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AN ANALYSIS OF FOOD RELATIONS BETWEEN THE SPIDERS – *ARANEUS CORNUTUS* CLERCK AND *ARANEUS QUADRATUS* CLERCK – AND THEIR PREY IN MEADOWS*

In this paper an analysis is presented of the prey found in spider webs, as well as of the relations between the number of prey captured and the number and species composition of the insect fauna of the environment and the changes taking place in the population of the predator. The paper also analyses the relations between the size of the spider populations and the supply of food in the environment as well as the degree of differentiation in the structure of vegetation.

CONTENTS

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I. INTRODUCTION

The present paper contains an analysis of the changes, occurring during the vegetative season, in the number of prey caught in the meadow by two species of web-spinning spiders – *Araneus cornutus* Clerck and *Araneus quadratus* Clerck.

Trials were made for finding a relationship between the varying amount of the prey captured by the spiders and: 1) variations in the number, mobility and species composition of the insects found in the meadows, 2) changes in the activity and age distribution of the spiders themselves and 3) changes in environmental conditions. This analysis of the relations between the situation in the environment and the intensity of predation was carried out in order to determine the role of spiders as a factor controlling the abundance of insects.

One of the important aims of this investigation was to adjust one of the known methods of studying food for a quantitative assessment, and a search for methods allowing of a comparison of the amount of food in the spider webs with the density of the fauna present in the environment under observation.

The web-spinning spiders are a fairly convenient object for the study of food relations. The external digestion and the remaining of small insects and indigested chitinous remnants of bigger preys in the webs for some time, make it possible to determine the composition and the amount of food captured.

The papers concerned with the investigations of the prey captured by spiders most frequently discuss, more or less widely, the composition of the food taken by the spiders, but they almost entirely neglect the composition and the abundance of the fauna in the area in which the food analyses were made (Ewing 1918, Bilsing 1920, Rau 1922, Cuthberson 1926, Hobby 1930, 1940, Poulton 1934, Pratt and Hatch 1938, Bristowe 1941, Knowlton 1952, Théodoridès 1952, Parmenter 1953, Turnbull 1960a, Tretzel 1961, Prószyński 1962). Although in some of the more extensive studies (Bilsing 1920, Bristowe 1941, Turnbull 1960a) some notes can be found regarding the species composition of the fauna present in the environment, the fauna itself is not however the object of study.

The influence of the spiders on a specified population of preys was studied mainly by the authors connected with agriculture and forestry, who tried to use spiders for controling the pests. The findings reported by various authors regarding the possibility of introducing spiders to crop-fields, i.e. opinions concerning their importance for the reduction of pests, have been collected in the papers elaborated by Bristowe (1941) and Vité (1953). Bristowe quotes American and English studies (Comstock 1879, Burgess and Crossman 1929, Fluke 1929, Alexander 1920, Maclagan 1932), and Vité the German ones (Keller 1883, Nolte 1938, Subklev 1939, Schimdt 1930) which indicate that spiders are an important factor reducing the size of the populations of a number of pests. Dunn (1949) and Gałecka (in the press) write that spiders may play an important role in the reduction of aphids. On the other hand, Vité quotes data given by another author (Engel 1942) according to whom spiders, in comparison to other entomophages, are not very important as a control factor for insects, their importance increase in only those cases where they are the only insect controlling factor.

Special attention should be given to the paper of Harrison (1913) who found that in the woods where there were few spiders and particularly *Bolyphantes expunctus*, the tops of the pines were to a considerably larger extent infested by pests (mainly *Chermesidae*) than in areas where spiders were numerous. He even suggested that spiders should be brought into the woods infested by pests.

In recent years the role of spiders has been investigated mainly by Japanese scientists – Kayashima 1960, 1961, Itô, Miyashita and Sekiguchi (1962), who ascribe a great importance to the activity of spiders in the fields. Kayashima (1960, 1961) found that *Oxyopes sertatus* L. Koch effectively reduced one population of the prey – *Contarinia inouyei* Mann (*Itoniidae*). He introduced spiders reared in the laboratory into *Cryptomeria* woods (*Taxodiaceae*) by which procedure he obtained a considerable decrease in the infestation of trees.

The above data suggests that in many situations the spiders may play an important role as one of the significant factors controlling the number of insects. So it is necessary to know more closely their role in the biocenosis.

II. METHODS

Two kinds of methods were used:

1. methods determining the abundance and mobility of the spider fauna in the environment,

2. methods determining the abundance, activity and the number of prey captured by the spiders.

1. The first method group included the use of sweep-nets and sticky traps. A single sample consisted of 25 sweeps with a sweep-net of a standardized size. Each catch consisted of 10 samples. The total number of samples collected is illustrated by Table I.

The sweep-net catches the fauna living in the upper part of field-layer, i.e. in the same layer as that in which the predatory species under observation are distributed. The material collected in this way may be regarded as an information about the abundance of the potential food for the spiders present in the environment.

As has been shown in a number of papers, the sweep-net method gives a clear picture of the variations in the abundance and of the dominance within individual groups (Carpenter 1936, Kontkanen 1950, Barnes and Barnes 1955, Łuczak 1958, Łuczak and Wierzbowska 1959). It does not however give the estimation of the density, although some authors (Smalley 1960, Turnbull 1960b) try to adjust this method for the estimation of the number of individuals per surface unit. But as the sweep-net acts selectively, Number of samples taken and the amount of material collected

Tab. I

Methods	Stations	Number of samples			Total	Number of individuals captured			Total
		1960	1961	1962		1960	1961	1962	
Sweep-net	1		60				1544		
	2		90		290		2354		6939
	3		140				3041		
Sticky traps	1		190				3113		
	2		180	120	630		2679	2465	10588
	3		140				2331		
Quadrate method	1	340	180			324	474		
	2	200	180		980	172	679		1795
	3		80				146		
Food of spiders (number of individuals considered)	1	344	387			213	950		
	2	194	409	143	1634	297	665	1928	3246
	3		157				193		

Additional material

Methods	number of samples		total	number of individuals		total
	1954	1955		1954	1955	
Sweep-net	776	280	1056	12400	2393	14793
Quadrate method	1504	784	2288	2307	1007	3314

frightens a part of the fauna (Łuczak 1958), such calculations do not show the real picture of the density.

The mobile fauna was caught in the present investigation by using sticky traps. These were small bags of the size of 30 by 50 cm made of a thin polyethylene film, fastened to wire frames. Two sides of these bags were covered by a thin layer of a sticky substance, one of those used in orchards; the bags were set up vertically, 10 at each station. The species and the number of individuals caught were recorded at approximately the same time every day, for three consecutive days. These 3 days' cycles of catching were repeated every fortnight, from July to September 1961 and in July 1962. Sticky traps catch first of all small insects carried by air currents (Johnson 1950, Staples and Allington 1959, Roth 1963).

This method was applied on account of its functioning which is similar to that of spider web. The sticky trap catches fauna similar in size to that caught by the webs of the spiders, and like the webs, it catches mobile, mainly flying and jumping, and to a lesser extent walking insects. This method was a necessary supplementation of the sweep-net method, because it gives evidence regarding the abundance of that part of the fauna which may be available to the webs of the predators in question.

The differences that may arise between the sticky traps and the webs are mainly differences in deflection of air currents by surfaces one of which is impermeable and the other permeable to these currents. Roth (1963) made a comparison of the catching rate of three different nets of a surface of 425 cm^2, varying in mesh-density – a metal net very dense (mesh size 3×3 mm) and two loose thread-nets of different densities (one of them consisted of 32 threads interwoven around a frame, the other one of 64 interweavings). The species composition of the fauna caught by the three methods was very similar despite the fact that each of the nets had a different resistance to air currents. However, the number of animals captured was different. The net made of metal used to catch about twice as many insects as the thread-nets; the loosest of the nets appeared to be the most effective, the number of animals caught by it, calculated per a unit of thread length, was the largest of all.

From the above experiments it can be presumed that the difference in the resistance to air currents of the two methods – sticky traps and nets – should not play a decisive role in the composition of the fauna captured.

2. The number of spiders was determined by the quadrate method, i.e. each time spiders present in a square 50×50 cm were counted. The series consisted of 20 such squares. Sampling by this method was carried on from May to September in 1960 and 1961; data collected in 1954 and 1955 was used as an additional material (Tab. I). This method was used for the determination of the abundance of spiders in the herb-layer, omitting the ground layer.

The number of prey captured by the spiders was in 1960 and 1961 estimated by collecting about once a week insects hanging on twenty webs and spider retreats. The number of spiders encountered, those with and those without webs, with or without preys, and also body-size classes were taken into account. The data was used for the calculation of the average number of prey per each spider and also for the estimation of the feeding activity of the spiders (see chapter V, 1). In 1962 a series of samples was collected to find how long a period of time was needed for the accumulation of that amount of food which was collected each time. For this purpose 100 webs had been marked and subsequently controlled at the same time-intervals (between 10 and 12 a.m.), for 4 consecutive days. At first food was collected at shorter time-intervals, but after 3 and 6 hours most of the webs, which had been damaged during the preceding collecting, appeared to be still unrepaired. The method used in the present investigation was a modification of the method introduced by Turnbull (1960a) for the observation on the food preference of *Linyphia triangularis* Clerck. The material that came from the first day of observation was collected chiefly by the same method as that used in 1960–1961 for the estimation of the quantity of food, whereas the material collected during the following days was clearly related to time, it had been caught during 24 hours. The average numbers of insects captured by 10 spiders on each of the consecutive days of observation were as follows:

9 VII – 111.8
10 VII – no webs, strong wind
11 VII – 82.1
12 VII – 107.6

The differences between the first and the following two dyas were not considerable. All the results are of a similar order so it may be concluded that the material collected each time roughly represents the number of prey falling into the webs during a period not longer than about 24 hours.

The above results are supported also by the data found in the literature concerning the frequency of web replacing by the species belonging to *Argiopidae*. Wiehle (1927) reports that in the field, the time between two successive replacings of webs may be, at the longest, 2 days. Only in laboratory conditions may a starving spider not renew its web for several consecutive days. Similar conclusions were drawn by Bristowe (1941) and Cherrett (1964), who have found that spiders renew their webs every day.

Only in one of the arachnological studies known to me (Turnbull 1960a) was the food of the spiders collected in a continuous way throughout the season, using a precise quantitative method of collecting which gave an estimation of the amount of food falling into the webs; the other papers were most frequently dealing with qualitative observations. The amount of food captured and eaten by the spiders was usually estimated by tests in which a spider was given appropriate food and an observation was subsequently made to find how much it could eat (Bilsing 1920, Bonnett 1930, Bristowe 1941, Tretzel 1961, Prószyński 1962). Such observations are valuable, but they do not give any information concerning the situation in the field or the average number of insects falling into the web. The method applied in this investigation was to supply evidence regarding variations in the intensity of food catching throughout the period of the activity of the spiders concerned.

The main methodical difficulty encountered is the difficulty with the comparing of the results obtained by using three different methods (sweep-net, sticky traps, webs) each of which acts selectively, but in a different way. Perhaps this is why so few papers make comparisons of the quantitative relations of the fauna and an analysis of the predator's food. Arachnological papers (Bilsing 1920, Bristowe 1941, Turnbull 1960a) report that although numerous in the environment, certain species were not found on webs or were found in small numbers only. But, as in the above-discussed problem relating to the amount of food captured, these are only notes and observations of experienced observers, with no detailed analysis to support them.

In connection with the alterations introduced by each of the above-named methods, in the comparison made in the present study the following procedure was used:

1. Only the major and frequently occurring differences between the results obtained by the various methods were taken into consideration and all the minor deviations were neglected.

2. The courses of the curves and not the particular numerical values obtained by the various methods were compared.

3. Only when the differences between the methods appeared to be different at several stations were trials made to find conditions to account for the situation and so the particular values were then compared.

A very significant difficulty that had to be overcome was the determination of the material collected. The material caught by the sticky traps must be identified at the spot, because the taking-off of the individuals stuck to traps usually causes damage of their bodies. This of course could have be done only by a specialist familiar with the given taxonomical group. Two most diverse insect groups, most numerous in the meadows, have been identified — *Diptera* (determined down to the family) and *Homoptera-Auchenorrhyncha*. With the material collected from the webs the same degree of accuracy in determination was used with regard to these two groups and, in addition, two other groups, relatively numerous in the spiders' food, were identified — *Coleoptera* and *Hymenoptera* (to families)[1].

Besides the well preserved individuals, the material collected from spider webs included specimens which were heavily damaged, these were the remains of the food eaten by the spiders. A closer identification or even a classification into the order was sometimes impossible.

III. DESCRIPTION OF THE STUDY AREA

The investigation was carried out in the Strzeleckie meadows, a complex of midforest meadows 66 hectares in surface, located in the north-eastern part of the Kampinos Forest near Dziekanów Leśny.

The field studies were carried out in three environments different floristically and ecologically.

Station I was located on patches of the association *Caricetum elatae* (W. Koch 1926) belonging to the alliance of tall sedges — *Magnocaricion* (W. Koch

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[1] I wish to extend my cordial thanks to L. Andrzejewska, M.Sc., (*Auchenorrhyncha*) and to Prof. K. Tarwid (*Diptera*) who were kind enough to determine the material in the field and in the laboratory, as well as to Dr. B. Burakowski and Dr. S. Wiąckowski for identifying the beetles and *Hymenoptera*.

Thanks are due also to Dr. T. Traczyk for the phytosociological description of the Strzeleckie meadows.

1926). This community develops during heavy and prolonged floods of ground waters. The water remains stagnant above the ground almost throughout the year, and only during a summer drought does it drop a little below the surface of the ground. Heavy flooding favours the development of tall immersed herbaceous perennials such as: *Carex hudsonii* Bennet, *C. acutiformis* Ehr., *C. riparia* Curt., *C. paradoxa* Willd, *Ranunculus linqua* L., *Iris pseudoacorus* L., *Rumex hydrolapathum* Huds. and others.

Species which dislike floods and only require areas with permanently waterlogged soil are found on the tops of the tussocks formed by the tussock sedges, mainly by *Carex hudsonii*. *C. hudsonii* species clearly dominates in this community giving it a specific character and look. It forms fairly high (about 0.5 m) tussocks separated from one another by flooded flat depressions.

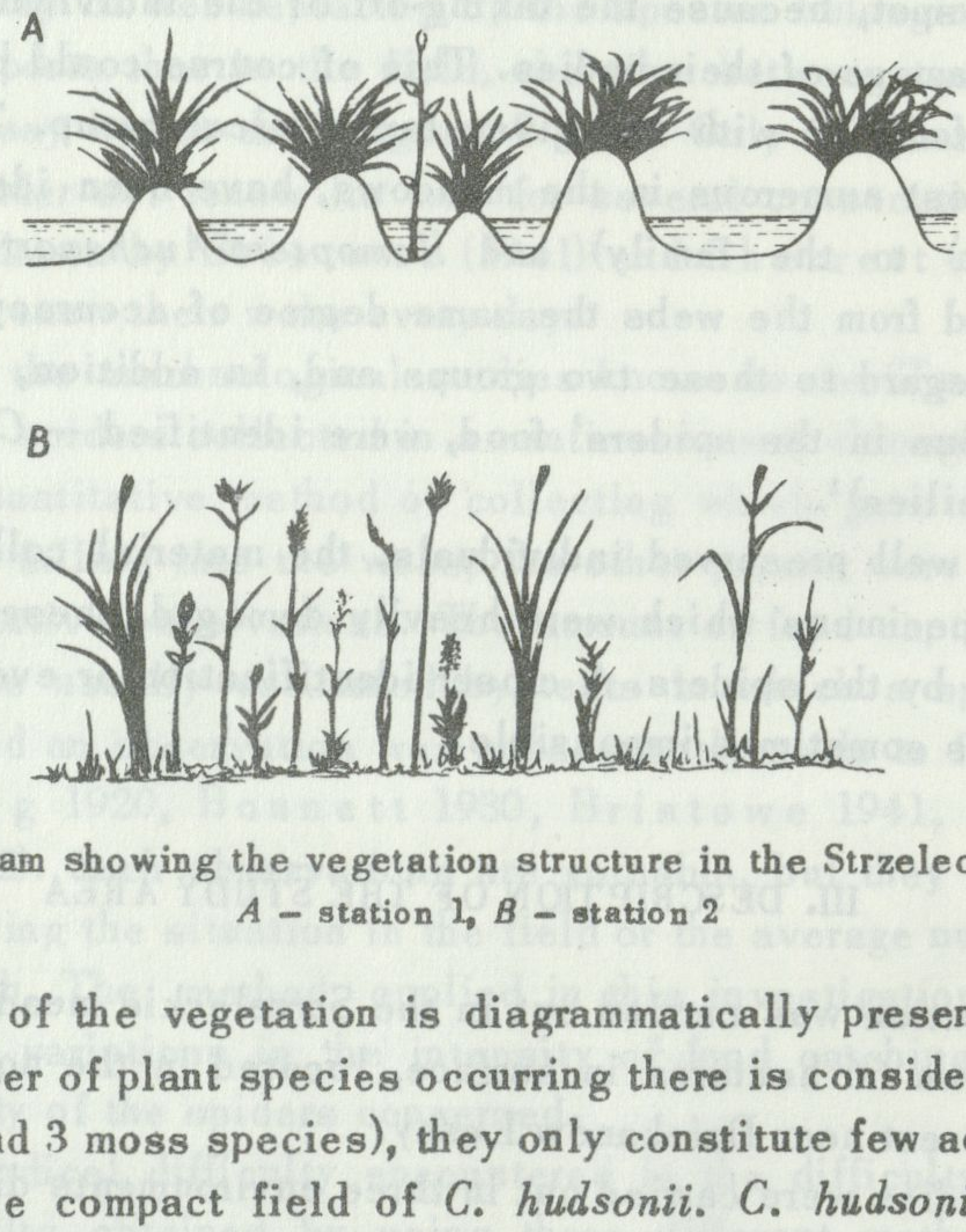

Fig. 1. Diagram showing the vegetation structure in the Strzeleckie meadows
A – station 1, *B* – station 2

The structure of the vegetation is diagrammatically presented in Figure 1. Although the number of plant species occurring there is considerable (34 species of higher plants and 3 moss species), they only constitute few admixtures, loosely dispersed over the compact field of *C. hudsonii*. *C. hudsonii* shows a great density and sociability, oftenest about 5.5. In spite of its immense bulk, the vegetation shows a poorly varied structure due to the dominance of one species.

In both the years during which the investigation was carried on the area was partially mown.

Station 2 covers an area which is not uniform floristically or as a habitat. There occurs a mosaic of mineral and peaty soils. In the small area bordering, from the south and from the north, on an alder forest three plant associations are found: 1) *Carici canescentis-Agrostetum caninae* (R. Tx. 1937), 2) *Stellario-*

Deschampsietum caespitosae (A. Freitag 1957), 3) *Caricetum gracilis* (R. Tx. 1937).

