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PREY AND PREDATOR DENSITY AND THEIR REACTIONS  
IN THE PROCESS OF MOSQUITO REDUCTION BY SPIDERS  
IN FIELD EXPERIMENTS

The predation of two spider species, *Tetragnatha montana* Simon and *Dolomedes fimbriatus* (Clerck), on mosquitoes has been investigated in field experiments. The rate of reduction was studied at various prey and predator densities. The food activity of spiders, as well as the relative activity and distribution of mosquitoes in the isolator, were analysed in various relations of prey and predator density. The authors studied the effect of the spider and mosquito reactions mentioned on prey reduction. Besides, the modifying effect of vegetation structure in the isolators and of different periods of the season when the experiments were carried out was taken into account in its bearing on the character and rate of prey reduction.

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## 1. INTRODUCTION

In the literature of the last ten years there have been published a number of scientific papers on the subject of the importance of predation in nature. The scientists have started investigating biological and ecological aspects of this process and they came to be particularly interested in the regulating role of predation in the community. But as the facts concerned with the numerical reduction of prey by predators are relatively wellknown and do not give rise to any doubts, then the idea of their regulation effect on the prey is still the subject of scientific discussions. Refraining from offering the final verdict, the scientists are bent on investigating the course of predation and basic factors affecting its level.

One of the most frequently analysed problems is the question arising from the effect of the prey and predator density on the course of predation. The relations occurring here can be considered from the following two points of view: the effect of predators on the numbers and other features of prey (Blondel 1967, Holling 1959), or the effect of prey on the numbers and other features of predators (Tinbergen 1960, Frochat 1967). Each type of approach concentrates on different regularities recorded in the phenomenon of predation, stresses different aspects of the problem, and only the two taken together can give a complete picture of the process and signify its importance in nature. The authors have put forward as their aim to investigate both the types of the dependency experimentally with spiders as predators and mosquitoes as prey.

Spiders as predators have already been taken up as the subject of investigation. It can be deduced from them that spiders possess a number of ecological features common with such vertebrate predators as carnivorous and insectivorous birds. That was born out by a comparison of the two groups' significance carried out in the paper by Miyashita in 1963. Spiders are poliphags feeding on a large number of insect species but each particular spider species has its own range of prey, and differs from other species by the quality and quantity of prey consumed (Bristowe 1941, Turnbull 1956, 1965, as well as others). This is closely connected with the qualitative supply of prey in the given habitat, their numbers and accessibility. Within the group usually can occur rare species specializing in only one type of prey. Most of all spiders feed on the most abundant food in the habitat (Vité 1953, Turnbull 1960). Taking into account these features of spiders Ruppertshofen (after Kirchner 1965) advocated the method of the species *Linyphia triangularis* introduction into the forests when they are threatened by pests. This author described this species as an equivalent of "the Tit among birds". In the webs of the spider species investigated he recorded about 40% of forest pests. The author mentioned advocated a combined method of forest protection including the use of ants, spiders, and birds. Bristowe (1941) expressed an opinion that the number of

insects captured by spiders exceeds the respective number attributed to birds, and he supplied his estimates. However, he pointed out that the lack of food specialization renders them less effective than, for example, some parasites or bird species.

Vité (1953) arrived at a conclusion, as a result of an analysis taking into account the up-to-date achievement of arachnology, that spiders could contribute much to the biological balance in the forest ecosystem, and that they exert a strong pressure, first of all, on phytophagous insects, parasites, and insect predators. He described, for the sake of example, their attitude towards *Bupalus piniarius*: the larger the numbers of the pest in the habitat, the more intensive was it captured by spiders with as much as 12 to 23% of the population being exterminated. Vité considered spiders being most effective as predators in the undergrowth and herb layer of the forest.

Kirchner (1964) singled out, on the basis of the literature and his own results, a number of factors which could affect and modify spider predation on insects or its estimates, in particular the method of trapping, the period of 24-hours and seasonal activity of spiders, the behaviour of prey, the character of the biotop, the density of the spider population and their prey, as well as the seasonal dynamics of their numbers. He considered web spiders as more effective than wandering spiders.

Turnbull (1960) worked out the qualitative and quantitative composition of prey being trapped in the webs of *Linyphia triangularis*, he considered the way of prey trapping by spiders (1964), and analysed the effect of the varying spiders' diet on their growth and development. He also pointed out (1966) the significance of spider migrations for pressure changes of these predators in relation to all the prey in the habitat in different periods of the season.

Haynes and Sisojevič (1966) investigated the effect of hunger, moults, and the process of egg-laying on the intensity of predation, as well as the effect of the prey density on the number of fruit flies trapped and the degree of the prey body usage. They also studied the problem of the stimulation of spiders just sucking their prey by other prey in their vicinity, and the effect of hunger or satiation on this phenomenon.

Japanese arachnologists and entomologists attributed much significance to spiders as predators of many agriculture pests (Ito, Miyashita, and Sekiguchi 1962). They also analysed the activity of poliphagous predators, spiders included (Miyashita 1963).

Kajak (1965a, 1965b) carried out a quantitative investigation on the food of the spiders *Araneus cornutus* and *A. quadratus* occurring in forest meadows. The author analysed the faunistic composition of insects trapped in spider webs and occurring in the habitat. She concluded that *Tendipedidae* and aphids, not so strong or adroit flyers, were trapped in webs proportionally to their density in the habitat. Other groups did not display this correlation at all or only in

a small degree. Adult females trapped more insects than juvenile individuals disregarding the number of insects in the habitat. There also occurred, under certain conditions, a correlation between the numbers of insects in the habitat and the total number of spiders.

Spider predation on mosquitoes was mentioned in the literature mainly in the form of reports on the trapping of mosquitoes by certain spider species as well as feeding on them (Jenkins 1964). It was already mentioned as early as in 1889 by McCook who observed in some periods frequent trapping of mosquitoes in webs of large *Argiopidae*. Bristowe (1941) pointed out that species from the family *Linyphidae* and genus *Tetragnatha* mainly feed on insects from the group *Nematocera*. Jenkins (1950) investigated *Aedes communis* predators, as well as other species of this genus, by checking their radioactivity caused by the feeding on mosquitoes marked by radioactive isotopes. He concluded that a number of spider species (*Araneus nordmanni*, *Meta patagiata*, *Tetragnatha extensa*, *Pithyophantes subarcticus*, *Pardosa mackenziana*, *Theridion zelotypum*, *Xysticus triangulosus*) fed on mosquitoes. A number of investigators (Bacot 1916, Marchoux, Salimbeni, Simond 1903, Howard, Dyar, Knab 1912, Gordon 1922) mentioned also other spider genera and species feeding on the mosquitoes *Aedes aegypti* and *Culex pipiens*, occurring in human environment.

Fontoynt (1922) (after Jenkins 1964) reported that *Nephila madagascariensis* feeds on mosquitoes of the genus *Anopheles*. The author suggested that the extermination of these spiders may cause an increase in populations of malarial mosquitoes. Turnbull (1960) concluded that species of the group *Diptera* constitute the main prey of the species *L. triangularis*. *Nematocera* made up only 18% of the species trapped in webs in early spring, while in June they made up 80% of the spiders prey. Laird (1947) observed numerous mosquitoes in the webs of *Meta* sp. He also pointed out that certain spiders of the genus *Epeira* (*Araneus*) and *Meta*, which spin webs around the pools, could be treated as important mosquito predators. James (1964) observed the occurrence of spider females of the genus *Dolomedes* in the breeding places of the mosquitoes *Aedes atropalpus*. McDuffie and Weidhaus, discussing new methods of mosquito control, concluded that parasites, predators, and pathogenes are very important in the biological control of mosquitoes, but that new intensive investigations on their activity against mosquitoes are necessary.

The authors of the present paper have already published data on the subject of pressure exerted by various spider species on mosquitoes in field experiments (Łuczak, Dąbrowska-Prot 1966), data concerned with the rate and character of mosquito reduction by spiders (Dąbrowska-Prot, Łuczak, Tarwid 1966), and data concerned with the effect of spiders on the behaviour of mosquitoes (Dąbrowska-Prot 1966). The aim of the present paper is to sum up the result of the two years of investigations on spider predation on mos-

quitoes, particularly taking into account the factor of prey and predator density in the process of prey reduction and the reaction of the two components to their presence.

## 2. DESCRIPTION OF THE STUDY AREA

The investigation was carried out in Kampinos Forest, in the vicinity of the villages Zamość and Cisowe (near Dębowskie). Large number of the spiders *T. montana* and *D. fimbriatus* and mosquitos were recorded in the area of a wet alder forest where the isolators were set up. This is their natural environment, from which the animals were picked up for the experiments.

The isolators, for technical reasons, were set up in two slightly differing plant communities<sup>1</sup>.

One of the series of isolators (10) was set up in the alder forest near Zamość where in the tree layer there were isolated groups of the alder (*Alnus glutinosa*), the common birch (*Betula pubescens*) and the willow (*Salix cinerea*). The density of canopies amounted from 50% to 75%. The alder buckthorn (*Frangula alnus*), the rowan (*Sorbus aucuparia*) the raspberry (*Rubus idaeus*), *Rhamnus cathartica*, and the black currant (*Ribes nigrum*) occurred abundantly in the undergrowth. The herb layer included 37 species of herbaceous vascular plants. Of dicotyledonous plants *Urtica dioica* was very common, and then *Ranunculus repens*, *Lycopus europaeus*, *Rumex hydrolapathum*. Of monocotyledons the following occurred: *Scirpus silvaticus*, *Agrostis canina*, *Poa trivialis*, *Poa palustris*, *Dryopteris thelypteris*.

The isolators distributed in this area included sections of the natural habitat with the species of the undergrowth and herb layer growing there. In 1965 5–10 plant species, on average 7.5, occurred under the isolators; while in 1966 from 4 to 9 species, on average 6. The bottom of the isolators was covered in 60 to 100% by herbaceous vascular plants of the herb layer in 1965, and in 30 to 90% in 1966.

Of the undergrowth species the rowan (*Rubus* sp.) was commonest, and of the herb layer species – *Agrostis canina*, *Galium aparinae*, *Geum urbanum*, *Urtica dioica*, *Galeobdolon luteum*, *Deschampsia caespitosa*, *Geranium robertianum*. The height of the vegetation in the isolators was on the whole not very considerable and amounted from 30 to 60 cm and that constituted more or less 1/5 to 1/3 of the isolator's height, only great nettles and some tems of grass reached higher.

The second series of isolators (10) was set up near the Dębowskie, also in

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<sup>1</sup> The qualitative and quantitative analysis of the area and the vegetation occurring under the isolators was carried out by Dr. Zdzisława Wójcik, and our best thanks are due to her for it.

the alder forest which was an ecotone habitat – the edge of a willow shrub and meadow. Beside the alder, dominating in the tree layer (*Alnus glutinosa*), there also commonly occurred the common birch (*Betula pubescens*), and the young ash (*Fraxinus excelsior*). The density of the tree canopies amounted to about 75%. In the undergrowth, much richer than in the previous area, the willow (*Salix cinerea*), the alder buckthorn (*Frangula alnus*), the common birch (*Betula pubescens*), the ash (*Fraxinus excelsior*), and the oak (*Quercus robur*) were dominating. The rowan (*Sorbus aucuparia*) and the raspberry (*Rubus* sp.) occurred in places. The herb layer was richer than in the previous area and occurred in isolated patches. It was mainly made up of monocotyledonous species – *Deschampsia caespitosa*, *Scirpus silvaticus*, *Calamagrostis lanceolata*, *Juncus effusus*, *Poa trivialis*, and of dicotyledonous species – *Geum urbanum*, *Lisymachia vulgaris*, *Urtica dioica*, *Lycopus europaeus*, and the fern (*Aspidium thelypteris*). In all, 25 herbaceous vascular plants and 8 tree species occurred in the herb layer.

First of all the *Rhamnus catartica*, the alder buckthorn (*F. alnus*), the oak (*Q. robur*), the raspberry (*Rubus* sp.), and the willow (*Salix cinerea*) were found among the vegetation of the isolators, and besides, about 15 species of vascular plants in 1965, and about 10 species in 1966.

The bottom of the isolators was covered in 70 to 90% by vascular plants in 1966, and only a small number of mosses were recorded. The most common vascular plants were *Deschampsia caespitosa*, *Geum urbanum*, *Agrostis canina*, *Scirpus silvaticus*, *Lycopus europaeus*. The average vegetation height in the isolators was more considerable in this area, and in some of the isolators it reached in places up to the ceiling (young trees), on average to 1 m, and that made up about 2/3 of the isolator's height. The floristic composition of the vegetation under the isolators indicated that the bottom was wetter than in the case of the previous isolators.

Thus the vegetation in the isolators was mainly composed of species occurring in the surrounding forest habitat, and its presence in the isolators gave shelter for preys and predators, and enabled the web spiders to trap their prey on the webs.

The investigation proved that the microclimate of the isolators did not show almost any differences from the microclimate of the surrounding habitat. Besides the initial check on the microclimate in the isolators when the experiment was commenced, systematic microclimatic observations were carried out in the course of 24 days (from August 15 till September 8, 1966). The temperature and air moisture were measured at the level of 5 cm and 70 cm above the ground. The temperature was read on the thermometers within 0.1°C, while hygrographs helped to measure the moisture.

