrophia<sup>2</sup>: 1) spiders which spin webs at low levels, 2) which hunt while running, 3) jumping spiders. Running spiders in turn are included in one syntrophium with ants and *Carabidae*. Unfortunately, there is no more accurate analysis of the connections in syntrophia given in the study referred to, the authors citing only the interesting observations made by Dahl (1908) (after Balogh and Loksa 1948) on this subject. Dahl considers that in the tropics, where there is a complete absence of *Carabidae*, ants predominate numerically. In the warm part of Central Europe, on the other hand, the reverse applies. It would seem that the authors accept Dahl's opinion as to the ecological equivalence of these two groups. Williams (1959), however, in his investigations of the daily activity of epigeic fauna, assumes that of the groups penetrating the surface of the soil spiders and *Carabidae* complement each other and reciprocally exclude each other.

Kaczmarek (1963) analyses the competition between groups of predatory soil and litter macrofauna in pine woods. He attributes a particularly important role in this competition to ants, as being abundant, active and wide specialized, and in his opinion they form the link between the habitat and the other specialized soil predators connected with them by competition. Thus the relations between the different groups of predators are effected through the medium of ants; in the litter, for instance, they determine both the abundance and activity of spiders.

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<sup>2</sup>Syntrophium – according to Balogh (1946) this is “a natural biocenotic unit composed of the same life forms”. The term “life form” is a concept borrowed from phytosociologists (Gams 1918, Raunkiaer 1934) and was defined in the field of zoocology by Remane (1943) as follows: organisms, which due to their similar way of life form a complex of similar structures belong to the same life form. These will therefore be, e.g. organisms moving in a similar way (running, jumping), obtaining food in a similar way, etc. Such a group of organisms leading a similar way of life in a definite biocenosis is termed a syntrophium.



## I. CONDITIONS UNDER WHICH MATERIAL WAS COLLECTED

### 1. Study area and stations

The material used in the present study was collected in the Sieraków Reserve on the north-east fringe of the Kampinos Forest near Warsaw. The study stations were distributed over a radius of about 3 km, and consisted of patches of coniferous or mixed woods of different ages and several portions of meadows in the group of meadows in the middle of wooded land known as the Strzeleckie Meadows. The area of one station was at least 200–300 m<sup>2</sup>. In 1960 a total of 5 stations were explored, 3 of which were situated close to each other: VPin – a pine wood near the Strzeleckie Meadows, Ml – a deciduous wood with patches of meadowland on the fringe of the Strzeleckie Meadows, D<sub>1</sub> – part of a meadow and PQs and PQm – two belts of mixed forest lying about 3 km away from the foregoing three and adjacent to each other within one area of an island of the *Pino-Quercetum*<sup>3</sup> association surrounded by marshland. Exploration of all these stations was continued in 1961, except that station D<sub>1</sub> was moved slightly into the middle of the meadow on to a part which was identical from the floristic aspect, and which was termed D<sub>2</sub>. Two further meadow stations were added, called DC and C. Thus in 1961 a total of 7 stations were explored: 4 forest and 3 meadow stations.

The phytosociological description of these stations, arranged in a gradient according to the degree of humidity, was as follows:

1. VPin – *Vaccinio myrtylli-Pinetum* association. This is the driest of the study stations: pine wood about 35 years old, density of the tree-stand 80%, density of shrubs negligible, coverage of herb layer 30%. The station is situated on a small hill. The litter is minimum, and only the mosses (coverage 90%) can maintain humidity and form a suitable habitat niche for the invertebrates penetrating the bottom of the forest. Soil podzolization medium.

2. PQs – *Pino-Quercetum* association: the mixed coniferous association clearly allied to the *Carpinion betuli* alliance. Density of tree-stand 60% (*Carpinus betulus*, *Quercus robur*, *Pinus silvestris*), shrub density 10%, herb layer 70%. The mixture of coniferous and *Carpinion* species is particularly evident among these latter. Scanty moss, the litter is formed by decomposing parts of *Vaccinium* and leaves. This station is formed by the dry, central part of a large stretch of forest surrounded by marshes.

3. PQm – a wet near-marsh belt adjacent to the preceding stations. The area is uneven, tufted, with species of the *Carpinion betuli* alliance entering on the higher parts, and *Alnus* in the lower-lying parts. Negligible density

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<sup>3</sup>Nomenclature of plant associations after Szafer (1959); nomenclature of plant species after Szafer, Kulczyński and Pawłowski (1953).



of mosses, some leaf humus on the line of contact with the water of the muddy substratum. Density of tree-stand 80%, of shrubs and herb layer 60%.

4. M1 – complex association, composed of parts of alder beds, and in treeless places of meadow of the *Molinietalia* order (periodically flooded) on which alder and birch grow. Density of tree-stand 60%, of shrub layer 40%, herb layer 90%. The ground vegetation and litter are very varied (at least 5 times denser coverage than on the nearby VPin), consisting of mosses, herbs, grasses and laeves. The station gives a very luxuriant and rich impression: the higher parts which were not subject to flooding were explored.

5. D<sub>1</sub>, D<sub>2</sub> – wet meadows, associations of the *Deschampsietum* group. Density of herb layer 70%, of mosses 80%. Station D<sub>1</sub> is situated nearer the edge of the meadow, D<sub>2</sub> nearer to the centre, but it is also more uniform and better formed. Both stations are periodically flooded.

6. DC – *Carici-Agrostetum* association: a non-uniform station, in drier places parts of *Deschampsietum*, and *Caricetum elatae* in the depressions. Density of herb layer 100%, mosses 70%. There is water standing in the depressions for the greater part of the year. The station is situated near the edge of the meadow.

7. C – *Caricetum elatae* association, uniform, very well formed. The station consists of ten patches of sedge growing in water standing there throughout the whole year. Density of herb layer 10%, mosses 30%. There is a certain amount of broken, decomposing or dried sedge leaves in the interior of the patches.

## 2. Weather conditions

The years 1960 and 1961 differed from each other chiefly as to the amount of precipitation, and in consequence as to atmospheric humidity. The data obtained from the Meteorological Station of the Institute of Ecology (Fig. 1) are as follows: the spring of 1960 was relatively dry; heavy rain began in July and lasted more or less intensively to the end of June. During these two months there was not a single week without rain. Water in the meadows and marshes rose so much that the traps placed on the wet stations were flooded. September introduced far drier weather, while the longer, autumn rains began in October. The weather was different in 1961: the spring and summer were relatively rainy (during the period from April to August there were only three weeks without rain), and the autumn dry. In general 1960 was characterized by heavy rain in July, which flooded the study stations, whereas in the spring and summer of 1961 there was long-lasting, but lighter rainfall.

The distribution of temperatures during these two years is similar: the maximum mean monthly temperature occurred in June, being 16.8°C for 1960, and 17.8°C for 1961. In addition the spring and autumn of 1961 were warmer than in the preceding years – the differences being about 2°C in mean monthly temperatures.



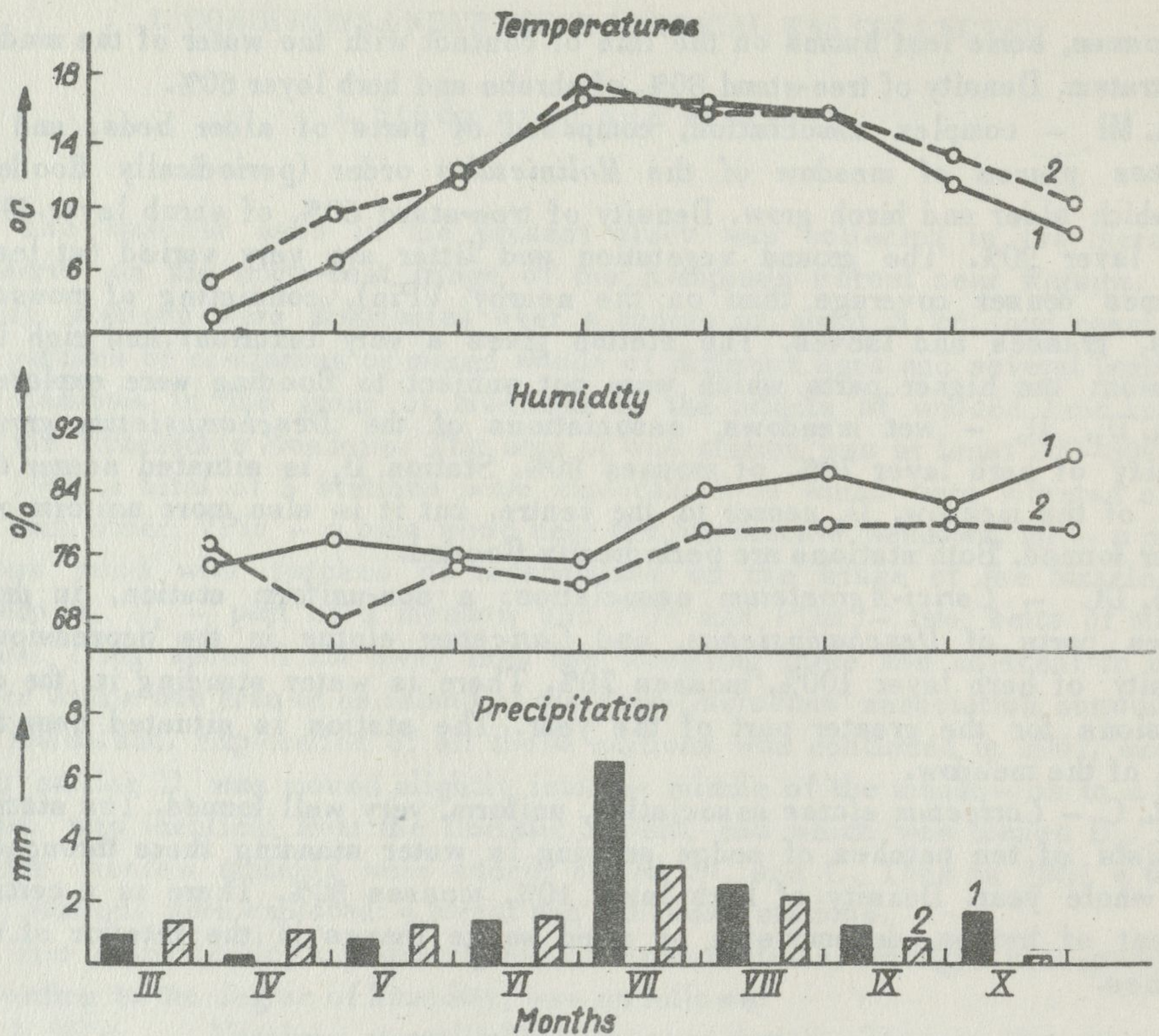


Fig. 1. Comparison of meteorological measurement for the years 1960–1961  
1 – 1960, 2 – 1961

### 3. Methods

Barber traps (Barber 1931, Stammer 1948, Tretzel 1955) were used for collecting material. The actual trap was formed of a vessel of hard, smooth plastic measuring 5 cm in diameter and about 10 cm in depth, which was sunk sufficiently deep into the soil for the edge of the vessel to be level with the surface of the soil. The traps were one-third filled with ethyl glycol or diluted formalin. Live traps were not used as it was found that the number of spiders caught in them exhibits a negative correlation with the number of other *Arthropoda* caught in the traps – the spiders are probably eaten in the traps or frightened away from them (Breymeyer 1960). In order to avoid the traps being flooded by rain holes, through which the water ran out, were drilled in the sides of the vessels (about half-way up the sides). The covers recommended by many authors (Tretzel 1955, Balogh 1958) were not



placed above the traps in order to avoid forming a constant microclimate beneath them, which might attract certain animals (e.g. all cryptozoa) to the traps.

At least 10 traps were placed on one station: this number guarantees the capture of the less numerous species also (Breymeyer 1961). In general the traps were arranged at random every 5–10 m, endeavour being made not to be influenced by the mosaic character of the habitat: traps were arranged in this way in 1960 on stations VPin, Ml, D<sub>1</sub> (10 traps on each) and on stations in 1961 (VPin, Ml – 15 traps each; PQs, PQm, D<sub>2</sub>, DC, C – 10 traps each). Stations PQs and PQm in 1960 were explored in a different way: that is, the considerably mosaic-like character of these stations was taken into consideration. The traps were arranged in groups of four in well separated defined spots in the habitat, 8 such points (32 traps) were arranged on PQs, and 7 (28 traps) on PQm.

The traps were emptied every four days in 1960 and every ten days in 1961. Captures were made over the whole year, but in the present study only materials from the periods from March to October were taken into consideration.

A total of 13,283 specimens of predatory *Arthropoda*, which included 4,597 spiders<sup>4</sup> were caught during 1960–1961.

Material for work on the diurnal rhythms of epigeic *Arthropoda* was collected on the above stations in 1962; it was supplemented by material collected in 1958 in the nearby pine wood (description similar to the description of station VPin) and on the meadow situated on the fringe of the Kampinos Forest. In 1958 the traps were emptied twice a day (at dawn and dusk), while in 1962 the day was divided into shorter sections – 3 a.m., 9 a.m., 5 p.m., 9 p.m., midnight. The periods 3–9 a.m. and 5–9 p.m. were treated as dawn and dusk, the period from 9 a.m. – 5 p.m. as the full day, and from 9 p.m. to 3 a.m. as night. Collections were made in three series, each of 10 days. The series were spread out from May to September so that almost the whole period of the growing season was covered by the samples. The whole of the material collected for this purpose consisted of 3,140 *Arthropoda* caught over the period of thirty days and thirty nights in from eighty to one hundred traps each day and each night.

The smallest forms, the body dimensions of which were below 4–5 mm were rejected from the material obtained in this way for the present study, since it was considered that such individuals have little chance of entering into competition for occupation of the area with the larger predators which were most numerous there. All spiders of the family *Micryphantidae* were also omitted from the analyses. These are web spiders. The fact that their wandering – and in consequence their being caught in the traps, are not

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<sup>4</sup>We have given all these data only for those predators with larger body dimensions, taken into consideration in this study – that is, according to Fenton's (1947) classification – mesofauna; Van der Drift (1951) and Kaczmarek (1963) term these animals macrofauna.



connected with a search for food, qualifies them as a group separate from all the other predators investigated.

Without solving the problem as to whether the material obtained by the trapping method corresponded to variations in numbers, or whether it only indicated the different activity of the animals caught, it was considered that the material obtained constituted an index of the penetration of the area. It is therefore intensity of penetration and variations in it which will be discussed in the continuation of this study.

In order to obtain an idea of the differences and similarities in the results obtained by the trapping method and the method making it possible to obtain the number of individuals per unit of area (sifting, searching the litter) it is worth while citing certain data. Pillai (1922), Pfetten (1925), Vité (1953) include among the results of their researches on the litter fauna of Central European coniferous forests the variations in abundance over the whole year of the spiders caught in these habitats. All three of the authors mentioned above collected material by the method of sifting and searching forest litter. There are two periods of increased abundance distinctly evident in the collections obtained by this method (Fig. 2): the first, a spring increase, during the period from April-May or April-June, and a second, a winter increase, during the period from October-December. From the material presented in the present study it can be seen that we are concerned with one peak only, the spring peak in the abundance of spiders (Fig. 2). The difference here is undoubtedly due to the character of the methods used. In the warm half of the year the spiders wander over the surface of the soil: they hunt here and during the maturity period search for the other sex. During this period of normally active life the traps register variations in their activity and abundance: the results of trap captures and sifting are similar. During the winter, on the other hand, not only the spiders normally running over the surface of the litter disappear into its interior but also many of the forms living on herbs, shrubs and trees (Weese 1924). This is at the same time

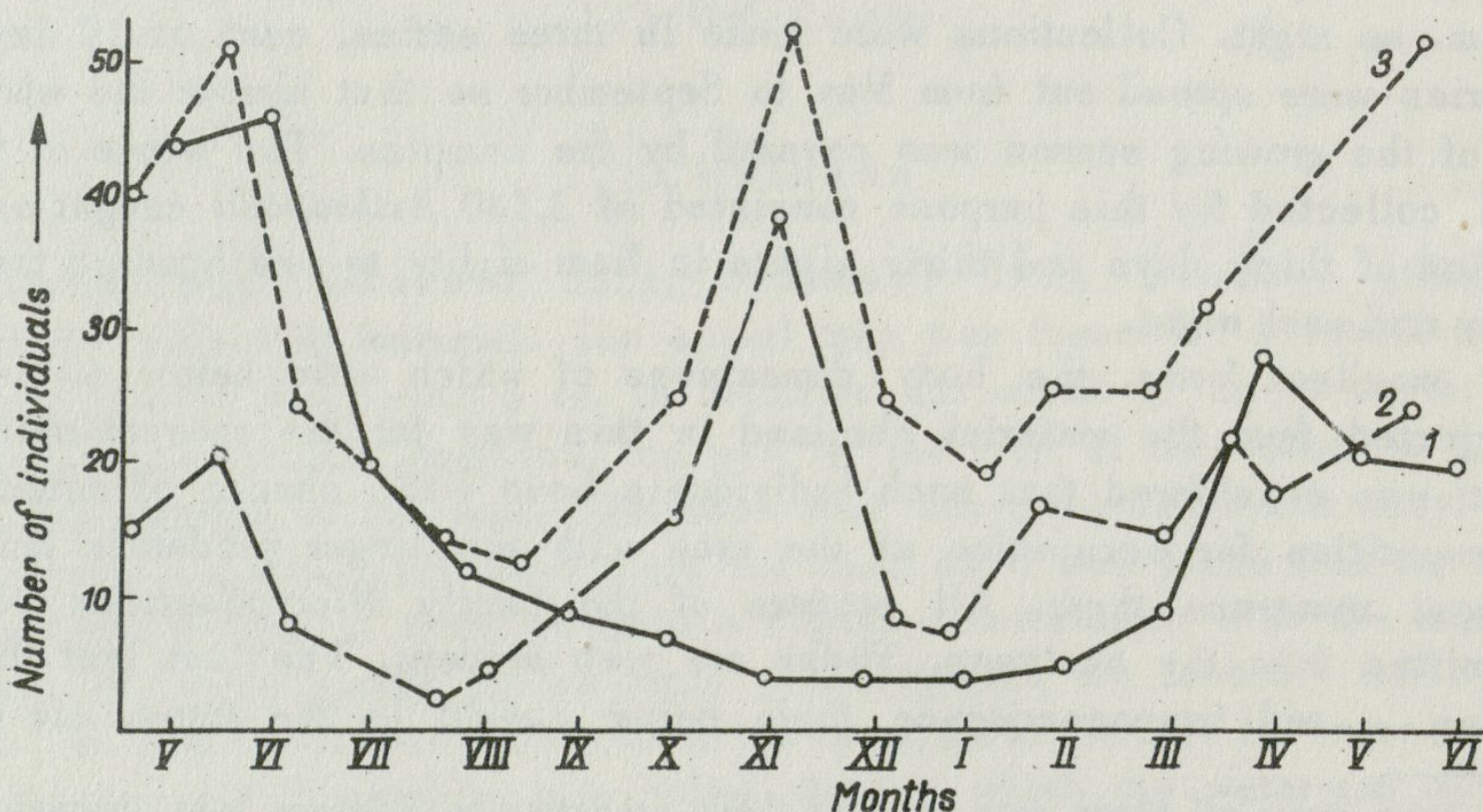


Fig. 2. Annual variations in the abundance of wandering spiders  
 1 — author's trapping material, 2, 3 — material from searching the litter of two forest stations after Vité (1953)



the transition to a passive, inactive way of life. The traps do not of course catch all these spiders, but they are caught when sifting the litter layer several centimeters deep. Hence the difference in the results obtained from the trapping and sifting methods. Bearing the above in mind, only the results from the warm half of the year were analysed in the present study, that is, from the period from March to October.