The highest and the driest places are occupied by the second association, the lowest and moistest by the third one, whereas in localities of intermediate conditions the first association is found. These associations appear to have a mosaic-like arrangement and often mix with one another. As a result a very complex and largely varied vegetation is formed. Although the species composition is here slightly poorer than at the former station (30 species of higher plants), there is no clear dominance of one or several species. The structure of the vegetation is much varied (Fig. 1) in both the horizontal and vertical directions. Several layers can be distinguished there. The highest layer is made up of tall sedges: *Carex gracilis* Curt., *C. acutiformis* Ehr., *Calamagrostis canescens* (Web.) Roth, *Iris pseudoacorus* L. (elements of the association *Caricetum gracilis*), the lower layer consists mainly of grasses of medium height, mostly the representatives of the association *Stellario-Deschampsietum*, they are *Deschampsia caespitosa* (L.) P.B., *Holcus lanatus* L., *Festuca rubra* L., *Poa pratensis* L., *Agrostis canina* L., *A. stolonifera* L., and also *Filipendula ulmaria* (L.) Maxim., *Cirsium palustre* (L.) Scop., *Juncus effusus* L. The still lower layer consists of *Carex panicea* L., *C. fusca* Bell. et al., *Ranunculus acer* L., *Lychnis flos-cuculi* L., *Lotus uliginosus* Schk., *Plantago lanceolata* L. The ground layer is formed by a compact carpet of mosses.

This part of the meadows was not mown.

Station 3 represents a uniform plant community belonging to the alliance *Molinion* (W. Koch 1926), to the group found in temporarily moist meadows. This association is floristically similar to the association *Stellario-Deschampsietum caespitosae*. This is the driest of all the environments discussed, only temporarily does here the water come up to the surface of the ground. The density of herbs constitutes 70% and that of mosses 80%. In comparison to other environments the number of plant species found here is the smallest of all (23 species). As there is only one association present there, the structure of the vegetation is obviously less varied than at the former station, but as at the formerly-discussed station, there is no distinct dominance of one species. Among the species forming the largest proportion of the vegetation cover are *Carex panicea*, *Deschampsia caespitosa*, *C. fusca* and *Potentilla anserina* L.

The area under investigation was partially mown.

The chapter dealing with the analysis of the factors controlling the abundance of spiders includes the material collected between 1954—1955 in the lowland peat bogs constituting part of the Kuwasy marshes complex. A detailed description of the localities investigated is given in other papers (A. Kajak 1960, 1962). Samples were then taken in two artificial and in five natural meadows. The environments were selected so as to form a clear gradient of vegetation differentiation. During the investigations one of the artificial meadows (S_1)

became invaded by weeds which caused a change in the degree of differentiation of that meadow. Three natural meadows belonged to the meadow group temporarily flooded, with a relatively uniform vegetation composed mainly of sedges (N_1, N_2, N_3); two meadows (N_4, N_5) were characterized by a considerable diversity of the vegetation. Besides sedges and grasses there were also many dicotyledonous species present, forming a varied vegetation structure.

IV. THE BIOLOGY OF THE INVESTIGATED SPECIES OF SPIDERS

Araneus cornutus and *A. quadratus* build large, radial webs in the top layer of the meadow vegetation. The size of the catching part of the web of adult individuals of *A. cornutus* may be as large as 60 cm in diameter, the webs of *A. quadratus* are slightly bigger (Wiehle 1927, 1931). *A. cornutus* renews its web before dusk and catches insects at both daytime and during the night (Wiehle 1931), *A. quadratus* also renews the web before dusk or dawn (Wiehle 1927) so probably both these species catch at about the same time of the day. Besides webs, they both build retreats placed in inflorescences or in bent leaves of grass. The retreats of the young individuals of *A. cornutus* are most frequently placed in flower heads, they are therefore generally located higher up than those of the young *A. quadratus* spiders which are usually placed among leaves. The adult individuals of both these species are distributed at about the same height.

The two species capture their prey in a similar manner. Also their webs are similar in structure and arrangement and so is the time of catching.

The life cycle of *A. quadratus* is completed during one vegetative season. Nests with developing young individuals are found in May and June. The beginning of July is the-time when the young individuals are most numerous; at the end of July and in August adult individuals appear and at the end of September the females build cocoons and die.

The life cycle of *A. cornutus* is a more complex one. Throughout the vegetative season individuals at various developmental stages occur side by side. In spring (V, VI) the proportion of adult individuals is the largest. The number of adult forms decreases gradually during July and August, young individuals predominating numerically, and in the autumn more numerous are medium size spiders (Fig. 2) which will eventually winter.

V. ANALYSIS OF SPIDER PREDATION

1. THE INDICES USED

In his analysis of predation in three species of small mammals Holling (1959, 1961) says that the intensity of predation is related to the number of prey

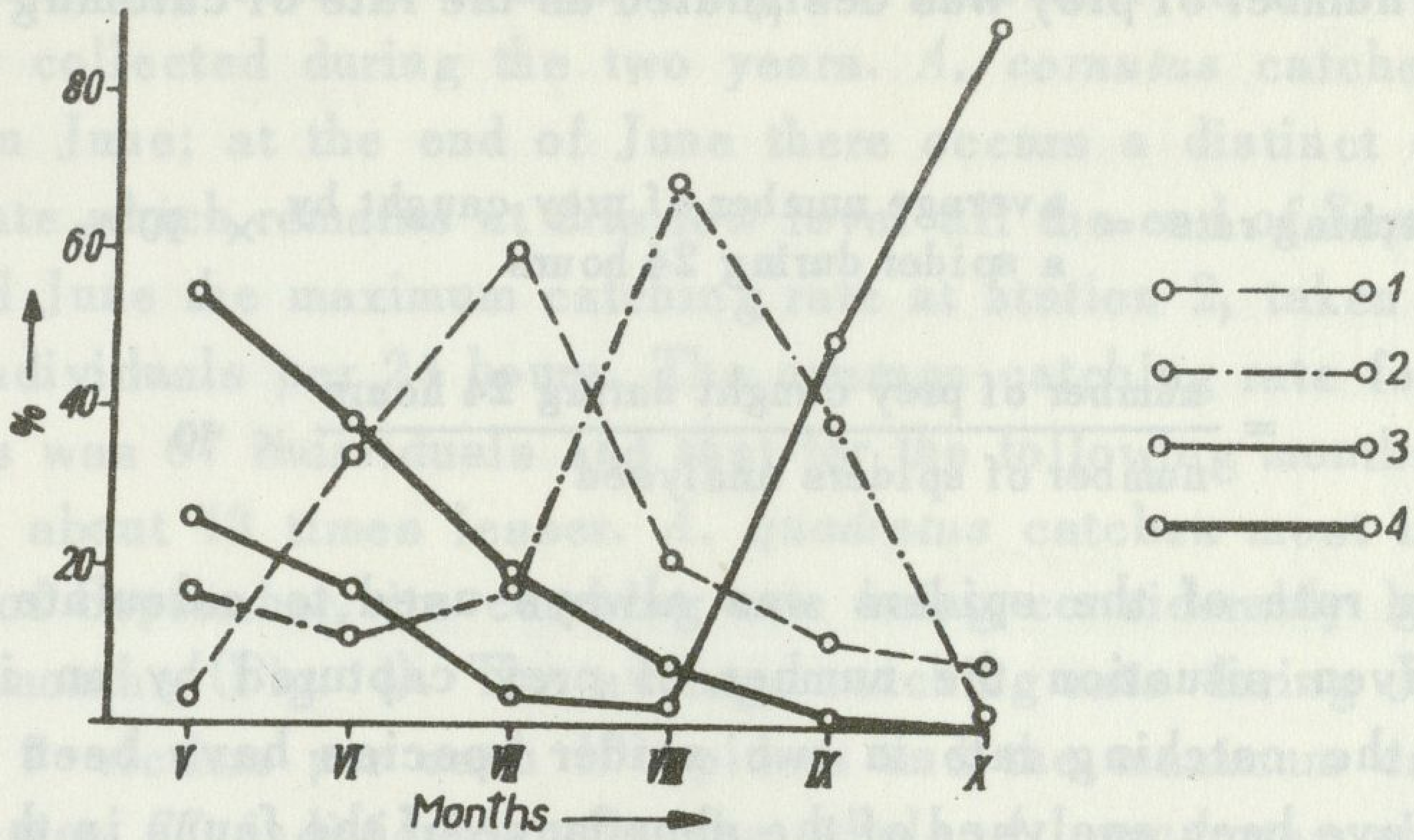

Fig. 2. Age distribution of *A. cornutus*. 1961
1 – very small individuals, *2* – small, *3* – medium size, *4* – adult

eaten by one predator and to the total number of predators. He separately analyses the intensity of feeding and the variations in the abundance of predators, and then the way in which the two parameters overlap. All his investigations Holling carried out against the variations in the number of the prey (pupae of *Neodiprion sertifer* Geoffr.).

In the present study a similar analysis of predation was applied – I considered changes in the average numbers of prey captured by a single spider, changes in the density of spiders and subsequently the course of the resultant of the component agencies. Below are given the indices applied in order to give an approximate estimation of the intensity of spider predation.

The intensity of the action of a specified spider population on the preys was expressed by means of an index of intensity of predation which shows the number of prey captured by the spiders present in a definite area, in this case, over a surface of 5 m^2. The index was obtained by multiplying the average number of prey per one spider by the density of the spiders. The number of spiders was estimated by using the quadrate method, and the number of preys per a spider – by the formerly-discussed method of collecting prey from 20 webs.

$$\text{intensity of predation} = \begin{array}{c}\text{average number of prey}\\ \text{caught by one spider}\\ \text{during 24 hours}\end{array} \times \begin{array}{c}\text{number of spiders}\\ \text{per an area of 5 m}^2\end{array}$$

By means of this index it was possible to show changes occurring during the season in the number of prey captured by the spider populations discussed.

Most attention was given to the first component of the product – to the average number of prey caught by the spiders. To avoid small numbers the average number of prey caught by 10 spiders, and not by only one, was used. The index of average number of prey was designated as the rate of catching by individual spiders.

$$\text{catching rate} = \frac{\text{average number of prey caught by a spider during 24 hours}}{} \times 10 =$$

$$= \frac{\text{number of prey caught during 24 hours}}{\text{number of spiders analysed}} \times 10$$

The catching rate of the spiders was always used to calculate the mean value, in the given situation the number of prey captured by an individual. Fluctuations in the catching rate in two spider species have been presented and the effects have been analysed of the abundance of the fauna in the environment and of the feeding activity of the predator on that catching rate.

By the feeding activity of the spiders I mean the ratio of the number of hunting individuals (those possessing webs) to the total number of individuals in the population (those possessing as well as those lacking webs); it was expressed in per cent.

$$\text{feeding activity (activity)} = \frac{\text{number of spiders with webs}}{\text{number of all spiders (with and without webs)}} \times 100$$

In some cases, to determine the supply of food in the environment or to compare fluctuations in the number of insects caught by the sticky traps and by individual webs the catching rate of the webs was used. This expresses the number of prey caught by 10 webs.

$$\text{catching rate of webs} = \text{average number of prey caught by the web during 24 hours} \times 10 =$$

$$= \frac{\text{number of prey caught during 24 hours}}{\text{number of web-possessing spiders analysed during one catch}} \times 10$$

This index makes it possible to render the data independent of the feeding activity of the population. It may also be expressed in another way:

$$\text{catching rate of webs} = \frac{\text{catching rate of spiders}}{\text{feeding activity}} \times 100$$

2. VARIATIONS IN CATCHING RATE OF THE SPIDERS DURING VEGETATIVE SEASON

In spite of the great similarity of the webs of the two spider species discussed the curves representing the changes in their catching rate have quite different courses. This is indicated by the data derived from various environments and collected during the two years. *A. cornutus* catches most prey in May and in June; at the end of June there occurs a distinct decrease in the catching rate which remains at this low level till the end of September (Fig. 3). In May and June the maximum catching rate at station 2, taken as an example, was 138 individuals per 24 hours. The average catching rate for each of these two months was 67 individuals and that for the following months only 5 individuals, i.e. about 13 times lesser. *A. quadratus* catches most intensely at the beginning of September, its catching rate being considerably lower during the preceding months (Fig. 4). The average catching rate during July and August was about 9 victims per each 10 spiders and the maximum catching rate for September was 77 individuals. On the whole *A. quadratus* showed a higher

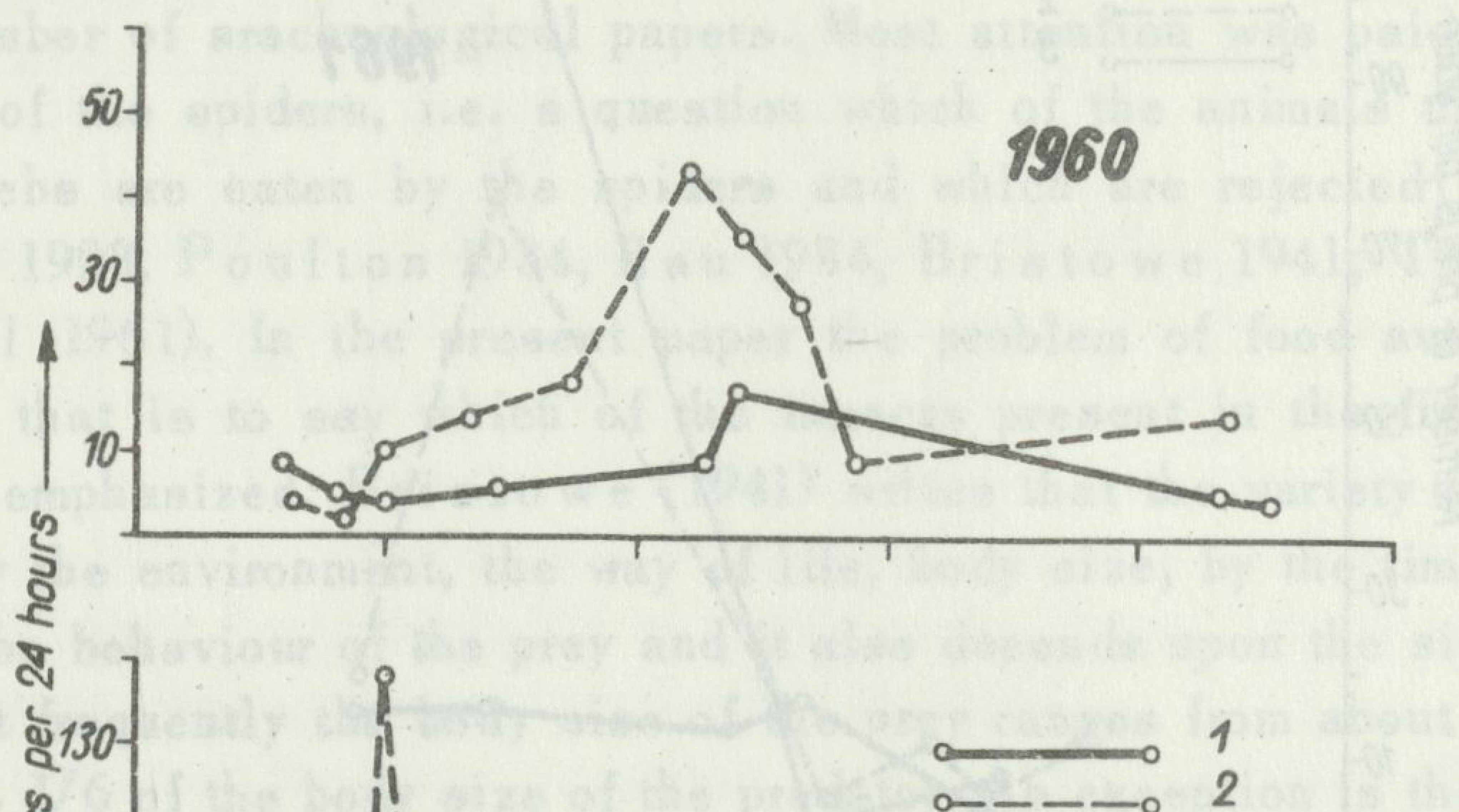

Fig. 3. Variations in the number of preys captured by individual spiders (rate of catching) *A. cornutus*
1 — station 1, 2 — station 2, 3 — station 3

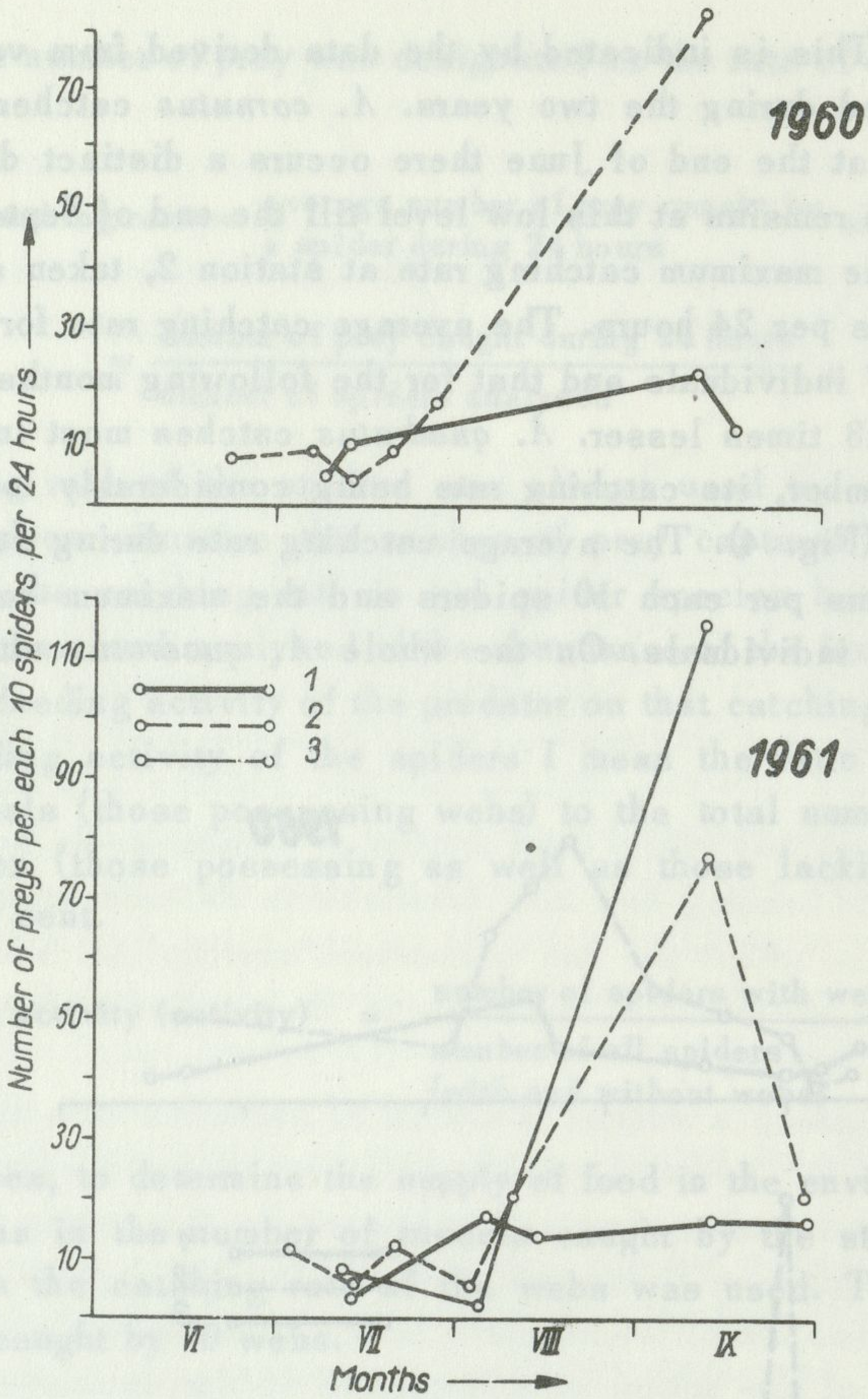

Fig. 4. Variations in the number of preys captured by individual spiders *A. quadratus*
For explanation see Fig. 3

catching rate than *A. cornutus*. In July and August, for instance, *A. cornutus* would catch an average of 5.7 individuals, whereas *A. quadratus* 9 individuals.