In the hours of the highest temperature in the daytime the temperature in the isolators did not differ significantly from the one in the forest at the same

height above the ground (Tab. I). The 24-hours changes in temperature, and particularly any decrease in the temperature were delayed in the isolators. In the evening, at night, and in the morning it was usually warmer in the isolators, the difference reaching about 0.3 to 0.7°C, and sometimes it reached 1.0°C. The air moisture in the isolators was more or less the same as in the surrounding forest, or sometimes it was slightly higher (the difference amounted to 5%). No drop in the moisture in the isolators was recorded in connection with the gradient of height, and so we could suppose that this factor, so important from the point of view of the modification of spider activity, did not limit their movements in the daytime all over the isolator. The animals in the isolators were protected from strong winds as compared with animals living in natural conditions.

Deviations in the air temperatures in the isolator in relation to the temperatures of the environment in the period August 16-September 7, 1966

Tab. I

The kind of weather	Temperature differences in the morning	Temperature differences in the early afternoon	Temperature differences in the evening
Warm weather above 20°C	*	0.1 to +0.3 on average +0.1	+0.3 to +0.4 on average +0.3
Cold weather below 15°C	+0.1 to +0.9 on average +0.4	*	+0.2 to +0.7 on average +0.4

\*Insufficient data.

These relatively insignificant modifications in the microclimate caused by the isolators were the results of the choice of the experimental sites. They were situated in a wet alder forest, with dense canopies, providing much shade, while the rich herb layer supplied favorable, not so changeable, microclimatic conditions for the organisms habitating there.

The problem is what the natural density of mosquitoes and spiders in their environment was, and how the experimental density differed in the isolators. Some information on this subject was obtained at the time of setting up the isolators in the forest. Certain data on the numbers of mosquitoes and spiders occurring within the isolator were recorded at that time applying necessary precaution measures (area 1.5 sq.m, volume 2.25 cu. m). The density of *Tetragnatha montana* was variable in natural conditions. In one of the isolators as many as 7 individuals of this species were captured. Up to 5 mosquito individuals occurred. In certain cases the isolators covered large clumpings of mosquitoes in the herb layer. About 50 individuals were recorded.

Although these data are very fragmentary and relative, they can give some idea of the degree of natural density of the prey and predator species investigat-

ed. However we should also take into account the mosaic-like pattern of the habitat and, connected with it, occurrence of sites particularly favourable for mosquitoes and the spider species mentioned above. In such places large clumpings of spiders – up to 15 individuals of *T. montana* per 1.0 sq. m. – could be observed in the herb layer.

### 3. METHOD

The investigation was carried out in the isolators set up in a wet alder forest (see the description of the area). The isolators were made of metal rods covered with a nylon net and divided by a partition wall, made of the same material, in the middle of their length. Thus two smaller compartments were formed – their size  $1.5 \times 1.5 \times 1.0$  m, the herb layer area 1.5 sq. m, and the volume 2.25 cu. m. The partition wall could be removed and then the area was 3.0 sq. m and the volume 4.5 cu. m. The lower edge of the net was dug into the ground to prevent the animals from the outside to get into the isolators and those from the isolators to the surrounding habitat. A hole covered with a sleeve made of net, and used for observations, was cut in the middle of an external wall of the “small” isolators. Each isolator included a section of the undergrowth and herb layer which provided the necessary microclimate for the animals and their hiding places.

Experiments connected with spider predation on mosquitoes – the species *Aedes maculatus* Meig., *A. punctor* Kirby, *A. cinereus* Meig. chiefly – and control experiments only with mosquitoes were carried out. The animals were put into the isolators after thoroughly cleaning the walls and vegetation of the isolators\*. Such cleaning of isolators was carried out in the course of a few days. Besides, when the experiments got under way, any “alien” species of animals that turned up there were carefully removed.

The observations were carried out three times a day: in the morning, in the afternoon, and just before dusk. The time of observation was limited to 5 minutes (mosquitoes were observed for 2 minutes, spiders for 3 minutes). The control observations carried out at the beginning of the investigation period with all the observers showed that in the course of 5 minutes the numbers of animals recorded by separate observers were quite similar.

As far as mosquitoes were concerned the observers recorded the number of individuals staying on the vegetation and walls of the isolators (in the vegetation and above it), and the number of individuals flying in the vegetation and above it. The observations yielded data on the occurrence of mosquitoes in different parts of the isolator and the present numbers of mosquitoes in the isolator. Changes in the numbers of mosquitoes in isolators with and without spiders

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\*That is removing all the other animals spotted there.



in successive days of the experiment from the moment of its commencement to the complete extermination of mosquitoes gave grounds for concluding about the pressure exerted by spiders on mosquitoes. The division into mosquitoes sitting and flying at the time of the observations enabled to determine the relative activity of mosquitoes in different conditions of the experiment.

As far as spiders were concerned, the observers recorded their total numbers, the number of individuals staying on the walls and on the vegetation, moving and immovable individuals, and in the case of web spiders, individuals staying in the web and those without webs. The behaviour of spiders was also observed — web spinning, spider moves on the isolator walls, etc. The observations enabled to determine the part of the population visible on the vegetation and isolator walls and the part of population actively waiting for preys in the period of observations.

Spiders were put into the isolators at least three days before letting in the prey to give them time to settle down in the habitat and to be able to determine the character and strength of the spider reaction to the appearance of their prey.

Spiders observed in the isolators made up a large part of the population introduced there, but never was it possible to observe all the individuals, partly hidden in the herb layer. The investigation of the 24-hours cycle of the spiders *T. montana* and *D. fimbriatus* (Horn, in press) showed that they turned up in the largest number in the period of their evening and nocturnal activity. The numbers of the spiders visible in the isolators were dependent on the weather, character of the herb layer, and the real numbers of spiders in the isolators. A detailed analysis of this problem is given in chapter 4.1.

As the experiments were to determine the character of the relation between the number of prey and their predators and the course of predation process, it was important to find out what part of predators was reduced in the course of the experiment. To do that spiders *Tetragnatha montana* Simon and *Dolomedes fimbriatus* (Clerck) were removed for a few days from some of the isolators in the middle of the investigation period and then new experiments with spiders and mosquitoes in the same quantitative relations were carried out. Besides, after the experiments were terminated, the remaining spiders in the majority of isolators were removed. The results obtained in such a way enabled to verify the experiments from the point of view of the real numbers of predators occurring in the isolators. The data indicate that *D. fimbriatus* suffered a small reduction in the course of the experiment, while the number of *T. montana* individuals gradually decreased in the course of the season as the adult individuals were dying out. These phenomena were taken into account when analysing the data on the reduction of mosquitoes by spiders.

#### 4. RESULTS OF THE INVESTIGATION

##### 4.1. Natural reduction of spider populations in isolators and "visibility" of the population

###### Method of calculating the index of predator reduction

Experiments with the species *T. montana* were carried out in the period from the end of May to the end of July, while those with the species *D. fimbriatus* in August and September in view of their seasonal life cycle.

It was found out in the investigation, as already mentioned in the chapter on the method, that spiders put into the isolators suffered a certain reduction in the course of the experiment. Even a casual observation showed that the course of the reduction was different for *D. fimbriatus* and *T. montana*. This was also indicated by the results of spider removals from the isolators in the middle of the experimental period and when the experiments with these species were terminated. As the number of actively predating spiders is important in the investigations of this type, the determination of the spider population reduction comes to the front.

The second problem, connected with the previous one, is whether there could be any relation between the present density of spiders in the isolator and their numbers recorded by the observer i.e. the visibility of spiders. This problem is concerned with the space distribution of the populations of the two spider species.

When estimating the mortality of spider populations habitating in the isolator the following method was applied: it was assumed that spiders decreased in the population according to the exponential distribution. This assumption was based on the results of experimental data\*.

The numbers observed were the result of both mortality and visibility of spiders. The index of mortality was determined on the basis of pairs of observations separated from each other by  $S$  days. This  $S$  was such that the numbers observed were within the period of the same spider density, and on days with a similar weather.

Value  $\mu$  was estimated on the basis of the formula:

$$\mu = \frac{\ln N_t - \ln N_{t+S}}{S} \quad (1)$$

where  $N_t$  is the number of spiders recorded on day  $t$ , while  $N_{t+S}$  is the number of spiders recorded on day  $t+S$ .

\*We want to express our best thanks to mgr. Teresa Wierzbowska who elaborated these problems from the statistical point of view.

However it happened that the sequence of number of spiders recorded was not constantly decreasing but that in the ensuing moments of time the values recorded were higher than those previously recorded. It seems evident that the sequence can not be increasing, and so the earlier values were increased to the level of those which were recorded in the ensuing days. Thus a new sequence of values was obtained, constant in parts, constantly decreasing (more precisely – not increasing).

Next, to estimate  $\mu$ , the terminal points of the constant intervals were included, taking into account weather conditions and density of spiders. This value was estimated on the basis of formula (1). Value  $\mu$  for the initial period was taken to be the index of decrease for the spiders introduced ( $N_0$ ) and the theoretical values expected were calculated on the basis of the formula:

$$N_t = N_0 e^{-\mu t} \quad t \geq 0 \quad (2)$$

Successive mortality indices (estimated for respectively homogenous, in view of mortality, periods of time) were taken as values of  $\mu$  occurring in formula (2).

For *T. montana* the per cent of spiders decreasing in the course of a week amounted in June, that is just when young adult individuals occur, to 17% of the population (index of decrease  $\mu = 0.027$ ), and in the first half of July to 25% (index of decrease  $\mu = 0.042$ ). In the second half of July, that is when this species starts naturally dying out, it amounted, on average, to 34% (index of decrease  $\mu = 0.057$ ) (Fig. 1).

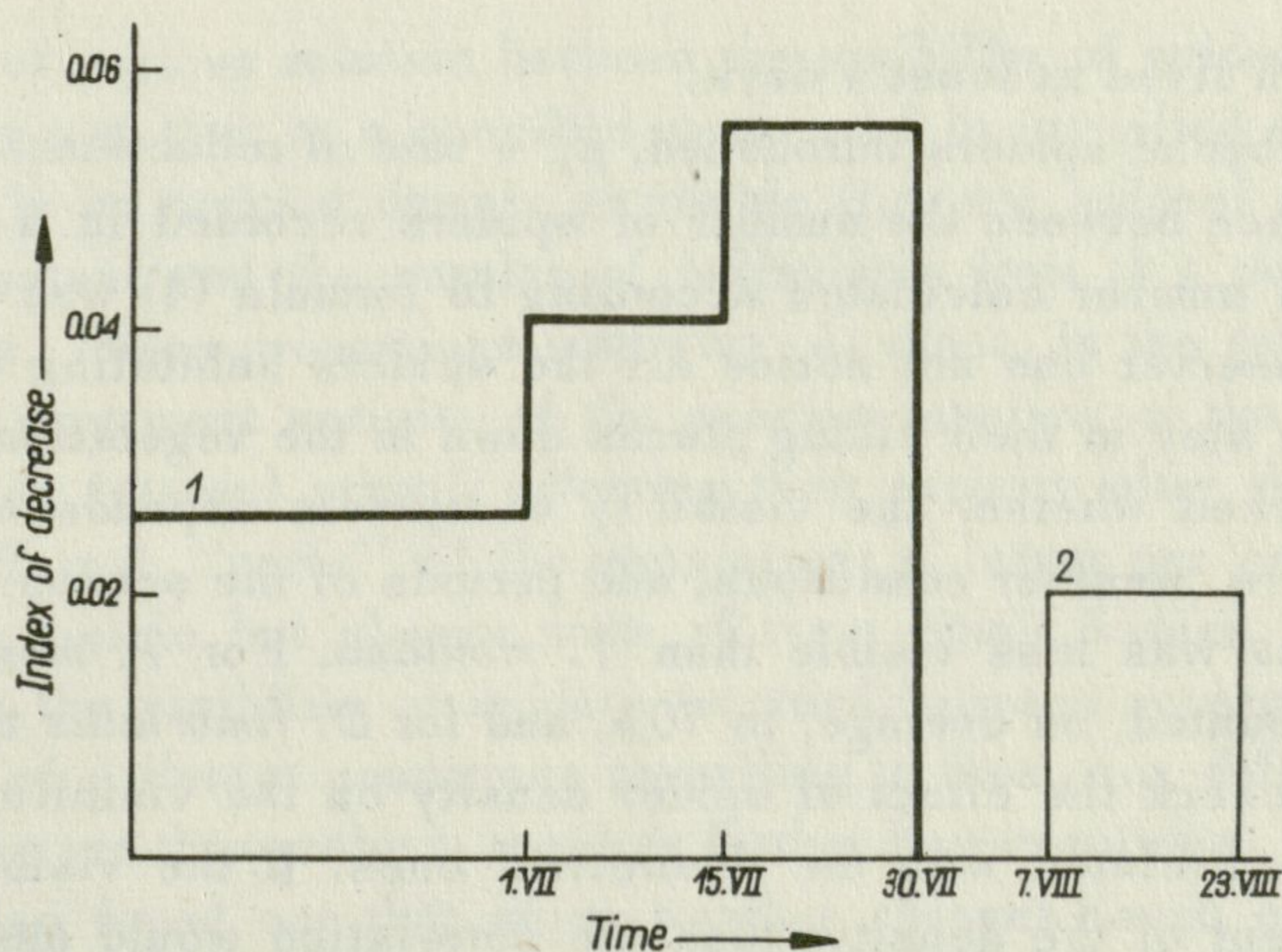


Fig. 1. Indices of the spider population decrease in the isolators in different periods of the season

1 – *Tetragnatha montana*, 2 – *Dolomedes fimbriatus*

The per cent of spiders decreasing in the course of a week was calculated on the basis of the formula:

$$100 \cdot (1 - e^{-7\mu}) \quad (3)$$

where  $\mu$  is the rate of reduction in the respective period. The results obtained can lead us to a conclusion that the period of the season affects the reduction rate of the spider population. This is most probably connected with the age of the individuals in the population, and those biological phenomena which are connected with the age.