Another question is the age structure of the population of spiders caught in the traps, which is definitely shifted in favour of the adult forms. This was observed by Łuczak (1953) and Hackman (1957); in the materials of the latter, obtained by trapping, the adult individuals formed on an average 78% of the whole. This is even more clearly evident in my material (Tab. I), in which the participation of adult animals in the community does not fall below 80%. Duffey (1962), however, states that in the material obtained by the method of registering abundance, the percentages of adult spiders never exceed 48% of the abundance of the whole population. Therefore in the case of trapping material we are concerned with populations of adult animals. Breymeyer (1961a) demonstrates that the young specimens of *Trochosa terricola* Thor. tend to live in the litter more frequently than on the soil surface, where the adult animals are more frequent. Kuenzler (1958) in investigating three species of the genus *Lycosa* found that these animals when uneasy escape and hide below the ground: in particular the immature, smaller spiders rapidly squeeze into holes and cracks in the soil. It is probable that we have to do here with similar behaviour in relation to the remaining species of wandering spiders — these animals are not fully active on the soil surface until they reach the period of maturity. While young they hide in the litter and holes in the soil, where they are afforded both protection from their enemies and abundance of fine, accessible food. Heydemann (1960) reached similar conclusions, and stated that the "density of activity" ("Aktivitätsdichte") of young individuals is far below that of adults.

In his study of methods Heydemann (1961) compares material from collections made by trapping and from sifting litter. He defines the first of these as "Aktivitätsdichte", the second as "Besiedlungsdichte". With the same density of settlement ("Besiedlungsdichte") the larger wandering spiders have a nine times greater "density of activity" ("Aktivitätsdichte") than the small *Micryphantidae*, and from 90–100 times greater "biomass of activity" ("Aktivitätsbiomasse"). In general the ratio *Besiedlungsdichte*: *Aktivitätsdichte* for *Lycosidae* is 1:3. The author stated that one trap set for 4 weeks traps a similar amount of animals to that which would be obtained from sifting an area of 1–2 m<sup>2</sup>. Breymeyer (1961) recommends using about 10 traps per station in order to obtain a sufficient number of specimens for analyses of variations in penetration of the less numerous species. Of course collection of animals from an area of 10–20 m<sup>2</sup> in order to obtain this number of specimens would be difficult to carry out. It would therefore seem that in relation to the comparatively scanty, and very active predatory *Arthropoda* of the soil surface, trapping constitutes the most convenient and suitable method. Analysis of the relations between populations of these animals must be based on data estimating both their abundance and activity. It is highly probable that the influence of the biotic environment on animals of this type primarily affects their activity, and later their abundance, in view of the fact that the first of these properties is more plastic than the second.



Percentage of adult and juvenile spiders  
in 1960

Spiders	Study					
	PQs	PQs	PQm	PQm	VPin	VPin
	1960	1961	1960	1961	1960	1961
Adult	82.8	87.4	89.9	92.1	87.9	84.5
Juvenile	17.2	12.6	10.1	7.9	12.1	11.5

## II. ARACHNOFAUNA IN THE STUDY AREAS

### 1. Systematic remarks and elements of biology

During the two-year study period a total of 88 species of wandering spiders<sup>5</sup> were found on all the stations discussed above, 79 species on forest stations, and 36 on meadow stations. Of these 27 species were common to the whole study area, thus giving a total of 52 species characteristic of the forest stations on which they were found, and only 9 such species characteristic of the meadow stations on which they were found<sup>6</sup> (Tab. II).

<sup>5</sup>In my opinion three of the species identified may prove dubious. They are: 1) Differentiation between *Zelotes apricorum* (L. Koch) and *Z. subterraneus* (C.L. Koch). Locket and Millidge (1951) state that these species are identical and refer to Simon (1874–1937), who gives the shape of the stylus as the character distinguishing them. The recommended preparation of the copulation organs was made, but distinction made between species otherwise identical on this basis only gives rise to doubts. 2) The species *Tricca lutetiana* (Dahl) given only by Dahl (1927), described by Simon (1874–1937) as *Lycosa lutetiana* (E.S.). The characteristic arrangement of the eyes, general shape and place of occurrence incline me to identify the species I found as *Tricca lutetiana*. Dahl (1927) unfortunately gives the drawing of the whole animal and description of external appearance for only one adult female found in the Berlin museum; he does not give a description of males, which formed the majority of the specimens in my material. Simon (1874–1937) does not give any illustrations, only a short description which makes identification uncertain. 3) *Lycosa* from the *monticola* group; this is most probably *Lycosa tarsalis* Thorell. Identification was made according to Locket and Millidge (1951), on the basis of drawing of the cephalothorax and the copulation organs. It was, however, found that there are situations in which the drawings given for one species fit the copulation organs of a second. Similar cases of finding specimens with characters corresponding to several species are noted in literature in connection with the *L. monticola* group; for instance they are given by Fedotov (1912) (after Petruszewicz 1933) – the specimens which he examined were similar to four species from the *monticola* group, Petruszewicz (1933) and Prószyński (1961).

<sup>6</sup>Identification in the material collected was made on the basis of the following studies: Simon (1874–1937), M. Dahl (1926, 1931), F. Dahl and M. Dahl (1927), Roever (1929), Petruszewicz (1935), Palmgren (1939, 1943, 1950), Tullgren



in collections made over the whole year  
and 1961

Tab. I

stations						Average on all stations
M1	M1	D <sub>1</sub>	D <sub>2</sub>	DC	C	
1960	1961	1960	1961	1960	1961	
92.7	89.7	85.8	81.2	91.5	79.1	86.8
7.3	10.3	14.2	18.8	8.5	20.9	12.6

The 88 species found belong to 8 families. They are all exclusively wandering spiders, catching their prey actively by attacking it. Single individuals were also found in the traps of spiders belonging to the upper layers (*Cercidia prominens* (Westring), *Linyphia clathrata* Sundevall and *L. triangularis* (Clerck), *Theridion ovatum* (Clerck)), which either reached the trap accidentally after falling from shrubs or trees, or were caught in the late autumn, when they searched in the litter for shelter for the winter. Spiders building houses and holes in the litter, as shown by the fairly numerous captures, must often leave their hiding places and wander over the surface of the soil (e.g. *Coelotes inermis* (L. Koch) found numerously in the material). Evidence that these are not wandering undertaken entirely to search for partners in copulation is provided by the fact that the males and females were caught at different times, whereas *Coelotes inermis* referred to above had clearly defined reproduction periods (Tretzel 1954).

The occurrence of wandering spiders in general primarily depends on such habitat factors as humidity and light (Petrušewicz 1933, 1933a, Knülle 1951, Tretzel 1952-3, Mikulska 1955, Prószyński 1961 and others). Bogs, meadows, well-lit deciduous woods are all well known as among the richest habitats in arachnofauna of this kind. An important factor here is also the structure of the area – the presence of litter, decaying tree stumps, stones – that is, places which provide shelter in the critical moments of the spider's life and which maintain a constant and suitable microclimate.

A relatively small number of authors draw attention to the fact that the abundance of spiders also depends on the abundance of food in a given habitat (Bilsing 1920, Tischler 1947, Tretzel 1955a, Prószyński 1961). It is considered in this connection that the qualitative composition of potential prey is not of importance here; spiders are exclusive but omnivorous predators and probably attack almost all invertebrates accessible to them from the aspect of size and strength. Bilsing (1920), Bristowe (1939-40)

(1944, 1946), Locket and Millidge (1951-53), Buchar (1958). Nomenclature was in principle used according to Locket and Millidge (1951); in the case of species not described by these authors the nomenclature used in the studies from which they were identified, was adhered to.



## List of species of wandering spiders caught on different stations\*

Tab. II

Species	Forest stations				Meadow stations			
	PQs	VPin	PQm	MI	D <sub>1</sub>	D <sub>2</sub>	DC	C
<i>Gnaphosidae:</i>								
<i>Drassodes signifer</i> (C. L. Koch)	+++	+		+				
<i>Drassodes sörenseni</i> (Strand)	++	++	+					
<i>Drassodes silvestris</i> (Blackwall)	++		++	+				
<i>Drassodes lapidosus</i> (Walckenaer)				+				
<i>Drassodes pubescens</i> (Thorell)				+				
<i>Drassodes minor</i> (O. P. — Cambridge)	+							
<i>Zelotes clivicolus</i> L. Koch	+							
<i>Zelotes electus</i> (C. L. Koch)	+							
<i>Zelotes latreillei</i> (Simon)	+	+		+	+			
<i>Zelotes praeficus</i> (L. Koch)	+							
<i>Zelotes serotinus</i> (L. Koch)	+							
<i>Zelotes subterraneus</i> C. L. Koch	++	+		+				
<i>Zelotes lutetianus</i> (L. Koch)		+		+			+	+
<i>Zelotes apricorum</i> (L. Koch)			+	+				
<i>Zelotes pusillus</i> (C. L. Koch)				+	+	+		
<i>Micaria pulicaria</i> (Sundevall)		+		+				
<i>Micaria scintillans</i> (O. P. — Cambridge)				+				
<i>Haplodrassus cognatus</i> Westring		+						
<i>Clubionidae:</i>								
<i>Apostenus fuscus</i> Westring	+		+					
<i>Clubiona compta</i> C. L. Koch			+					
<i>Clubiona lutescens</i> Westring			+					
<i>Clubiona coeruleascens</i> L. Koch	+							
<i>Agroeca brunnea</i> (Blackwall)	+	+	+	+				
<i>Agroeca proxima</i> (O. P. — Cambridge)		+		+				
<i>Agreacina striata</i> (Kulczyński)			+	+				
<i>Zora spinimana</i> (Sundevall)	+	+	+	+				
<i>Zora nemoralis</i> (Blackwall)	+		+					
<i>Phrurolithus minimus</i> C. L. Koch	+	+						
<i>Thomisidae:</i>								
<i>Xysticus lanio</i> C. L. Koch	+		+					
<i>Xysticus cristatus</i> (Clerck)	+			+	++	+	+	
<i>Xysticus kochi</i> Thorell.	+			+	+			
<i>Xysticus luctuosus</i> (Blackwall)	+	+		+				
<i>Xysticus ulmi</i> (Hahn)	+	+		+				
<i>Xysticus luctator</i> L. Koch		+	+					
<i>Xysticus audax</i> (Schrank)		+			+			
<i>Xysticus erraticus</i> (Blackwall)							+	
<i>Oxyptila atomaria</i> (Panzer)	+							
<i>Oxyptila praticola</i> (C. L. Koch)	+		+					
<i>Oxyptila trux</i> (Blackwall)			+	+	+		+	
<i>Tmarus piger</i> (Walckenaer)				+				
<i>Philodromus histrio</i> (Latreille)	+							
<i>Philodromus margaritatus</i> (Clerck)	+	+						



Tab. II (con.)

Species	Forest stations				Meadow stations			
	PQs	VPin	PQm	Ml	D <sub>1</sub>	D <sub>2</sub>	DC	C
<i>Philodromus fuscomarginatus</i> De Geer.		+						
<i>Thanatus formicinus</i> (Clerck)	+	+		+				
<i>Thanatus arenarius</i> Thorell	+				+			
<i>Tibellus maritimus</i> (Menge)						+		
<i>Salticidae:</i>								
<i>Ballus depressus</i> (Walckenaer)			+					
<i>Euophrys frontalis</i> (Walckenaer)	+	+		+				
<i>Euophrys petrensis</i> C. L. Koch			+					
<i>Sitticus floricola</i> (C. L. Koch)						+	+	
<i>Evarcha falcata</i> (Clerck)	+	+		+				
<i>Lycosidae:</i>								
<i>Lycosa lugubris</i> (Walckenaer)	+++	+++	++	+++				
<i>Lycosa tarsalis</i> Thorell.					+++	+++		
<i>Lycosa amentata</i> (Clerck)		+		+				
<i>Lycosa paludicola</i> (Clerck)				+	+			
<i>Lycosa pullata</i> (Clerck)		+		+	+++	+++	+++	
<i>Lycosa rubrofasciata</i> (Ohlert)	+	+	+	++	+		+	
<i>Lycosa prativaga</i> L. Koch				+	+	++	+++	+
<i>Lycosa proxima</i> C. L. Koch	+							
<i>Xerolycosa nemoralis</i> (Westring)	++	+	+					+
<i>Xerolycosa miniata</i> (C. L. Koch)	+	+						
<i>Tarentula pulverulenta</i> (Clerck)	++	+		++	+++	++		
<i>Tarentula aculeata</i> (Clerck)				+				
<i>Tarentula fabrilis</i> (Clerck)		+			+			
<i>Trochosa spinipalpis</i> (O. P. — Cambridge)			+	+++	+	+	+	
<i>Trochosa terricola</i> Thorell	+++	+++	++	+++				
<i>Trochosa ruficola</i> (De Geer)					+	++	+	+
<i>Arctosa leopardus</i> (Sundevall)					+++	++	+	
<i>Arctosa cinerea</i> (Fabricius)				+				
<i>Pirata hygrophilus</i> Thorell	+		+++	++		+	+	
<i>Pirata latitans</i> (Blackwall)			+	+	++	+++	++	+
<i>Pirata piraticus</i> (Clerck)			++		+		++	+
<i>Pirata piscatorius</i> (Clerck)	+		+		+	+	++	++
<i>Pirata ulginosus</i> (Thorell)				+				
<i>Aulonia albimana</i> (Walckenaer)	+	+		+				
<i>Tricca lutetiana</i> (Dahl)	+	+	+	+				
<i>Pisauridae:</i>								
<i>Dolomedes fimbriatus</i> (Clerck)	+		+				+	+
<i>Pisaura mirabilis</i> (Clerck)	+		+		+			
<i>Agelenidae:</i>								
<i>Cicurina cicur</i> (Fabricius)	+	+	+	+				
<i>Coelotes inermis</i> L. Koch	++	++	+++	+	+			
<i>Amaurobius terrestris</i> (Wider)	+							
<i>Antistea elegans</i> (Blackwall)				+	++	+	++	+
<i>Hahnia pusilla</i> C. L. Koch						+		



Tab. II (con.)

Species	Forest stations				Meadow stations			
	PQs	VPin	PQm	Ml	D <sub>1</sub>	D <sub>2</sub>	DC	C
<i>Tetragnathidae:</i>								
<i>Pachygnatha clercki</i> Sundevall	+		+	+	+	+	++	
<i>Pachygnatha listeri</i> Sundevall	++	+	++	+			+	
<i>Pachygnatha degeeri</i> Sundevall		+		+	++	+++	+	
<i>Tetragnatha obtusa</i> C. L. Koch	+							
<i>Tetragnatha</i> sp.	+							

\* Together with small species, few in number, which were later discarded.

\*\* Symbol + used to indicate abundance of the species on a station according to the scale: + up to 10 individuals, ++ up to 50, +++ over 50.

and Tretzel (1961) give examples of spiders' attacking animals far larger than themselves, such as, for instance, *Bombus* sp., large *Muscidae*, *Tabanidae*, and also beetles, e.g. *Pterostichus vulgaris* L., *Helops* sp. and others.

That the occurrence of wandering spiders depends on the presence and abundance of species or groups of species competing with them is suggested by the authors referred to in the introduction: Łuczak (1953, 1954), Tretzel (1955a), Buchar and Zdarek (1960) – competition between different species of spiders, and Balogh and Loksa (1948), Williams (1959, 1962) and Kaczmarek (1963) – competition between spiders and other predatory *Arthropoda* on the surface of the soil.