The catching rate of *A. quadratus* had a very similar course in 1960 and 1961 (Fig. 4), while the catching rate of *A. cornutus* in the two years differed considerably (Fig. 3). In 1960 the characteristic spring-maximum related to the mass emergence of insects, whose larvae live in the water, did not occur. In the spring of 1960 the level of ground water was so low that the emergence of insects was not intense. Maximum catching rate occurred only in July and was as small as 44 individuals per 10 spiders that is to say about 3 times lower than in 1961 (Fig. 3). The average catching rate in 1960 was even higher than in 1961, not including the period of maximum catching rate, it was on the average 10 victims per 10 spiders, whereas in 1961 – only 5.

The data derived from various environments shows a considerable accordance in the course of the catching rate curve. The maximum and the lowered numbers of prey occurred in the majority of cases simultaneously at all the stations compared (Figs. 3 and 4). This similarity of the data derived from the various localities confirms the reality of the courses and at the same time makes it possible to discuss the main regularities on the basis of one example of locality.

3. ANALYSIS OF THE COMPOSITION OF FOOD AGAINST THE SPECIES COMPOSITION OF THE FAUNA PRESENT IN THE MEADOW

The composition of the food of spiders has been for many years dealt with by a number of arachnological papers. Most attention was paid to the food preference of the spiders, i.e. a question which of the animals that fall into the spider webs are eaten by the spiders and which are rejected (Bilsing 1920, Savory 1928, Poulton 1934, Rau 1934, Bristowe 1941, Turnbull 1960a, Tretzel 1961). In the present paper the problem of food availability to the spiders, that is to say which of the insects present in the field fall into the webs is emphasized. Bristowe (1941) writes that the variety of prey is determined by the environment, the way of life, body size, by the time of occurrence and by the behaviour of the prey and it also depends upon the size of the predator. Most frequently the body size of the prey ranges from about the size of the spider to 1/6 of the body size of the predator. An exception is the spiders of the genus *Araneus* which, when starting the building of a new web, utilize even the smallest insects hanging in the old webs. Vité (1953) estimated the food availability to spiders by the method similar to that used by Bristowe (1941). Among the most important factors on which the availability depends he names the distribution of the prey and the period of their occurrence (season, time of the day) as well as the size of the web and the way it is arranged. In his paper Turnbull (1960a) gives most detailed description of a very important factor determining the availability of food, namely the manner of locomotion of the insects.

The food of spiders, collected by me contained representatives of all the insect orders that had been found by using other methods of catching (Tabs. II and III). So the spider species discussed had the possibility to capture a large variety of forms, the most frequent were however very small insects in which the product of the length of the body by its width does not exceed 2 mm². The smallest of insects always constituted over 65% (65–97%) of the individuals captured by webs (Tab. IV). The insects included in the second size-class (the product ranging from 2.1 to 10 mm²) constituted at the most 10%; usually, each of the following size-classes constituted less than 10% of the food.

Average numbers of insects in webs and in comparative methods of catching during the period of uniform food

Tab. II

Captured arthropods	Stations and methods: station 1 — average numbers caught by: 10 spiders *A. cornutus*	station 2 — 10 spiders *A. cornutus*		10 sticky traps	10 sweep-net samples
	1961	1961	1962	1962	1961
1	2	3	4	5	6
Diptera	43.8	60.7	109.8	155.9	67.7
Tendipedidae	29.3	46.6	101.6	111.3	
Lycoriidae	1.8	1.1	0.6	9.6	
Limnobiidae	0.9	0.4	0.4	–	
Ephydridae	0.9	–	–	2.6	
Heleidae	0.5	1.4	0.6	3.0	
Itoniidae	0.3	1.1	1.6	3.0	
Melusinidae		+	0.5		
Scatopsidae	+		+	13.6	
Culicidae	+			+	
Stratiomyidae	+				
Cypselidae	+				
Anthomyiidae		+		+	
Sciomyzidae		+		+	
Chloropidae		+		+	
Empididae		+			
Phoridae			+		
Cyrtidae			+	+	
Fungivoridae			+	+	
Bibionidae			+		
Dolichopodidae				3.3	
Other families				0.4	
Homoptera-Auchenorrhyncha	0.1	–	0.1	30.2	15.0
Aphidoidea	3.9	11.1	9.5	23.2	1.7
Psyllodea	–	–	+	–	–
Hymenoptera	0.5	1.6	1.1	3.5	4.0
Braconoidea	+	0.7			
Cynipidae	+				
Apidae	+		+		
Formicidae			+		
Coleoptera	0.5	0.4	0.1	8.0	14.3
Plateumaris consimilis (Schrank)	+				
Staphylinidae	+	+		+	
Malachius marginellus Oliv.		+			
Ancmala sp.			+		

Tab. II cont.

1	2	3	4	5	6
Hydrophilidae			+		
Thysanoptera	$\boxed{0.7}$	$\boxed{0.4}$	$\boxed{7.1}$	0.8	–
Acridoidea	–	–	–	1.0	0.3
Heteroptera	–	–	+	1.2	2.3
Psocoptera	+	–	–	+	–
Neuroptera	–	–	–	+	–
Trichoptera	–	–	+	–	–
Lepidoptera	–	–	+	$\boxed{2.3}$	$\boxed{2.3}$
Araneae	–	–	$\boxed{0.2}$	–	$\boxed{33.7}$
Total number	$\boxed{50.1}$	$\boxed{76.0}$	$\boxed{134.0}$	$\boxed{226.1}$	$\boxed{141.3}$

\+ very small number of individuals,
– no representatives of the order,
framed numbers represent the total number of individuals captured, the remainder of numbers concern the fauna that could be identified more closely.

A similar size distribution is represented by the insects caught by the sticky traps. There too the most frequently captured were the smallest forms (46–73%), but the difference between the number of individuals in classes I and II was not very great. The proportions of the following size-classes (III-V) were more or less the same as on the webs. The fauna caught by the sweep-net consisted mainly of larger forms included in size-classes II and III; the size class I was poorly represented and constituted only 1.2–2.5%.

Two orders of the fauna occurring there can be unquestionably described as permanently very little available to the webs, these are *Heteroptera* and *Araneae*, much less frequent in the webs than in the environment (Tab. II and III). The availability of other groups varies with the periods.

Two very distinct periods of varying food availability can be observed – a period of uniform food, occurring usually in the spring or early summer (as observed in the spring of 1961 and in July, 1962) when the food is not varied but abundant, and a period of varied food during which the catching rate of the webs is lower, but the food is more diverse (as observed in the spring and summer of 1960 and in the summer of 1961).

A. Period of uniform food

During the period of uniform food the species composition of the fauna caught by the webs is much less differentiated than that of the fauna caught by the sticky traps. At this time the differentiation of the mobile fauna caught by the sticky traps (*Diptera* and *Homoptera-Auchenorrhyncha*), the number of individuals being the same, is about four times as great as the differentiation of the

Average numbers of insects in … of catching during the

Captured arthropods	station 1			
	10 spiders:		10 sticky traps	10 sweep-net samples
	A. cornutus	*A. quadratus*		
1	2	3	4	5
Diptera	1.5	7.8	128.9	165.0
Tendipedidae	0.6	1.7	1.8	
Lycoriidae	0.1	2.6	22.0	
Itoniidae	+	0.5	2.9	
Scatopsidae	+			
Trypetidae	+			
Clythiidae	+			
Sepsidae	+		+	
Tabanidae	+		2.1	
Larvaevoridae		+	+	
Chloropidae		+	+	
Anthomyiidae		+	11.0	
Muscidae		+	—	
Phoridae		+	+	
Dolichopodidae			7.0	
Fungivoridae			3.5	
Coenosiinae			1.7	
Sciomyzidae			2.1	
Cyrtidae			+	
Musidoridae			+	
Heleidae			+	
Psychodidae			+	
Dixiinae		+	+	
Limnobiidae			+	
Ephydridae				
Tipulidae			+	
Agromyzidae				
Asilidae				
Syrphidae				
Bibionidae				
Drosophilidae				
Melusinidae				
Homoptera-Auchenorrhyncha	0.9	1.0	30.4	29.8
Tettigella viridis (L.)	0.5	0.2	6.7	
Strongylocephalus agrestis (Fall.)	0.1	0.2	1.2	
Aphrodes bicinctus (Schrk.)	+			
Calligypona pallens (Stal.)	+			

webs and in comparative methods
period of varied food, 1961

Tab. III

Stations and methods							
station 2				station 3			
average numbers caught by:							
10 spiders:		10 sticky traps	10 sweep-net samples	10 spiders:		10 sticky traps	10 sweep-net samples
A. cornutus	*A. quadratus*			*A. cornutus*	*A. quadratus*		
6	*7*	*8*	*9*	*10*	*11*	*12*	*13*
1.3	12.2	96.5	101.0	3.0	23.6	186.0	103.0
0.3	0.8	+		0.4	2.6	5.0	
0.2	3.3	29.0		1.3	9.4	61.4	
+	0.8	6.7			0.9	10.7	
+	1.0	+			1.2		
		+					
		2.0				4.0	
		1.4				+	
	+	+				+	
		13.4		+	+	21.8	
	+	+		+	+		
		3.7				7.4	
		4.1				6.7	
		1.9			+	16.1	
+		1.3				+	
+		1.9		+			
+		+					
+	+				+		
	0.3						
						+	
	0.3	+		+	0.9	3.7	
						+	
	+	+		+		+	
	+						
	+						
				+		+	
				+			
						+	
		0.9				+	
0.3	1.0	36.6	43.5	0.5	2.1	18.3	33.8
	+	5.6			+	1.2	
		6.3				+	
+		1.8		+	+	1.6	
		+		+		2.2	

1	2	3	4	5
Megamelus notula (Germ.)	+		2.8	
Notus flavipennis (Zett.)		0.5	5.2	
Cicadula sp.			0.8	
Metalimnus formosus (Boh.)			2.1	
Palus costalis (Fall.)			1.0	
Conomelus sp.				
Lepyronia coleopterata (L.)				
Kelisia ribauti Wagn.				
Aphrophora salicina (Goeze)				
Arthaldeus pasquellus (Fall.)				
Neophilaenus lineatus (L.)				
Macrosteles sexnotatus (Fall.)				
M. opacipennis (Leth.)				
Philaenus spumarius L.				
Euconomelus sp.				
Euscelis obsoletus (Kbm.)				
Athysanus argentatus (Fabr.)				
A. quadrum (Boh.)				
Aphidoidea	0.4	1.7	–	–
Psyllodea	+	–	–	–
Hymenoptera	0.5	1.7	12.2	3.7
Proctotrupoidea	+	0.5		
Braconoidea	0.2	0.7		
Cynipidae	+	+		
Apidae	+			
Ichneumonidae		+		
Formicidae				
Coleoptera	0.2	–	9.6	13.2
Staphylinidae	+			
Curculionidae	+			
Anisosticta sp.	+			
Phaedon cochleariae (F.)				
Haltica sp.				
Thysanoptera	0.2	–	–	–
Acridoidea	+	0.3	0.6	20.0
Anisoptera	+	–	–	–
Heteroptera	+	–	+	1.8
Psocoptera	–	–	–	–
Neuroptera	–	–	–	–
Trichoptera	–	–	0.5	–
Lepidoptera	+	–	1.5	2.0
Araneae	–	+	2.4	27.6
Theridion sp. juv.		+		
Araneus sp. juv.				
Lycosa sp. juv.				
Total number	4.4	13.1	186.1	263.1

Explantations as for Table II.

Tab. III cont.

6	7	8	9	10	11	12	13
				+			
	+	1.4				+	
		1.5		+		1.1	
					+		
+	+						
+						+	
+		0.6				1.6	
+	+						
	0.2	2.9				+	
	0.2	3.7				+	
	+	1.5				1.3	
		2.6				+	
		1.3				+	
		2.1					
		1.4				+	
		1.0.				+	
						+	
0.3	1.5	–	–	0.5	0.9	–	0.2
–	–	–	–	–	–	–	–
0.2	0.9	12.2	5.8	0.5	1.5	7.9	1.9
0.1					+		
+	0.2			0.2			
	0.2			0.2			
				+			
+				+			
0.2	0.7	4.8	10.7	0.2	+	6.3	6.7
	+						
+							
	+						
+	0.7	–	–	+	1.8	–	–
–	0.8	5.5	23.2	+	–	6.0	29.0
–	–	–	–	–	–	+	–
–	0.1	0.6	59.8	–	–	+	15.9
–	+	–	–	–	–	–	–
–	–	–	0.7	–	–	+	0.1
+	0.2	–	+	–	–	–	0.1
0.1	–	0.5	2.5	–	–	3.4	1.9
+	+	1.0	66.5	+	–	0.5	22.5
	+			+			
+							
3.4	19.9	157.7	313.7	4.7	29.9	228.4	215.1

Differentiation of body size of insects in the various methods of catching, in per cent. 1961

Tab. IV

Size classes (product of length by the width of the body in mm²)		sweep-net	sticky traps	webs of *A. cornutus*	
Period of uniform food					
I	0–2	1.2	73.4	97.2	
II	2.1–10	66.4	18.5	2.2	
III	10.1–20	22.9	7.9	0.5	
IV	20.1–50	0.4	0.2	0.1	
V	>50	9.1	–	–	
Period of varied food					
Size classes (product of length by the width of the body, in mm²)		sweep-net	sticky traps	webs of: *A. cornutus*	webs of: *A. quadratus*
I	0–2	2.5	46.1	65.0	80.6
II	2.1–10	57.8	32.4	10.5	10.7
III	10.1–20	16.7	16.9	17.5	3.5
IV	20.1–50	6.6	2.6	5.5	2.8
V	>50	16.4	2.0	1.5	2.4

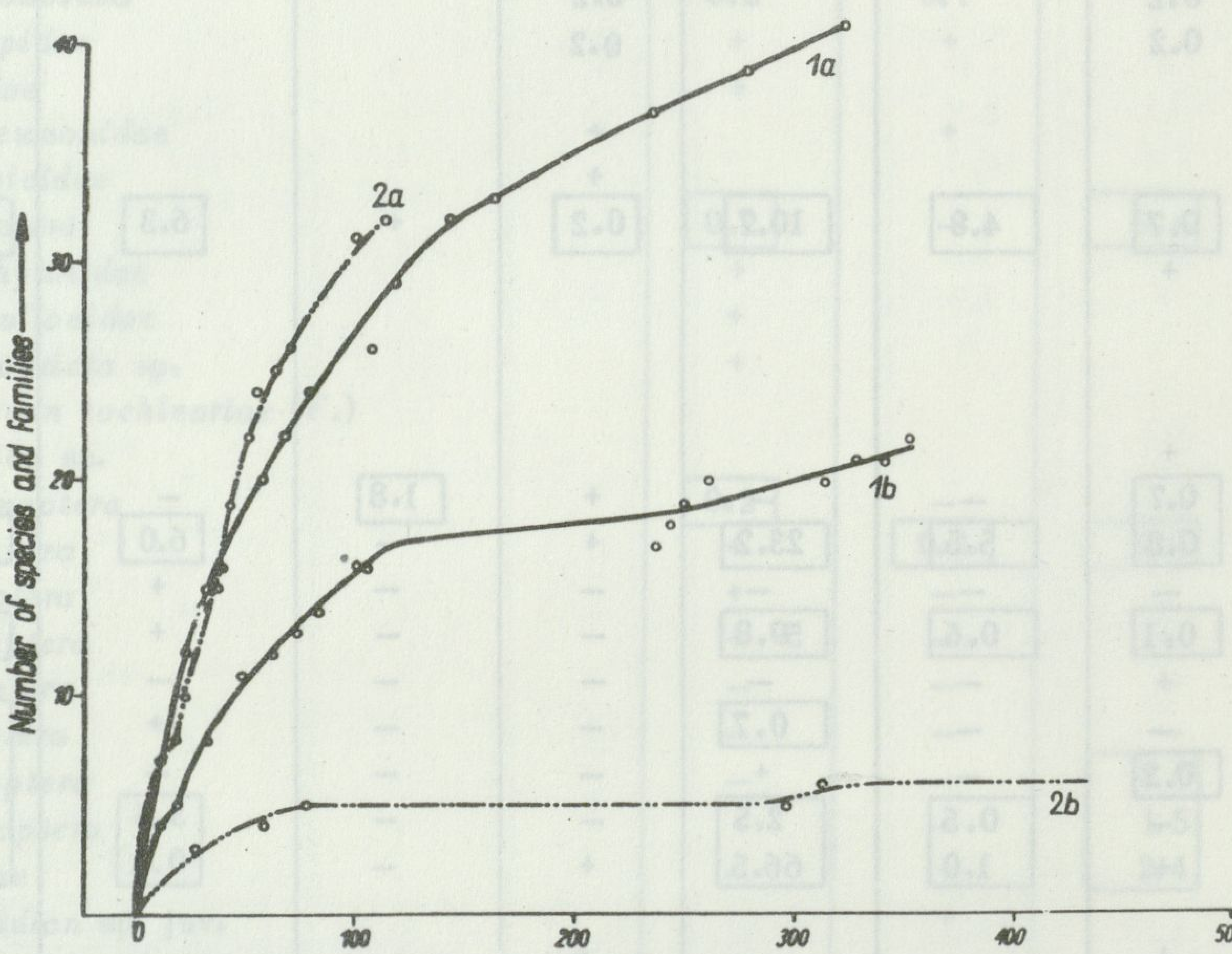

Fig. 5. Differentiation of the fauna of *Diptera* and *Homoptera-Auchenorrhyncha* in webs and on sticky traps

1 – sticky traps, *2* – webs, *a* – period of varied food, *b* – period of uniform food fauna caught by the webs (Fig. 5). In the following period, the period of varied food, no differences are found, in respect of the number of families or species, between the material collected from the webs and that from sticky traps (Fig. 5).

The period of uniform food is simultaneous with the mass emergence of *Tendipedidae* and with the migration of winged aphids to new environments. These two groups are the main components of the abundant food of this period, *Tendipedidae* constituting from 68.8 to 78.8% of the fauna caught by the webs, and the aphids from 7 to 14% (in different years and in various localities). These groups were also most numerous on the sticky traps, but there they constituted about 60%, that is to say less than in the webs where their proportion amounted to about 80% or even more.