For *D. fimbriatus* the index of decrease amounted, in the period between August 7 to August 23, to 0.02, and that makes up about 11% of the population (Fig. 1). Experiments with this species were carried out with grown though not yet mature individuals.

The pictures of reduction obtained for the spider species investigated most probably depend on their development stage. Grown individuals of *D. fimbriatus* passed already the phase of a strong reduction of juvenile stages, but they did not enter the phase of a strong reduction connected with the final period of their life.

Having the rate of reduction estimated on the basis of formula (1) we could calculate the theoretical number of spiders in the isolator for each day according to the following formula:

$$N_t = N_0 \cdot e^{-\sum_{k=0}^m \mu_k} \quad t \geq 0 \quad (4)$$

for spiders which lived at least  $k$  days,

where  $N_0$  – number of spiders introduced,  $\mu_k$  – rate of reduction.

The difference between the number of spiders recorded in a given day and their theoretical number calculated according to formula (4) was a result of the fact that the observer can not notice all the spiders habitating in the isolator, as some of them stay in their hiding places down in the vegetation.

It was checked whether the visibility of spiders depends on the species, density of spiders, weather conditions, and periods of the season.

*D. fimbriatus* was less visible than *T. montana*. For *T. montana* the index of visibility amounted, on average, to 70%, and for *D. fimbriatus* to 56%.

In order to check the effect of spider density on the visibility, the numbers observed were correlated with the theoretical ones. If the visibility were constant, independent of the density, then the correlation would assume the linear character:

$$N = a \cdot N'$$

where  $N'$  – theoretical numbers, and  $N$  – empirical numbers.

It turned out that the relation is of the following type:

$$N = a \cdot (N')^k \quad (5)$$

For *T. montana*  $N = 0.88 (N')^{0.91}$   
 For *D. fimbriatus*  $N = 0.75 (N')^{0.89}$

It follows from formula (5) that there is a tendency to a decrease in the visibility together with an increase in the density (Fig. 2).

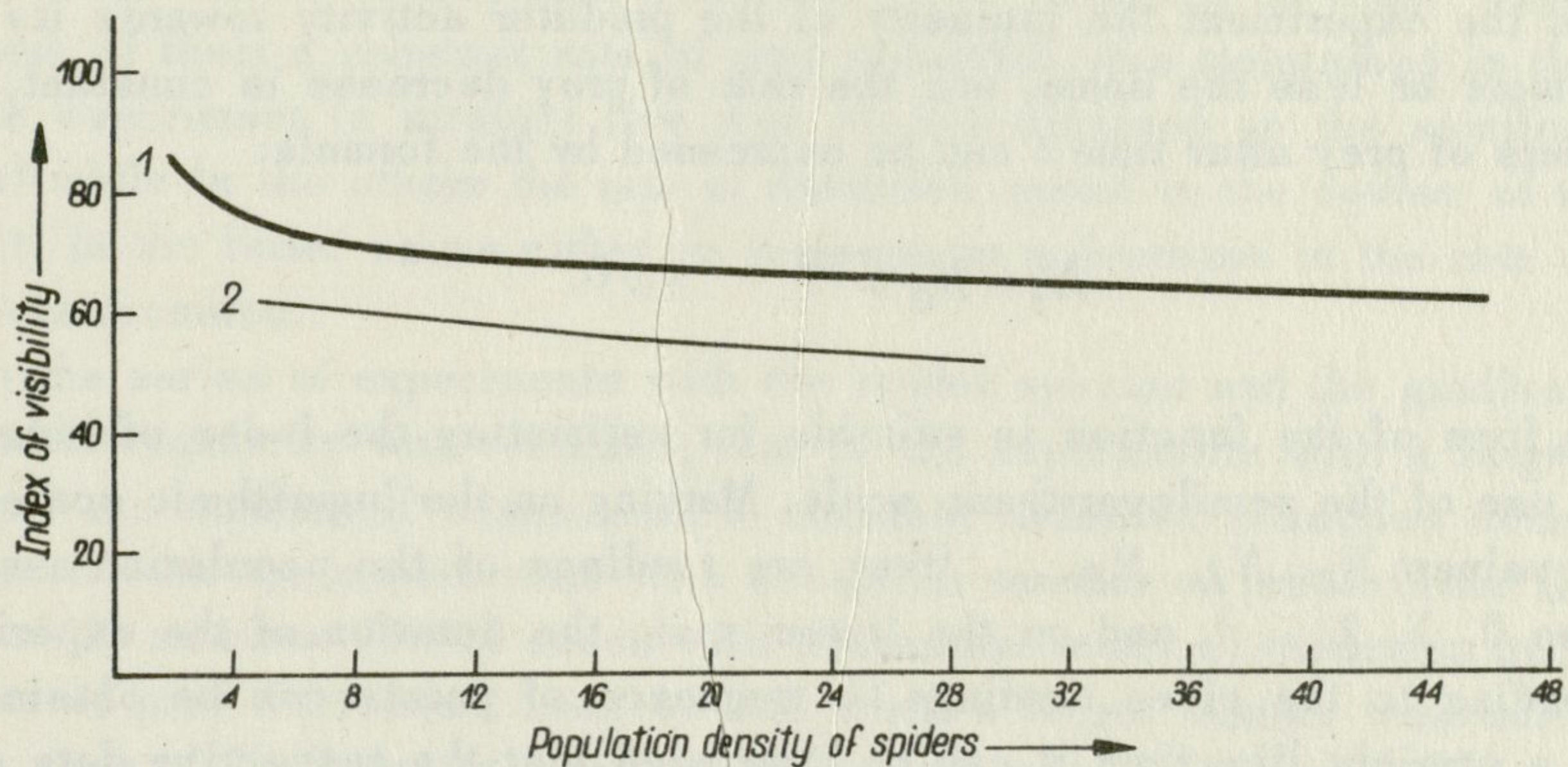


Fig. 2. Dependence of spider visibility on their density in the isolator  
 1 - *Tetragnatha montana*, 2 - *Dolomedes fimbriatus*

The lack of a close relation between the visibility of spiders and their density might suggest that in a specified space and in specified environment conditions there is an optimal number of visible (i.e. not hidden) spiders which is relatively constant and the surplus of individuals from this population hide in the vegetation. These proportions may vary. At night, in the period of the highest food and movement activity of the species (studies of the 24-hours cycle, E. Horn) strong internal stimuli affecting their activity alter the proportions of these two different "parts" of the population. A larger per cent of the spider population is visible but always some of them remain hidden. Some permanent differences in the visibility of spiders recorded between separate isolators may be the result of different conditions prevailing in them, e.g. different vegetation structure. However this problem requires further investigations.

It was also found out that sharp weather changes (such as long spells of rain, strong winds) alter, to a certain degree the visibility of spiders, while moderate changes in the weather do not have any effect whatsoever.

No effect of the season period on the visibility of spiders was recorded.

### Method of calculating the index of prey reduction

We can use formula (1) also when we want to calculate the rate of prey reduction.

The reduction rate of prey not breeding in the given conditions, and constantly under the pressure of the predator, depends on the chance of meeting the individuals of predator and prey populations. It could be assumed in the conditions of our experiment that these chances depend on the following two circumstances: 1) behaviour of the individuals of both the populations in the given ecological conditions, and 2) numbers of the two populations. If in the course of the experiment the intensity of the predator activity towards its prey remains more or less the same, and the rate of prey decrease is constant, then the numbers of prey after time  $t$  can be expressed by the formula:

$$N_t = N_0 e^{-\mu t} \quad t \geq 0.$$

This form of the function is suitable for estimating the index of reduction with the use of the semilogarithmic scale. Marking on the logarithmic scale successive values  $N_0, N_1, N_2, \dots$  (they are readings of the population numbers after time 0, 1, 2, ...), and on the linear scale the duration of the experiment corresponding to the given readings, a sequence of points can be obtained. If it forms a straight line then it can be concluded that the respective data solve function (1) and its assumptions. The graphical picture of this relation enables to find out directly the value of the reduction index. It can be measured by the inclination angle of this straight line. The respective data were obtained graphically by relating the angle to the index of reduction expressed in per cent for 24-hours.

The effect of the changeable visibility of the population and various random deviations in the precision of calculation by the observer, are expressed in the distribution of points with certain deviations on each side of the straight line.

#### 4.2. Effect of predator population density and initial prey density on mosquito reduction

On the basis of an analysis of mosquito reduction by three spider species (*D. fimbriatus*, *T. montana*, and *L. triangularis*) four different types of reduction were recorded in field experiments (Dąbrowska-Prot, Łuczak, Tarwid 1966). It was found out that certain types of reduction occur more frequently in experiments with specified spider species. The correlation analysis of the prey reduction type with prey and predator density was carried out on the basis of

materials obtained in the series of experiments realized in 1966. One series were experiments with various densities of prey – 10, 30, 90, and 180 mosquitoes – introduced into the isolators into which predators had been put beforehand – 24 spiders of *T. montana* or 20 individuals of *D. fimbriatus*. The other series was made up of experiments with a constant density of mosquitoes (50 individuals) and a varying numbers of predators – 6, 12, 24, 48 spiders of *T. montana* or 6, 12, 20, and 30 individuals of *D. fimbriatus*. Each one of the experiments lasted from a few to more than several days until all the mosquitoes introduced into the isolator were exterminated.

Various cases of mosquito reduction were observed in these experiments: in some of them a constant rate of prey reduction was maintained in the course of the experiment (a straight line was always obtained on the semilogarithmic scale) while in the others the rate of reduction varied in the course of the experiment. In the latter cases either an increase or a decrease in the rate of reduction was recorded.

In the series of experiments with the spider species and the gradient of prey a general regularity was recorded, that in the experiments with a larger number of prey the number of cases with a constant index of reduction decreased as compared with the experiments with a smaller number of preys (Tab. II). In the case of *T. montana* 75% of cases with a constant index of reduction and a small number of prey decreased down to 36% when a larger number was taken, while in the case of *D. fimbriatus* the respective data were 100% and 14%.

Dependence of the character of prey reduction on their density (data from the series of experiments with the gradient of preys)

Tab. II

Number of mosquitoes in the series of experiments with the gradient of preys	Number of experiments with separate prey densities				Small number of preys (10–30) per cent of cases	Large number of preys (90–180) per cent of cases
	10	30	90	180		
Experiments						
<i>Tetragnatha montana</i>						
Number of experiments with a variable rate of reduction	1	2	4	5	25	64
Number of experiments with a constant rate of reduction	1	8	3	2	75	36
<i>Dolomedes fimbriatus</i>						
Number of experiments with a variable rate of reduction	0	0	3	3	0	86
Number of experiments with a constant rate of reduction	7	8	1	0	100	14

As it was mentioned above changes in the rate of reduction are expressed either by its increase or its decrease. In the case of *T. montana* in the experiments with the gradient of prey the two types of changes occurred equally frequently, and in *D. fimbriatus* changes in the rate of reduction were mainly expressed by its intensification in the course of one experiment.

In the series of experiments with the gradient of predators, the two spider species reacted differently. When the number of *D. fimbriatus* individuals was small, only about half the experiments showed a constant rate of reduction, while when a large number of predators were involved all the experiments were characterized by a constant index of reduction (Tab. III). In the experiments with *T. montana* any type of density usually resulted in cases with a variable rate of reduction.

Dependence of the character of prey reduction on the density of predators (data from the series of experiments with the gradient of predators)

Tab. III

Number of spiders in the series of experiments with the gradient of predators	Number of experiments with separate predator densities				Small number of predators (6-12) per cent of cases	Large number of predators (24-48) (20-30) per cent of cases
	6	12	24(20)	48(30)		
Experiments						
<i>Tetragnatha montana</i>						
Number of experiments with a variable rate of reduction	5	3	7	4	67	73
Number of experiments with a constant rate of reduction	1	3	1	3	33	27
<i>Dolomedes fimbriatus</i>						
Number of experiments with a variable rate of reduction	1	2	0	0	60	0
Number of experiments with a constant rate of reduction	2	0	3	3	40	100

And so we can assume that the initial density of the prey-predator relation components (spiders-mosquitoes) can have an effect on whether the rate of prey reduction on the course of the experiment is constant or variable. A decrease in the rate of reduction was usually recorded in such experiments in which there was a larger number of prey per one predator (a large number of prey introduced into the isolator, or a small number of predators introduced). When the number of prey per one predator was smaller, then the constant rate of reduction was maintained in the course of an experiment.

The phenomena discussed are concerned with the qualitative aspect of the



problem. We have also investigated the effect of the predator population density and the initial prey density on the value of the mosquito reduction indices obtained in separate experiments. It was concluded that the course of mosquito reduction by spiders depends on the initial density of preys introduced into the isolator (experiments with the gradient of prey) (Fig. 3). This is indicated by the maximum values of indices obtained in separate groups of experiments. These indices were taken into account as they were concerned with the period of the most intensive prey reduction. In the experiments with *T. montana* the values of indices were higher when the initial prey density was higher. On the other hand the experiments with *D. fimbriatus* proved that the highest values of reduction indices were similar even for various initial prey densities (except the experiment with 30 prey individuals). This is due to the fact that *D. fimbriatus* is a species effectively exterminating mosquitoes and hence the maximum values of mosquito reduction indices are high for each initial prey density (Fig. 3).