## 2. Description of the spider communities in different habitats

The richest of the forest stations are PQs – 49 species of spiders, and Ml – 48 species. These are followed in turn by VPIn – 35 species, and PQm – 32 species. The meadow stations are as a rule poorer in species of wandering spiders: D<sub>1</sub> – 25, D<sub>2</sub> – 18, DC – 20 and C – 9 species<sup>7</sup>. The richest of the meadow stations does not therefore reach the level of the poorest of the forest stations, which afford wandering spiders greater "qualitative" opportunities, i.e. have a larger number of varied spatial niches. The case as regards the "quantitative" opportunities of the habitats is different. On forest stations there is never so intensive penetration by spiders as there is on meadows (Tab. III). The density of spiders caught in one trapping day on stations D<sub>1</sub> and D<sub>2</sub> clearly exceed the analogical numbers on the forest stations. In addition calculation was made of the index of mean abundance per species (total

<sup>7</sup> These differences would be slightly smaller if all the meadow stations had been explored in 1960 also – this was a year far more abundant in spiders. Even when the mean numbers of species per year are taken into consideration the forest stations are richer: PQs – 35, Ml – 31, VPIn – 26, PQm – 19 species.



## Occurrence of wandering spiders\* in the two study years

Tab. III

Occurrence of spiders	Years	Study stations						
		VPin	PQs	PQm	MI	D <sub>1</sub> -D <sub>2</sub>	DC	C
Abundance for one trapping day	1960	0.42	0.23	0.23	0.57	0.86		
	1961	0.13	0.13	0.10	0.20	0.62	0.23	0.06
Number of species	1960	29	44	30	39	25		
	1961	24	26	9	24	18	20	9

\* Together with small species, later discarded (cf. Tab. V).

abundance was included in the numerator, and the number of species of spiders in a given habitat in the denominator) and a similar result obtained. This index shows the abundance for 1 species and is also a measure of the "quantitative" capacities of the habitat. Values of this index for the different stations were as follows: PQm - 16.7; MI - 12.1; PQs - 11.7; VPIn - 7.2; D<sub>1</sub> - 29.2; D<sub>2</sub> - 28.2; DC - 14.3; C - 6.0. Therefore comparison of forest and meadow stations produces results contrary to those obtained when comparing species wealth: the meadow stations (although explored in a "worse" year), are quantitatively richer than the forest stations, and each species is represented here by a larger number of individuals than in the forests (of the forest stations those in wet woods are more abundant in spiders).

In order to describe the specific nature of the settlement by spiders of different stations comparison was made of the domination of species in collections made over the whole season (Fig. 3). It is an accepted fact that the sharply marked domination of one species is evidence of the relative uniformity of the habitat for the group investigated; simultaneous domination of several species, on the other hand, is evidence of its richness and the variety of the ecological niches. In the present material we have to do with different domination structure: on VPIn and PQm the predominance of one species is maintained, and even increases, from year to year. The situation is different in the case of MI and PQs - the distinct domination of one species in 1960 is effaced, and in fact in 1961 we find several dominants, the most numerous of which attains 20% of the total numbers in the community. The habitats discussed could not, of course, alter from year to year from the aspect of the basic abiotic factors. The causes of the variations in numerical relations might be sought for in the influence of climate - 1960 and 1961 differed as to intensity of rainfall. The fact that analogical variations in structure occurred on several stations completely different from the humidity aspect is, however, remarkable. It would seem that the settlement of all humid habitats should change in one direction under the influence of similar climatic changes, and analogically, all dry habitats.



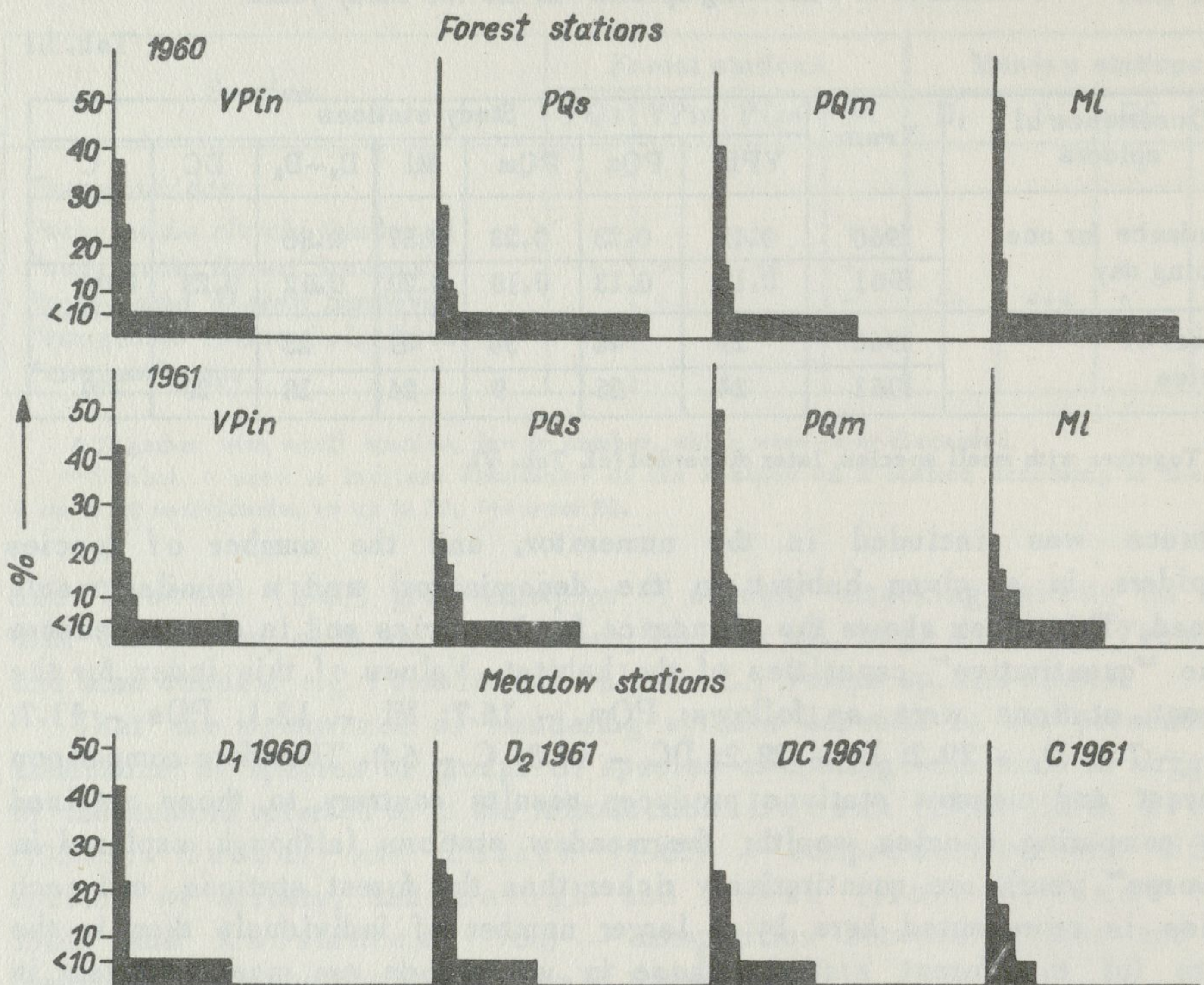


Fig. 3. Domination structure in *Araneida* communities (one column indicates the percentage of one species)

Both stations maintaining the domination structure – VPin and PQm, retain the same dominants in both study years, while those on PQs and ML – change (Tab. IV). It is extremely interesting that the change in both cases consists in the withdrawal from the position of the dominant *Lycosa lugubris* – a species considered as one of the most euryvalent forest species. On all 4 forest stations *L. lugubris* always occurs in 1960 only – in 1961 it either decreases in numbers to below 10%, or does not appear at all (Tab. IV). As we are concerned with such varied habitats it is difficult to assume that this degradation of the greatest eurytope is connected solely with the effect of climate. 1960 and 1961 were very rainy years, yet this factor most certainly exerted a different effect on distinctly dry stations (VPin, PQs) from that on flooded (ML) or near-marshy PQm stations, yet *L. lugubris* disappears from all the stations.

Tretzel (1954, 1955a) postulates that investigation should be made of euryvalent species as being indicators of definite interspecies relations.



## Percentage of more numerous species of spiders in communities

Tab. IV

Species	Study stations												
	VPin		PQs		PQm		Ml		D <sub>1</sub> -D <sub>2</sub>		DC	C	
	1960	1961	1960	1961	1960	1961	1960	1961	1960	1961	1961	1961	
<i>Trochosa terricola</i> *	38	44		17		15		16					
<i>Lycosa lugubris</i>	23		27		10		50						
<i>Pirata hygrophilus</i>					42	50							
<i>Trochosa spinipalpis</i> *							15	24					
<i>Lycosa tarsalis</i>									42	23			
<i>Lycosa pullata</i>									11	26	21		
<i>Lycosa prativaga</i>											24	11	
<i>Pirata piscatorius</i> *												22	
<i>Drassodes silvestris</i> *			13										
<i>Coelotes inermis</i> *					15	12							
<i>Lycosa rubrofasciata</i> *								12					
<i>Pirata piraticus</i>											10	17	
<i>Trochosa ruricola</i> *												17	
<i>Pachygnatha listeri</i>				10									

\* Large species.

These species find optimum sets of abiotic factors in many places; the fact that they occur in limited and different densities is due to the action of biotic factors, primarily of competition with other species.

Kaczmarek (1963) emphasizes the special role of polytopic species pointing out that they are more numerous than the remainder and considering them as conveyors of the relations between more narrowly specialized forms.

Margalef (1963) assumes that the presence and great abundance of unspecialized species are evidence of disturbance of the organisation of the group. Under stabilized conditions the euryoecious species are replaced by more highly specialized species, more capable of withstanding competition.

It is interesting that Tretzel (1954, 1955) reaches the stage of consideration of the particular role of widely specialized species through analysing the occurrence of *Lycosa lugubris*. He found that the great differences in the density of this species on similar stations cannot be explained by microclimatic factors, that the influence of biotic factors is distinctly evident here, that is, interspecies competition. *L. lugubris* attains greater densities on the stations on which other larger epigeic spider species (chiefly *Trochosa terricola*, *Coelotes inermis* and *C. atropos*, *Agroeca brunnea*) occur scantily.



## Classification of spider species according to size of body

Tab. V

Medium species (5–10 mm)	Large species (over 10 mm)
1. <i>Agroeca proxima</i>	1. <i>Agroeca brunnea</i>
2. <i>Cicurina cicur</i>	2. <i>Arctosa leopardus</i>
3. <i>Clubiona compta</i>	3. <i>Arctosa cinerea</i>
4. <i>Drassodes sörenseni</i>	4. <i>Clubiona coerulescens</i>
5. <i>Lycosa prativaga</i>	5. <i>Clubiona lutescens</i>
6. <i>Lycosa pullata</i>	6. <i>Coelotes inermis</i>
7. <i>Lycosa tarsalis</i>	7. <i>Dolomedes fimbriatus</i>
8. <i>Lycosa lugubris</i>	8. <i>Drassodes silvestris</i>
9. <i>Lycosa proxima</i>	9. <i>Drassodes signifer</i>
10. <i>Lycosa amentata</i>	10. <i>Drassodes lapidosus</i>
11. <i>Oxyptila trux</i>	11. <i>Drassodes pubescens</i>
12. <i>Pachygnatha clerckii</i>	12. <i>Evarcha falcata</i>
13. <i>Pachygnatha listeri</i>	13. <i>Haplodrassus cognatus</i>
14. <i>Philodromus histrio</i>	14. <i>Lycosa paludicola</i>
15. <i>Philodromus margaritatus</i>	15. <i>Lycosa rubrofasciata</i>
16. <i>Philodromus fuscomarginatus</i>	16. <i>Pirata piscatorius</i>
17. <i>Pirata piraticus</i>	17. <i>Pisaura mirabilis</i>
18. <i>Pirata hygrophilus</i>	18. <i>Tarentula fabrilis</i>
19. <i>Thanatus arenarius</i>	19. <i>Tarentula pulverulenta</i>
20. <i>Thanatus formicinus</i>	20. <i>Tarentula aculeata</i>
21. <i>Zelotes lutetianus</i>	21. <i>Tibellus maritimus</i>
22. <i>Zelotes latreillei</i>	22. <i>Tmarus piger</i>
23. <i>Zelotes apricorum</i>	23. <i>Trochosa terricola</i>
24. <i>Zelotes subterraneus</i>	24. <i>Trochosa spinipalpis</i>
25. <i>Zelotes serotinus</i>	25. <i>Trochosa ruricola</i>
26. <i>Zora spinimana</i>	26. <i>Tricca lutetiana</i>
27. <i>Zora nemoralis</i>	27. <i>Xysticus luctuosus</i>
28. <i>Xerolycosa nemoralis</i>	
29. <i>Xerolycosa miniata</i>	
30. <i>Xysticus erraticus</i>	
31. <i>Xysticus cristatus</i>	
32. <i>Xysticus audax</i>	
33. <i>Xysticus kochii</i>	
34. <i>Xysticus lanio</i>	
35. <i>Xysticus ulmi</i>	
36. <i>Xysticus luctator</i>	

Mean percentage of large spiders and *Lycosa lugubris* in spider communities in the two study years

Tab. VI

Years	Large spiders	<i>Lycosa lugubris</i>
1960	37.0	27.7
1961	55.0	4.7



Endeavour was made to ascertain whether the above relation is found in the material discussed in this paper. Comparison was made of the percentages of *L. lugubris* and the group of spiders qualified as large (cf. Tab. V) on

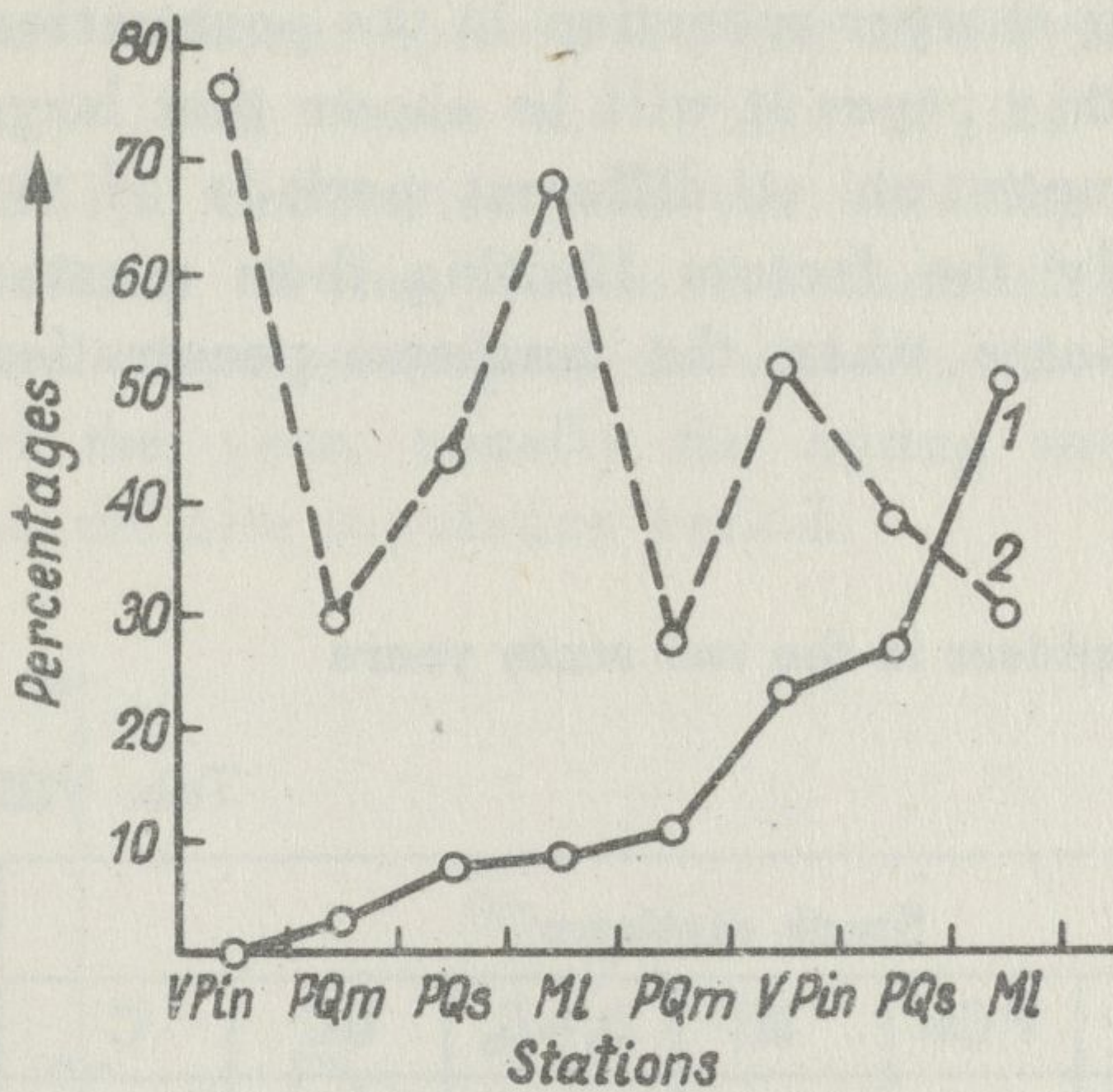


Fig. 4. Percentages of *Lycosa lugubris* and large spiders on different stations in the whole spider community in 1960 and 1961

1 - *Lycosa lugubris*, 2 - large spiders

different stations (Fig. 4) and in both study years (Tab. VI). In both cases the relation indicated by Tretzel (1954, 1955) was established as present: *L. lugubris* tends to interchange with large epigeic spiders both on different stations and in consecutive years; it is therefore a species particularly sensitive to the pressure of biotic factors, probably competition.

In study year II the percentage of large spiders in the community increases on the forest stations (Tab. IV). If the large species was a dominant in 1960, then in 1961 its domination increases (VPin), and on two stations the large species rises from second in order of abundance to the position of dominant (PQs, Ml), while on station PQm it occupies the next two places

after the dominant. This interesting shift in the proportions between the species of large and medium size of body is confirmed by a more exact analysis (Tab. VII). On all the forest stations in 1961 there is a decrease in penetration by spiders of medium size; the question therefore arises as to whether the increase in the percentage of large spiders in the community is parallel to an increase in their numbers in the traps?