In 1962 the average number of individuals of these two groups, caught by 10 spiders during 24 hours amounted to 111 and the number of individuals of these groups, caught by the sticky traps was 130.

For the comparison of the species composition of the fauna caught by the webs with that of the fauna caught by the sticky traps I used the preference index applied by Ivlev (1955) for the estimation of the food preference of fish.

$$E = \frac{r - p}{r + p}$$

r – per cent of the given group in the webs, p – per cent of the given group in sticky traps.

The index varies from –1 to +1. Values positive for groups whose contribution in the webs is greater than in the sticky traps, and negative for groups whose proportion in the material from the sticky traps is larger than in the food.

For the majority of groups the index for the period in question has negative values. The proportions of only two groups were in 1962 large in the webs than on the sticky traps – these were *Tendipedidae* and *Thysanoptera* (Fig. 8). The percentage of *Itoniidae*, winged aphids and parasitic *Hymenoptera* was in both methods similar. Comparatively frequent in the webs were, during the period of uniform food, *Lycoriidae*, *Heleidae* and *Limnobiidae*, but each of these families represented no more than 5% of the *Diptera* captured.

Among the fauna caught by the sticky traps there was a larger number of *Diptera* families – besides *Lycoriidae* (6% of *Diptera*) and *Heleidae* (2% of *Diptera*), there occurred also in similar numbers, *Scatopsidae*, *Dolichopodidae*, *Ephydridae*, i.e. families that were very infrequent or missing in the webs at this time. Similarly, *Auchenorrhyncha* and *Coleoptera*, though relatively numeorus on sticky traps, were hardly ever caught by the webs (Fig. 6).

As can be concluded from the data mentioned above, the uniformity of food during the period discussed is not the result of a real absence of the various groups – the mobile fauna found in the meadow is varied, but only certain part of it is available to the webs.

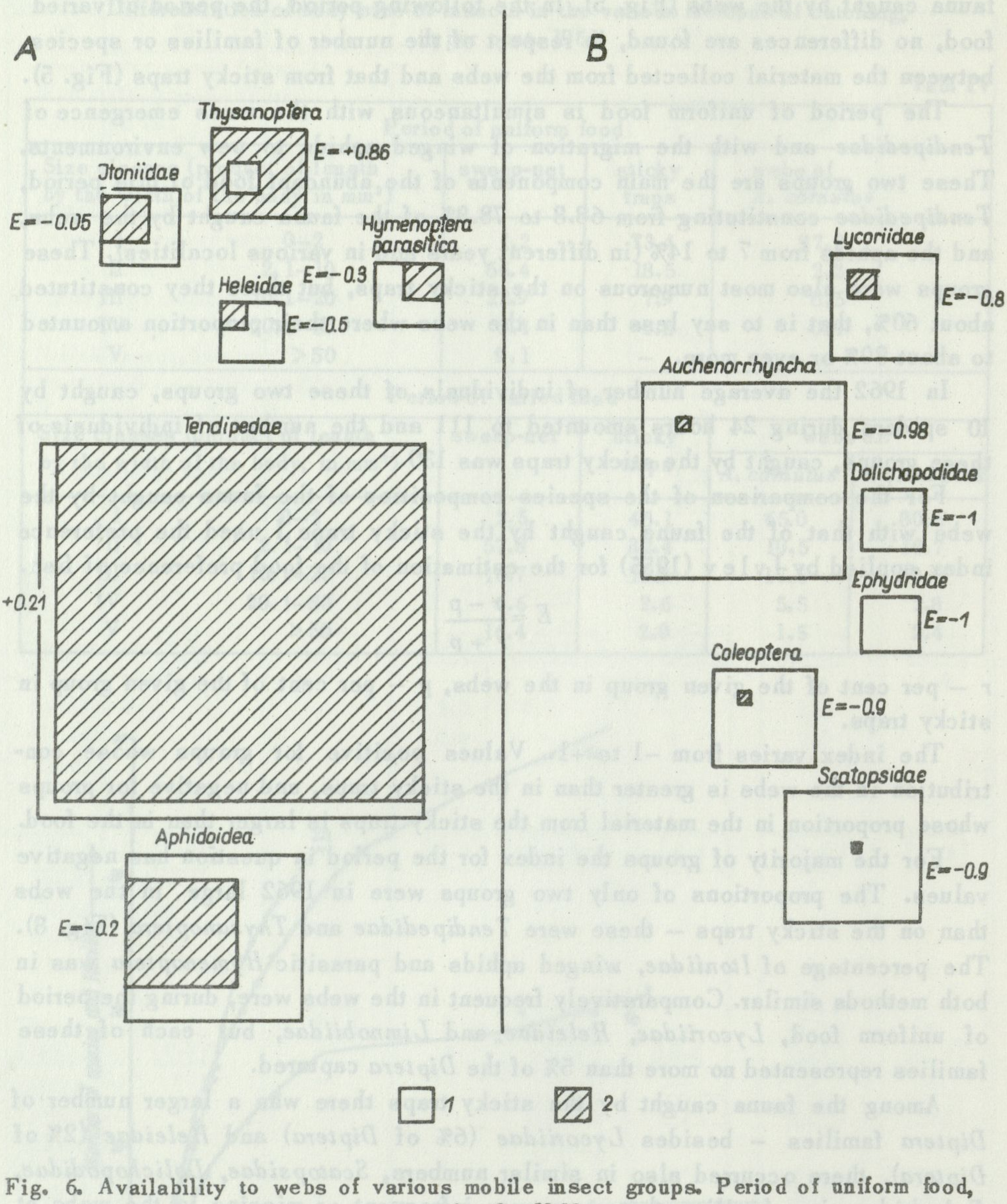

Fig. 6. Availability to webs of various mobile insect groups. Period of uniform food, station 2, 1962

A – fauna available to webs and sticky traps, *B* – fauna available mainly to sticky traps, *1* – 1 individual caught by 10 sticky traps during 24 hours, *2* – 1 individual captured by 10 spiders *A. cornutus* during 24 hours, *E* – preference index

B. Period of varied food

During the period of varied food none of the insect groups is so abundant in the webs as in the preceding period, but the composition of the fauna is much more varied.

The composition of the food of the two spider species under observation and the size distribution of the individuals captured are similar (Fig. 7, Tab. IV).

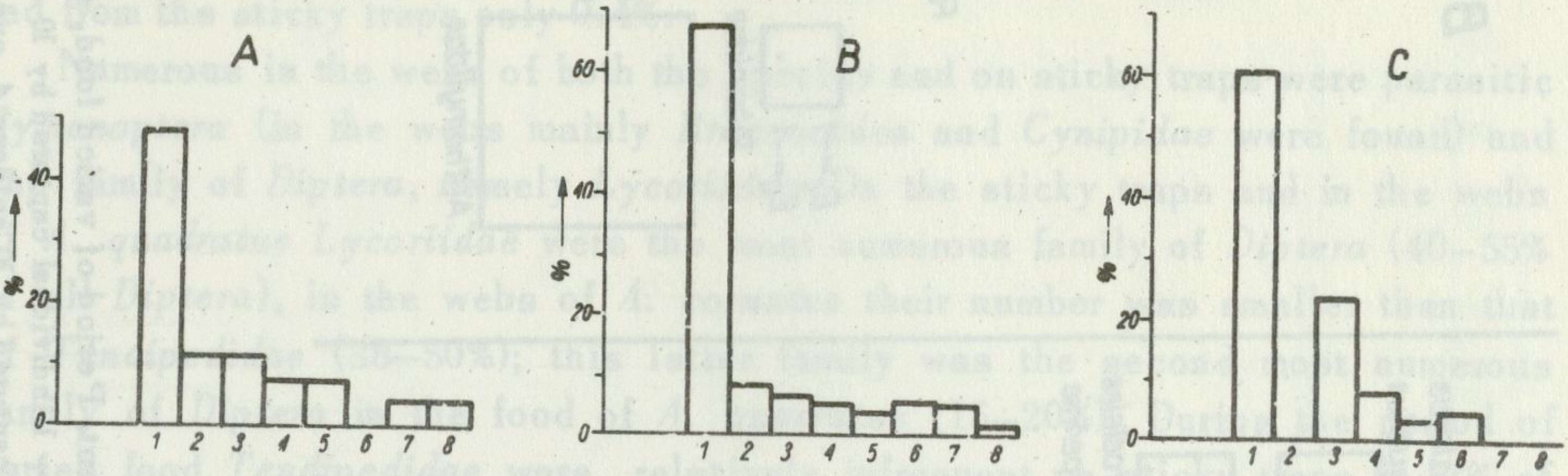

Fig. 7. Species composition of the fauna caught by webs and sticky traps. Period of varied food, station 2

A – webs of *A. cornutus*, *B* – webs of *A. quadratus*, *C* – sticky traps, *1* – *Diptera*, *2* – *Aphidoidea*, *3* – *Homoptera-Auchenorrhyncha*, *4* – *Hymenoptera*, *5* – *Coleoptera*, *6* – *Acridoidea*, *7* – *Thysanoptera*, *8* – *Trichoptera*

When arranged according to their decreasing contribution, insect groups captured in the largest numbers in the food of the two species they were found to occur oftenest in the same order. There occurred of course certain shifting in the contribution of the groups represented by small number of individuals, for instance in the food of *A. quadratus Acridoidea* were comparatively more numerous (4.3%) than in the food of *A. cornutus*, this does not however change the principal, considerable similarity in the composition of the food of both the species. The preference index for both the spider species, in relation to the same insect groups, was also, nearly always, of a similar value (with the exception of *Coleoptera* for which the index was found to be positive in *A. quadratus* and negative in *A. cornutus*, Fig. 8). As in *A. cornutus* during the preceding period, in the webs of both species comparatively frequent were *Tendipedidae*, winged aphids, *Itoniidae* and *Thysanoptera*. Preference index was for these groups positive, approaching +1 (Fig. 8). The per cent share of these groups in the webs considerably exceeded their contribution on the sticky traps. In spite of the fact that the composition of the exploited populations was much richer in comparison with the period of uniform food, the webs of both the species retained a positive preference in relation to those groups which were most frequent in the webs of *A. cornutus* during the preceding period. The abundance of the majority of these groups in the environment decreased considerably so that they

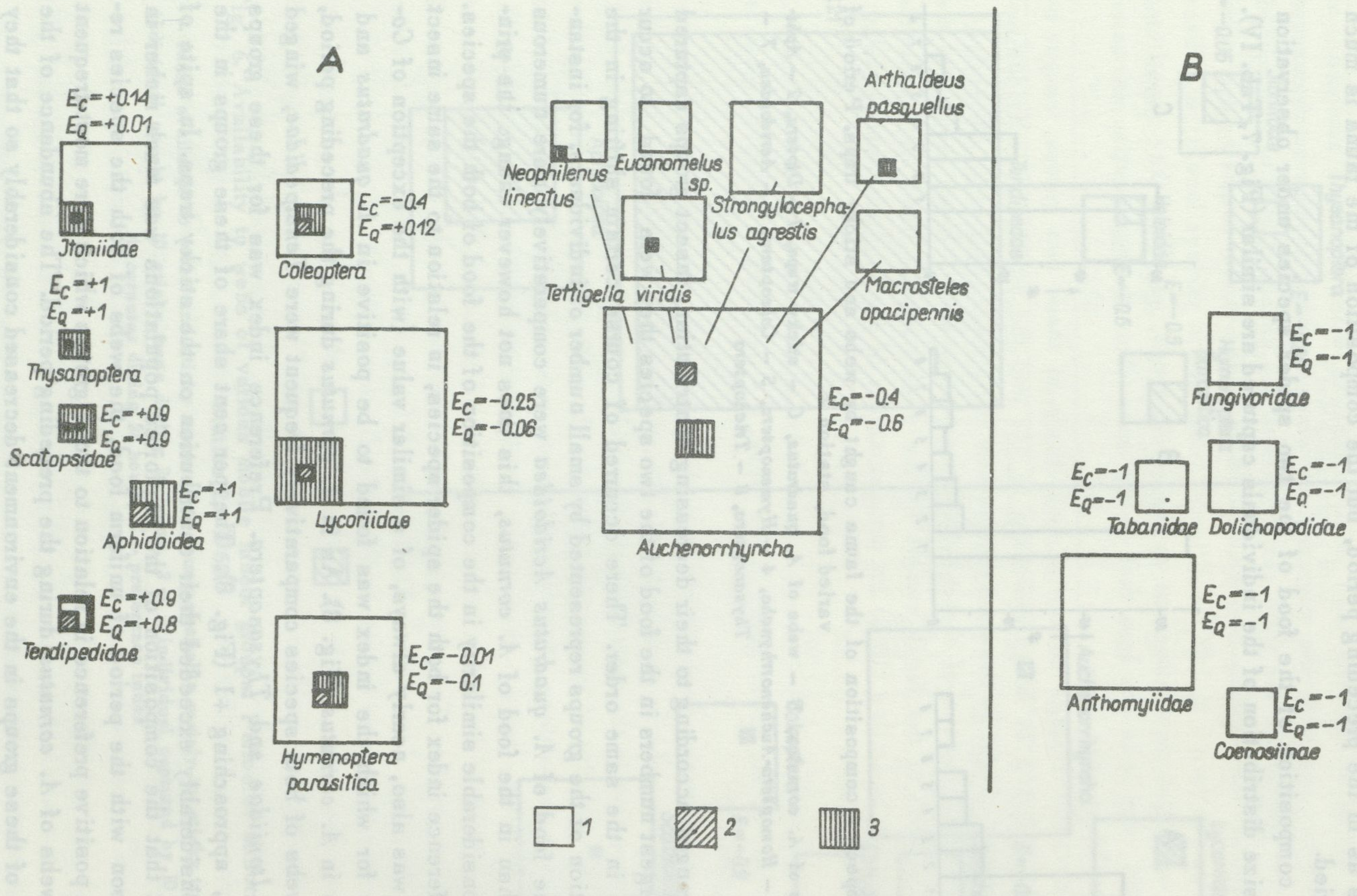

Fig. 8. Availability to webs of various mobile insect groups in the environment. Period of varied food, station 2. 1961
A – fauna available to webs and sticky traps, *B* – fauna available mainly to sticky traps. *1* – 1 individual captured by 10 sticky traps during 24 hours, *2* – 1 individual captured by 10 spiders *A. cornutus* during 24 hours, *3* – 1 individual captured by 10 spiders *A. quadratus* during 24 hours

hardly ever occurred on the sticky traps, much smaller was also the number of individuals captured by the spiders. The average catching rate of the spiders in relation to the groups which were most numerous in the preceding period – *Tendipedidae* and *Aphidoidea* – decreased about 95 times. However, in view of the general decrease in the numbers of prey they continued to be an important component of the food, and in the webs of *A. cornutus* at station 2 they constituted jointly 22%, in the food of *A. quadratus* 13% and among the fauna collected from the sticky traps only 0.4%.

Numerous in the webs of both the species and on sticky traps were parasitic *Hymenoptera* (in the webs mainly *Braconoidea* and *Cynipidae* were found) and one family of *Diptera*, namely *Lycoriidae*. On the sticky traps and in the webs of *A. quadratus Lycoriidae* were the most numerous family of *Diptera* (40–55% of all *Diptera*), in the webs of *A. cornutus* their number was smaller than that of *Tendipedidae* (38–50%); this latter family was the second most numerous family of *Diptera* in the food of *A. quadratus* (15–20%). During the period of varied food *Tendipedidae* were relatively infrequent on sticky traps (1–3% of *Diptera*). But a number of *Diptera* families which were never caught in the webs were found in large numbers on sticky traps. These were *Anthomyiidae* (15–21% of *Diptera*), *Dolichopodidae* (5–11%), *Fungivoridae* (about 6%), *Coenosiinae* (3–11%) and *Tabanidae* (about 3%) (Fig. 8). Species of these families were caught on the sticky traps oftener than *Tendipedidae*, very numerous in the webs.

In the period of varied food the contribution of *Auchenorrhyncha* and *Coleoptera* in the webs increased considerably in comparison to the preceding period. Although the preference index in relation to these groups was still negative, its value was much higher than in the preceding period, when it approximated – 1.

As has been mentioned, the prey caught by the webs during the period of varied food is as diverse as that caught by the sticky traps (Fig. 5). The main difference in comparison to the sticky traps lies in the fact that *Tendipedidae*, *Aphidoidea* and *Thysanoptera*, being still an important component in the webs, were hardly ever caught by the sticky traps. The webs also recorded a considerable decrease in abundance of the species representing these groups, but not to that extent as the sticky traps method. However, a number of *Diptera* families, as in the previous period, did not get into the webs.

4. THE INFLUENCE OF VARIATIONS IN THE ABUNDANCE OF FAUNA ON THE CATCHING RATE OF THE SPIDERS AND THEIR WEBS

The web mechanically catches all the insects of the appropriate size which in their flight encounter its surface. It can therefore be presumed that an important factor, having an influence on the number of individuals caught by the webs, is the number and the mobility of the insects in the environment.

The kinds of influence on the webs of the following factors have been considered: a) changes in the abundance and mobility of the insects found in the same vegetation layer as the spiders, and particularly the changes in the species composition and the numbers of *Diptera*, the most numerous order in the webs and b) changes in the catching rate of the spiders, due to changes in the environment (hay-making).