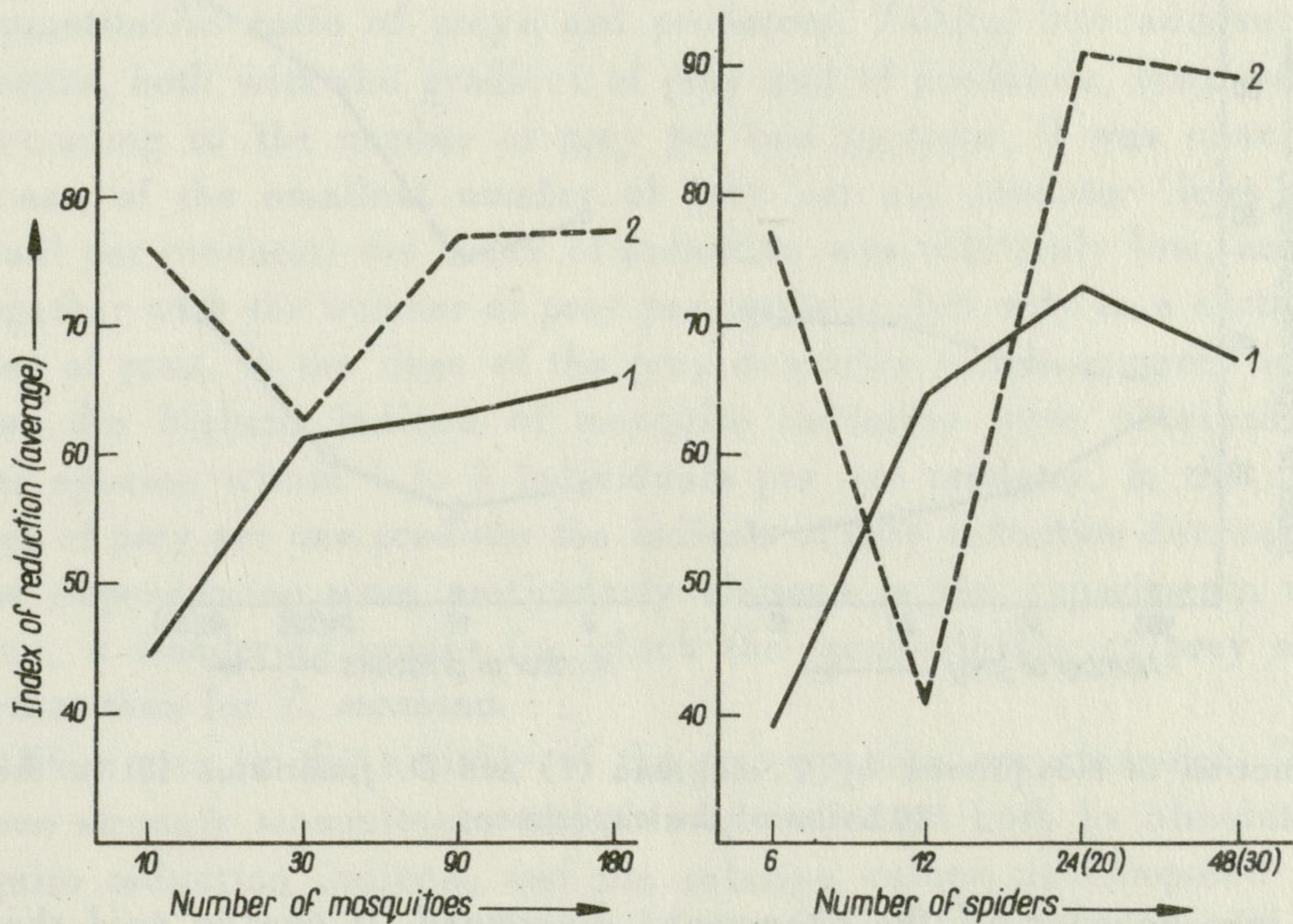


Fig. 3. Rate of mosquito reduction by *T. montana* (1) and *D. fimbriatus* (2) at different numbers of predators and preys introduced

Such is the picture of the process of mosquito reduction by spiders in the experiments with the gradient of prey when we take into account the experiments from the moment of mosquito introduction into the isolators until their complete reduction. However it is possible to take into account only the first stage of the experiment, that is the introduction of mosquitoes into the isolators and spider reaction to them expressed by the value of their reduction in the course

of the first 24 hours. The index of this reduction was calculated directly on the basis of the formula  $\frac{a - b}{a} \times 100$ , where  $a$  is the number of mosquitoes introduced into the isolator, and  $b$  their number after 24 hours. The analysis of these materials concerned with the initial spider reaction to the mosquitoes supported the conclusion about the character of *T. montana* reaction to the density of mosquitoes introduced into the isolator: the higher was their initial density, the more intensive was the reduction by this spider in the first 24 hours (Fig. 4). *D. fimbriatus* displayed, on the other hand, a negligible dependence of its initial reaction to the prey on their density. Values of reduction indices were higher in the experiments with *D. fimbriatus* than in the experiments with the other species. As compared with *T. montana* it was a stronger and more effective predator (Fig. 4).

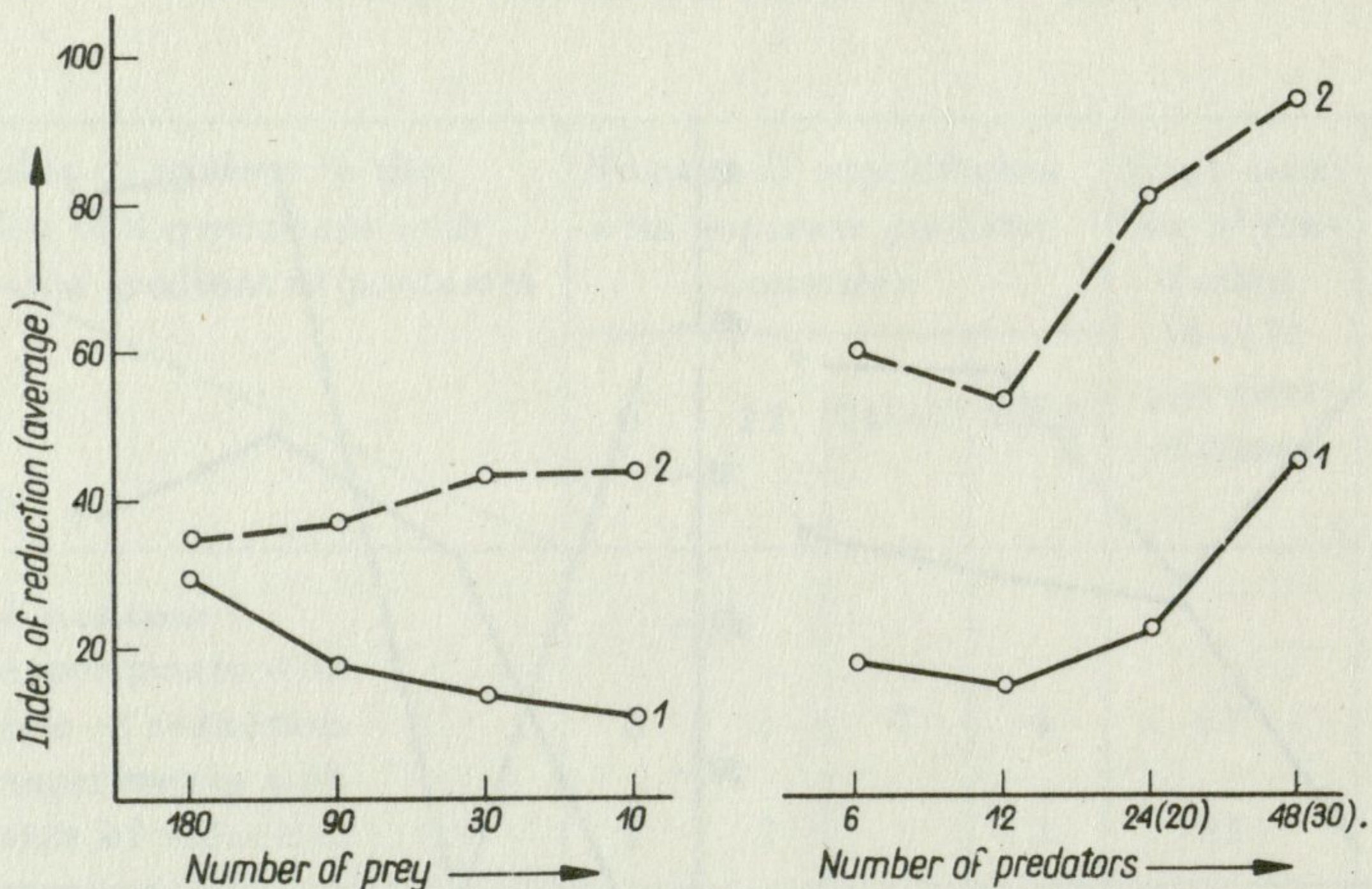


Fig. 4. Reduction of mosquitoes by *T. montana* (1) and *D. fimbriatus* (2) in the first 24 hours of the experiment

Taking into account all the phenomena discussed, it can be said that the initial prey density may affect both the numerical value of the index of reduction, and the change in the rate of reduction.

Experiments with the gradient of predator density (Fig. 3) showed that the higher predator density in the isolators with a constant number of prey, resulted in a higher prey reduction, and so higher indices of reduction were obtained. As it could be expected this increase in density was accompanied by an intensification in the pressure of predators on their prey. Such a picture was obtained both for *T. montana* and for *D. fimbriatus* (Fig. 3). It was only surprising that the reduction was weakened when there were 12 *D. fimbriatus* indivi-

duals. It also gave food for thought that smaller values of the index of reduction were arrived at in the experiments with the two species at the highest predator densities. The reason here must have been phenomena occurring inside the predator population.

A general conclusion concerning the intensification of the predator pressure together with an increase in its density was supported by an analysis of the mosquito reduction by the two predator species in the course of the first 24 hours (Fig. 4).

The pictures of mosquito reduction described above were undoubtedly caused by predator activity, and that was indicated by a comparison of the results with the control experiments (Tab. IV). In the control isolators the indices of mosquito reduction were lower than in the experiments with spiders. The reduction in the control experiments was caused by the natural mortality of mosquitoes, however we can not exclude their partial extermination by predators accidentally leaving the litter of the isolators, in spite of its careful cleaning.

Density dependences were also expressed in the prey-predator relation by the quantitative ratio of preys and predators. Taking into account all the experiments, both with the gradient of prey and of predators, they were segregated according to the number of prey per one predator. It was concluded that in the case of the smallest number of prey per one predator (less than one individual per predator) the index of reduction was relatively low, and it increased together with the number of prey per predator, but only to a certain specified number of prey. In the case of the prey densities which occurred in our experiments, the highest indices of mosquito reduction were obtained by the two spider species within 1 to 3 individuals per one predator. In the case of other number of prey per one predator the indices of prey reduction decreased (Fig. 5). These dependences were particularly obvious in the experiments with *D. fimbriatus*, a wandering spider for which the accessibility of prey may be more important than for *T. montana*.

Differences in the activity of the two species are clear-cut. *D. fimbriatus* reduces strongly mosquitoes, and this is indicated both by absolute values of mosquito reduction indices, and the relative values as compared with the indices arrived at in the control experiments (Tab. IV). A comparison of the pressure exerted by the three spider species *Linyphia triangularis* (Clerck), *T. montana* Simon, and *D. fimbriatus* (Clerck), at the same prey and predator densities even more clearly stressed differences in the activity of separate species (Fig. 6). The least intensive pressure on mosquitoes was exerted by the web spider *L. triangularis*, slightly more intensive by *T. montana* as a species trapping mosquitoes in the isolators in its webs and also outside it on the walls of the isolator. The strongest pressure was exerted by *D. fimbriatus*, a wandering spider actively searching for its prey.