Penetration of large and medium spiders in the two study years, in percentages

Tab. VII

Percentage in penetration	Year	Study stations						
		VPin	PQs	PQm	Ml	D <sub>1</sub> →D <sub>2</sub>	DC	C
Large species	1960	56	38	27	39	23		
	1961	74	45	32	67	25	17	60
Medium species	1960	44	62	73	61	77		
	1961	26	55	68	33	75	83	40



It proved that this was not the case (Tab. VIII), since both groups – large and medium spiders, are less numerous in the traps in the second study year, and this decrease affects both the numbers per trapping day and the number of species caught. The shift of proportions in favour of the large spiders therefore takes place at the cost of the far sharper reduction in the penetration of medium spiders. In the further part of this paper it will be shown that large and medium spiders have maxima of penetration at different periods of the growing season and of the day. Probably the factors limiting them exerted a stronger effect in 1961 at those moments when the maximum penetration of medium spiders took place.

Occurrence of large and medium spiders in the two study years

Tab. VIII

Occurrence of spiders		Years	Study stations						
			VPin	PQs	PQm	Ml	D <sub>1</sub> -D <sub>2</sub>	DC	C
Large spiders	abundance for one trapping day	1960	0.20	0.07	0.06	0.20	0.20		
		1961	0.10	0.06	0.05	0.13	0.10	0.03	0.03
	number of species	1960	11	12	10	15	10		
		1961	7	11	3	10	6	6	3
Medium spiders	abundance for one trapping day	1960	0.13	0.16	0.18	0.35	0.60		
		1961	0.02	0.07	0.05	0.05	0.38	0.15	0.02
	number of species	1960	12	21	14	17	11		
		1961	15	15	6	11	7	12	4

To sum up, the conclusions in this section are as follows:

1. Comparison of 8 study stations showed that the forest habitats are richer in regard to the number of species, and the meadow habitats richer in density of large and medium wandering spiders penetrating the surface of the soil.

2. Comparison of the settlement by spiders of the habitats discussed during the two study years showed that in 1961:

a. The number of species and density of all the spiders decreases.

b. The proportions of the participation in penetration of large and medium species shift in favour of the large species.

c. The euryvalent species particularly sensitive to the pressure of biotic factors disappears from the forest habitats.

d. In places where the euryvalent species was dominant in 1960, as a result of its disappearance the domination structure is obliterated in the community in 1961.



### 3. Seasonal variations in penetration by the spiders

Wandering spiders maintain their activity through the whole year; although, it decreases markedly, especially on meadow stations where there is no litter, yet in forest spiders are one of the most abundant components of active epigeic and litter fauna the whole of the winter (Kaczmarek 1958, Pilawski 1961). Copulation and the hatching of the young are distributed in different periods of the year in the case of wandering spiders; there are species with one copulation period, diplochronic species (copulating during two seasons of the year, usually the spring and autumn), and also species which have no definite copulation period.

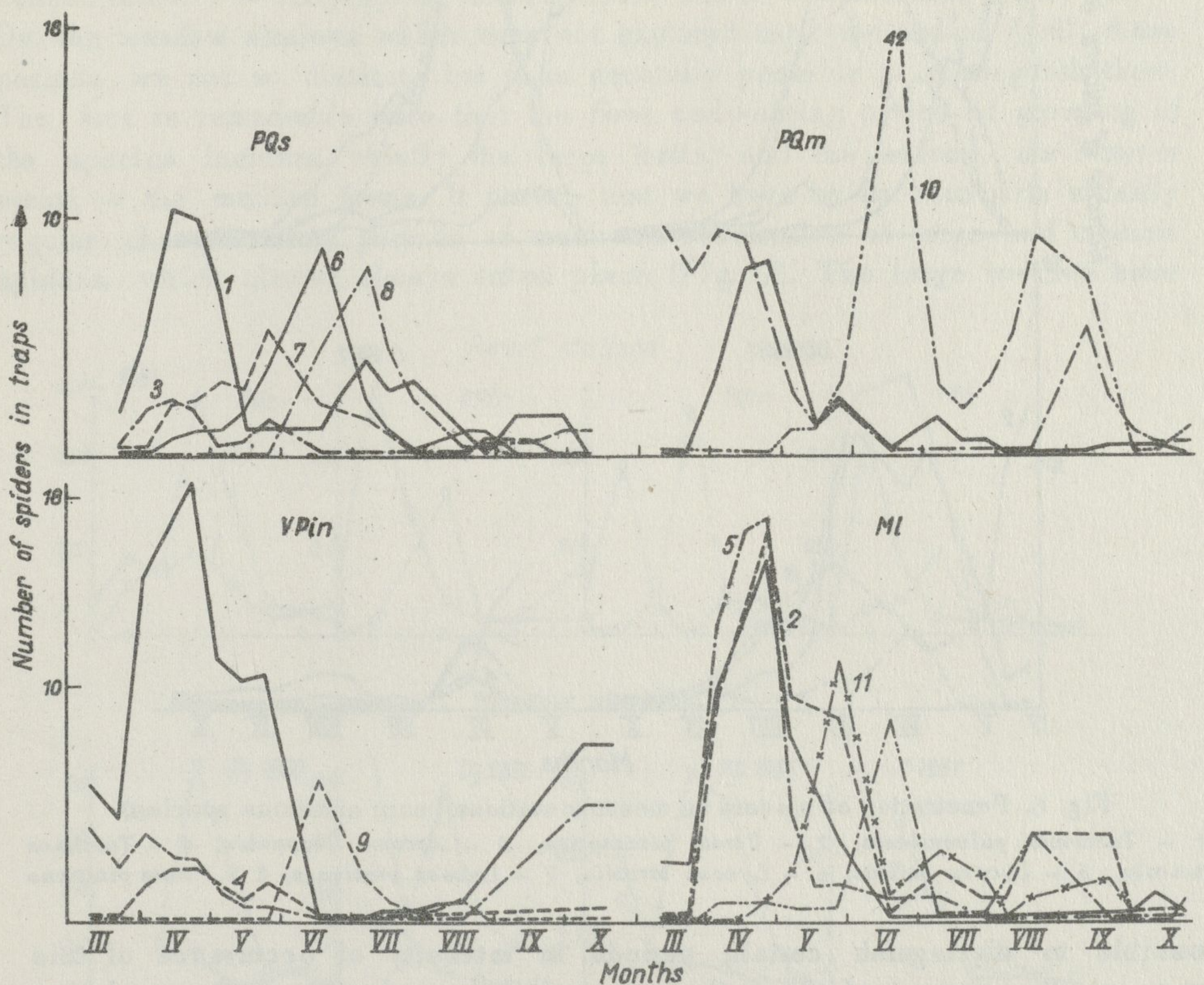


Fig. 5. Penetration of spiders on forest stations in 1961 (more numerous species)  
 1 - *Trochosa terricola*, 2 - *Trochosa spinipalpis*, 3 - *Coelotes inermis*, 4 - *Agroeca brunnea*,  
 5 - *Lycosa rubrofasciata*, 6 - *Zelotes subterraneus*, 7 - *Pachygnatha listeri*, 8 - *Xerolycosa nemoralis*,  
 9 - *Drassodes sörenseni*, 10 - *Pirata hygrophilus*, 11 - *Lycosa lugubris*

Thus the activity and way of hatching of these animals, spread out over the whole year, makes it possible to consider wandering spiders as a group permanent occurring in a habitat. This does not of course mean that it is not



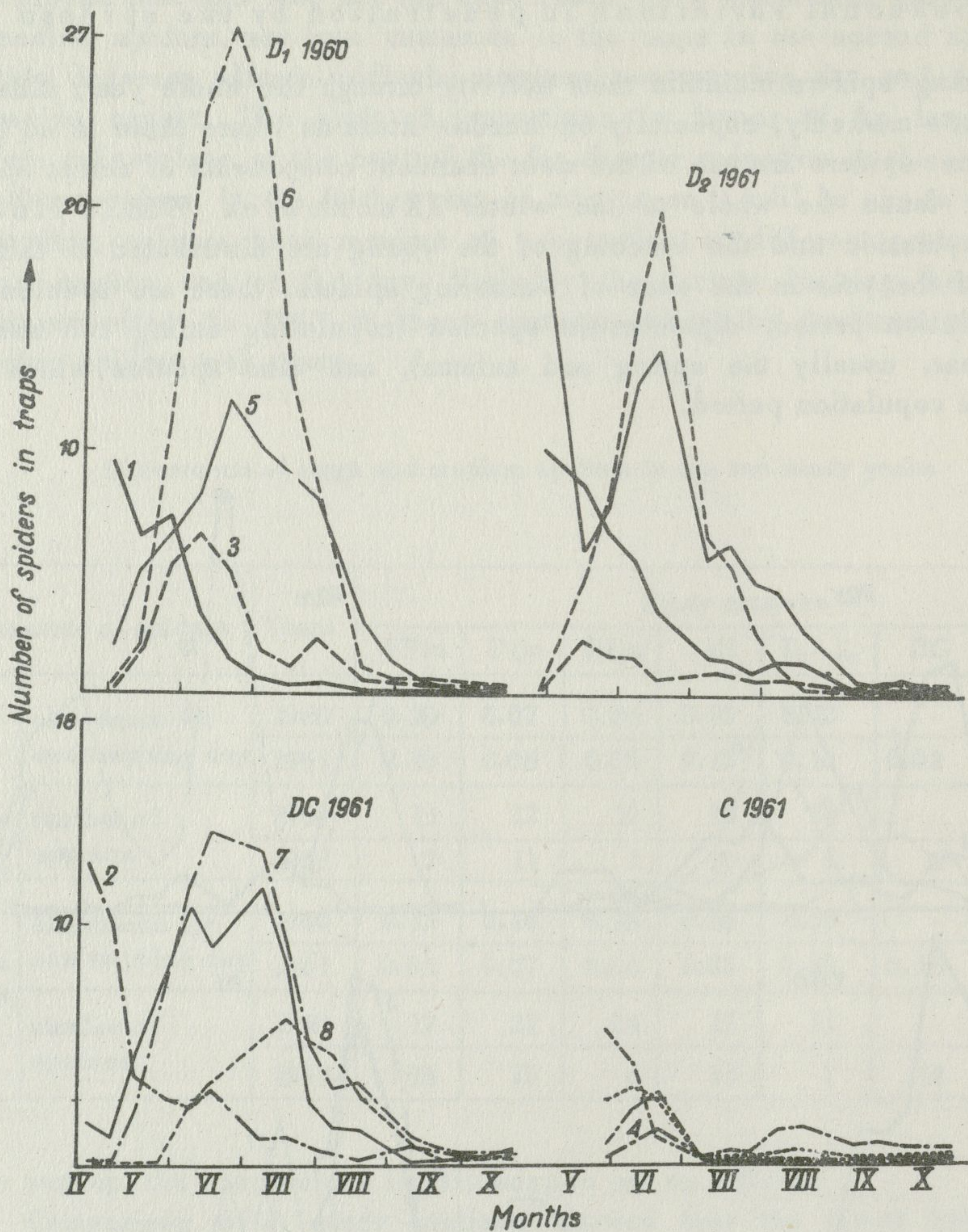


Fig. 6. Penetration of spiders on meadow stations (more numerous species)

1 - *Tarentula pulvenulenta*, 2 - *Pirata piscatorius*, 3 - *Arctosa leopardus*, 4 - *Trochosa ruricola*, 5 - *Lycosa pullata*, 6 - *Lycosa tarsalis*, 7 - *Lycosa prativaga*, 8 - *Pirata piraticus*

possible to distinguish certain periods in intensity of occurrence of this group on the surface of the soil. It is well known that the main copulation period, and in consequence intensified activity of wandering spiders, takes place in the spring and early summer, the main reproduction period covers the middle of the summer and therefore towards the end of summer young spiders are observed to appear (Petrusewicz 1933, Tretzel 1954, 1955). The autumn is a second copulation period, a period of growth of juvenile forms and death of the majority of the adults. Some of the species copulate in the winter.



On all the stations which I examined the wandering spiders form a group which in the spring is the earliest of all the predatory arthropods to occupy the soil surface – and is fully active by April. Practically speaking they then form the only active group – the predators accompanying them in the winter have then disappeared (e.g. the numerous *Cantharidae* larvae found in my material), and the predators of the warm half of the year have not as yet made their appearance (the next to follow the spiders will be ants).

Details of the course taken by variations in penetration of different species during the season are shown in Figures 5 and 6.

On all the forest stations and part of the meadow stations two distinct periods can be seen, in which the maxima of penetration of the species are concentrated: I – early spring (March, April) and II – midsummer (June, July)<sup>6</sup>. On the meadow stations which were not explored until the end of April, these periods are not so distinct, but it is generally possible to distinguish them. The fact is remarkable here that the first early-spring period of grouping of the species includes chiefly the large forms, and the second, the summer period – the medium forms. It proves that we have to do here with a fairly regular changeover of periods of maximum penetration of large and medium spiders, which almost always takes place (Fig. 7). The large species have

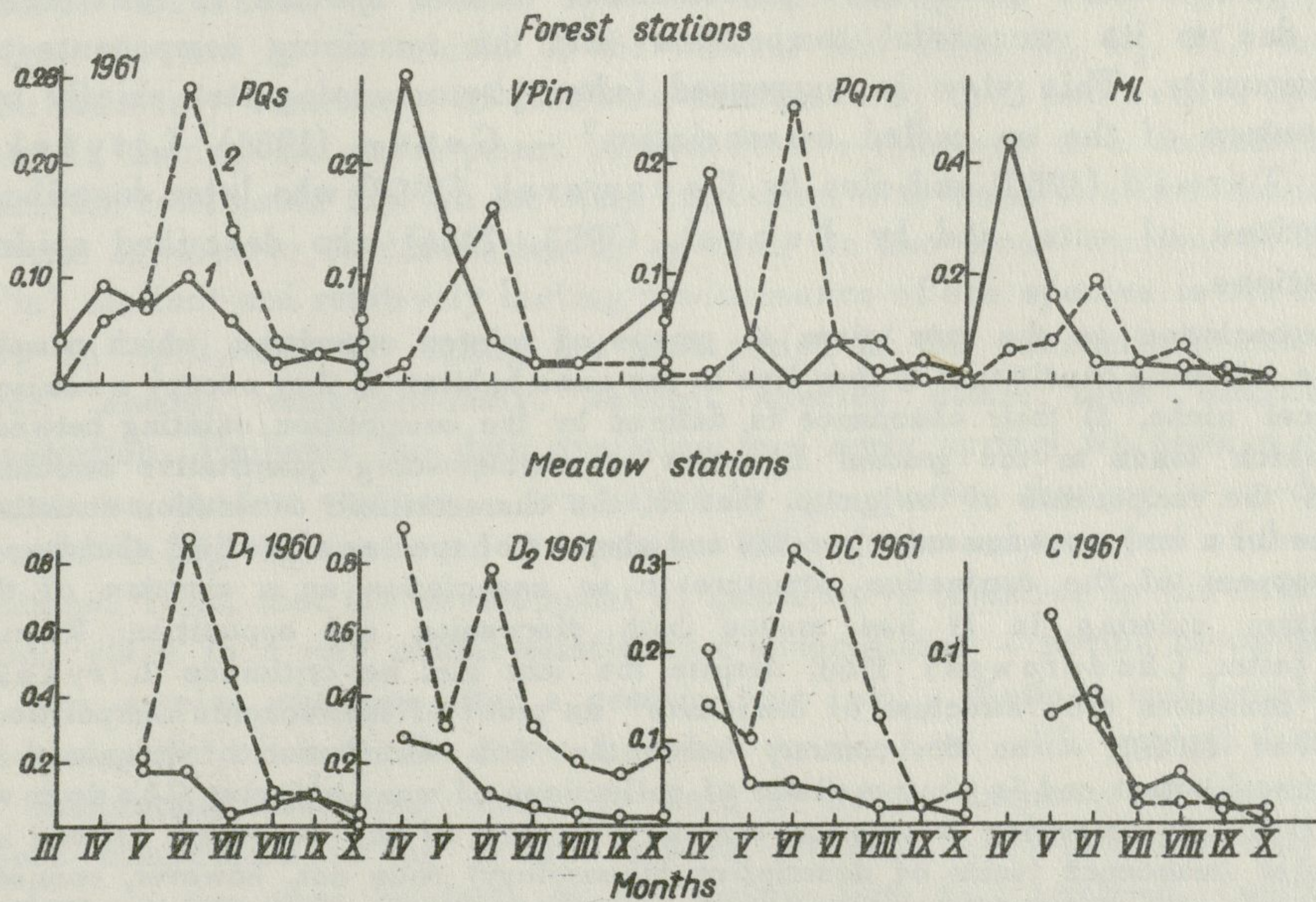


Fig. 7. Penetration of large and medium spiders during the season (mean numbers for one trapping day)

1 – large species, 2 – medium species

<sup>6</sup>A further, third autumn maximum of penetration is observed on forest stations (in September).



their maximum earlier – usually in April, and the medium spiders penetrate most intensively in June.

The regularity and commonness of this phenomenon on the majority of the stations, which yet differ from each other, and the different behaviour, described in the preceding section, of the large and medium spiders from year to year lead to the assumption that wandering spiders do not form a compact functional unit in the biocenosis. Probably the group of large early-spring species, which penetrate the surface of the soil almost in solitude, is exposed to the influences of biotic factors of a different type than is the group of medium species, competing for occupation of space with other groups, numerous during the summer, of predatory arthropods. As will be convincingly shown later, the decrease, demonstrated earlier in this study, in the percentage of medium species in the community in the second study year is concomitant with considerable increase in simultaneous penetration by the other predatory arthropods in 1961.