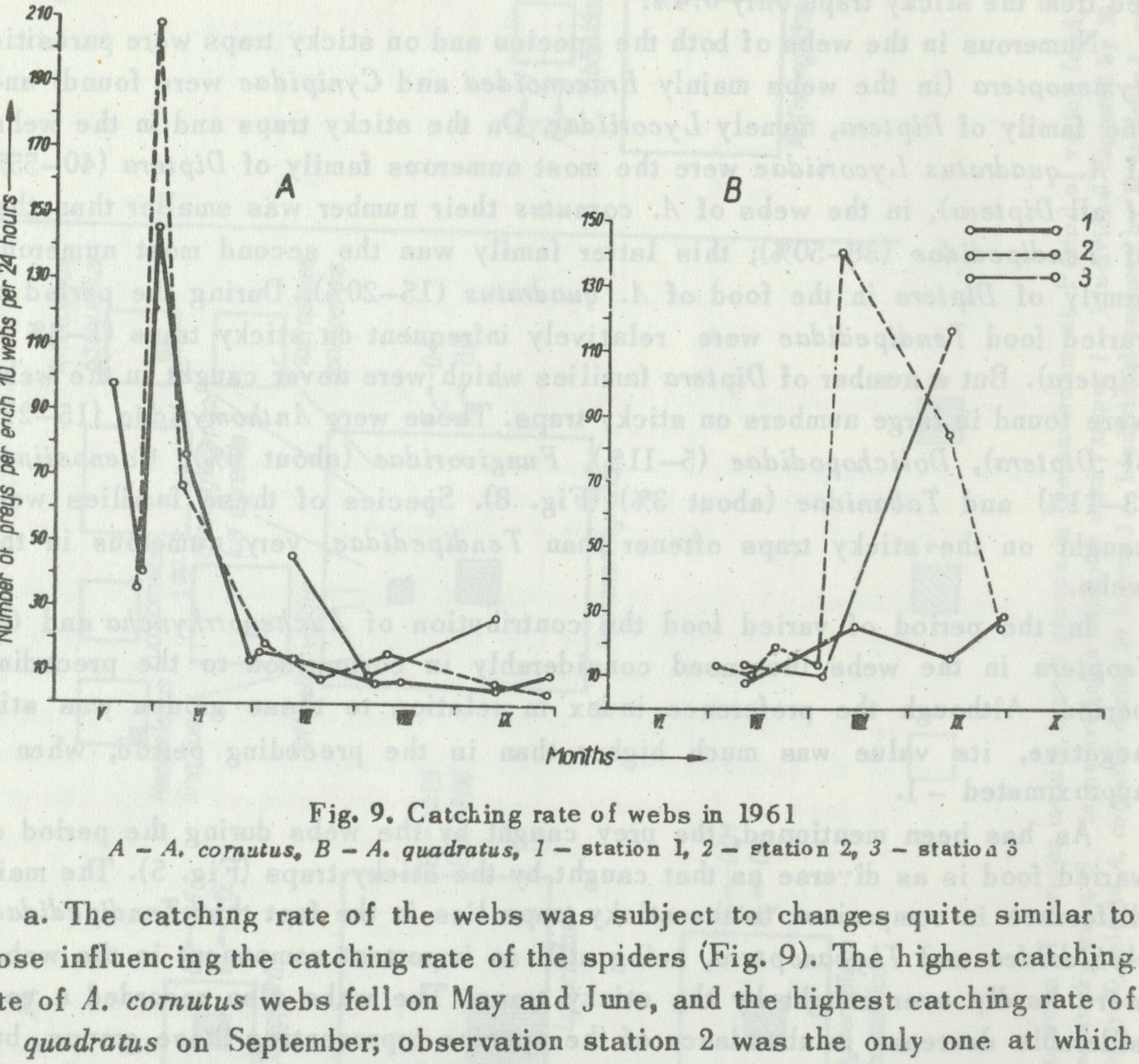

Fig. 9. Catching rate of webs in 1961
A – A. cornutus, B – A. quadratus, 1 – station 1, *2* – station 2, *3* – station 3

a. The catching rate of the webs was subject to changes quite similar to those influencing the catching rate of the spiders (Fig. 9). The highest catching rate of *A. cornutus* webs fell on May and June, and the highest catching rate of *A. quadratus* on September; observation station 2 was the only one at which the catching rate of the webs increased as early as August, thus being different from the catching rate of the spiders.

The maximum abundance of insects was observed in July and the first half of August, so it was not simultaneous with the maximum catching rate of the spider webs (Fig. 10). In *A. cornutus*, the highest catching rate of the spiders and that of the webs were observed before the occurrence of the largest numbers of insects and in *A. quadratus* – after this period.

Maybe, a part of the fauna, though living in the same vegetation layers as

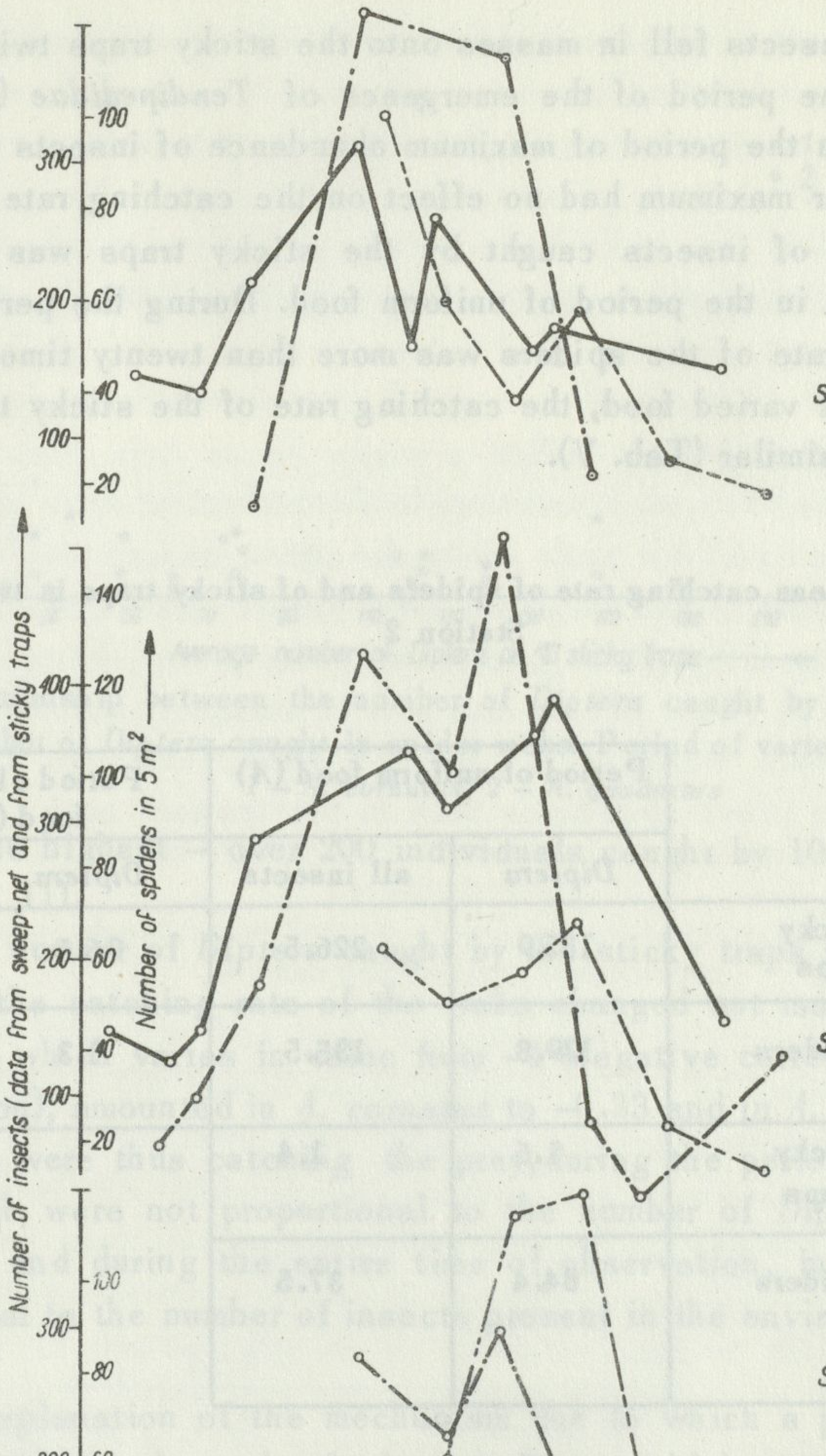

Fig. 10. Variations in the abundance of insects and of spiders in the environment. 1961
1 – number of insects, data from sweep-net, *2* – number of insects, data from sticky traps, *3* – number of spiders, data from the quadrate method

the spiders concerned, is not available to the webs and that is why there is no relationship between the abundance of all the insect fauna in the environment and the number of prey captured by the spiders.

Small, mobile insects fell in masses onto the sticky traps twice during the season – during the period of the emergence of *Tendipedidae* (the period of uniform food) and in the period of maximum abundance of insects (July, August, Fig. 10). The latter maximum had no effect on the catching rate of the webs, though the number of insects caught by the sticky traps was at that time nearly as large as in the period of uniform food. During the period of uniform food the catching rate of the spiders was more than twenty times higher than during the period of varied food, the catching rate of the sticky traps being in both these periods similar (Tab. V).

Comparison of mean catching rate of spiders and of sticky traps in two periods.
Station 2

Tab. V

		Period of uniform food (*A*)		Period of varied food (*B*)	
		Diptera	all insects	*Diptera*	all insects
Average number caught by 10:	sticky traps	155.9	226.5	96.5	157.7
	spiders	109.8	135.5	1.3	3.6
Increase of catching rate $\frac{A}{B}$	sticky traps	1.6	1.4		
	spiders	84.4	37.5		

The groups whose presence in the environment caused a high catching rate of the webs were first of all *Tendipedidae* caught, as has been mentioned, in masses only in the period of uniform food, and *Aphidoidea* – another group caught in large numbers in the webs, though forming a considerably decreased population. Variations in the abundance of these two groups in the environment have a great influence on the catching rate of the webs; an increase in the number of individuals of these groups is immediately recorded by the webs, whereas an increase of the populations of other insect groups was not observed to have a similar effect on the catching rate of the webs.

An attempt was made to find, for the period of varied food, a relationship between the average number of *Diptera* caught on the sticky traps and the number of individuals caught simultaneously by the webs. The abundance of *Diptera* was at that time subject to considerable variations, from the lowest value of

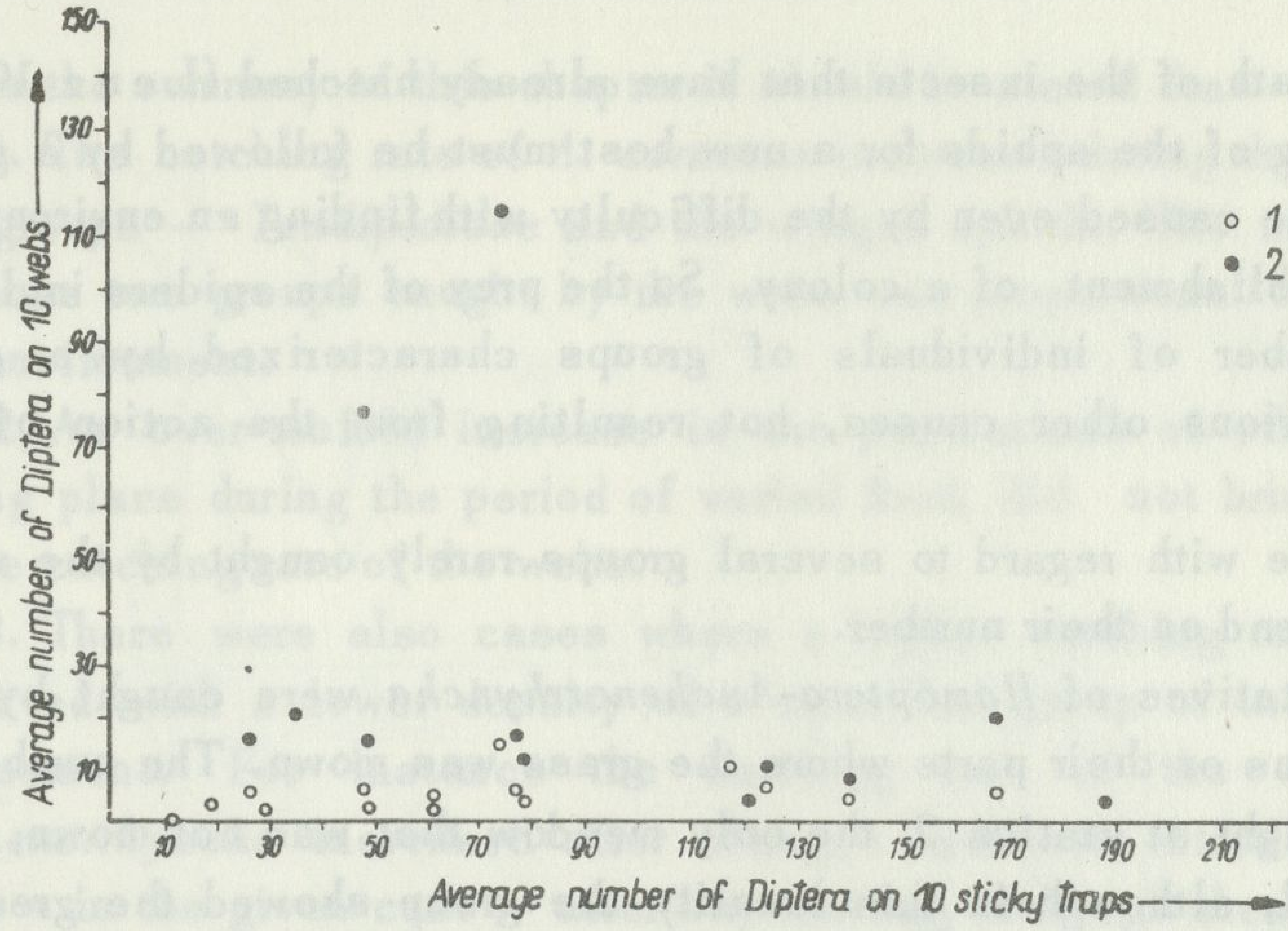

Fig. 11. Relationship between the number of *Diptera* caught by sticky traps and the number of *Diptera* caught in spider webs. Period of varied food, 1961
1 – *A. cornutus*, 2 – *A. quadratus*

about 25 to the highest – over 200 individuals caught by 10 sticky traps during 24 hours (Fig. 11).

While the number of *Diptera* caught by the sticky traps was at its maximum or minimum, the catching rate of the webs changed not much. The correlation coefficient ρ, which varies in value from -1 (negative correlation) to $+1$ (positive correlation), amounted in *A. cornutus* to -0.33 and in *A. quadratus* to -0.20.

The webs were thus catching the prey, during the period of varied food, in numbers which were not proportional to the number of *Diptera* caught by the sticky traps, and during the entire time of observation, in numbers that were not proportional to the number of insects present in the environment under observation.

For the explanation of the mechanism due to which a part of the fauna is slightly available to the webs further studies would be required. This may be due to physiological adaptations enabling some insects to actively avoid the webs; the insects may move in the space in such a manner that the line of flight will most frequently run across a zone in which there are no webs of these spider species or there may be some other factors acting. These mechanisms may be various but the result is that two groups, mainly, are available to the webs and are caught in large numbers during their great abundance in the environment. These are *Tendipedidae* and *Aphidoidea* at the stages which remain in the environment for a short time and which may be expected to show a considerable mortality regardless of the action of the predators. In *Tendipedidae* the larval stages cover 99% of the life span, while the adult stages that can be caught by the webs live for a very short time. In this group a great natural mortality can be observed. They also depend, to a large extent, on meteorological conditions. An unfavourable weather checks the hatching of *Tendipedidae* or causes a mass-death of the insects that have already hatched (Lenz 1962). Similarly, the looking of the aphids for a new host must be followed by a great mortality that may be caused even by the difficulty with finding an environment suitable for the establishment of a colony. So the prey of the spiders includes a considerable number of individuals of groups characterized by a great mortality due to various other causes, not resulting from the action of the predators.

The catching rate with regard to several groups rarely caught by the webs was not found to depend on their number.

b. Most representatives of *Homoptera-Auchenorrhyncha* were caught by the webs at those stations or their parts where the grass was mown. The number of *Auchenorrhyncha* caught at station 2, the only meadow that was not mown, was relatively very small, although in this locality the group showed the greatest abundance and mobility (Tab. III). In that part of station 1 where the grass was mown more individuals were caught by the webs, although the sweep-net materials indicated a lower abundance than in the unmown area (Tab. VI). The

Comparison of the number of *Homoptera-Auchenorrhyncha* caught in two parts of the meadow – mown and unmown

Tab. VI

Method		Part of station: mown	Part of station: unmown
Average number of *Homoptera* in 10 sweep-net samples		29.5	43.0
Average catching rate of spiders:	*A. cornutus*	0.24	0.00
	A. quadratus	0.17	0.07

comparison of the two parts of the meadow was made in the second half of August and in September, when the number of insects found in the webs was very small, but since a similar difference in the catching rate was observed in both the spider species, it seems that this difference may be regarded as a confirmation of the suggestion that hay-making increases the availability of *Homoptera-Auchenorrhyncha* to the webs. Hay-making results, first of all, in a change in the arrangement of the webs, the webs must then be built at a lower level and all at the same height. It may also evoke in this group of prey a tendency to spreading. In *Homoptera* the migratory tendencies vary considerably with the stages of the development of the populations (Andrzejewska 1960). It is probable that by disturbing the previous stratification hay-making increases the tendency to migration on which the availability of the insects to the webs depends to a considerable extent.

In the summary of this chapter it should be stated that:

1. The catching rate of *A. cornutus* increased during the mass-occurrence of the groups – *Tendipedidae* and the winged aphids. The number of individuals of those two groups caught by the webs was proportional to their abundance in the environment.

2. An over-tenfold increase in the populations of other *Diptera* families, taking place during the period of varied food, did not bring about an increase in the catching rate of the webs.

3. There were also cases where a higher catching rate of the webs was observed with a lower density of a specified group of insects present in the environment. For instance the catching rate of the webs in relation to *Auchenorrhyncha* increased after changes had been introduced to the environment – in the given case – after hay-making, although these caused a decrease in the number of this group.

5. THE INFLUENCE OF THE STATE OF THE POPULATION ON THE FEEDING RATE OF THE SPIDERS

So far the influence has been discussed of the changes in abundance and the composition of the insect fauna present in the environment on the average catching rate of the spiders. The catching rate depends also on the changes in the population of the predator, i.e. on how many individuals of the population are hunting the prey (feeding activity) and on the web-size distribution in the population, which in turn is related to the age of the individuals.

Variations in the activity of *A. cornutus*, and in particular those taking place at station 1, were to a some degree dependent on the variations in the temperature (Fig. 12 *A*). The most intense activity of the spiders was observed to occur at the beginning of August, when the temperatures were at their highest. About the middle of August, almost simultaneously with the falling of the temperature, the activity of the spiders decreased. Finally, at the end of September or early in October the activity almost died out which was also related to the lowest average temperatures of that period.