Indices of mosquito reduction (average)

Tab. IV

Number of mosquitoes	10	30	90	180	Average indices for all the experiments	Number of spiders	6	12	24 (20)	48 (30)	Average indices for all experiments
Experiments with <i>T. montana</i>	32.5	48.0	47.9	40.8	42.3	experiments with <i>T. montana</i>	29.3	54.4	54.0	55.0	48.2
Control experiments	25.9	24.5	40.0	34.8	32.3	Control experiments with 50 mosquitoes	29.5				29.5
Experiments with <i>D. fimbriatus</i>	76.1	62.0	52.4	53.1	60.9	Experiments with <i>D. fimbriatus</i>	66.6	35.6	91.0	89.0	70.6
Control experiments	44.0	32.7	35.7	37.0	37.3	Control experiments with 50 mosquitoes	39.2				39.2

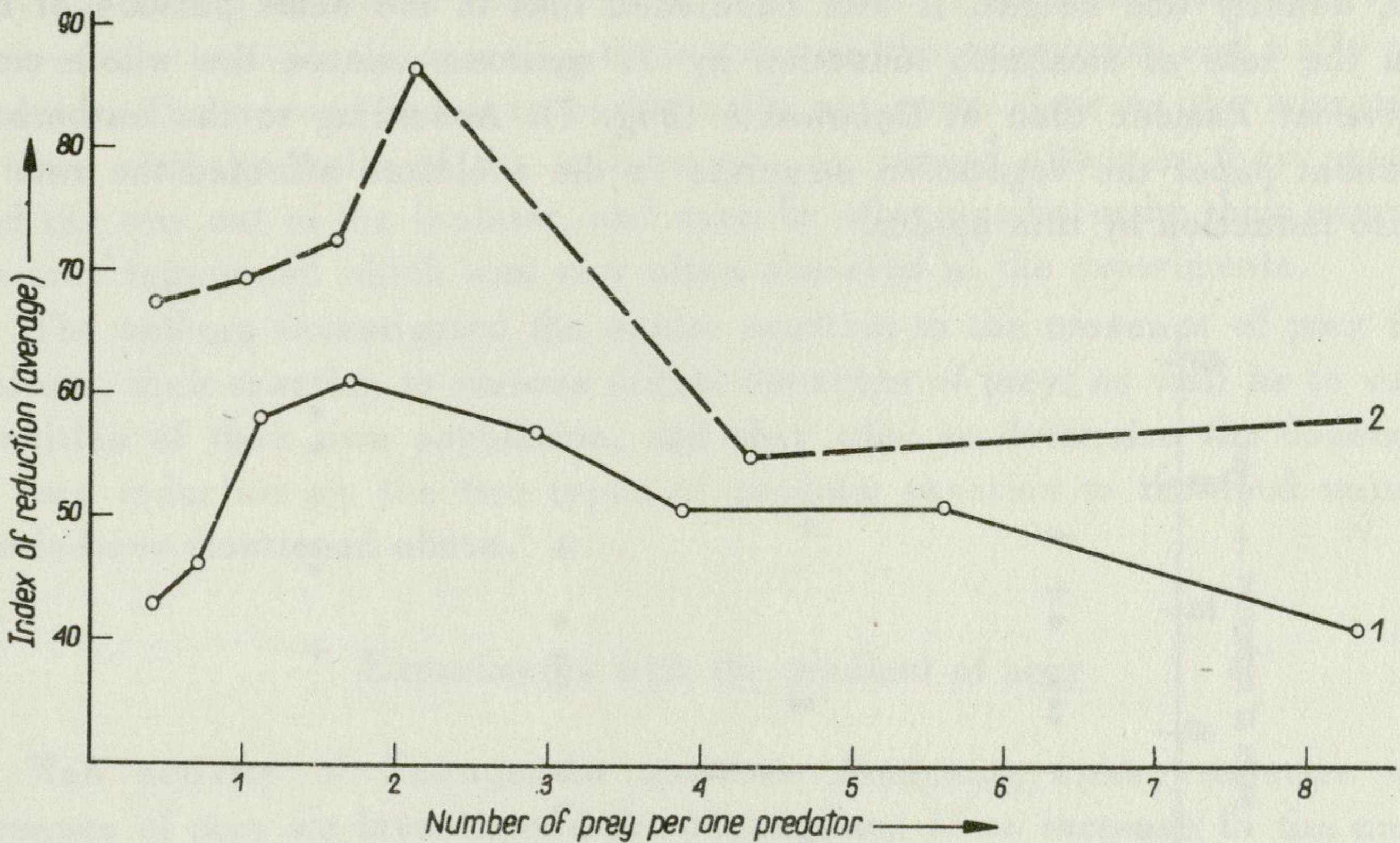


Fig. 5. Dependence of reduction index value on the number of preys per one predator in the experiment

1 - *T. montana*, 2 - *D. fimbriatus*

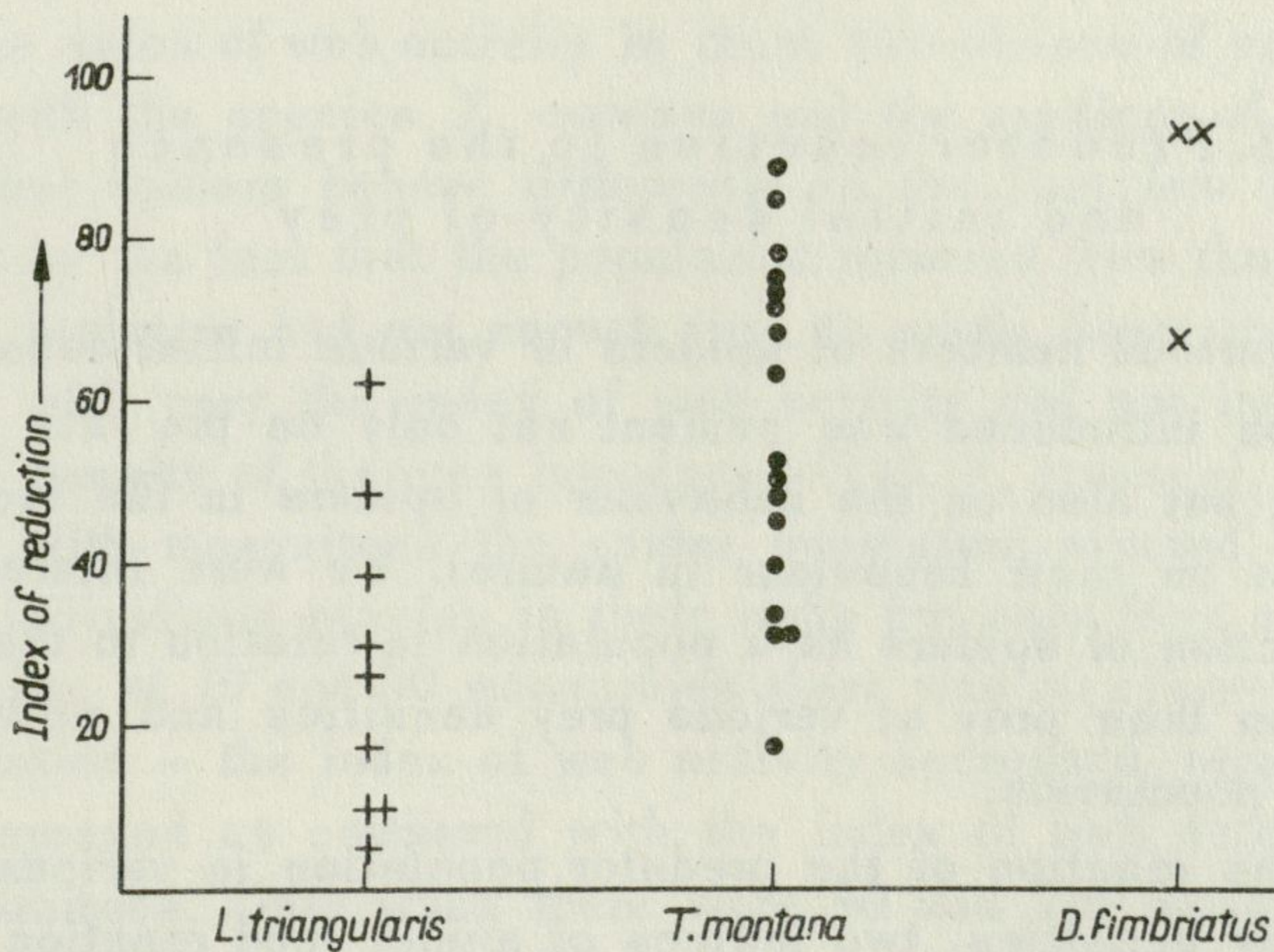


Fig. 6. Mosquito reduction by three spider species in the same density conditions of preys and predators (experiments were carried out in 1965)

Not only specific differences modified the effect of prey-predator densities on the value and rate of prey reduction. The environment is also quite an important factor. When describing the study area we pointed out the fact that in the isolators put up at Dębowski, the vegetation occurring there was more suitable for mosquitoes than the vegetation at Zamość in view of its differen-

tiation, density and height. It was concluded that in the same periods of the season the rate of mosquito reduction by *T. montana* was on the whole more intensive at Zamość than at Dębowskie (Fig. 7). According to the authors of the present paper the vegetation structure in the isolators affected the rate of mosquito reduction by this spider.

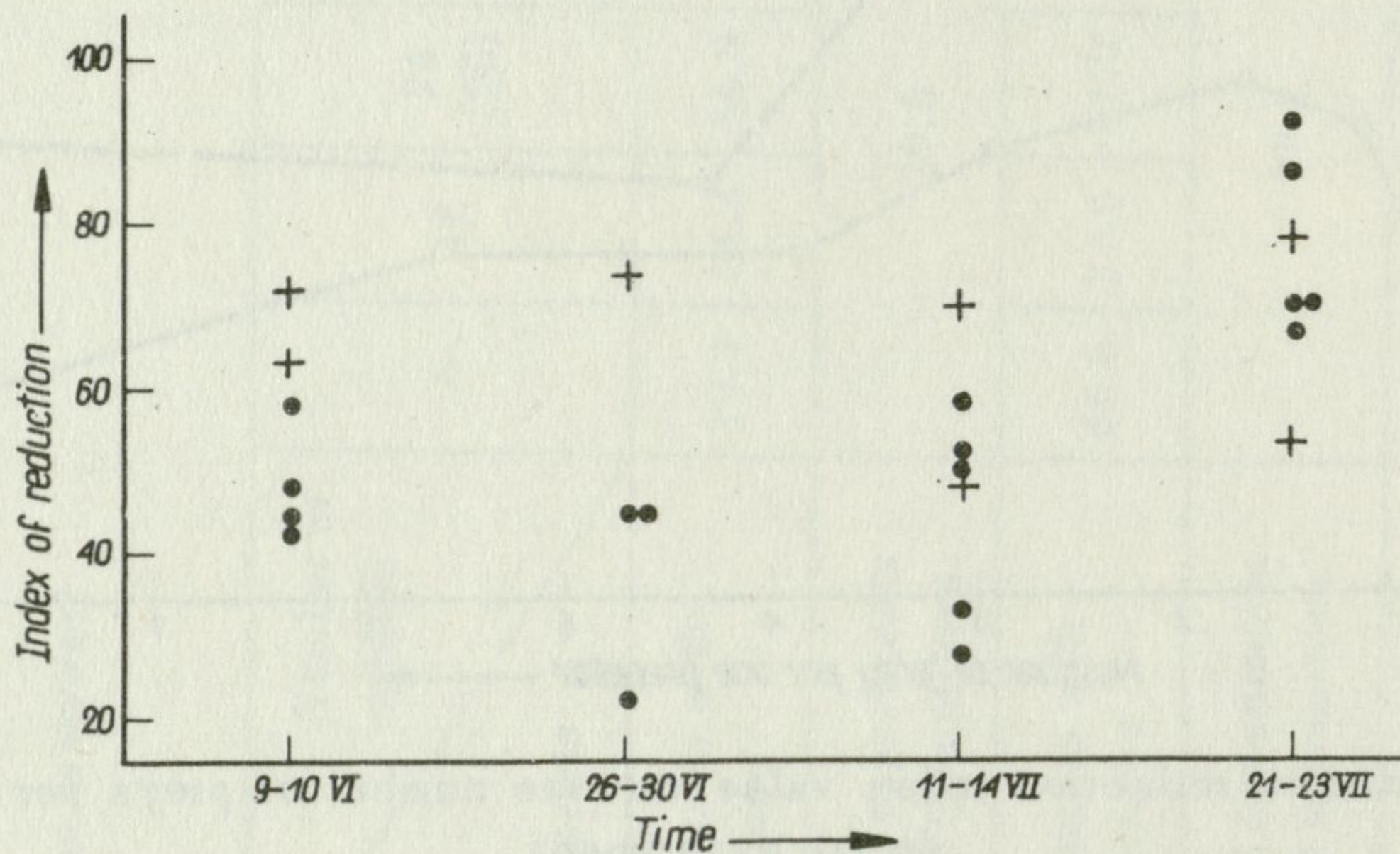


Fig. 7. Mosquito reduction by *T. montana* in different environmental conditions  
● Dębowskie, + Zamość

#### 4.3. Predator reaction to the presence and initial density of prey

The effect of various numbers of spiders or various initial densities of the mosquito population introduced was evident not only on the rate and way of mosquito reduction but also on the behaviour of spiders in the isolators (and most probably also on their behaviour in nature). We were interested in the problem of the reaction of spiders as a population in relation to their food and pressure exerted on their prey at various prey densities and at various densities of their own population.

Investigating the reaction of the predator population in various conditions of prey and predator densities, two indices of spider food reaction were used: the index of the population "web activity" (invented by Kajak in 1966 and called by her index of food activity; the name had to be changed as the food activity was also investigated with the help of another index) — measured in per cent by the ratio of the number of spiders in webs to the total number of spiders recorded in the isolator — and the index of "spider movement" on the walls of the isolator — expressed in per cent by the ratio of the number of spiders staying on the walls to the total number of spiders in the isolator. The two indices determine quantitatively the per cent of the spider population dis-

playing certain specified reactions to their food. The first determines the per cent of the individuals spinning their webs on the vegetation and walls of the isolator. The second index is biologically not quite clear as the migration of spiders over the walls of the isolator may be caused either by their search to find the way out of the isolator, and even by other needs, or by their search for the prey introduced which was very often observed in the experiments.

The authors investigated the spider reaction to the presence of prey in the isolator, their reaction to various initial densities of prey, as well as to various densities of their own population, and they tried to determine the dependence of prey reduction on the two types of predator reaction to the food using the two indices mentioned above.