Examination was next made of the variations in the quantitative proportions between the species forming the community. It is considered that the defined quantitative relations among species of an ecologically similar group of organisms occupying the same habitat are due to biotic relations. The formation of marked quantitative predominance of one species is considered to be due to its successful competition with the remaining components of the community. This view is expressed (after phytosociologists) chiefly by the creators of the so called c-association<sup>9</sup> – Gause (1936), Lityński (1938), Tarwid (1952) and also by Kaczmarek (1953) who later described associations of ants, and by Łuczak (1953, 1954) who described spider associations.

C-association is the term given to groups of related organisms, which comply with the following conditions: 1) they live in the same habitat, 2) they occupy a common ecological niche, 3) their abundance is defined by the competition existing between them which leads to the gradual formation of corresponding quantitative structure between the components of the group, that is, the characteristic domination structure with one (or a few) most numerous species and absence of species of medium abundance.

Treatment of the domination structure in an association as a symptom of the competition existing in it has roused both discussion and opposition: Wautier (1952) (after Chodorowski 1960) despite the fact that he criticises Lityński (1938), considers the "structure of dominants" as proof of interspecies competition; Margalef (1958) – on the contrary holds that this distribution of frequency is a statistical effect and is characteristic of collections of many objects; Chodorowski (1960), in proposing domination structure as one of the necessary criteria in distinguish taxocenes (units of descriptive biocenology) does not, however, connect it distinctly with competition existing in the taxocene (cf. also Breymeyer 1960a, Chodorowski 1960a); Kaczmarek (1963) supports the objections made by Margalef (1958) but proposes that attention should be drawn to the discontinuity of domination structure – the absence of species of medium abundance in his opinion is evidence of the "biocenotic ordering of relations between species".

<sup>9</sup>The term "c-association" is the formal abbreviation of the term "association of competing species", and I use it according to K. Tarwid's verbal proposition.



The associations of spiders described by Łuczak (1953, 1954) (including "the group of large wandering spiders" named from the dominant the *Trochosa terricola* association) comply with the criteria of c-associations, together with the formation of the characteristic domination structure, which according to this author is evidence of the interspecies competition existing in the association. In her later paper (Łuczak 1963) she reaches the conclusion that the domination structure of the web spider community which she investigated in a more favourable year from the climatic aspect, alters under the influence of interspecies activity, while in a climatically unfavourable year it depends on weather factors.

What are the numerical relations in the communities of spiders which we investigated? The comparison of material from entire seasons has already been given (Fig. 3). We would recall that in the second study year the domination structure on two different forest stations (PQs and Ml) was observed to have been effaced. Of the communities on meadow stations only one ( $D_1$ ) is characterized by predominance of one species; on the remaining stations there is parallel domination of several species.

Also detailed analysis of the variations in penetration over the season (Fig. 5, 6) lead to the conclusion that frequently we have to do with simultaneous domination of several species. Both during the early spring period (PQm, Ml) and in the middle of the summer (Ml, PQs,  $D_1$ ,  $D_2$ , DC) there is simultaneously attainment of maximum abundance by 2, 3 and even 4 species. Here in tracing the development of quantitative relations in a community, we reach the conclusion that we are often concerned with transition from domination by one species to co-domination by several. On two forest stations (PQs and VPIn) distinct and relatively lasting predominance of one species is observable only in April, that is, during the first period of the community's existence; later, almost simultaneously, several species attain their maximum of penetration. Probably (no data available from early spring) we have a similar picture on meadow stations – domination by one species changes to co-domination of 2 ( $D_1$ ,  $D_2$ ) or even 3 species (DC). It is only on one of the study stations, PQm, that the development of quantitative relations in the community takes place in a way characteristic of c-associations – spring co-domination of two species changes after a certain time into a distinct and long-lasting predominance of one. We have therefore to do here with gradual formation of domination structure, which is held to be an indicator of increasingly fierce competition in the group. This is, however, a single case only. The spiders in the other habitats do not comply with this criterion. Comparison of the participation of dominants in the communities in three aspects – early spring, summer and autumn (Tab.IX) indicates that in all the communities except PQm, the most sharply marked domination is encountered in the early spring period, a period when the spiders are the only group penetrating the soil surface. Later, that is, from the moment when other arthropods emerge



Intensity of domination in spider communities in three periods of the season  
(spring, summer, autumn) in 1961

Tab. IX

Percentage of the dominant during the period:	Forest stations				Meadow stations		
	PQs	VPin	PQm	MI	D <sub>1</sub>	D <sub>2</sub>	DC
March-April	57	76	60	33	72	40	50
May-June	26	41	66	25	42	36	33
July-September	24	50	60	25	41	24	28

into the surface of the soil, the participation of the dominant in the spider community decreases.

In summing up this section it is found that:

1. The wandering spiders form a group which appears in large numbers in the spring on the soil surface, the earliest of all the predatory arthropods.
2. Their maxima of penetration occur during two periods: early spring and in the middle of summer.
3. The penetration of large species of spiders is concentrated in the early spring period, and that of the medium species in the summer period.
4. Most often the gradual formation of sharply marked predominance of one species, characteristic of c-association is not observed, in fact the reverse is the case.
5. Sharply marked domination of one species is observed in the early spring period, this domination becoming effaced usually with the appearance on the soil surface of other groups of predatory arthropods.

### III. SPIDERS AND OTHER PREDATORY ARTHROPODA

#### 1. Preliminary remarks

In the material which I collected the predatory *Arthropoda*, apart from spiders, belong to the following groups: *Formicidae*, *Carabidae*, *Opiliones*, *Chilopoda*, *Staphylinidae* (I have given them in order of abundance, from the most numerous to least numerous). These groups are not either identical or homogenous as regards range of food specialization; if the nomenclature proposed by Kaczmarek (1963) is adopted it may be said that they contain all three degrees of specialization of zoophages (zoophages, hemizooophages; parazoophages). The lists of species according to which more detailed classification could be made are given at the end of this paper. Only whole groups, however, were taken for analysis. The animals were, however, classified from the aspect of size of the body – as was the case with spiders, forms smaller than 4–5 mm in length were not taken into consideration.



From material prepared in this way analysis was made of the possibilities of the spiders' encountering the predatory arthropods mentioned – attention was paid chiefly to their occurrence in time: during the season and during the day.

## 2. Daily cycles of penetration by predatory *Arthropoda*

In the '40s and '50s of this century many papers and original elaborations were published on the subject of the daily rhythms in the animal world (Park 1940, Calhoun 1944–6, Cladsley-Thompson 1954, 1957, Harker 1958, 1964 and others). Among others Park (1941) puts forward the hypothesis that the evolution of biocenoses takes place in the direction of symmetry of activity over the 24-hour cycle. The case is here that with an increase in the number of species in a biocenosis they must continually adapt themselves differently to utilisation of its food resources. Thus species with similar ecological requirements make differences in their behaviour in order to avoid competition, for instance alter the time of their activity during the day. The 24-hour period is increasingly evenly filled with activity of different animals with similar ecological requirements endeavouring to avoid encounters. The degree to which this activity is plastic may differ.

Park's (1941) idea was taken up by Williams (1959). In comparing material composed of epigeic arthropods from three habitats of different ages he obtained a tendency to symmetry of daily activity with increasing age of the biocenosis. In his next studies (Williams 1959a, 1962) he also made experiments in which he altered the rhythm of activity of certain species of *Opiliones* and *Carabidae*. He demonstrates that these animals, usually nocturnal, change under the influence of hunger to a daytime way of life, and that their daily rhythm of activity is therefore plastic and relatively easily adopts itself to different ecological situations. In the light of these data the statement made by Park (1941) on the tendency to formation of a "shift" system of activity in biocenosis, and in particular the results obtained by Williams (1959a, 1962) forming evidence of the interchanging activity of species from groups connected by competition, would appear very convincing.

In the present study attention has been concentrated on analysis of the following problems:

1. The daily activity of the different groups of predatory arthropods. Following the suggestions made by the authors referred to above, consideration was given to whether these animals have a tendency to even occupation of the 24-hour period by activity in older biocenoses.

2. The possibilities of encounter between different groups of predators and wandering spiders at different times of the day.

3. The rhythm of activity over the 24-hour period of certain species of spiders.



The study stations were arranged in age gradient of the plant associations (PQs, VPin, PQm, Ml, D), variations in the symmetry of daily activity of these arthropods was expressed by means of diagrams (Fig. 8). From these it can be clearly seen that the two stations considered as the oldest (PQs, VPin) are characterized by an incomparably more symmetrical distribution of daily activity of predators. On the younger stations the distributions of activity are less even.

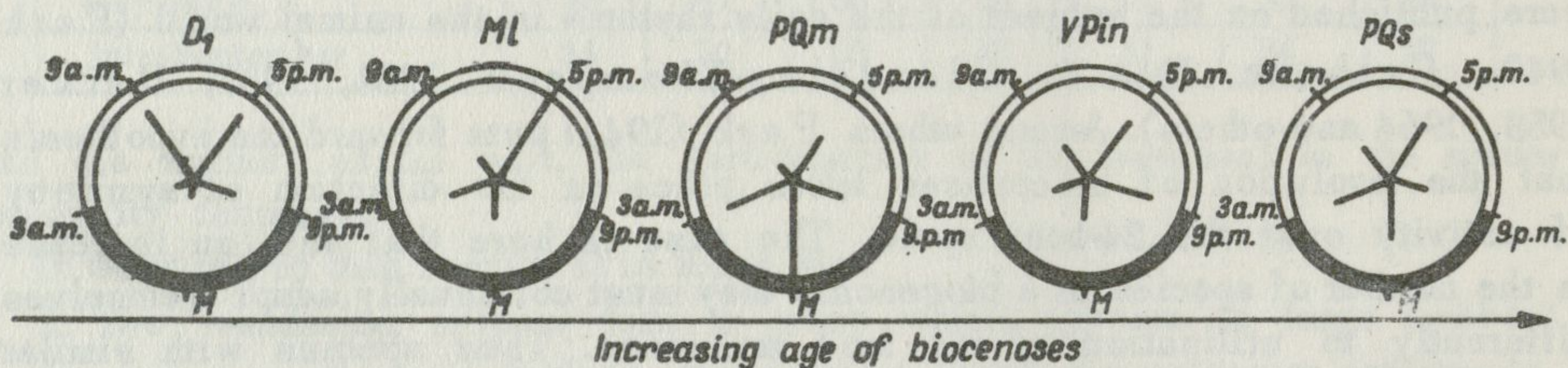


Fig. 8. Diurnal distribution of penetration of predatory *Arthropoda* in biocenoses of different ages (in 1962)  
M - midnight

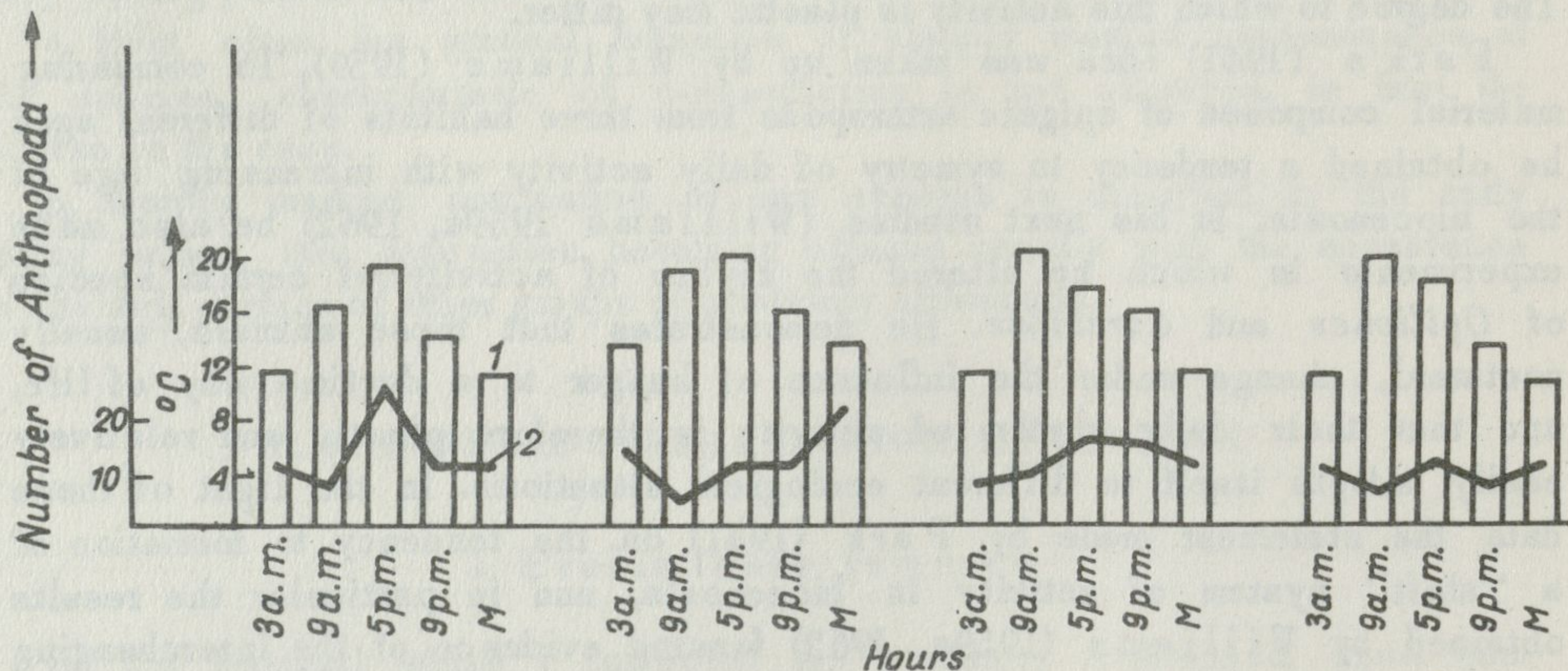


Fig. 9. Penetration of predatory *Arthropoda* during the day in relation to temperature variations in 1962

1 - temperature on the surface of the soil, 2 - number of predatory *Arthropoda* on the surface of the soil, M - midnight

Comparison was made for the forest stations also of the distributions of the predators' penetration and the daily distributions of temperature in the litter on the stations (Fig. 9); the tendency to a certain degree of independence of intensity of penetration on variations in temperature would seem clear: the curve of penetration in the older biocenoses is close to a straight line despite the fact that the distribution of daily temperatures in these biocenoses is the same as in the remainder.



Diurnal variations in the intensity of penetration of the most numerous families  
of *Arthropoda*

Tab. X

Group	Abundance for one trapping day		Intensity of penetration during different periods of the day in per cent				
	during the day	at night	mid-night— —3 a.m.	3 a.m.— —9 a.m.	9 a.m.— —5 p.m.	5 p.m.— —9 p.m.	9 p.m.— —mid-night
<i>Opiliones:</i> <i>Phalangidae</i>	1.20	12.23	42	4	2	6	46
<i>Araneida:</i> <i>Gnaphosidae</i>	2.11	2.13	23	6	32	22	17
<i>Clubionidae</i>	0.77	0.56	42	20	16	21	0
<i>Thomisidae</i>	8.16	0.70	15	7	66	12	0
<i>Salticidae</i>	0.71	0.00	0	40	60	0	0
<i>Lycosidae</i>	32.17	23.88	8	23	47	14	8
<i>Agelenidae</i>	1.18	2.69	0	0	12	24	64
<i>Tetragnathidae</i>	4.83	5.10	19	19	10	32	20
<i>Coleoptera:</i> <i>Carabidae</i>	9.90	76.73	28	6	13	14	39
<i>Staphylinidae</i>	2.50	1.90	0	15	43	21	21
<i>Hymenoptera:</i> <i>Formicidae</i>	22.15	3.39	8	22	40	26	4
Large spiders	13.71	16.62					
Medium spiders	35.60	21.87					
Large <i>Carabidae</i>	3.52	63.16					
Small <i>Carabidae</i>	3.83	5.43					

It was therefore found that the older the station, and in consequence the denser the group of insects living on it, the more evenly distributed over the 24-hour period the activity of epigeic predatory arthropods on the stations. The conclusion was therefore reached that the predatory arthropods of the habitats examined are connected with each other by competition relations, leading to their interchanging with each other in time.

Analyses of the abundance of these groups of *Arthropoda* for day and night show that *Opiliones* and *Carabidae* are decidedly nocturnal animals (Tab. X); these latter are, however, internally differentiated. After dividing them into large and small species<sup>10</sup> it proved that small *Carabidae* penetrate

<sup>10</sup> All species of the genus *Carabus* and two species of the genus *Pterostichus*



the soil surface both during the day and night. The nocturnal character of the whole group is imposed here by the numerous and decidedly nocturnal large species. Spiders are active in both day and night; among the families with, particularly speaking, all-day activity are *Gnaphosidae*, *Clubionidae*, *Tetragnathidae*. The nocturnal families are *Agelenidae*, while *Thomisidae* and *Salticidae* are clearly daytime families.

The *Lycosidae* family is most numerously represented in my material. Williams (1962) caught species of this family more often during the day than during the night; he found that the genus *Lycosa*, common in his stations, is in general a daytime genus, and the less frequently encountered genus *Trochosa* – nocturnal. In the present investigations also slightly more *Lycosidae* were caught during the day – the maximum of their activity occurs between 9 a.m. and 5 p.m. (Tab. X). The species of the genus *Lycosa*, frequently encountered in the study areas, are all daytime with the exception of young animals. The fact is worthy of attention that the majority of the young spiders (not only *Lycosidae*) lead a completely or partly nocturnal way of life; this applies also to the young animals of species which when adult are clearly daytime animals (Breymeyer in press).