The maximum, almost 100 per cent, activity of the other species – *A. quadratus* – was not determined by any particular meteorological situation, it occurred at the time of maximum catching rate which usually took place in September. This is evidenced in a surprisingly accordant way by data from all the observation stations, collected during the years of study (Fig. 12). The webs of the other spider species investigated, or the sticky traps, did not record at that time any increase in their catching rate (Figs. 9 and 10). In *A. quadratus*, the maximum activity and the catching rate appeared to be simultaneous with

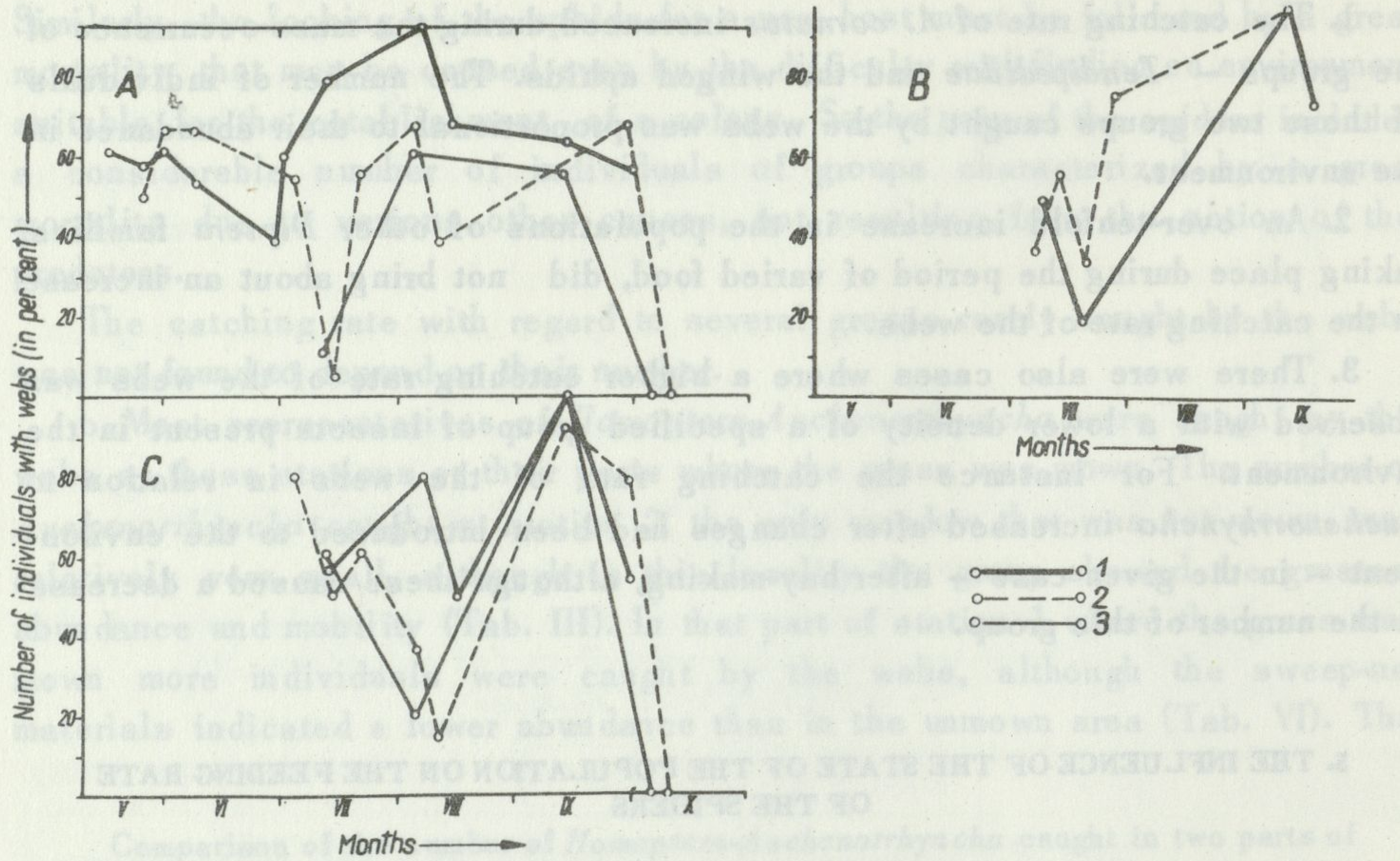

Fig. 12. Changes in the activity of spiders
A – *A. cornutus*, 1961, *B* – *A. quadratus*, 1960, *C* – *A. quadratus*, 1961, *1* – station 1, *2* – station 2, *3* – station 3

oviposition. The population was clearly increasing its catching rate during the time preceding the breeding season.

Most intense egg laying in *A. cornutus* population occurred in the spring, though cocoons were found almost throughout the vegetation season. In 1961 the period prior to intense oviposition was accompanied by the most intense catching rate of the spiders. In 1960 the maximum catching rate was shifted to July; however, the intense cocoon formation took place in the spring, with no changes. So in *A. cornutus* populations the breeding season was not always convergent with the time of intense catching.

The maximum catching rate of *A. cornutus* was not accompanied by an increased activity of the population; at the time of the highest rate of prey catching this activity approximated the average value, being about 60% (Fig. 12).

The relationship was analysed between the size of the web and the number of prey. Of course, the bigger the web the more and the bigger prey it can catch. As the size of the web depends on the size of the spiders that build it, the size of the individuals was regarded as the web-size index. The food of small and very small individuals and on the other hand that of the medium-size and adult individuals were considered separately. Variations in the average catching rate for these two age groups are presented separately (Fig. 13). The differences

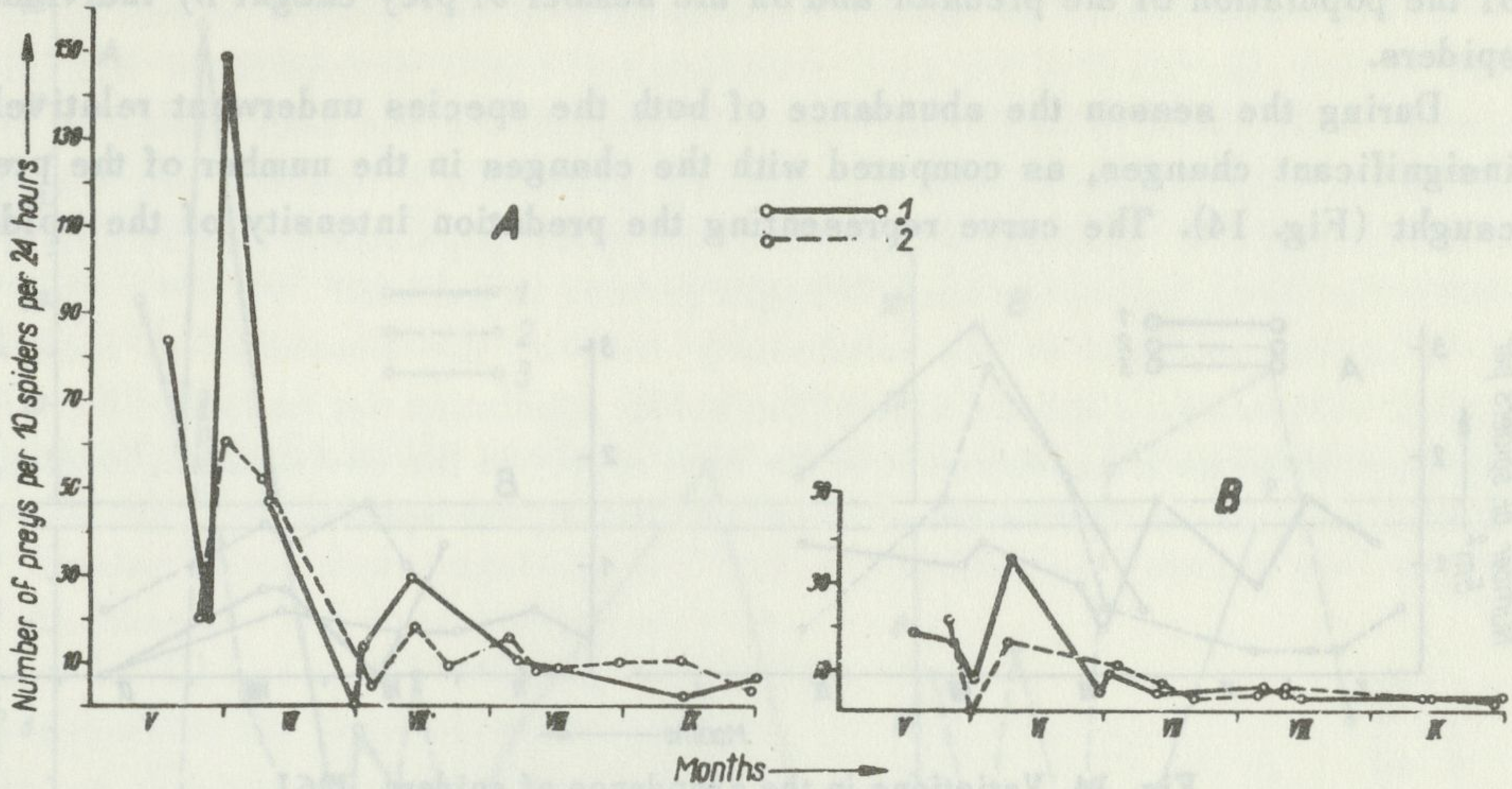

Fig. 13. Differences in catching rate between spiders of two age groups. *A. cornutus* 1961
A – medium age and adults, *B* – small and very small, *1* – station 1, *2* – station 2

in the catching rate between the small and the large individuals are particularly distinct in *A. cornutus* in which individuals of various ages occur simultaneously throughout the season. Indeed, small spiders used to catch fewer victims, but the course of the catching rate was in both groups very similar. The largest numbers of prey were found in the webs during May and June, whereas during the following months fewer victims got into both small and big webs. In *A. quadratus* small and large individuals occur simultaneously for only a short time between July and August. Here also a separate analysis of the two age-groups does not change the basic picture of the catching rate.

The condition of the populations, and its activity in particular, had a considerable influence upon the catching rate of the spider *A. quadratus*, the activity of the other species did not undergo any great changes and did not increase during the time of most intense catching.

6. INTENSITY OF PREDATION

I have so far considered the course of the variations in the number of the prey caught by individual spiders *A. cornutus* and *A. quadratus*. There still remains the problem of the changes in the intensity of predation (see chapter V, 1) that is to say, variations in the pression exerted upon the prey by each of the populations observed. The intensity of predation depends on the size of the population of the predator and on the number of prey caught by individual spiders.

During the season the abundance of both the species underwent relatively insignificant changes, as compared with the changes in the number of the prey caught (Fig. 14). The curve representing the predation intensity of the spider

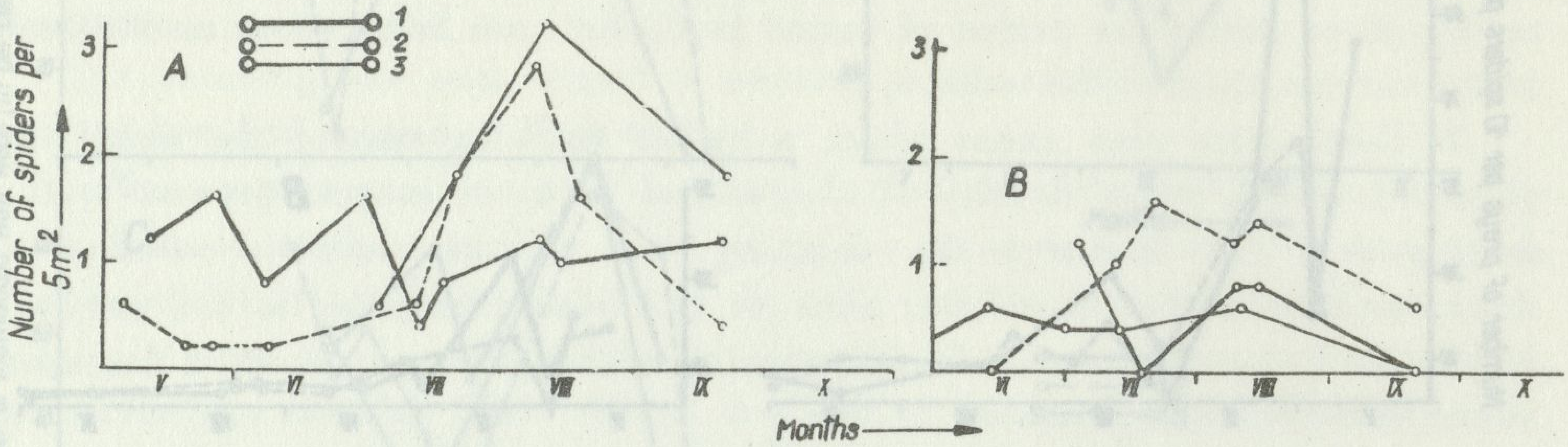

Fig. 14. Variations in the abundance of spiders, 1961

A – A. cornutus, B – A. quadratus, 1 – station 1, 2 – station 2, 3 – station 3

populations studied has a similar course as the curve showing the variations in the catching rate of individual spiders. The population of *A. cornutus* catches most victims in May and at the beginning of June, the population of *A. quadratus* in September (Fig. 15). The most intense predation of these populations is not simultaneous with the occurrence of the largest numbers of insects and their intense mobility in the environment. The greatest abundance of the insects is observed during the same period as the largest abundance of the spiders. The above concerns all the spiders living in the field layer and not only the two species discussed (Fig. 10). The number of all the spiders of this layer began to increase in June, its maximum occurred in July and August and in September the process of decreasing started (Fig. 10). The growth of the number of insects started at a later time, when the number of spiders was quite considerable. The period of maximum abundance and mobility of the insects entirely overlaped the period of maximum abundance of the spiders. This course was repeated in the areas under consideration which is a good evidence of its reality (Fig. 10).

Spring time during which the intensity of predation by *A. cornutus* populations was so considerable is at the same time the period of relatively small density of all the spiders present in the grass layer. Similarly, September during which the greatest predation intensity of the other species was observed is the period of decreasing density of all spider species. As the maximum density of the spiders took place during the time when the insects were most numerous, it may be presumed that the action exerted by them all together on the insects was at that time the strongest. If it were possible to sum up the action of all the spider species, it would probably appear that July and August are the months when the strongest action of the spiders on the density of insects is observed.

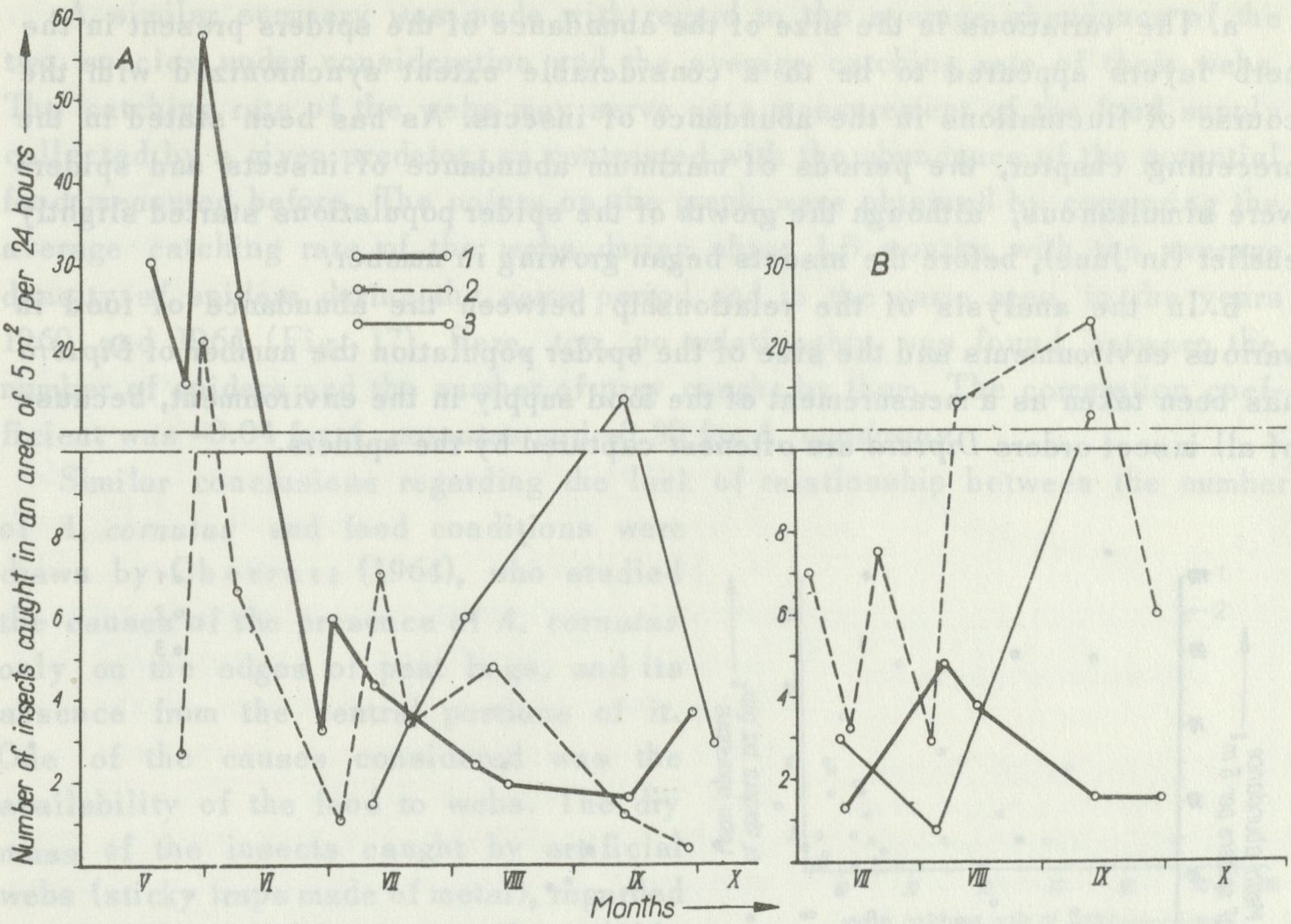

Fig. 15. Variations in predation intensity, 1961

For explanations see Fig. 14

In *A. cornutus* and *A. quadratus* the highest predation intensity lasted a relatively short time during the year. During that period the density of other spiders was relatively low. Probably, the strong action exerted by these species compensated at least in part for the weak, due to a low, at that time, density, action on insects of other spiders present in the field layer.

VI. ANALYSIS OF THE FACTORS DETERMINING THE SIZE OF SPIDER POPULATIONS

1. RELATIONSHIP BETWEEN THE NUMBER OF SPIDERS AND THE SUPPLY OF FOOD

So far only the influence of the spiders on the population of insects was discussed, whereas the other side of the predator-prey relationship, namely the determination of the density of spiders by the amount of food, was not considered.

The influence of the food supply on the size of the spider populations was searched for by: a) comparing the population dynamics of the spiders and insects in yearly cycles and b) comparing the abundance of spiders in environments differing in respect of the supply of food.

a. The variations in the size of the abundance of the spiders present in the herb layers appeared to be to a considerable extent synchronized with the course of fluctuations in the abundance of insects. As has been stated in the preceding chapter, the periods of maximum abundance of insects and spiders were simultanous, although the growth of the spider populations started slightly earlier (in June), before the insects began growing in number.

b. In the analysis of the relationship between the abundance of food in various environments and the size of the spider population the number of *Diptera* has been taken as a measurement of the food supply in the environment, because of all insect orders *Diptera* are oftenest captured by the spiders.