#### Experiments with the gradient of prey

Web activity of *Tetragnatha montana*. Analysing spider reaction to the presence of prey we investigated the phenomenon of an increase in the numbers of spiders staying in their webs in the spider population of the isolator, and we used for that purpose average indices of spider reaction in the period of three days before and three days after introducing the mosquitoes. We were not interested at that stage in the real value of indices in various experiments, only if there was any increase or not in the value of the index. Comparing average values of the index of web activity in these two phases of each of the 26 experiments, with the species *T. montana* and the gradient of prey, the authors concluded that spiders behave differently in the first few days. It may have been caused by the fact that the population removed from their natural environment to the isolators had not enough time to settle down properly. In the first experiments with prey the index of web activity did not increase, as a rule, whatever the density of the prey introduced (Tab. V, crosses). In the successive experiments with mosquitoes the spider population reacted by increasing the per cent of individuals staying in their webs but only from a certain threshold of prey density: at 10 and 30 mosquitoes there was no clear-cut reaction of the spider population — the index of web activity decreased, remained at the same level, or increased as compared with the index of web activity in the period without mosquitoes. Only when there were 90 and 180 mosquitoes introduced, the index, as a rule, increased (Tab. V). Thus there is a spider reaction to the prey but this reaction is delayed as a result of the adaptation of the spider population to the new environment in the first few days after getting into the isolator.

The authors followed closely value changes in the index of web activity obtained in separate experiments with various prey densities for periods of the most intensive prey reduction by spiders. It was then recorded that the per cent of webs in the spider population was, on average, smaller when there were 180

Dependence of food activity of *Tetragnatha montana* on the presence and density of mosquitoes in the field experiments (24 individuals of *T. montana* in each of the experiments)

Tab. V

Number of mosquitoes	Increase in the per cent (+) of individuals from the population staying in their webs after the introduction of preys	Increase in the per cent (+) of individuals moving on the walls of the isolator after the introduction of preys
10*		+
30*		+
30*		+
90*		+
90*		
180*		+
180*		+
10		+
30		+
30	+	+
30		
30		+
30		+
30	+	
30	+	
30	+	+
90	+	+
90	+	+
90	+	
90		+
90	+	+
180	+	+
180	+	+
180	+	+
180	+	+
180	+	+

\* — Initial experiments with *T. montana*.

mosquitoes than with 90, and smaller with 90 mosquitoes than with 30. That could indicate the situation that when there are more mosquitoes there are relatively fewer spiders staying in their webs (Fig. 8). This dependence of the spider population reaction on the prey density can be explained by the fact that the strong stimulus, i.e. a considerable prey density, makes some of the individuals of *T. montana* leave the web or prevents them from spinning one if the prey can be trapped on the walls of the isolator without spinning a regular web (Łuczak, Dąbrowska-Prot 1966). To calculate these values of the web activity index the results of all the experiments from all the periods of the season in which they were carried out were taken into account.



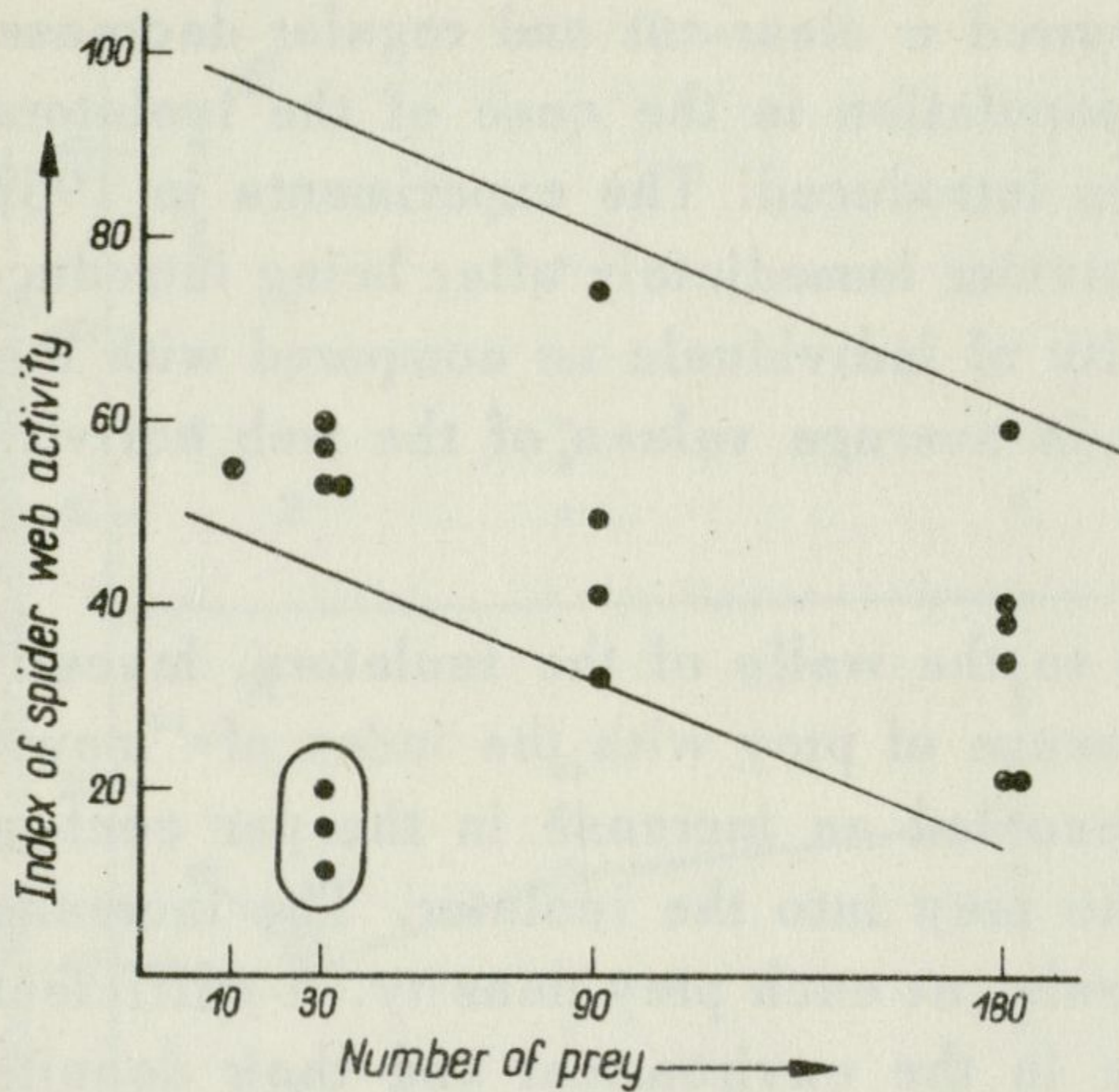


Fig. 8. Dependence of the web activity index of *T. montana* on the numbers of preys introduced (initial experiments not included)

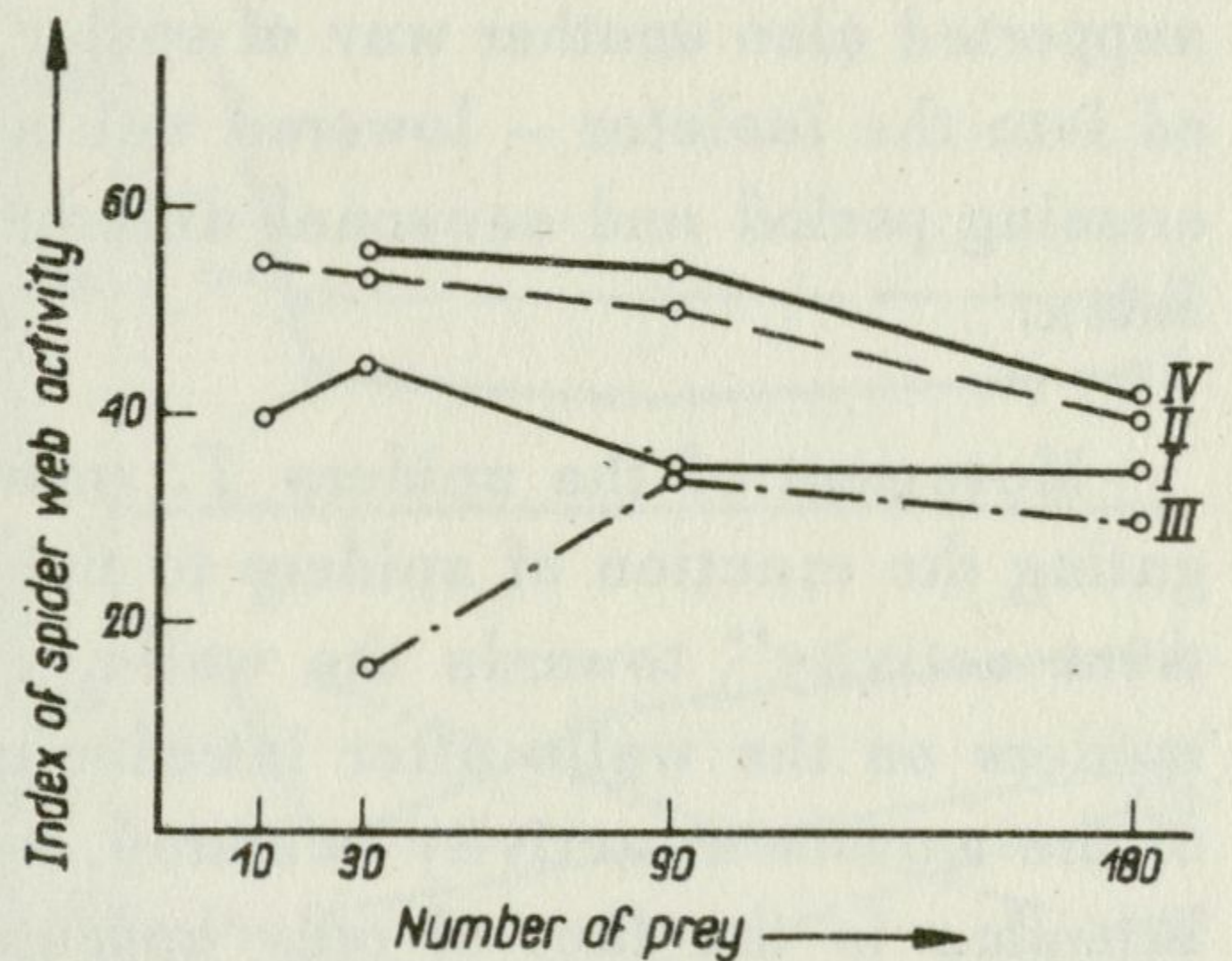


Fig. 9. Value of web activity index of *T. montana* in relation to the period of prey introduction into the isolator  
I, II, III, IV – periods of the season (detailed explanations in the text)

When we compare the indices of web activity obtained in various periods of the season (I – June 1 to 15, II – June 15 to 30, III – July 1 to 20, IV – July 21 to August 10), then we can see that each period has its characteristic level of the index value (Fig. 9) differing, sometimes not much but always clearly, from other periods. This means that in different periods of the season somewhat different per cent of individuals of the given population stay in their webs. This can be important, besides the effect of prey density, for estimating the ecological role of spiders in the community in different periods of the season. The periods were determined according to the following assumption based on the biology of the given species – I is the period when spiders settle down in the isolators, II is the period of the most intensive sexual activity of the young adult spiders, III – period of the most intensive breeding, IV is the period when the mature individuals start dying out. Seasonal differences recorded may be caused by changes occurring inside the spider population which alters its way of behaviour entering the new biological stages of development. We must also take into account the effect of various weather conditions. These effects of various factors on the web activity of *T. montana* population complicate the dependence of their behaviour on the prey density. Data for separate periods of the season support the regularity described above and consisting in a small decrease in the per cent of spiders in their webs when there are 180 as compared with 90 mosquitoes (Fig. 9). This interesting regularity was most decidedly supported by the experiments carried out in 1967 in which the pressure of prey on the predator was increased several times. It was recorded, particularly dur-

ing evening observations, that there occurred a clear-cut and regular decrease of spiders staying in their webs in the population in the case of the isolators which had a higher density of mosquitoes introduced. The experiments in 1967 supported also another way of spider behaviour immediately after being introduced into the isolator – lowered web activity of individuals as compared with the ensuing period and seasonal differences in average values of the web activity index.

Movement of the spiders *T. montana* to the walls of the isolators. Investigating the reaction of spiders to the presence of prey with the index of “movement activity” towards the walls, we recorded an increase in the per cent of spiders on the walls after introducing the prey into the isolator. The increase of the movement activity occurred, as a rule, at each prey density. A sufficient stimulus is the fact of prey appearance in the environment and their density

was immaterial (Tab. V). Analysing changes in the values of indices, recorded in the same experiment before and after introducing the prey it could be supposed that the most important difference in the intensity of movement in the two stages of the experiment – with and without the prey – occurred when the number of prey was either smallest or largest, with a very weak reaction when the prey density was moderate (Fig. 10). This means that spiders move all over the walls more intensively when there are 10 or 180 mosquitoes than when there are 30 or 90. So far we have not been able to find a completely satisfactory explanation of this phenomenon.