Of the remainder of the spiders caught – apart from *Lycosidae* – the activity of 3 species of *Pachygnatha* are interestingly distributed over the 24 hours. These are *Pachygnatha clerckii* and *P. listerii* – day-time-nocturnal, with predominance of activity at night, *P. degeeri* – a clearly daytime species. Williams (1962), referred to above, who discusses in his study *P. clerckii* and *P. degeeri*, considers that the daytime way of life of this latter is determined by the greater resistance to drying up, while *P. clerckii* requires greater atmospheric humidity.

Referring this assumption to the remaining species it should be expected that all the less resistant forms would shift their activity to the night time, when the greater relative atmospheric humidity would make it possible for them to leave their shelters inside the litter (or turf) or in holes in the ground. Many authors, who emphasize the importance of atmospheric humidity to the activity of litter fauna are of this opinion (Crawford 1934, Davies and Edney 1952, Cladsley-Thompson 1954, Edney 1957) and point to the correlation of the periods of this activity with the degree of water-tightness of the cuticle of the organisms examined. In this situation it is the smallest forms which should prove most sensitive – the ratio of surface of body accessible to drying up to its volume is the least favourable in their case, whereas when separating the group of large individuals from among all the spiders caught (after the classification given earlier in Table V) it proves that nocturnal forms predominate among them; the large species

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were considered as large; these two species are: *Pterostichus niger* Schall. and *P. vulgaris* L. All the other species of *Carabidae* caught were classified as small.



of spiders form 67% of species considered as distinctly nocturnal, and only 31% of the species considered as daytime species. The distribution of daily activity of the above three species of the genus *Pachygnatha* is similar – the daytime way of life is led by the smallest species (*Pachygnatha degeeri*). Also comparison of the abundance of all large and medium spiders caught suggests that the first of these have a tendency to slightly more intensive penetration at night, while the second are more often active during the day (Tab. X).

This tendency of the large spiders to shift their activity to the nighttime, and of smaller ones to the daytime, suggests the action of factors of an ecological nature – these may be dependence on food (as held by Williams 1959a, 1962), or dependence on the activity of other arthropods penetrating the surface of the soil together with the spiders.

The group of animals which is decidedly nocturnal are *Carabidae*. Of the 20 species caught only 2 are active during the day, and 4 during the day and night; the remaining 14 species, which includes all species of the genus *Carabus*, and therefore almost all large species, lead a nocturnal way of life.

Ants are characterized by daytime activity, although their penetration at dawn and dusk is also considerable. The only species leading a partly nocturnal way of life is *Myrmica scabrinodis*; *Opiliones* – as has already been demonstrated – are decidedly nocturnal.

It would seem that on the basis of the material presented it would be possible to reply as follows to the second of the questions put: it is primarily the species of spiders and ants of medium size which have chances of encounter during the day on the study stations. Also certain of the smaller *Carabidae* may penetrate the surface of the soil during this time. The large species of spiders often leading a nocturnal way of life might encounter other animals during penetration (chiefly large *Carabidae* and *Opiliones*). As, however, we shall see in a short time, both *Carabidae* and *Opiliones* occur more numerous on the surface of the ground in the later months than the large wandering spiders – therefore the chances of these groups meeting during their penetration of the soil are slight.

### 3. Variations in penetration during the season and in the two study years

Similarity and regularity of seasonal variations in penetration on all the forest stations are exhibited only by *Araneida* and *Carabidae* (Tab. XI): the first of these exhibit maximum of penetration always during the first half of the season, the second are always most numerous later, usually in August. It may be said of *Opiliones* that this is a summer-autumn group, not correctly speaking present on the surface of the ground in the spring. The other groups of predators are characterized by irregular variations – even the course taken



by variations in penetration by this same group on the same station differs completely in the two years. Forest ants in particular must be carefully treated here: the results of their captures depend primarily on the distance from the ant-heap or the ants' paths at which the trap was situated. It is true that endeavour has been made to avoid the immediate vicinity of ant-heaps, and samples markedly greater than average have been rejected from the material collected, but even so it would seem that different, special methods are required to assess the degree of penetration of a given area by ants. For this reason a general assessment of the level of ants' occurrence in a habitat has continued to be used, without attaching importance to variations in the ants' abundance.

Returning to the two regularly varying groups it must be stated that the maxima of the penetration distinctly interchange with each other during the season (Fig. 10 – more exact diagrams of variations in the numbers of *Araneida* and *Carabidae* in the traps). The spiders have their maximum of occurrence during the period from April to June, *Carabidae* – as a rule in August. Therefore large spiders occurring in the early spring have no chance at all of encountering *Carabidae*. The spiders of medium dimensions, however, have such opportunities, since the peak period of their activity occurs in midsummer, that is, during the period by which *Carabidae* are already numerous. It must be pointed out here that the medium species of spiders are usually daytime animals, while *Carabidae* are usually nocturnal. Thus it is clear from the above reasonings that wandering spiders and *Carabidae* have somewhat small chances of meeting each other during their penetration of the soil surface on the forest stations examined. It is the small *Carabidae* (partly daytime animals) which have relatively the greatest chances of encounter, and also the medium spiders (occurring numerously in the second half of summer). Also the large species of diplochronic spiders having a second reproduction period in the autumn have chances of encounter in September and October with the by then disappearing *Carabidae*. At other periods of the season and 24-hours these two groups interchange in their penetration of the area.

On the meadow stations ( $D_1$ ,  $D_2$ , DC, C) the spiders' behaviour is similar to that exhibited in the forest (Tab. XI), whereas in the case of *Carabidae* we sometimes have to do with two maxima of activity, of which the earlier coincides with the period of intensive penetration of spiders. *Carabidae* occur on meadows in negligible numbers – they form 5–10% of the whole of the predator community. Spiders and ants divide the penetration of the soil surface between themselves – these two groups form over 80% of the predator community and distinctly complement each other (Fig. 11): station  $D_1$  may be considered as occupied by spiders, DC – by ants,  $D_2$ , C – intermediate stations, occupied by both groups.

It would appear to be of interest here to recall the fact that the domination structure among the spiders of meadow stations is effaced with time. It is











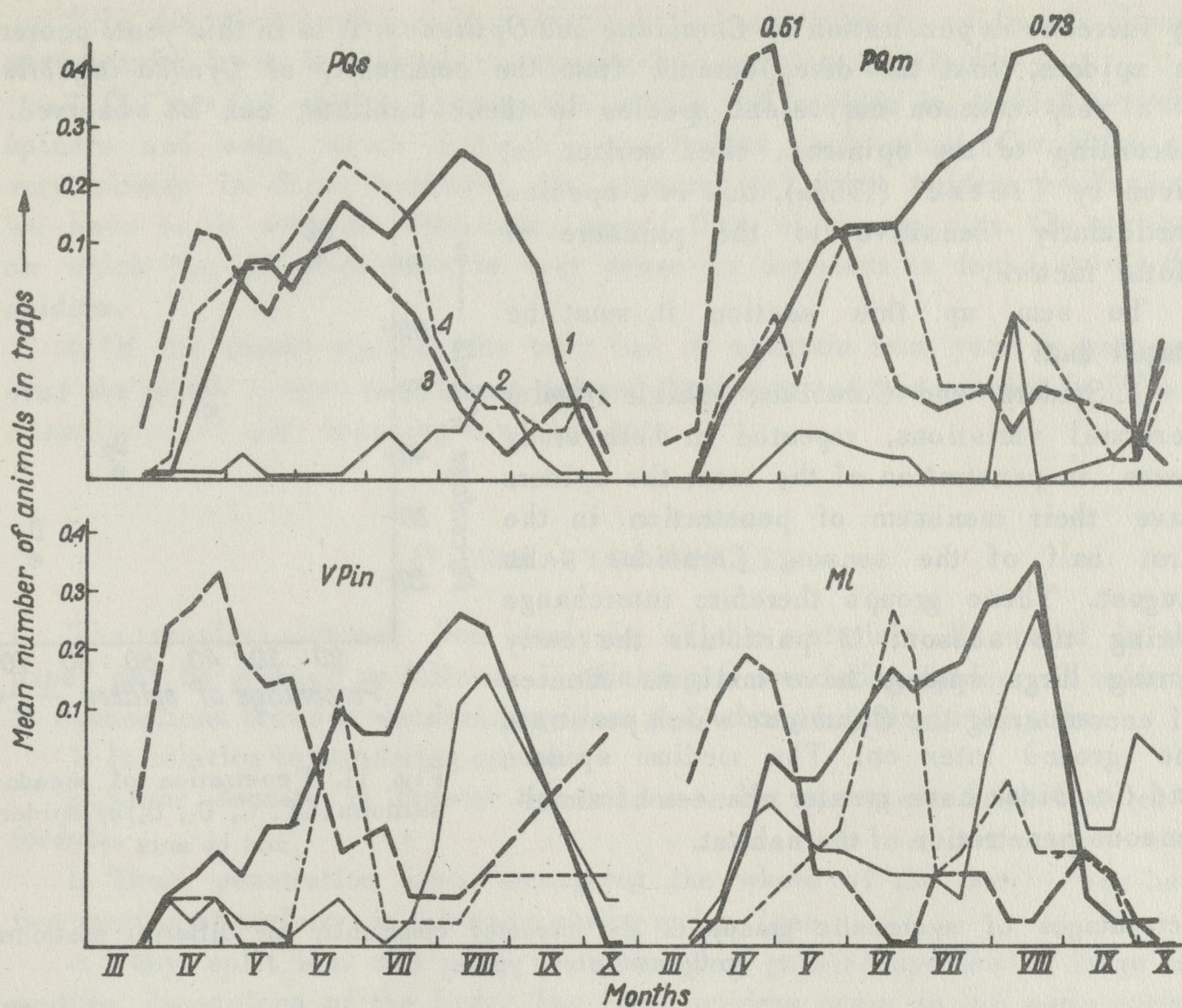


Fig. 10. Variations in penetration of spiders and *Carabidae* on forest stations in 1961 (mean number for one trapping day)

1 – large *Carabidae*, 2 – small *Carabidae*, 3 – large *Araneida*, 4 – medium *Araneida*

possible to speak of a domination structure during the first period in the early spring (Tab. IX), when the spiders penetrate the surface of the ground almost independently. Later, after other groups enter the area (on meadows, to be exact, after ants have entered) the domination structure is obliterated. Similar effacement of the domination structure was observed among spiders during the period that other groups enter the area, that is, in relation to forest stations. The fact is remarkable here that the only station on which the characteristic domination structure among spiders is maintained throughout the whole season and in both study years – PQm – is a station practically devoid of ants.

When tracing the variations in the participation of different groups of predators in the two study years on forest stations it is easy to notice their regularity – in general the participation of the group varies in a similar direction on the stations, although these differ from each other (Tab. XII). In 1961 the participation of spiders decidedly decreases – this is accompanied



by increase in penetration by *Carabidae* and *Opiliones*. It is in this year, poorer in spiders, that the disappearance from the community of *Lycosa lugubris* – a very common euryvalent species in these habitats, can be observed. According to the opinions, cited earlier on, given by Tretzel (1955a), this is a species particularly sensitive to the pressure of biotic factors.

To sum up this section it must be stated that:

1. Spiders and *Carabidae* exhibit regular seasonal variations, repeated in both study years, in penetration of the area; the spiders have their maximum of penetration in the first half of the season, *Carabidae* – in August. These groups therefore interchange during the season; in particular the early spring large spiders have minimum chances of encountering the *Carabidae* which penetrate the ground later on. The medium spiders and *Carabidae* have greater chances of simultaneous penetration of the habitat.

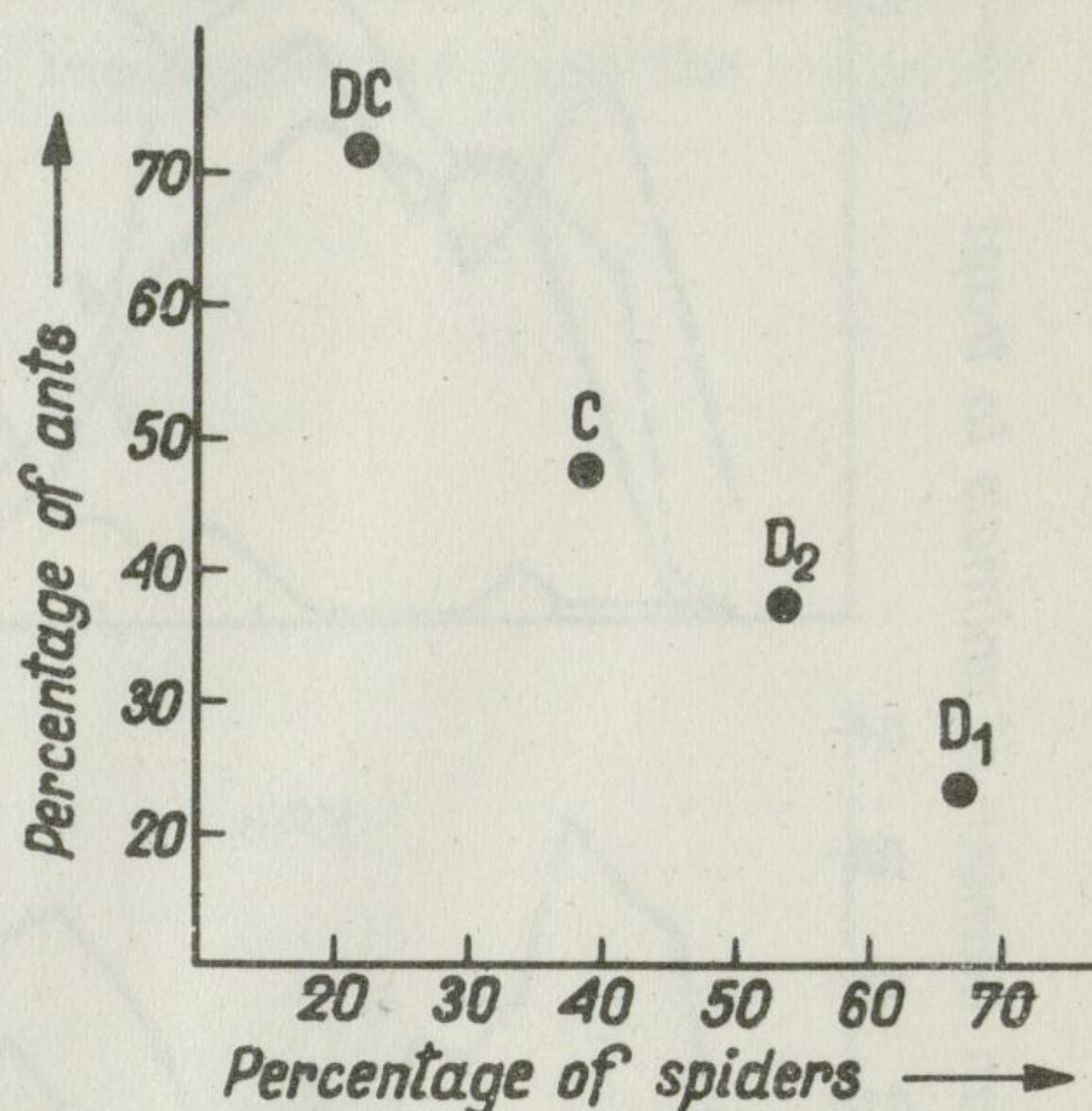


Fig. 11. Penetration of meadow stations (DC, C, D<sub>1</sub>, D<sub>2</sub>) by spiders and by ants

Percentages of systematic groups in the predator community on different stations in the two study years

Tab. XII

Group	Years	Forest stations				Meadow stations		
		PQs	VPin	PQm	Ml	D <sub>1</sub> -D <sub>2</sub>	DC	C
<i>Araneida</i>	1960	45.4	37.0	27.6	32.1	67.2		
	1961	39.0	19.0	21.0	15.0	54.2	21.0	39.0
<i>Formicidae</i>	1960	31.8	42.2	7.1	46.1	23.3		
	1961	9.0	44.0	3.0	40.0	39.4	72.0	47.0
<i>Carabidae</i>	1960	13.0	13.7	49.9	11.9	5.3		
	1961	36.0	27.0	50.0	25.0	5.0	6.0	10.0
<i>Opiliones</i>	1960	3.3	2.3	11.4	6.4	0.2		
	1961	10.0	5.0	18.0	14.0	0.3	0.1	2.0
<i>Chilopoda</i>	1960	2.1	3.4	2.5	1.8			
	1961	4.0	4.0	5.0	3.0			
<i>Staphylinidae</i>	1960	1.4	1.3	1.4	1.8	4.0		
	1961	3.0	0.6	1.0	1.0	1.2	1.0	1.0



2. In the second study year a decrease in penetration by spiders is always accompanied by an increase in penetration by *Carabidae* and *Opiliones*.

3. On meadow stations penetration of the soil surface is divided between spiders and ants, which distinctly complement each other (*Carabidae* are very scanty in these habitats). On stations on which spiders predominate we have to do with the domination among them of one species. On stations on which the ant population is very dense no dominant is found among the spiders.

4. Of the forest stations the only one to maintain from year to year and over the whole season the sharply-defined domination of one species is PQm — a station practically speaking devoid of ants.

#### IV. SUMMARY OF RESULTS

The results obtained from analysis of the materials discussed in this paper may be grouped as follows: 1) referring to wandering spiders, 2) referring to connections between wandering spiders and other predatory arthropods.

1. In relation to wandering spiders:

a. Their density is greater on meadows, but there are more species in forests.

b. Their penetration lasts throughout the whole of the year. They have two maxima of activity: in the early spring and in June.

c. They split into two partly interchanging groups: species of large and medium dimensions of the body. The large spiders occur in the early spring, are less exposed to encounter with other predatory arthropods also penetrating the surface of the soil. During the 24-hour cycle the large species are active both during the day and at night, the medium — are decidedly daytime animals.

d. The euryvalent species avoids stations which are intensively occupied in a given year by other species of larger spiders probably competing with it.

e. In the majority of the spider communities examined a characteristic domination structure which is the criterion of existence of c-association, is not formed.