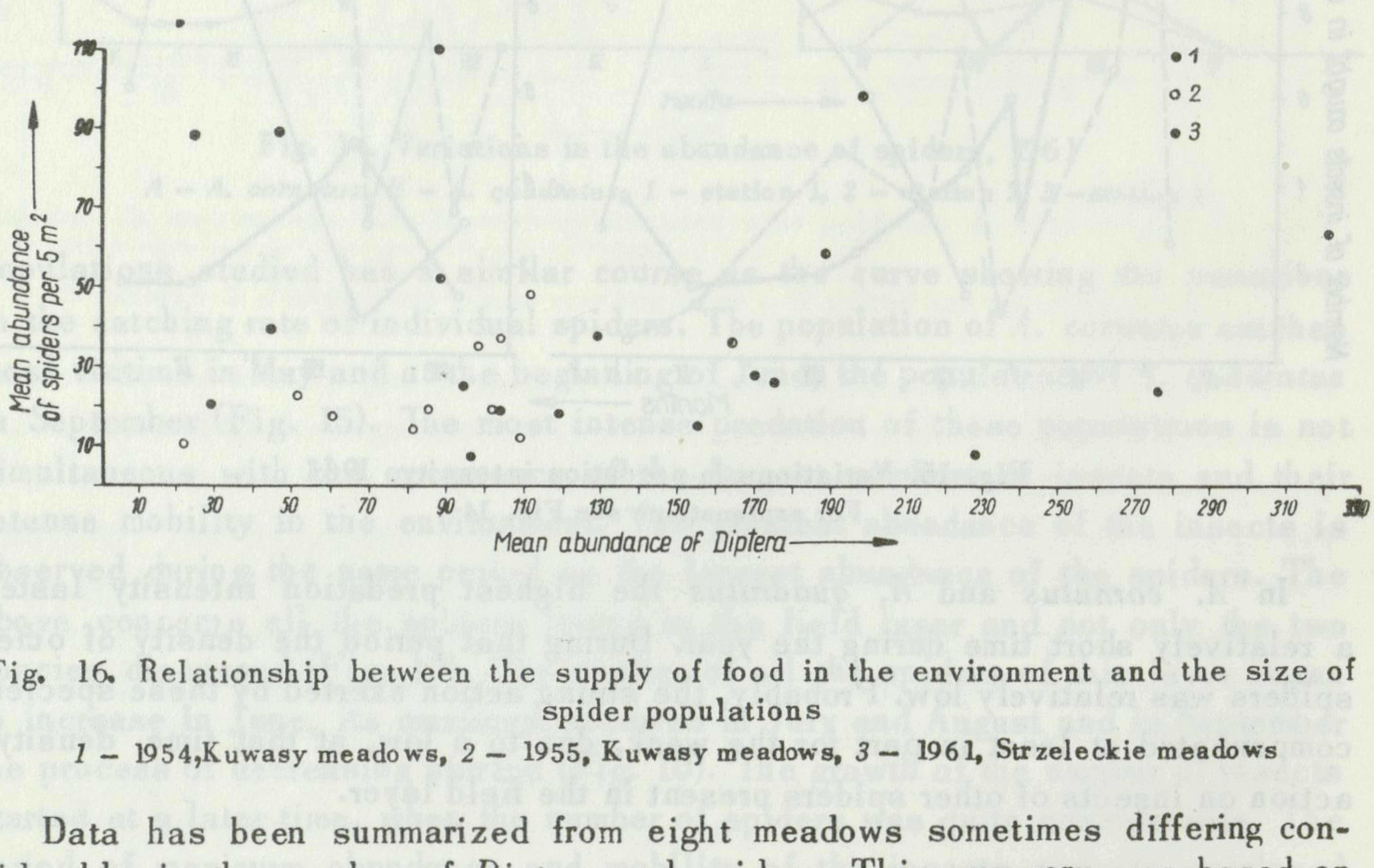

Fig. 16. Relationship between the supply of food in the environment and the size of spider populations

1 – 1954, Kuwasy meadows, *2* – 1955, Kuwasy meadows, *3* – 1961, Strzeleckie meadows

Data has been summarized from eight meadows sometimes differing considerably in the number of *Diptera* and spiders. This summary was based on materials collected between July and September in the years 1954 and 1955 in the Kuwasy meadows as well as evidence supplied by the observation carried out in the Strzeleckie meadows in 1961. The average number of *Diptera* in a specified month was each time compared with the average number of spiders occurring at this time in the same area (Fig. 16). Each of the mean values was calculated from at least 50 samples. The number of *Diptera* present in the environments under observation varied from about 20 to over 300 in particular series of sweep-net catches. With this range of variation in the number of *Diptera* there was no correlation between the abundance of the potential food and that of the spiders. The correlation coefficient calculated from the material collected in 1954 and 1955 amounted to –0.30, and that estimated from the material of 1961 – –0.15, thus being invariably negative.

A similar summary was made with regard to the average abundance of the two species under consideration and the average catching rate of their webs. The catching rate of the webs may serve as a measurement of the food supply collected by a given predator, as contrasted with the abundance of the potential food measured before. The points on the graph were obtained by comparing the average catching rate of the webs during about 1.5 months with the average density of spiders during the same period and in the same area, in the years 1960 and 1961 (Fig. 17). Here, too, no relationship was found between the number of spiders and the number of prey caught by them. The correlation coefficient was -0.04 for *A. cornutus* and +0.30 for *A. quadratus*.

Similar conclusions regarding the lack of relationship between the number of *A. cornutus* and food conditions were drawn by Cherrett (1964), who studied the causes of the presence of *A. cornutus* only on the edges of peat bogs, and its absence from the central portions of it. One of the causes considered was the availability of the food to webs. The dry mass of the insects caught by artificial webs (sticky traps made of metal), regarded as an index of the amount of available food, was in both environments similar.

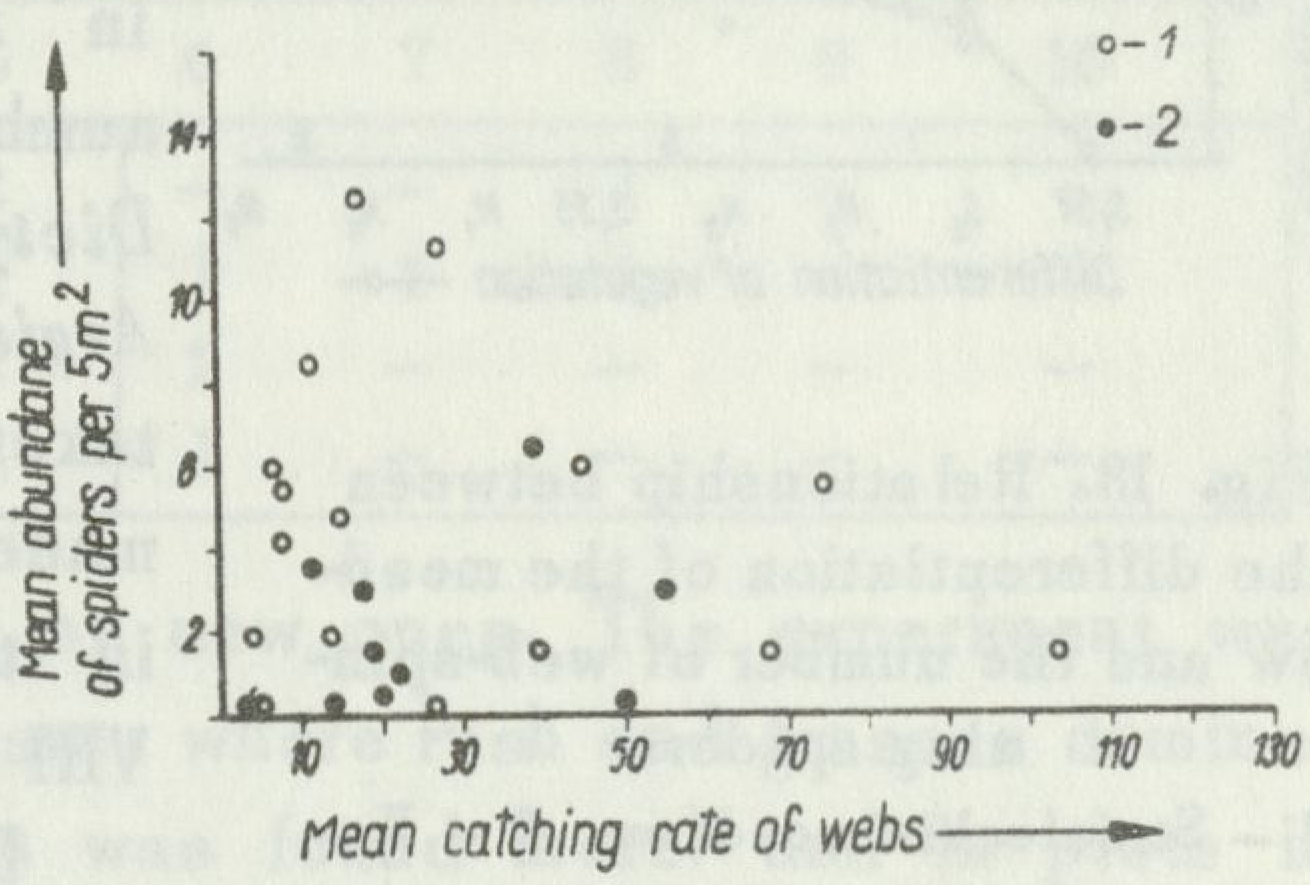

Fig. 17. Relationship between the catching rate of webs and the size of populations of the spiders
1 – *A. cornutus*, 2 – *A. quadratus*

Bristowe (1941) writes that there exists a close correlation between the abundance of the exploited populations and the size of spider populations. Such a correlation may, perhaps, be found if one is comparing a number of quite different habitats; however, it has not been observed within the range of food supply found in various meadows.

When compared over a yearly cycle, the variations in the number of spiders were found to be simultaneous with changes in the number of insects; when however different environments are compared, no relationship was found between the number of spiders and the food supply.

2. RELATIONSHIP BETWEEN THE NUMBER OF SPIDERS AND THE NATURE OF THE ENVIRONMENT

When the meadows were arranged according to vegetation structure, from most uniform meadows to those with diverse vegetation structure, a picture was obtained showing a gradual growth of the number of spiders with the increase in the diversity of the environment (Fig. 18).

The diversity of vegetation depends on the presence among grasses and sedges of dycotyledonous plant admixtures, especially of herbaceous perennials, on the occurrence side by side of plants differing in their habitus – their height, structure of inflorescences – due to which they do not form a compact field, but a mosaic with an uneven, multi-level surface. The nature of the vegetation determines the number of micro-habitats in the environment, suitable for making cocoons, retreats for living as well as webs.

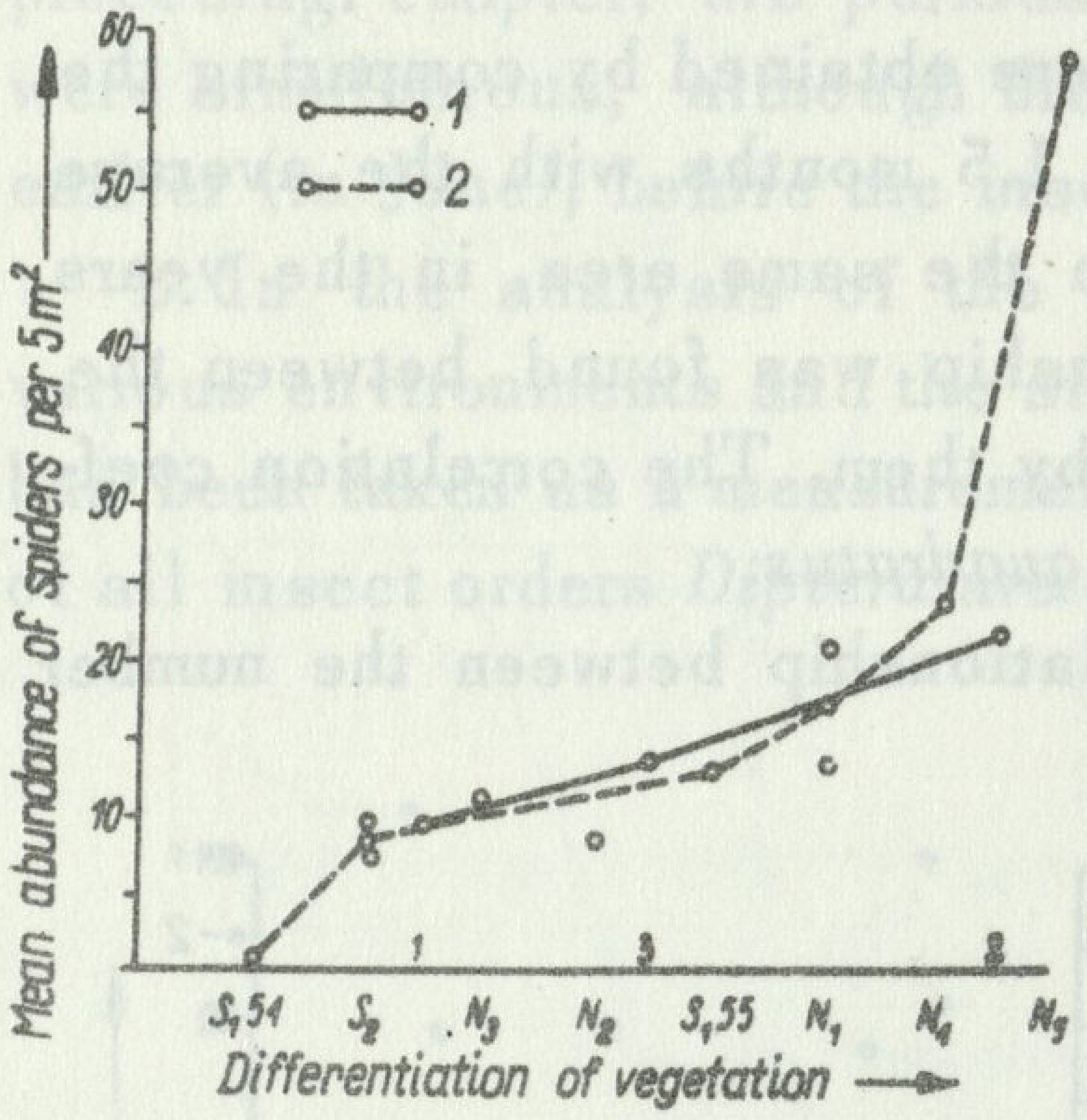

Fig. 18. Relationship between the differentiation of the meadow and the number of web-spinning spiders

1 – Strzeleckie meadows, 2 – Kuwasy meadows

In a search of a relationship between the number of spiders and the diversity of the environment the materials collected in 1954, 1955 and 1961 in 10 meadows at Kuwasy and in the Kampinos Forest were used. The number of the web-spinning spiders (species of *Dictynidae*, *Theridiidae*, *Tetragnathidae* and *Argiopidae*) found on herbaceous plants was taken into consideration. A comparison was made of the average density of these spiders in the meadows during three months – VII, VIII and IX.

In the Kuwasy and Strzeleckie meadows the same regularity was found – the smallest populations of spiders were found in uniform meadows, in spite of the exuberant vegetation, and the largest were those occurring in varied meadows. This relationship is confirmed by the investigations carried out by Mikulska (1955). In the sedge meadows situated near lakes the density of the spiders of the above-named families was lower than in the meadows covered by rich meadow vegetation. Duffey (1962) and Cherrett (1964) have reported that the habitus of the plants present in the meadow may have a significant influence on the number of webs.

The reality of the regularity was confirmed by the material collected in 1954 and 1955. The statistical significance of differences between the average number of spiders found in the meadows under observation was tested by using the Student's *t*-criterion for two independent samples (Fisz 1954). In all cases (meadow S_1 and N_1, S_2 and N_2, N_1 and N_5) statistically real differences were obtained at the level of significance of 0.01 ($t_{s_1N_1} = 5.2$ $t_{0.01} = 2.7$; $t_{s_2N_1} = 2.9$ $t_{0.01} = 2.7$; $t_{N_1N_5} = 7.7$ $t_{0.01} = 2.6$).

From the above-cited data it seems that in the meadows an important factor determining the size of the populations of the web-spinning spiders is the presence of suitable micro-habitats required for the building of webs, and at the same time providing shelter.

To prove the above conclusions two additional experiments have been carried out.

In the first experiment individuals of *A. cornutus* were removed from 10 plots, each of the surface of 1 m². After a week the spiders, that had settled in the meantime, were counted and taken away. The above procedure was repeated four times; each time the number of spiders was found to be approximately the same as during the preceding counting (Tab. VII). So the individuals that had been removed were subsequently replaced by new ones. The experiment was carried out at two areas at station 2, in an area where rush and grasses dominated (generally a higher density of spiders was found there) and in plots in another area where sedges dominated with some grasses admixed. In the last two plots (9 and 10) where the vegetation consisted of sedges alone no individuals of this species were found throughout the time of observation. Only during the first removal of the spiders was their number in most of the plots very low. Later on, levels of density, each characteristic of particular plot, were established, the characteristic density being maintained in spite of the periodical removing of spiders.

Number of individuals of *A. cornutus* in individual plots

Tab. VII

Dates of the removal of spiders	Dominance of rush					Dominance of sedges				
	plot number									
	1	2	3	4	5	6	7	8	9	10
25 VII	—	7	1	nest	2	—	—	1	—	—
31 VII	11	11	2	5	1	1	2	1	—	—
7 VIII	9	16	5	6	2	2	—	—	—	—
16 VIII	6	12	6	12	1	—	—	—	—	—

It seems therefore probable that a proportion of the population penetrates the terrain in search of free and suitable places and if it finds such places it settles at them.

The second experiment was carried out in 1960 (A. Kajak 1961) and repeated in 1961. In this experiment dried *Hypericum maculatum* Cr. plants were introduced to the meadows and the extent of their settlement by the spiders was subsequently observed. In 1961 the experiment was started in May. At station 1 it was continued till July and at station 2 for only 3 weeks. 50 plants were placed at station 1 and 20 at station 2. After a week the plants appeared to have been already populated, the extent of population being established and approximating the average population observed throughout the experiment. At station 2 in both years about 40% of the plants introduced were found to be settled down (Tab. VIII), at station 1, in the mown portion of this area, over 60%. *A. cornutus* constituted about 15% of the settling spiders.

Number of plants occupied by spiders, in per cent

Tab. VIII

Stations and years		Per cent of plants occupied after a week	after 3 weeks	average for the whole period
Station 1	1961	50.0	90.0	64.4
Station 2	1960	33.3	47.5	49.6
	1961	42.1	44.4	43.2

In both the above-discussed experiments the micro-habitats from which the spiders had been removed, were populated anew. This does not mean that the environments are already fully populated by spiders, for there always are free plants. In the grasslands studied by Duffey (1962) the number of spiders was small in comparison to the number of the plants that could be occupied. The average number of spiders was 1.2 individuals per 1 m^2 and the average number of plants 9.2 per 1 m^2. In the meadows investigated by me the number of free plants, in relation to the populated ones, is even greater. In spite of this, the evidence supplied by the experiments and the data relating to the number of spiders in various meadows suggest that the nature of vegetation is an important factor influencing the abundance of web-spinning spiders. In the web-spinning spiders the relationship between the living conditions, the conditions suitable for web building and the food conditions is of course particularly close. The presence of localities supplying sites suitable not only for making webs, but also for the location of these in areas where insects fly frequently seems to be an important factor, for although abundant, the insect fauna is otherwise unavailable. It is possible that due to this close relationship between the conditions favourable for web building and the food supplies no relationship was found between the number of spiders and the number of insects, when different environments were compared, although such a relationship was observed when changes occurring during the season in the same area were compared. The relationship between the number of spiders and the amount of food is not direct, but is modified by the conditions required for web-building, which may be favourable or unfavourable, depending on the environment.

VII. DISCUSSION

Those authors, who are of the opinion that predation is one of the important mechanisms controlling the number of animals, often consider two groups of predators – the stenophagic and polyphagic predators – separately (Voûte 1946, DeBach 1958, Huffaker and Kennet 1956, Itô, Miyashita and Sekiguchi 1962, Kaczmarek 1963).

It is often thought that only the former group – stenophagic predators – has an effective influence on the abundance of the prey since the course of the abundance of these predators or the intensity of their feeding entirely depend on the variations in the population density of the prey. This view is supported by numerous studies dealing with these specialized predators (or parasites) and showing their effectiveness in fighting the pests (De Bach 1958, Huffaker and Kennett 1956, Burnett 1960, Kot 1964 and others).