Considering the values of the index in the experiments with various prey densities (excluding period III, July 1 to 20, as characterized by long rainy spells and

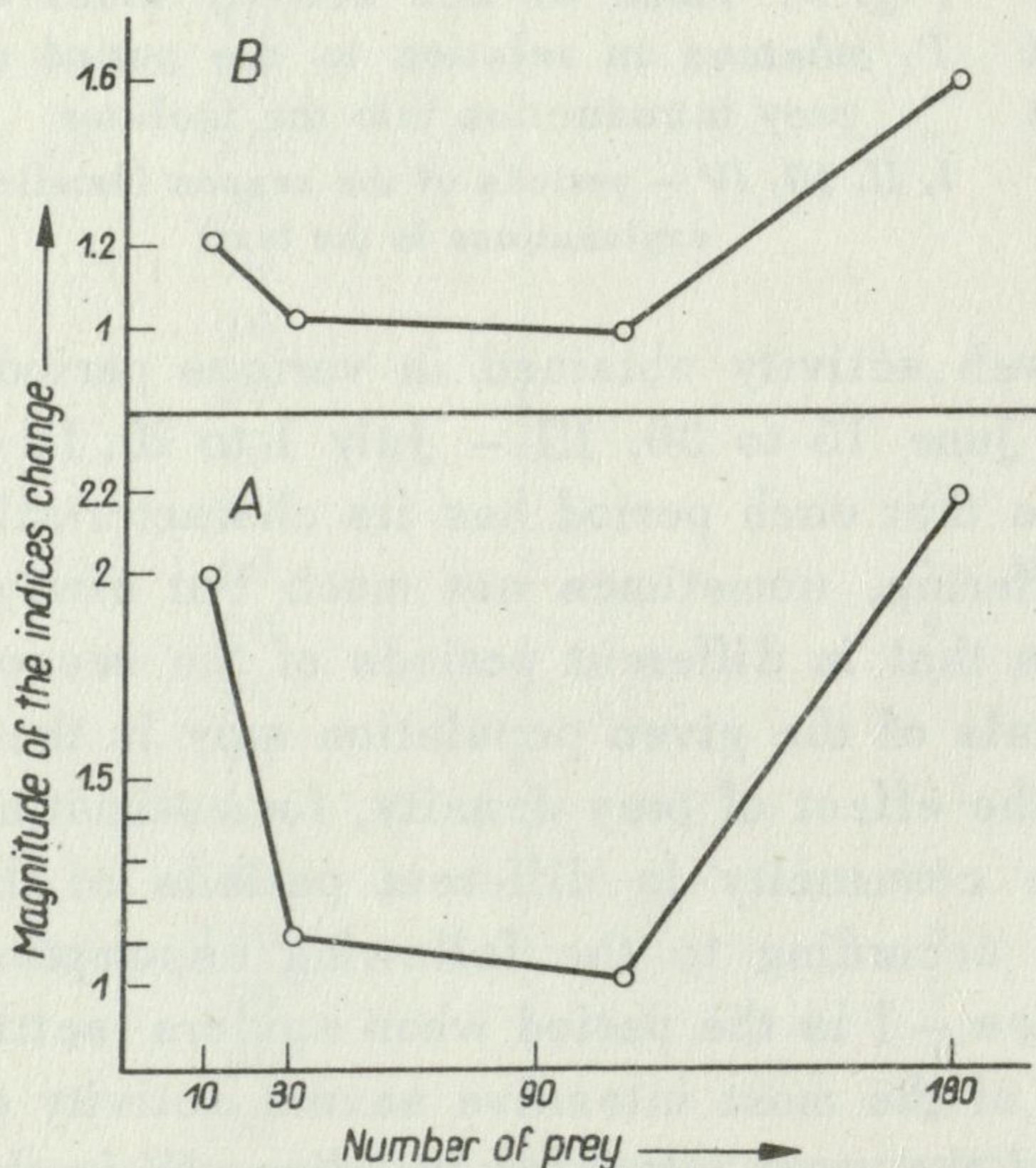


Fig. 10. Value of the change in the index of spider movement activity of *T. montana* (A) and *D. fimbriatus* (B) all over the walls of the isolator in the period following the introduction of mosquitoes as compared with the period when there were no mosquitoes, at different numbers of preys introduced

generally bad weather) we can notice a tendency to an increase in the number of individuals moving on the walls when there occurs an increase in the density of prey in the isolator (Fig. 11) in the gradient of 30, 90, and 180 mosquitoes.

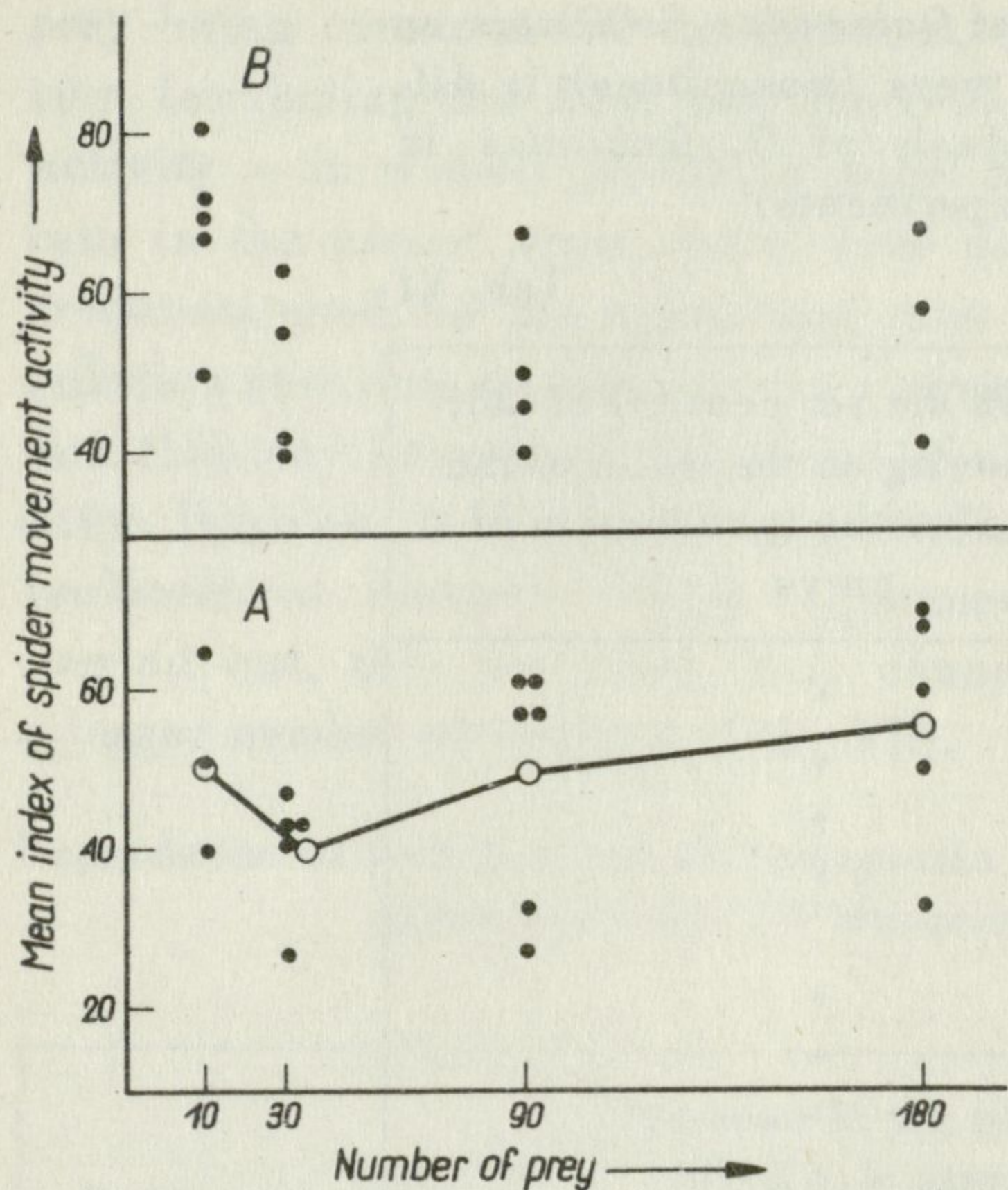


Fig. 11. Value of the index of movement activity on the walls of the isolator of *T. montana* (A) and *D. fimbriatus* (B) at different numbers of preys introduced

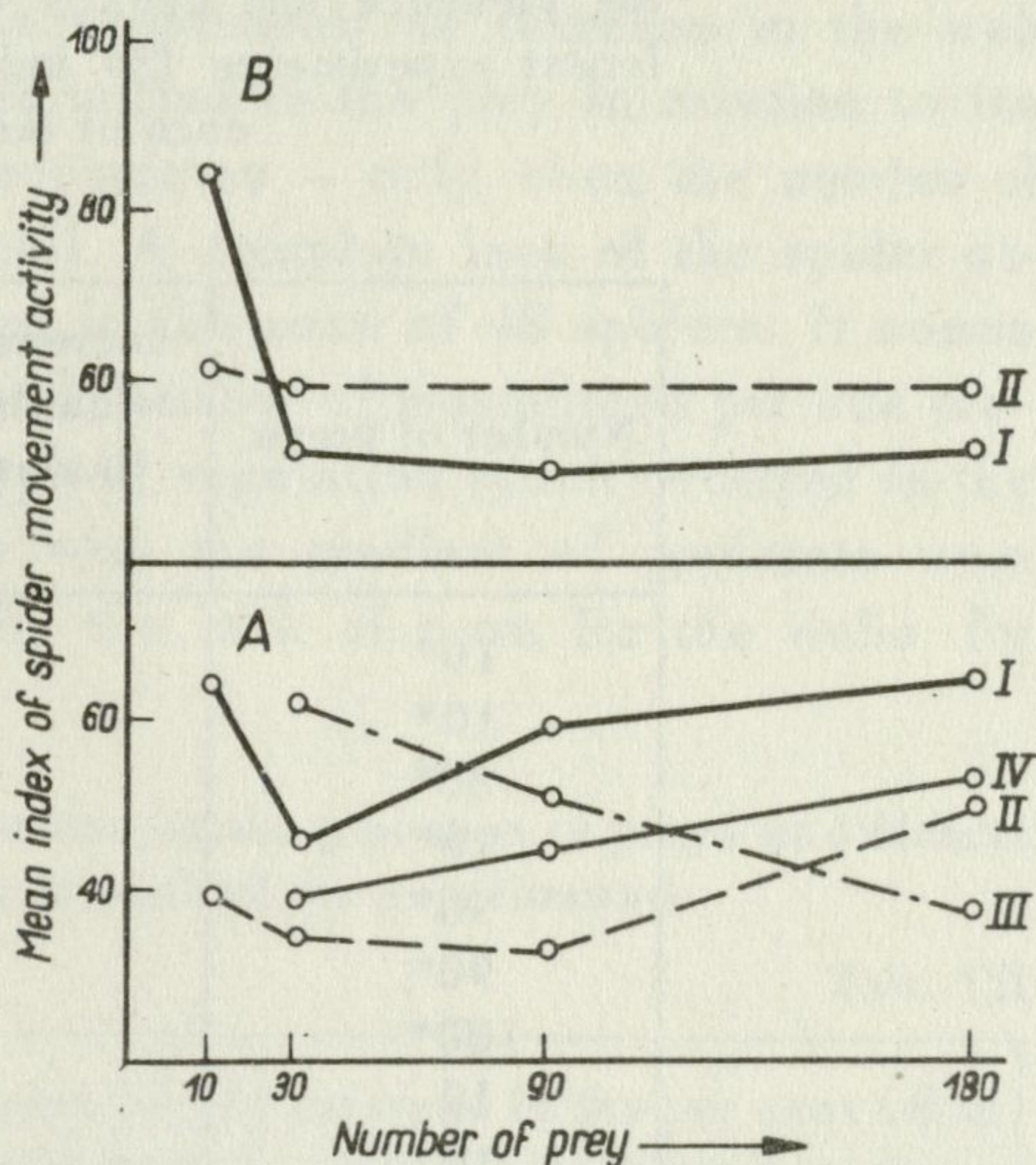


Fig. 12. Value of the index movement activity on the walls of the isolator of *T. montana* (A) and *D. fimbriatus* (B) in relation to the period of prey introduction into the isolator

I, II, III, IV — periods of the season (detailed explanations in the text)

Considering the level of average movement activity indices in the four periods of the season it should be stressed that, excluding period III, each period has its characteristic level of index values. A similar regularity occurs here as in the case of the web activity indices. It was also possible to record in each of the periods an increase in the per cent of spiders moving to the walls of the isolator when the prey densities were higher (Fig. 12).

Movement activity of *Dolomedes fimbriatus* individuals. The per cent of the wandering spider *D. fimbriatus* individuals staying on the walls shows, similarly as in the case of *T. montana*, a dependence on the presence of prey in the environment. This per cent is, as a rule, smaller in a period when there are no preys than after the introduction of the prey for each of the initial prey density (Tab. VI).

Besides, also as with *T. montana*, changes in the intensity of spider movement on the walls of the isolator in the phase of prey presence, as compared with the period when there are no preys, are greater for the lowest and highest initial prey density (Fig. 10). As with *T. montana* we are not able to explain sufficiently this phenomenon though the occurrence of such dependences in the case of two different spider species indicates its significance.

Dependence of food activity of *Dolomedes fimbriatus* on the presence and density of preys (mosquitoes) in different experiments (20 individuals of *D. fimbriatus* in each of the experiments)

Tab. VI

Number of preys	Increase in the per cent (+) of individuals moving on the walls of the isolator after the introduction of preys
10*	+
10*	+
30*	+
30*	+
90*	
90*	+
180*	+
10	+
10	
10	+
30	
30	+
30	+
90	
90	+
180	+

\* – Initial experiments with *D. fimbriatus*.

Analysing values of the movement activity index in the experiments with various prey densities we did not record any correlation between the per cent of the spider population staying on the walls and the value of the initial mosquito density (Fig. 11). This spider is stimulated only by the presence of prey (Tab. VI), and not by its initial density.