2. In relation to connections between wandering spiders and other predatory arthropods:

a. During the season the wandering spiders (chiefly medium species) in the study habitats have chances of encountering primarily ants, *Carabidae* and *Opiliones*.

b. During the 24-hour period, ants and certain small *Carabidae* penetrate the soil surface simultaneously with spiders. The large species of spiders, occurring partly nocturnally, may encounter *Opiliones* and large *Carabidae*.

c. There is a connection of a competitive character between spiders and the other predatory arthropods of the soil surface. The following facts, established in the present study, were taken as proofs of these connections:



the older the biocenosis, the more completely the 24-hour period is filled by the activity of predatory arthropods; increase in penetration by other predatory arthropods affects the domination structure in the spider community and the occurrence of the euryvalent species of spider.

Lists of species of the groups of predatory *Arthropoda*  
discussed in the study

*Arachnoidea – Opiliones:*

1. *Lacinius blackwalli* Md
2. *Lacinius ehippiatus* (C. L. K.)
3. *Lacinius horridus* (Panzer)
4. *Mitostoma chrysomelas* (Hem.)
5. *Nemastoma lugubre* f. *bimaculatum* (Fabr.)
6. *Oligolophus palpinalis* (Hb)
7. *Oligolophus tridens* (C. L. K.)
8. *Platybunus opilio* L.
9. *Platybunus triangularis* (Hb)
10. *Phalangium opilio* L.

*Hymenoptera – Formicidae:*

1. *Formica fusca* L.
2. *Formica rufa rufa* L.
3. *Formica rufa rufo-pratensis minor* Göswald
4. *Formica rufa rufo-pratensis major* Göswald
5. *Formica rufibarbis* F.
6. *Lasius flavus* F.
7. *Lasius niger* L.
8. *Leptothorax acervorum* Nyl.
9. *Myrmica laevinodis* Nyl.
10. *Myrmica ruginodis* Nyl.
11. *Myrmica rugulosoides* Forel
12. *Myrmica scabrinodis* Nyl.
13. *Myrmica schencki* Em.
14. *Polyergus rufescens* Latr.
15. *Tetramorium caespitum* L.

*Coleoptera – Carabidae:*

1. *Agonum livens* Gyll.
2. *Agonum viduum* Panz.
3. *Amara* sp.
4. *Badister peltatus* Panz.
5. *Calathus micropterus* Duft.
6. *Calathus erratus* Sahlb.
7. *Carabus arcensis* Herbst.
8. *Carabus cancellatus* Illig.
9. *Carabus clathratus* L.
10. *Carabus glabratus* Payk.
11. *Carabus granulatus* L.
12. *Carabus hortensis* L.
13. *Carabus nemoralis* Müll.
14. *Carabus nitens* L.
15. *Carabus violaceus* L.



16. *Clivina* sp.
17. *Cychrus rostratus* F.
18. *Chlaenius* sp.
19. *Chlaenius illigeri* Gnglb.
20. *Dyschirus* sp.
21. *Epaphius secalis* Payk.
22. *Harpalus* sp.
23. *Leistus ferrugineus* L.
24. *Nebria brevicollis* F.
25. *Oodes helopiodes* F.
26. *Patrobis excavatus* Payk.
27. *Poecilus coerulescens* L.
28. *Loricera pilicomis* Fbr.
29. *Pterostichus anthracinus* Ill.
30. *Pterostichus niger* Schall.
31. *Pterostichus nigrita* Fbr.
32. *Pterostichus minor* Gyll.
33. *Pterostichus oblongopunctatus* Fbr.
34. *Pterostichus vulgaris* L.
35. *Elaphrus cupreus* Duft.

*Coleoptera* – *Staphylinidae*:

1. *Bryoporus cernuus* Grav.
2. *Drusilla canaliculata* F.
3. *Lathrobium geminum* Kr.
4. *Lathrobium brunnipes* F.
5. *Mycetoporus brunneus* Marsh.
6. *Ocypus aeneocephalus* Degeer
7. *Olophrum assimile* Payk.
8. *Othius punctulatus* Goeze
9. *Othius myrmecophilus* Kiesw.
10. *Oxypoda lividipennis* Mann.
11. *Philonthus addendus* Sharp.
12. *Philonthus coneinnus* Grav.
13. *Philonthus fumarius* Grav.
14. *Philonthus fuscipennis* Mann.
15. *Philonthus mannerheimi* Fauv.
16. *Philonthus micans* Grav.
17. *Quedius fuliginosus* Grav.
18. *Quedius molochinus* ab. *denudatus* Steph.
19. *Quedius umbrinus* Er.
20. *Quedius nitipennis* Steph.
21. *Rugilus erichsoni* Fauv.
22. *Rugilus rufipes* Germ.
23. *Staphylinus erythropterus* L.
24. *Staphylinus fulvipes* Scop.
25. *Staphylinus latebricola* Grav.
26. *Stenus ater* Mann.
27. *Tachinus rufipes* Deg.
28. *Xantholinus linearis* Ol.
29. *Xantholinus longiventris* Heer
30. *Xantholinus* sp. from the group *X. longiventris* Heer (females)
31. *Xantholinus tricolor* F.



32. *Xantholinus* sp. (females)  
 33. *Zyras cognatus* Maerk.

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#### REFERENCES

1. Balogh, J. 1946 – The structure of the biocenoses – *Állat, Közlem.* 43: 1–14.
2. Balogh, J. 1958 – *Lebensgemeinschaften der Landtiere* – Budapest, Berlin, 562 pp.
3. Balogh, J., Loksa, J. 1948 – Quantitativ-biozoologische Untersuchung der Arthropodenwelt ungarischer Sandgebiete – *Arch. biol. hung.* 18: 65–100.
4. Barber, H.S. 1931 – Traps for cave-inhabiting insects – *J. Elisha Mitch. sci. Soc.* 46.
5. Barnes, H.D., Barnes, B. 1955 – The spider population of the abstract broom-sedge community of the Southeastern Piedmont – *Ecology*, 36: 656–666.
6. Bilsing, S.W. 1920 – Quantitative studies in the food of spiders – *Ohio J. Sci.* 20: 215–260.
7. Breymeyer, A. 1960 – Uwagi o łowieniu się pajaków w pułapki chwytne – *Ekol. Pol. B*, 6: 179–189.
8. Breymeyer, A. 1960a – Uwagi o taxocenach – *Ekol. Pol. B*, 6: 297–299.
9. Breymeyer, A. 1961 – Uwagi o stosowaniu różnych ilości pułapek Barbera – *Ekol. Pol. B*, 7: 103–110.
10. Breymeyer, A. 1961a – Zmiany liczebności populacji *Trochosa tericola* Thor. – *Ekol. Pol. A*, 9: 25–35.
11. Breymeyer, A. (in press) – The diurnal rhythms of certain arthropods – *Ekol. Pol. A*.
12. Bristowe, W.S. 1939–40 – *The comity of spiders* – London, 550 pp.
13. Buchar, J. 1958 – Beitrag zur Bestimmung der Mitteleuropäische Arten der Gattung *Trochosa* (C. L. Koch) – *Acta Univ. Carol.* 3: 159–164.
14. Buchar, J., Zdarek, J. 1960 – Die Arachnofauna der Mittelböhmischen Waldsteppe – *Acta Univ. Carol.* No 2: 87–102.
15. Calhoun, J.B. 1944–46 – Twenty-four hour periodicities in the animal kingdom – *J. Tenn. Acad. Sci.* 19: 179–200, 252–262; 20: 228–232, 291–308; 21: 208–216, 261–282.
16. Chodorowski, A. 1960 – Taxoceny wirków (*Turbellaria*) i metodyka ich badania – *Ekol. Pol. B*, 6: 95–114.
17. Chodorowski, A. 1960a – Taxoceny jako jednostka biocenologii opisowej – *Ekol. Pol. B*, 6: 301–303.
18. Cloudsley-Thompson, J.L. 1953 – The biology of hunting spiders – *Discovery*, 14: 286–289.
19. Cloudsley-Thompson, J.L. 1954 – The ecological significance of diurnal rhythms in terrestrial arthropods – *Sci. Progr.* 42: 46–52.
20. Cloudsley-Thompson, J.L. 1957 – Studies in diurnal rhythms. Nocturnal ecology and water relations of the British oribellate spiders of the genus *Ciniflo* Bl. – *J. linn. Soc. (Zool.)*, 43: 134–152.



21. Crawford, S. C. 1934 – The habits and characteristics of nocturnal animals – Quart. Rev. Biol. 9: 201–214.
22. Dahl, M. 1926 – Springspinnen (*Salticidae*) (Die Tierwelt Deutschlands, Teil 3) – Jena, 55 pp.
23. Dahl, M. 1931 – *Agelenidae* (Die Tierwelt Deutschlands, Teil 23) – Jena, 46 pp.
24. Dahl, F., Dahl, M. 1927 – *Lycosidae* s. lat. (Wolfspinnen im weiteren Sinne) (Die Tierwelt Deutschlands, Teil 5) – Jena, 11–79 pp.
25. Davies, M. E., Edney, E. B. 1952 – The evaporation of water from spiders – J. exp. Biol. 29: 571–582.
26. Duffey, E. 1962 – A population study of spiders in Limestone grassland – J. Anim. Ecol. 31: 571–599.
27. Duffey, E. 1962a – A population study of spiders in Limestone grassland, the field-layer fauna – Oikos, 13: 15–34.
28. Duffey, E. 1963 – Ecological studies on the spider fauna of the Malham Tarn Area – Field Stud. 1: 1–23.
29. Edney, E. B. 1957 – The water relations of terrestrial arthropods – Manage exp. Biol. No 5.
30. Fenton, G. R. 1947 – The soil fauna: with special reference to the ecosystem of forest soil – J. Anim. Ecol. 16: 76–93.
31. Gams, H. 1918 – Prinzipienfragen der Vegetationsforschung. Ein Beitrag zur Begriffsklarung und Methodik der Biocenologie – Vjschr. naturf. Ges. Zürich, 63: 293–493.
32. Gause, G. F. 1936 – The principles of biocenology – Quart. Rev. Biol. 11: 320–336.
33. Hackman, W. 1957 – Studies on the ecology of the wolf spider *Trochosa ruricola* Deg. – Comment. biol. Helsingfors, 16: 1–34.
34. Harker, J. E. 1958 – Diurnal rhythms in the animal kingdom – Biol. Rev. (Cambridge), 33: 1–52.
35. Harker, J. E. 1964 – The physiology of diurnal rhythms – Cambridge, 114 pp.
36. Heydemann, B. 1960 – Verlauf und Abhängigkeit von Spinnensukzessionen im Neuland der Nordseeküste – Verh. dtsh. zool. Ges. Bonn-Rhein, 431–457.
37. Heydemann, B. 1960a – Die biozönotische Entwicklung vom Vorland zum Koog. Spinnen (*Araneae*) – Abh. math.-nat. Kl. Akad. Wiss. Mainz, 11: 745–913.
38. Heydemann, B. 1961 – Untersuchungen über die Aktivitäts- und Besiedlungsdichte bei epigäischen Spinnen – Verh. dtsh. zool. Ges. Saarbrücken, 538–556.
39. Kaczmarek, M. 1958 – Obserwacje nad aktywnością zimową bezkręgowców gleb leśnych – Ekol. Pol. B, 4: 53–62.
40. Kaczmarek, W. 1953 – Badania nad zespołami mrówek leśnych – Ekol. Pol. I: 69–96.
41. Kaczmarek, W. 1963 – An analysis of interspecific competition in communities of the soil macrofauna of some habitats in the Kampinos National Park – Ekol. Pol. A, 11: 421–483.
42. Kajak, A. 1965 – An analysis of food relations between the spiders – *Araneus cornutus* Clerck and *Araneus quadratus* Clerck – and their prey in meadows – Ekol. Pol. A, 13: 717–764.
43. Knülle, W. 1951 – Die Bedeutung natürlicher Faktorengefälle für Tierökologische Untersuchungen demonstriert an der Verbreitung der Spinnen – Zool. Anz. 16: 418–433.
44. Knülle, W. 1952 – Die geomorphologischen Grundlagen der Meeresküsten-Ökologie und ihre Bedeutung für die räumliche Anordnung der Spinnen-Lebensgemeinschaften – Kieler Meeresforsch. 9: 112–125.
45. Knülle, W. 1953 – Zur Ökologie der Spinnen an Ufern und Küsten – Z. Morph. Ökol. Tiere. 42: 117–158.



46. Knülle, W. 1954 – *Lycosa purbeckensis* F. O. R. Cambridge (*Lycosidae: Araneae*), eine deutsche Küstenart – Kieler Meeresforsch. 10: 67–76.
47. Krogerus, R. 1960 – Ökologie Studien über nordische Moorarthropoden – Comment. Biol. Helsingfors, 21: 1–238.
48. Kuenzler, E. J. 1958 – Niche relations of three species of lycosid spiders – Ecology, 39: 494–500.
49. Lityński, A. 1938 – Biocenoza i biosocjacja – Arch. Hydrobiol. i Ryb. 11: 1–209.
50. Locket, G. H., Millidge, A. F. 1951–53 – British spiders, Vol. I, II – London, 310, 449 pp.
51. Łuczak, J. 1953 – Zespoły pajaków leśnych – Ekol. Pol. 1: 57–94.
52. Łuczak, J. 1954 – Dwa zespoły pajaków – Ekol. Pol. 2: 447–463.
53. Łuczak, J. 1963 – Differences in the structure of communities of web spiders in one type of environment (young pine forest) – Ekol. Pol. A, 11: 159–221.
54. Margalef, R. 1958 – Information theory in ecology – Gen. Syst. 3: 36–72.
55. Margalef, R. 1963 – Ecologie marine: nouvelles vues sur de vieux problemes – L'année biologique, 2: 3–16.
56. Mikulska, I. 1950 – Materiały do poznania pajaków jako elementu składowego biocenozy kilku lasów Karpat Śląskich – Pr. biol. Wyd. śląsk. PAU, 2: 113–140.
57. Mikulska, I. 1955 – Rozmieszczenie pajaków w pasie nadbrzeżnym jeziora Wigry – Ekol. Pol. A, 3: 33–64.
58. Mončadskij, A. 1949 – O tipach reakcii nasekomych na izučenija temperatury okružajuščej sredy – Izd. AN SSSR, 2: 171–200.
59. Nörgaard, E. 1951 – On the ecology of two lycosid spiders (*Pirata piraticus* and *Lycosa pullata*) from a Danish sphagnum bog – Oikos, 3: 1–21.
60. Palmgren, P. 1939 – *Lycosidae* (Die Spinnenfauna Finnlands, Vol. I) – Acta zool. fenn. 25: 1–86.
61. Palmgren, P. 1943 – *Pisauridae, Oxyopidae, Salticidae, Clubionidae, Anyphaenidae, Sparassidae, Ctenidae, Drassidae* (Die Spinnenfauna Finnlands, Vol. II) – Acta zool. fenn. 36: 1–112.
62. Palmgren, P. 1950 – *Xysticidae* und *Philodromidae* (Die Spinnenfauna Finnlands und Ostfennoskandiens, Vol. III) – Acta zool. fenn. 62: 1–43.
63. Park, O. 1940 – Nocturnalism – the development of a problem – Ecol. Monogr. 10: 485–536.
64. Park, O. 1941 – Concerning community symmetry – Ecology, 22: 164–167.
65. Petruszewicz, K. 1933 – Pogońce (*Lycosidae* s. lat.) okolic Wilna – Pr. TPN Wilno, 8: 1–30.
66. Petruszewicz, K. 1933a – Próba charakterystyki ekologicznej pogońców (*Lycosidae* s. lat.) – Pamiętnik Zjazdu Lekarzy i Przyrodników w Poznaniu, Poznań, 447–449 pp.
67. Petruszewicz, K. 1935 – *Lycosa riparia* C. L. Koch, *L. riparia sphagnicola* Dahl und *L. montivaga* Kulcz. – Ann. Mus. zool. pol. (Hist. nat.), 11: 21–25.
68. Petruszewicz, K. 1935a – Pogońce (*Lycosidae* s. lat.) północno-wschodniego Polesia i południowej Nowogródzczyzny – Pr. TPN Wilno, 9: 1–24.
69. Petruszewicz, K. 1936 – Podstawowe pojęcia biocenologii – Wilno, 48 pp.
70. Petruszewicz, K. 1938 – Badania pajaków na północnej krawędzi Podola – Kosmos, 63: 317–361.
71. Pfetten, J. 1925 – Beiträge zur Kenntnis der Fauna der Waldstreu. Fichtenstreu – Z. angew. Ent. 11.
72. Pilawski, S. 1961 – Późnojesienne aspekty pajaków kilku sąsiadujących biotopów w okolicy Lublińca (województwo katowickie) – Prz. zool. 5: 225–231.
73. Pillai, S. K. 1922 – Beiträge zur Kenntnis der Fauna der Waldstreu. Kiefernstreu – Z. angew. Ent. 8.