The authors who are concerned with the effect of the polyphages on the populations of the prey maintain that this group causes the greatest reduction in those populations which are just beginning to increase their abundance or have just begun to decrease it, but when the exploited population is in the phase of its highest density, the reduction per cent lowers. The above is stated, which is particularly worth emphasizing, by the authors dealing with various animal groups, who interpret the phenomenon itself in various ways (Tothill 1922, 1923, Betts 1955, Holling 1959, 1961, Tinbergen 1960, Itô, Miyashita and Sekiguchi 1962). During her study on the effect of various predators on the size of the aphid populations Gałecka (Breymeyer et al. 1964) found that the polyphagic predators (spiders) occur in the field already during the first stage of the development of the aphid population, when the specialized predators are almost absent. Acting during this first stage the polyphages may have an influence on the further course of population dynamics of the aphids.

Some authors investigating the importance of polyphages for the biocenosis (and not for the reduction of particular populations) arrive at the conclusion that these may prevent the insect populations from attaining great densities due to which they are important as a factor maintaining the stabilization of the community (Voûte 1946, MacArthur 1955, Kaczmarek 1961, 1963).

Similar conclusions concerning the role of the polyphagic predators, like spiders, can be drawn from the material gathered during the present investigation. In the meadows under observation spiders were present throughout the year. They started growing in number very early – already before the increasing of the insect populations. The two spider species studied in detail captured most prey not during the time of the highest density of insects, but earlier or later than that.

As has been demonstrated, the largest were the numbers of those insects in which a considerable mortality could have been expected – ephemeral ones, like the adult individuals of *Tendipedidae*, or migrating, like the winged aphids. Their numbers in the webs were proportional to the size of their population in the environment. Variations in the abundance of several other insect groups had no effect on the catching rate of the webs, though these insects were sometimes caught in quite large numbers by the sticky traps. Catching by the spiders of forms ephemeral for a given environment (male insects) was observed also by other investigators (Hobby 1930, 1940, Parmenter 1953).

From this data it can be presumed that the spider species which were investigated were supplementing the action of the stenophagic predators. They acted in periods when specialized predators were few in number (because these were the periods of low density of the exploited population) and they acted mainly on the migratory developmental stages of insects whose presence in the biocenosis was short (and which in this connection may not have had many specialized enemies).

On the other hand, it can be supposed that the action of all the spiders living in the field layer is most intense at the time when the density of insects is at its highest.

So the action of the spiders on the insects is on the whole fairly intense throughout the season. It is not restricted, like the action of the stenophages, to the periods of an increased abundance of the prey, it is no doubt to a lesser degree dependent on this abundance, being therefore less effective.

REFERENCES

1. Andrzejewska, L. 1960 – Inactivity of a stabilized *Tettigella viridis* L. population in resettling of environments – Bull. Acad. pol. Sci. cl. II, 8: 581–585.
2. Barnes, H. D., Barnes, B. 1955 – The spider population of the abstract broomsedge community of the Southeastern Piedmont – Ecology 36: 658–666.
3. Betts, M. M. 1955 – The food of titmice in oak woodland – J. anim. Ecol. 24: 282–323.
4. Bilsing, S. W. 1920 – Quantitative studies on the food of spiders – Ohio J. Sci. 20: 215–298.
5. Bonnett, P. 1930 – La mue, l'autotomie et la régenération chez les Araignées avec une étude des Dolomèdes d'Europe – Thèses Fac. sci. Toulouse 44: 1–464.
6. Breymeyer, A., Gałecka, B., Kajak, A., Łuczak, J. 1964 – Różne aspekty oddziaływania drapieżcy na liczebność ofiar i warunki modyfikujące to działanie – Pol. Pismo ent., B 1/2: 79–87.
7. Bristowe, W. S. 1941 – The comity of spiders. II – London, 560 pp.
8. Burnett, T. 1960 – Interactions in insect populations – Amer. Nat. 94: 201–211.
9. Carpenter, J. 1936 – Quantitative community studies of land animals – J. anim. Ecol. 5: 231–245.
10. Cherrett, J. M. 1964 – The distribution of spiders on the Moor House National Nature Reserve, Westmorland – J. anim. Ecol. 33: 27–48.
11. Cuthbertson, A. 1926 – Spiders as natural enemies of craneflies – Scot. Nat. 160: 127–129.
12. DeBach, P. 1958 – The role of weather and entomophagous species in the natural control of insect populations – J. econ. Ent. 51: 474–484.
13. Duffey, E. 1962 – A population study of spiders in limestone grassland, the field-layer fauna – Oikos 13: 15–34.
14. Dunn, J. A. 1949 – The parasites and predators of potato aphids – Bull. ent. Res. 40: 97–122.

15. Ewing, H. E. 1918 – The life and behaviour of the house spider – Proc. Iowa Acad. Sci. 25: 181.

16. Fisz, M. 1954 – Rachunek prawdopodobieństwa i statystyka matematyczna – Warszawa, 374 pp.

17. Gałecka, B. (in press) – Rola drapieżców w redukcji dwóch gatunków mszyc ziemniaczanych *Aphis nasturtii* Kalt. i *Aphis frangulae* Kalt. – Ekol. Pol. A.

18. Harrison, J. W. H. 1913 – Friends and foes of the *Coniferae* – Entomologist 46: 50–54, 96–98.

19. Hobby, B. M. 1930 – Spiders and their isect prey – Proc. roy. ent. Soc. London 5: 107–110.

20. Hobby, B. M. 1940 – Spiders and their prey – Ent. monthly Mag. 76: 258–259.

21. Holling, C. S. 1959 – The components of predation as revealed by a study of small mammal predation of the European pine sawfly – Can. Ent. 91: 293–320.

22. Holling, C. S. 1961 – Principles of insect predation – Ann. Rev. Ent. 6: 163–183.

23. Huffaker, C. B., Kennett, C. E. 1956 – Experimental studies on predation: Predation and cyclamen-mite populations on strawberries in California – Hilgardia 26: 191–222.

24. Itô, Y., Miyashita, K., Sekiguchi, K. 1962 – Studies on the predators of the rice crop insect pests, using the insecticidal check method – Japan. J. Ecol. 12: 1–11.

25. Ivlev, V. S. 1955 – Eksperimental'naja ekologija pitanija ryb – Moskva, 252 pp.

26. Johnson, C. G. 1950 – The comparison of suction trap, sticky trap and townet for the quantitative sampling of small airborne insects – Ann. appl. Biol. 37: 268–285.

27. Kaczmarek, W. 1961 – On the role of euryecious species in biocenotical regulation phenomena – Bull. Acad. pol. Sci. cl. II 9: 41–45.

28. 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: 421–484.

29. Kajak, A. 1960 – Zmiany liczebności pająków na kilku łąkach – Ekol. Pol. A, 8: 199–228.

30. Kajak, A. 1961 – Obserwacje nad zasiedlaniem dziurawca czterobocznego *Hypericum maculatum* Cr. przez pająki – Ekol. Pol. A, 9: 279–298.

31. Kajak, A. 1962 – Porównanie fauny pająków łąk sztucznych i naturalnych – Ekol. Pol. A, 10: 1–20.

32. Kayashima, I. 1960 – Studies on spiders as natural enemies of crop pests (I). Daily activities of spiders in the cabbage fields establishments of spiders liberated in the fields and evolution of the effectiveness of spiders against crop pest – Sc. Bull. Fac. Agric. Kyushu Univ. 18.

33. Kayashima, I. 1961 – Study on the lynx-spider *Oxyopes sertatus* L. Koch for biological control of the Cryptomerian leaf-fly *Contarinia inouyei* Mani (VI) – Publ. ent. Lab. Coll. Agric. Univ. Osaca 6: 167–169.

34. Kontkanen, P. 1950 – Quantitative and seasonal studies on the leafhopper fauna of the field stratum on open areas in North Karelia – Ann. Soc. zool.-bot. fenn. "Vanamo" 13: 1–91.

35. Kot, J. 1964 – Experiments in the biology and ecology of species of the genus *Trichogramma* Westw. and their use in plant protection – Ecol. Pol. A, 12: 243–303.

36. Knowlton, G. F. 1952 – Spiders feeding on insects – Bull. Brooklyn ent. Soc. 47: 83–84.

37. Lenz, F. 1962 – Gedanken zur Phaenologie der Tendipediden – Z. angew. Zool. 49: 15–24.

38. Łuczak, J. 1958 – O metodyce badania pająków runa lasu sosnowego – Ekol. Pol. A, 4: 283–292.
39. Łuczak, J., Wierzbowska, T. 1959 – Analysis of likelihood of material in relation to the length of series in the sweep method – Bull. Acad. pol. Sci. cl. II, 7: 313–318.
40. MacArthur, R. 1955 – Fluctuations of animal populations, and a measure of community stability – Ecology 36: 533–536.
41. Mikulska, I. 1955 – Rozmieszczenie pająków w pasie nadbrzeżnym jeziora Wigry – Ecol. Pol. A, 3: 33–64.
42. Parmenter, L. 1953 – Some spiders and their prey – Ent. monthly Mag. 89: 135.
43. Poulton, E. B. 1934 – Observations on the Thomisid spider, *Misumena vatia* Clerck – Proc. roy. ent. Soc. London, 9: 72–74.
44. Pratt, R. Y., Hatch, M. H. 1938 – The food of black widow spider on Whidby Island – J. N. Y. ent. Soc. 46: 191–193.
45. Prószyński, J. 1962 – Pająki leśnictwa Zawada nad Notecią – Fragm. faun. Mus. zool. pol. 10: 205–214.
46. Rau, P. 1922 – Ecological and behavior notes on Missouri insects – Trans. Acad. Sci. S.-Luis, 24: 68–70.
47. Roth, M. 1963 – Comparaisons de méthodes de capture en écologie entomologique – Rév. Pathol. végét. Ent. agr. France 42: 177–197.
48. Savory, T. H. 1928 – The biology of spiders – London, 376 pp.
49. Smalley, A. E. 1960 – Energy flow of a saltmarsh grasshopper populations – Ecology 41: 772–777.
50. Staples, R., Allington, W. B. 1959 – The efficiency of sticky traps in sampling epidemic populations of Eriophyid mite *Aceria tulipae*, vector of wheat streak mosaic virus – Ann. ent. Soc. Amer. 52: 159–164.
51. Thédoridès, J. 1952 – Araignés predatrices de Coléoptères de la garrique littorale – Vie et Milieu 3: 338.
52. Tinbergen, L. 1960 – The natural control of insects in pinewoods I. Factors influencing the intensity of predation by song birds – Arch. néerl. Zool. 13: 265–336.
53. Tothill, J. D. 1922 – The natural control of the fall webworm *Hyphantria cunea* Drury in Canada – Bull. canad. Dept. Agric. 3, n.s. (Ent. Bull. 19), 1–107.
54. Tothill, J. D. 1923 – Notes on the outbreaks of spruce budworm forest tent caterpillar and larch sawfly in New Brunswick – Proc. Acadian ent. Soc. for 1922, 8: 172–182.
55. Tretzel, E. 1961 – Biologie, Ökologie und Brutpflege von *Coelotes terrestris* (Wider) (*Araneae, Agelenidae*). II: Brutpflege – Z. Morph. Ökol. Tiere 50: 375–542.
56. Turbull, A. L. 1960a – The prey of the spider *Linyphia triangularis* (Clerck) (*Araneae, Linyphiidae*) – Canad. J. Zool. 38: 859–873.
57. Turnbull, A. L. 1960b – The spider population of oak (*Quercus robur* L.) in Wytham Wood, Berks., England – Can. Entom. 92: 110–124.
58. Vité, J. P. 1953 – Untersuchungen über die ökologische und forstliche Bedeutung der Spinnen im Walde – Z. angew. Ent. 34: 313–334.
59. Voûte, A. D. 1946 – Regulation of the density of the insect populations in virgin-forests and cultivated woods – Arch. néerl. Zool. 7: 435–470.
60. Wiehle, H. 1927 – Beiträge zur Kenntnis des Radnetzbaues der Epeiriden, Tetragnathiden und Uloboriden – Z. Morph. Ökol. Tiere 8: 468–537.
61. Wiehle, H. 1931 – Spinnentiere oder Arachnoidea VI: *Agelenidae* – *Araneidae* (Tierwelt Deutschlands 27) – Jena, 136 pp.

ANALIZA STOSUNKÓW POKARMOWYCH MIĘDZY PAJĄKAMI *ARANEUS CORNUTUS* CLERCK I *ARANEUS QUADRATUS* CLERCK I ICH OFIARAMI, W ZBIOROWISKACH ŁĄKOWYCH

Streszczenie

Przedstawiona praca składa się z dwu części – część pierwsza poświęcona jest analizie ilości zdobyczy trafiającej w sieci dwu gatunków pająków sieciowych w warunkach różnej obfitości owadów na łące, część druga – rozpatruje wpływ zasobów pokarmu w środowisku na liczebność pająków.

Pracę prowadzono w latach 1960–1962, na rozległych łąkach śródleśnych w Puszczy Kampinoskiej (Łąki Strzeleckie), w trzech różnych zbiorowiskach roślinnych (*Caricetum elatae, Carici canescentis-Agrostetum caninae, Daeschampsietum caespitosae*). W drugiej części pracy, w której potrzebny był materiał porównawczy zebrany z wielu łąk, posłużono się także materiałami zebranymi w latach 1954 i 1955 na torfowiskach niskich, wchodzących w skład kompleksu Bagien Kuwasy.

Stosowano dwa rodzaje metod – metody określające liczebność pająków oraz łowionej przez nie zdobyczy (a) i metody ustalające obfitość owadów w środowisku (b).

a. Liczbę ofiar ustalano w ten sposób, że zbierano pokarm zawieszony na 20 sieciach pajęczych, przy czym notowano równocześnie, liczbę wszystkich pająków napotkanych w czasie tego zbierania. Ustalono na podstawie literatury i na podstawie w inny sposób zebranej serii prób, że pokarm znajdowany na sieciach pochodzi z okresu nie dłuższego niż doba. Metoda ta dawała ocenę, jak dużo pokarmu łowi przeciętnie w ciągu dnia jeden osobnik.

Zagęszczenie pająków ustalano, stosując metodę kwadratów. Serię stanowiło 20 kwadratów o łącznej powierzchni 5 m^2. Dane uzyskane tymi metodami (zagęszczenie pająków, liczba zdobyczy łowiona przez każdego z nich przez okres około doby) przedstawione w postaci iloczynu, traktowano w pracy jako wskaźnik intensywności drapieżnictwa badanych gatunków.

b. Obfitość owadów w środowisku określano metodą czerpaka (pobierano 10 prób co 2 tygodnie) i metodą lepów (ustawione po 10 na stanowisku, na 3 dni w ciągu dwu tygodni). Czerpak dostarcza danych o liczebności fauny występującej w górnej warstwie roślinności, lepy łowią podobnie jak sieci – tylko faunę ruchliwą i głównie drobną (tab. IV).

Na podstawie zebranego pokarmu gatunku *A. cornutus* wyróżniono dwa okresy, w których różnie przedstawiał się skład i liczba zdobyczy w sieciach pajęczych (tab. II i III). Pierwszy – okres jednolitego pokarmu, najczęściej występuje późną wiosną, w maju i w pierwszej połowie czerwca. Pokarm trafia wówczas w sieci masowo, natomiast jest znacznie mniej zróżnicowany niż fauna trafiająca na lepy (fig. 5). Drugi – okres zróżnicowanego pokarmu, trwa najczęściej przez lipiec, sierpień i wrzesień. W pokarmie znajdowano wówczas wiele rzędów owadów, ale liczba łowionych osobników była niewielka.

A. quadratus łowi maksymalną liczbę ofiar we wrześniu, w okresie poprzedzającym składanie jaj, dokładnie w tym samym czasie w obu latach badań (fig. 4). Wzmożenie łowności tego gatunku wynikało raczej ze stanu populacji pająka (występowała np. bardzo duża aktywność – wszystkie osobniki posiadały sieci) niż ze wzrostu liczby owadów w środowisku. Wzrostu liczby owadów w tym okresie nie zarejestrowały ani lepy, ani sieci *A. cornutus*, ani połowy czerpakiem. Przebieg zmian liczby ofiar łowionych

przez poszczególne pająki — *A. cornutus* i *A. quadratus* — bardzo się różni (fig. 3 i 4), natomiast skład łowionych ofiar jest bardzo podobny.

Sieci obu gatunków pająków łowiły stale stosunkowo więcej aniżeli lepy przedstawicieli *Tendipedidae* i *Aphidoidea* i to zarówno w okresie jednolitego pokarmu, kiedy grupy te w środowisku były masowe (stanowiły w sieciach ponad 80% łowionej fauny, na lepach około 60% fauny) i w okresie zróżnicowanego pokarmu, kiedy w środowisku było ich niewiele (stanowiły około 20% w sieciach *A. cornutus* i około 13% w sieciach *A. quadratus*), a tylko 0,4% na lepach (fig. 6 i 8). *Tendipedidae* i przelotne mszyce łowione były przez sieci w sposób proporcjonalny do ich zagęszczenia w środowisku, podczas gdy inne grupy owadów trafiały w sieci rzadko, mimo nawet znacznej obfitości w środowisku. Wyciągnięto wniosek, że sieci pajęcze wyłapują głównie faunę przelotną, krótkotrwałą w danym środowisku.

Liczebność populacji *A. cornutus* i *A. quadratus* podlegała w ciągu sezonu wegetacyjnego stosunkowo niewielkim zmianom w porównaniu ze zmianami liczby ofiar (fig. 14), stąd wskaźnik intensywności drapieżnictwa, obrazujący siłę oddziaływania całej populacji drapieżcy na ofiary, ma podobny przebieg w ciągu sezonu, jak zmiany liczby ofiar łowionych przez poszczególne pająki. Oddziaływanie populacji *A. cornutus* było najintensywniejsze wiosną, populacji *A. quadratus* — na jesieni (fig. 15).

Intensywność drapieżnictwa pająków nie była określana przez obfitość owadów w środowisku. Pająki łowiły najwięcej ofiar albo przed okresem maksymalnej obfitości owadów (*A. cornutus*), albo już po nim (*A. quadratus*). Natomiast liczebność wszystkich pająków, występujących na roślinności (a nie dwu analizowanych gatunków), była największa właśnie w okresie maksymalnej liczebności owadów (lipiec, pierwsza połowa sierpnia, fig. 10).

Sumaryczne działanie wszystkich pająków razem mogło się więc nasilać w okresie wzmożonej obfitości owadów, mimo że działanie analizowanych populacji było wtedy słabe.

Drugą część pracy poświęcono rozważaniom znaczenia dla liczebności pająków piętra ziół — zasobów pokarmu i stopnia zróżnicowania środowiska. Okazało się, że brak jest zależności między liczebnością pająków i obfitością fauny pokarmowej (w tym wypadku fauny muchówek) na danej łące (fig. 16). Liczebność pająków zależy natomiast od stopnia zróżnicowania roślinności w środowisku. Więcej pająków sieciowych znajdowano w tych środowiskach, w których występowała mieszanka roślin o zróżnicowanej wysokości i budowie kwiatostanów (rośliny jednoliścienne i dwuliścienne) (fig. 18).

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