74. Prószyński, J. 1961 – Pająki Góry Nartowej w Puszczy Kampinoskiej – *Fragm. faun. Mus. zool. pol.* 8: 555–595.
75. Raunkiaer, C. 1934 – *The life forms of plants and statistical plant geography* – Oxford.
76. Remane, A. 1943 – Die Bedeutung der Lebensformtypen für die Ökologie – *Biol. gen.* 17: 164–182.
77. Roever, C. F. 1929 – *Echte oder Webespinnen, Araneae* (Tierwelt Mitteleur. Vol. III) – Leipzig, 143 pp.
78. Simon, E. 1874–1937 – *Les Arachnides de France* – Paris.
79. Stammer, H. J. 1948 – Die Bedeutung der Äethylenglycolfallen für tierökologische und phänologische Untersuchungen – *Verh. dtsh. Zool. (zool. Ges.)*, 53: 387–391.
80. Szafer, W., Kulczyński, S., Pawłowski, B. 1953 – *Rośliny polskie* – Warszawa, 1020 pp.
81. Szafer, W. (editor) 1959 – *Szata roślinna Polski*, Vol. I, II – Warszawa, 586, 333 pp.
82. Tarwid, K. 1952 – Próba charakterystyki zespołu komarów Puszczy Kampinoskiej – *Stud. Soc. Sci. tor.* 3: 1–29.
83. Thiele, H. U. 1956 – Die Tiergesellschaften der Bodenstreu in den verschiedenen Waldtypen des Niederbergischen Landes – *Z. angew. Ent.* 39: 316–367.
84. Tischler, W. 1948 – Biozönotische Untersuchungen an Wallhecken – *Zool. Jb. Syst.* 77: 284–400.
85. Tretzel, E. 1952–53 – Zur Ökologie der Spinnen (*Araneae*) – *SB. phys.-med. Soz. Erlangen*, 75: 36–131.
86. Tretzel, E. 1954 – Reife und Fortpflanzungszeit bei Spinnen – *Z. Morph. Ökol. Tiere*, 42: 634–691.
87. Tretzel, E. 1955 – Technik und Bedeutung des Fallenfanges für ökologische Untersuchungen – *Zool. Anz.* 155: 276–287.
88. Tretzel, E. 1955a – Intragenerische Isolation und interspezifische Konkurrenz bei Spinnen – *Z. Morph. Ökol. Tiere*, 44: 43–162.
89. Tretzel, E. 1961 – Biologie, Ökologie und Brutpflege von *Coelotes terrestris* (Wider) (*Araneae, Agelenidae*), Teil I, II – *Z. Morph. Ökol. Tiere*, 49: 658–745, 50: 375–542.
90. Tullgren, A. 1944 – *Salticidae, Thomisidae, Philodromidae och Eusparrassidae* (Svensk Spindelfauna, Vol. III) – Stockholm, 138 pp.
91. Tullgren, A. 1946 – *Clubionidae, Zoridae, Gnaphosidae* (Svensk Spindelfauna, Vol. III) – Stockholm, 141 pp.
92. Van der Drift, J. 1951 – Analysis of the animal community in a beech forest floor – *Tijdschr. Ent.* 94: 1–118.
93. Van der Drift, J. 1959 – Field studies on the surface fauna of forests – *Bijdr. Dierk.* 29: 79–103.
94. Vité, J. P. 1953 – Untersuchungen über die ökologische und forstliche Bedeutung der Spinnen im Walde – *Z. angew. Ent.* 34: 313–334.
95. Weese, A. 1924 – Animal ecology of an Illinois elm-maple forest – *Illinois biol. Monogr.* 9: 1–93.
96. Williams, G. 1959 – The seasonal and diurnal activity of the fauna sampled by pitfall traps in different habitats – *J. Anim. Ecol.* 28: 1–13.
97. Williams, G. 1959a – Seasonal and diurnal activity of *Carabidae* – *J. Anim. Ecol.* 28: 309–330.
98. Williams, G. 1962 – Seasonal and diurnal activity of harvestmen (*Phalangidae*) and spiders (*Araneida*) in contrasted habitats – *J. Anim. Ecol.* 31: 21–42.



## STOSUNKI MIĘDZY PAJAKAMI WĘDRUJĄCYMI A INNYMI EPIGEICZNYMI STAWONOGAMI DRAPIEŻNYMI

### Streszczenie

Pajaki wędrujące są jedną z głównych grup drapieżnych stawonogów żyjących na powierzchni gleby. W pracy niniejszej przedstawiono wyniki badań nad intensywnością penetrowania przez nie środowiska w ciągu sezonu i w ciągu doby. Jako czynniki warunkujące intensywność i charakter penetrowania analizowano zależności międzygatunkowe wewnątrz zgrupowania pajaków oraz pewne uzależnienia ich od pozostałych drapieżnych stawonogów epigeicznych. W badanych środowiskach towarzyszyły pajakom następujące grupy bezkręgowych drapieżców: mrówki, biegaczowate, kusakowate, kosarze, pareczniki<sup>11</sup>.

Materiały zbierano w Rezerwacie Sierakowskim na północno-wschodnim krańcu Puszczy Kampinoskiej. Wytypowane stanowiska (w liczbie 5 w pierwszym roku badań, 7 w drugim roku i 5 w trzecim roku badań) były płacami różnowiekowego, iglastego lub mieszanego lasu oraz fragmentami łąki w śródleśnym kompleksie Łąk Strzeleckich. Stanowiska leśne, wymienione w kolejności według wzrastającego stopnia zawilgoceń, stanowiły zespoły: *Vaccinio-myrtilli-Pinetum* (VPin), *Pino-Quercetum* (suchy, nieco podwyższony fragment – PQs), *Pino-Quercetum* (wilgotny, przybagienny fragment – PQm) oraz zarosnięty olchą i brzozą fragment łąki z rzędu *Molinietalia* (M1). Stanowiska łąkowe stanowiły dwa fragmenty łąki z grupy *Deschampsietum* (D<sub>1</sub>, D<sub>2</sub>), jeden fragment *Carici-Agrostetum* (DC) oraz jeden fragment *Caricetum elatae* (C). Stanowiska o powierzchni 200–300 m<sup>2</sup> rozłożone były w promieniu około 3 km.

Materiały zbierano w sposób ciągły przez dwa lata (1960–1961) oraz uzupełniano w 1962 roku. Zbiorów dokonywano posługując się pułapkami Barbera (1931). Jako pułapek używano naczyń z twardego, gładkiego plastiku (średnica – 5 cm, głębokość – 10 cm), które zakopywano tak, aby górne brzegi naczyń były równo z poziomem powierzchni gleby. Naczynia wypełniano do około 1/3 wysokości płynem trującym i konserwującym (4% roztwór formaliny lub glikol etylenowy). Na jednym stanowisku znajdowało się minimum 10 pułapek. Opróżniano je w roku 1960 co 4 dni, w roku 1961 co 10 dni, w okresie od marca do października. W roku 1962, w którym zbierano materiały do analiz dobowych rytmów aktywności badanych zwierząt, opróżniano pułapki w godzinach: 3, 9, 17, 21 i 24 (okresy między godzinami 3–9 i 17–21 traktowano jako świt i zmierzch, okres 9–17 jako pełny dzień, a okres 21–3 jako noc).

Równoległe ze zbieraniem materiałów do analiz cykli dobowych przeprowadzono pomiary temperatury przyziemnej warstwy powietrza (fig. 9). Dane meteorologiczne za cały badany okres czasu uzyskano ze Stacji Meteorologicznej Stacji Terenowej Instytutu Ekologii PAN w Dziekanowie Leśnym. Zestawienie ich wykazuje, że lata 1960 i 1961 różniły się przede wszystkim ilością i rozłożeniem opadów były natomiast podobne pod względem temperatur (średnie maksymalne temperatury miesiąca różniły się najwyżej o 2°C na korzyść roku 1961 – fig. 1).

W opracowaniu niniejszym uwzględniono tylko drapieżce o większych rozmiarach ciała. Jest to według klasyfikacji Fentona (1947) mezofauna, Van der Drift (1951) i Kaczmarek (1963) nazywają te zwierzęta makrofauną. Można przyjąć z pewnym przybliżeniem, że są to zwierzęta o długości ciała  $\geq 5$  mm. Dodatkowej klasyfikacji ze względu na wielkość poddano pajaki i biegaczowate. Wśród pajaków

<sup>11</sup>Grupy te charakteryzują się szerszą specjalizacją pokarmową niż pajaki; wykorzystują także martwy pokarm zwierzęcego i roślinnego pochodzenia. Zakwalifikowanie ich jako drapieżców w badanych biocenozach nie powinno jednak budzić wątpliwości.



wyróżniono zwierzęta średnie (5–10 mm długości) i duże (ponad 10 mm długości), wśród biegaczowatych: małe (do 12 mm) i duże (15–40 mm)<sup>12</sup>.

Przeprowadzono ocenę zastosowanej metody połowów. Ponieważ pułapki Barbera rejestrują zarówno liczebność jak i aktywność znajdujących się w terenie zwierząt, porównano uzyskane za ich pomocą materiały z materiałami uzyskanymi za pomocą metod dających oszacowanie samej liczebności pajaków (przesiewanie, przebieranie ściółki) (fig. 2). Stwierdzono, że:

1. Dynamika liczebności pajaków uzyskana na podstawie materiałów z przesiewania i materiałów z pułapek jest podobna w ciepłej połowie roku. W czasie zimy natomiast materiały pułapkowe są dużo uboższe ponieważ spada aktywność zwierząt na powierzchni gleby; skupiają się one wtedy we wnętrzu ściółki i w glebie.

2. Wyraźną przewagę (do 80% liczebności populacji) w materiałach pułapkowych mają formy dojrzałe (tab. I). Formy młode kryją się częściej w ściółce i w jamkach gleby, wskutek czego rzadko wpadają w powierzchniowe pułapki. Wyniki uzyskane za pomocą metody pułapkowej uznano na tej podstawie za wskaźnik intensywności penetracji zwierząt i praca niniejsza podejmuje zagadnienia zmian ich penetracji, a nie zmian liczebności.

W ciągu ponad dwu lat badań znaleziono na wszystkich omówionych wyżej stanowiskach 88 gatunków pajaków wędrujących (tab. II). Na stanowiskach leśnych znaleziono 79 gatunków, z czego 52 gatunki charakterystyczne dla lasu, na stanowiskach łąkowych 36 gatunków, z czego 9 gatunków charakterystycznych dla łąk. Stanowiska leśne są zatem bogatsze w gatunki pajaków wędrujących niż stanowiska łąkowe. Odwrotną sytuację stwierdzono jeśli chodzi o liczebność pajaków znajdowanych w pułapkach (tab. III). Jeden gatunek reprezentowany jest na stanowiskach leśnych przez następującą, średnią liczbę osobników: PQm – 16,7, Ml – 12,1, PQs – 11,7, VPIn – 7,2, a na stanowiskach łąkowych; D<sub>1</sub> – 29,2, D<sub>2</sub> – 28,2, DC – 14,3, C – 6,0.

Wyróżniono dwa okresy nasilenia penetracji pajaków wędrujących: pierwszym z nich jest przedwiośnie (marzec, kwiecień), drugim – miesiąc czerwiec. Wczesnowiosenne maksimum powstaje w wyniku wzmożonej penetracji dużych gatunków pajaków. Czerwcowe maksimum tworzą natomiast gatunki pajaków średnich rozmiarów (fig. 7). Czasem występuje jeszcze trzecie, jesienne nasilenie penetracji, powstałe w wyniku wzmożenia aktywności gatunków diplochronicznych, przebywających drugi okres kopulacyjny.

Duże gatunki pajaków mają tendencję do aktywności nocnej, podczas gdy u średnich przeważa zdecydowanie penetracja dzienna (tab. X). Wykazano dla trzech gatunków z rodzaju *Pachygnatha*, że większe z nich mają tendencję do aktywności nocnej, a mniejszy gatunek do dziennej. Ogólnie biorąc, 67% gatunków dużych pajaków można uznać za wyraźnie nocne, a tylko 31% gatunków – za dzienne. Jako przyczyny uaktywniania się gatunków w różnych porach doby przytacza się w literaturze dobowe zmiany temperatury, a zwłaszcza zmiany wilgotności. Ze względu na mniej korzystny stosunek wielkości ciała do jego powierzchni, wrażliwsze na wysychanie winny być gatunki mniejsze. Przesuwanie się aktywności dużych pajaków epigeicznych na okres nocy wydaje się być spowodowane zależnościami ekologicznymi, a mianowicie zależnościami konkurencyjnymi między pajakami, a innymi drapieżcami penetrującymi wraz z nimi powierzchnię gleby (fig. 8, 9).

Zależności międzygatunkowe w zgrupowaniu pajaków badano śledząc występowanie gatunku eurywalentnego i analizując zmiany struktury dominacji w zgrupowaniu.

Zgodnie z poglądami wielu autorów gatunki eurywalentne, stosunkowo mało za-

<sup>12</sup>Do dużych biegaczowatych zaliczono wszystkie gatunki z rodzaju *Carabus* i dwa gatunki z rodzaju *Pterostichus*: *P. niger* i *P. vulgaris*. Wszystkie pozostałe *Carabidae* zaliczono do klasy małych; w zebranych materiałach nie przekraczały one 12 mm długości.



leżne od środowiska fizycznego, są szczególnie czułe na działanie czynników biotycznych. Najbardziej eurywalentnym wśród branych pod uwagę w niniejszej pracy gatunków pajaków jest *Lycosa lugubris* (Walck.). Sledząc jej występowanie w różnych środowiskach i w dwu latach badań stwierdzono, że unika ona towarzystwa innych większych gatunków pajaków wędrujących (fig. 4, tab. VI). Wymijanie to powodowane jest niewątpliwie stosunkami konkurencji między *L. lugubris* a pozostałymi gatunkami zgrupowania.

Dominowanie jednego gatunku uważane jest za wynik konkurencji między gatunkami tworzącymi zgrupowanie. Dominacja jednego gatunku w zgrupowaniu pajaków epigeicznych jest wyraźna tylko wczesną wiosną, to jest w okresie kiedy tylko pajaki penetrują powierzchnię gleby. W miarę upływu czasu przewaga jednego gatunku zacierza się i w pełni sezonu mamy zazwyczaj do czynienia z równoczesnym licznym współwystępowaniem kilku – 2, 3, a nawet 4 gatunków (fig. 5, 6, tab. IX). Nasilenie konkurencji wewnątrz zgrupowania pajaków maleje prawdopodobnie w miarę zwiększającej się penetracji innych drapieżców.

Badając zależności między pajakami wędrującymi i innymi stawonogami drapieżnymi powierzchni gleby stwierdzono, że:

1. Pierwszymi stawonogami pojawiającymi się wiosną (marzec, kwiecień) na powierzchni gleby są gatunki dużych pajaków. Inne drapieżne stawonogi są jeszcze wtedy nieaktywne. Grupa przedwiosennych, dużych gatunków pajaków nie napotyka więc w tym czasie na powierzchni gleby innych drapieżców.

2. W dalszym ciągu sezonu pajaki wędrujące (głównie gatunki średnie) mają szanse spotkania się przede wszystkim z mrówkami, biegaczowatymi i kosarzami, te bowiem grupy, podobnie jak pajaki średnie, wykazują maksima penetracji w pełni lata (fig. 10, tab. XI).

3. W czasie doby (głównie w dzień) równocześnie z pajakami penetrują powierzchnię gleby mrówki i niektóre małe biegaczowate. Duże pajaki występujące częściowo nocą mogą spotykać się z nocnymi kosarzami i dużymi biegaczowatymi (tab. X).

4. Aktywność wszystkich badanych grup drapieżnych stawonogów rozkłada się w czasie doby tym równomierniej, im starsza jest biocenoza (fig. 8, 9). Fakt ten uznano za dowód trwających zależności konkurencyjnych między omawianymi grupami zwierząt.

5. Struktura dominacji w zgrupowaniu pajaków zacierza się w miarę nasilania się penetracji pozostałych badanych drapieżców. Prawdopodobnie jest to wynikiem przesunięcia się nasilenia konkurencji ze stosunków międzygatunkowych na stosunki międzygrupowe.

6. Spadkowi intensywności penetracji pajaków w 1961 roku na stanowiskach leśnych towarzyszy uaktywnianie się biegaczowatych i kosarzy.

7. Penetrowanie powierzchni gleby na stanowiskach łąkowych dzieła między siebie pajaki i mrówki, które wyraźnie się wymijają (fig. 11).

Na podstawie uzyskanych wyników rozważano również zagadnienie, czy pajaki wędrujące stanowią w biocenozach jednostki funkcjonalne, tak zwane zespoły konkurencyjne (Gause 1936, Lityński 1938, Tarwid 1952)<sup>13</sup>. Według tych autorów zespołami konkurencyjnymi są grupy organizmów, zajmujących te same nisze ekologiczne w środowisku oraz związanych wewnętrzną konkurencją. Symptodem tej konkurencji ma być charakterystyczna struktura dominacji z wyraźną przewagą liczebności jednego gatunku. Stwierdzono, że pajaki badanych środowisk nie tworzą typowych zespołów konkurencyjnych, gdyż nie obserwuje się stopniowego wykształca-

<sup>13</sup> Zgodnie z sugestią K. Tarwida wprowadzono w angielskim tekście pracy skrótowy termin „c-association” dla oznaczenia pojęcia „zespołów konkurencyjnych” przyjętego w języku polskim.



nia się charakterystycznej struktury dominacji, mającej być symptomem zawiązujących się zależności konkurencyjnych. Pewne z przedstawionych faktów świadczą jednak, że istnieje konkurencja wewnątrz zgrupowania pajaków. Zgrupowanie to podzielone jest na dwie grupy (gatunki duże i średnie), wykazujące tendencję do wymijania się z roku na rok (tab. VII), w czasie doby (tab. X) i w czasie sezonu (fig. 7). *Lycosa lugubris* unika stanowisk opanowanych jednocześnie intensywnie przez inne gatunki pajaków, bliskie pod względem wymogów ekologicznych (fig. 4, tab. VI). Dane zebrane w niniejszej pracy i pewne dane z literatury wskazują, że w zgrupowaniu wszystkich drapieżnych stawonogów powierzchni gleby wytwarzają się także zależności konkurencyjne. Intensywność penetrowania powierzchni gleby przez pajaki wędrujące uzależniona jest więc zarówno od nasilenia konkurencji międzygatunkowej w zgrupowaniu pajaków, jak i od presji innych grup drapieżnych stawonogów.

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