The per cent of *D. fimbriatus* spiders staying on the walls in the two arbitrary chosen periods of the season (I – August, II – September) remains on a level different for each of the periods, but similar for different prey densities in the same period (Fig. 12). Again as in the case of *T. montana* there is a strong effect of the “period of the season” on the reaction of the spider movement after its food.

#### Experiments with the gradient of predators

Web activity of *T. montana*. Considering the qualitative reaction of predators in the experiments with the gradient of predator numbers, the number of

prey being constant (50 mosquitoes), there could be observed in spider population (excluding the first few days of the experiment) an increase in the web activity – in a short period (3 days) after letting in the prey in relation to its rate in the period when there were no mosquitoes – only when the number of predators used for the experiment was small. A complete lack of the spider population reaction to the prey was observed in the case of 48 spiders. It seems that this may have been the result of a small number of mosquitoes per one predator. Besides, in the conditions of this type of vegetation which occurred in the isolators at Zamość, where experiments with the gradient of predators were carried out, this may have been caused by the lack of room for the webs for a larger number of spiders (Tab. VII).

Dependence of food activity of *Tetragnatha montana* on the presence of preys at different spider densities (50 mosquitoes in each of the experiments)

Tab. VII

Number of predators	Increase in the per cent (+) of individuals staying in their webs after the introduction of preys	Increase in the per cent (+) of individuals moving on the walls of the isolator after the introduction of preys
6*		+
6*		+
12*		
12*		+
24*		
24*		+
48*		+
48*		+
6	+	+
6	+	
6	+	
6		+
12	+	+
12		+
12		+
12	+	+
24		+
24	+	
24		+
24	+	+
24		+
48		+
48		+
48		+
48		+

\* – Initial experiments with *T. montana*.

Taking into account a number of experiments with various spider densities an interesting regularity can be recorded. Overlooking here the density of 12 spiders per isolator, when the average web activity of *T. montana* is lowest

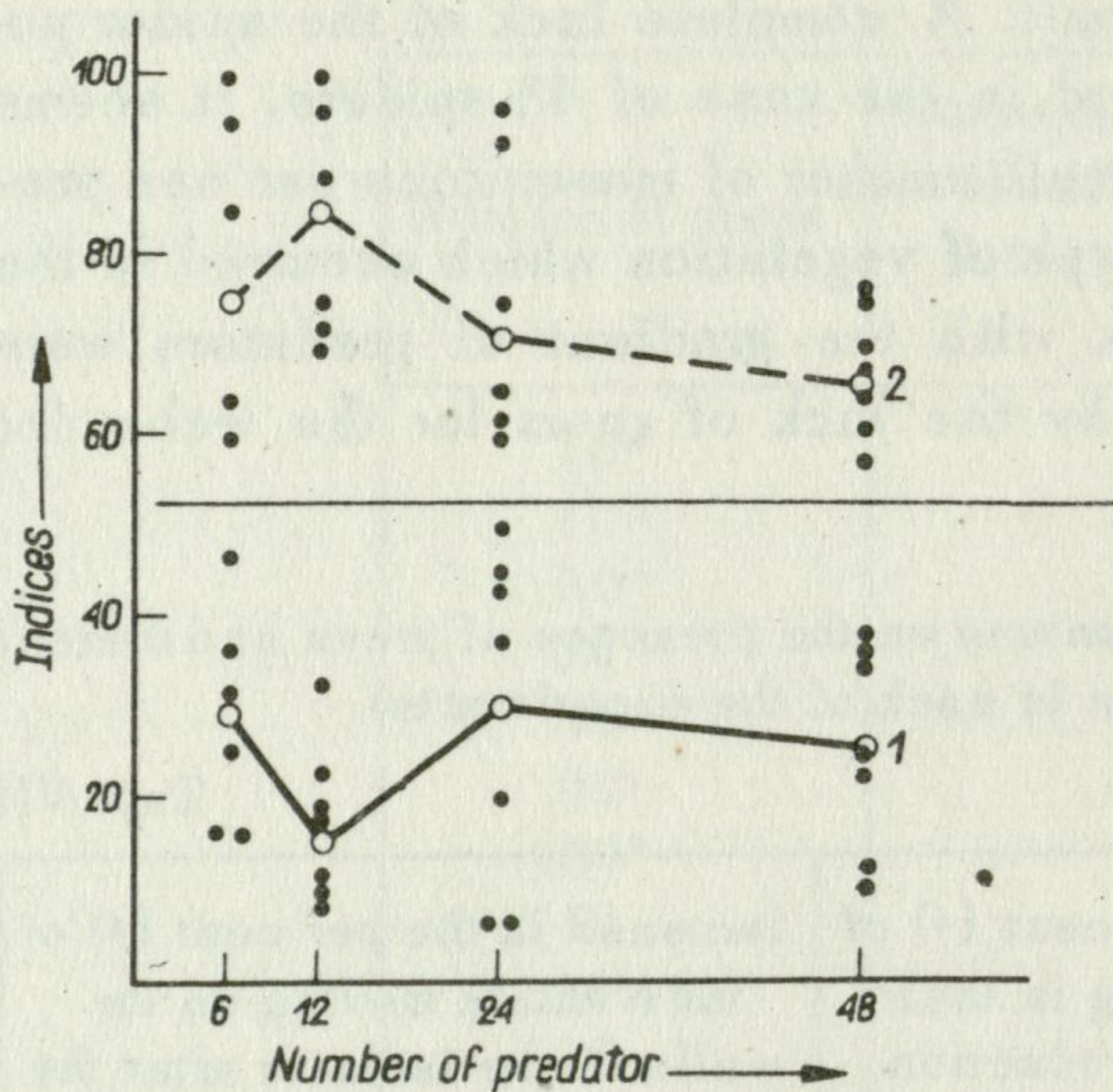


Fig. 13. Values of web activity and movement activity indices of *T. montana* at different densities of predators

1 — average index of web activity, 2 — average index of movement activity

In all the experiments with various predator densities the per cent of individuals staying on the walls (65 to 85%) was much higher than the per cent of spiders staying in their webs (17 to 30%) (Fig. 13). This was most probably caused, among other things, by the not so good conditions of vegetation in the isolators at Zamość, because this difference was not so strong in the isolators at Dębowskie. A negative correlation between the per cent of individuals staying on the walls and an increase in their density was recorded — their participation in the population decreased when the spider density increased. It seems possible that at high densities spiders of this species get in each other's way when wandering and some of the individuals leave the walls and pass to the plants (Fig. 13).

Movement activity of *D. fimbriatus*. In the gradient of predators there is no reaction of this spider population of the presence of prey. Differences in the movement activity in the period with the lack of prey and after the introduction of the prey in separate experiments are small and quite irregular. Nothing indicates any regular dependence on the density of predators. However it should be stressed that we had to deal with a small number of cases (11).

(may be as a result of special conditions in the isolator, e.g. particularly unsuitable vegetation) a similar web activity of spiders can be recorded when there are 6, 24, and 48 spider individuals: 25 to 30% of the population stay in their webs, and there is only a slight tendency to a decrease in the case of high spider densities (Fig. 13).

Movement activity of *T. montana*. The per cent of spider individuals wandering to the walls of the isolator (just as with the same species in the experiments with the gradient of prey) increased, as a rule, in the presence of preys in relation to its value in the period when there are no mosquitoes, at various densities of predators introduced (Tab. VII).

Taking into account a number of various experiments with different spider densities we can observe the following dependence of the per cent of spiders staying on the walls on the density of spiders: the highest per cent was recorded at the smallest (6) and the largest (30) number of predators (Fig. 14). It is very difficult to explain this phenomenon, and the small number of experiments with this spider species warns that we should be cautious when drawing conclusions. An increase in the per cent of spiders moving in the isolator occurs only in the gradient 12, 24, 30 individuals per isolator, excluding here the case of 6 individuals (Fig. 14).

The data above are the first attempt to analyse ecologically certain aspects of the behaviour of spiders as a population in relation to their food. We recorded the effect of the prey and predator density on the population food activity of *T. montana* and *D. fimbriatus*. However this effect was weakened by environmental factors, such as the effect of the "settling down" process of the spider population in the new habitat, the effect of the "period of the season", i.e. the development stage of spiders in the given period of time, the effect of long drastic weather changes, and the effect of the vegetation structure under the isolator.

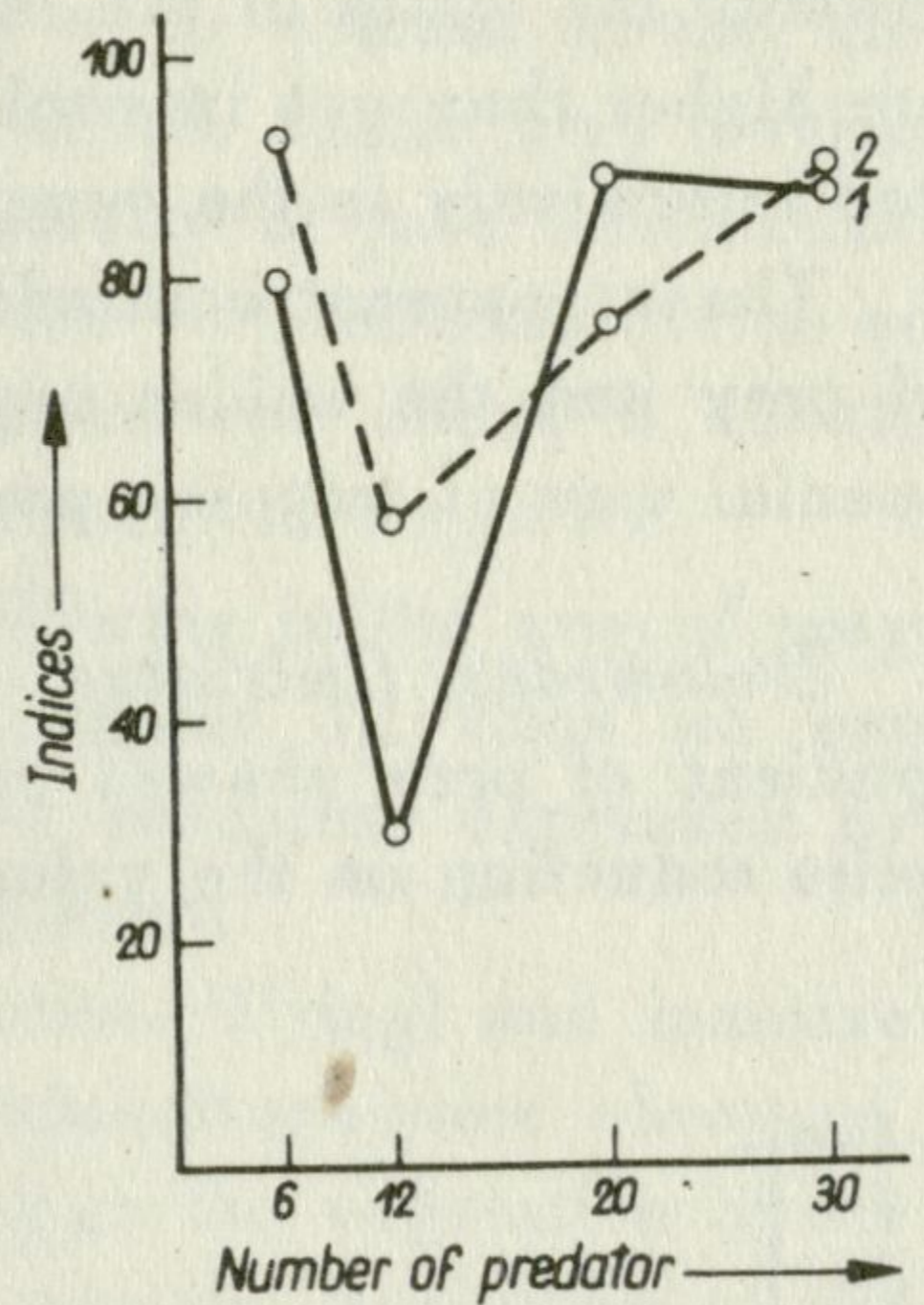


Fig. 14. Dependence between the index of mosquito reduction and the index of movement activity of *D. fimbriatus* in the experiments with the gradient of predators 1 — average index of mosquito reduction, 2 — average index of spider movement activity

#### Mosquito reduction and the indices of spider food activity

*Tetragnatha montana*. Between the reduction of mosquitoes and the movement activity of spiders towards the walls of the isolator only a weak correlation occurs. It was observed for high prey densities that this spider can trap them actively outside its web. When it is stimulated by the abundant prey in the environment it can either leave its web or even reach its prey quicker without spinning the web. Hence a certain correlation between the reduction of mosquitoes and the index of movement activity of spiders at high initial densities of prey.

Considering the web activity we can point out that a decrease in the web activity of *T. montana* spiders for the highest initial densities of prey was correlated with an increase in the index of mosquito reduction, and this is sufficiently supported by the explanation provided above.

In the experiments with the gradient of predators it is clear that there occurs an increase in the reduction of mosquitoes at higher predator densities, while (excluding the smallest density of predators) the increase in the reduction of mosquitoes was correlated with the decrease in the movement activity of spiders towards the walls of the isolator. It is possible that when densities of spiders are higher they get in each other's way and some of them leave the walls and trap intensively in the vegetation.

These apparent contradictions and vague correlations between the reduction of prey and the spider population food activity can be easily explained by a special way of trapping preys in the isolators by *T. montana* mentioned above.

*Dolomedes fimbriatus*. In the case of this species, experiments with the gradient of prey showed not a very strong dependence of the indices of mosquito reduction on the values of the indices of the movement activity (Fig. 15).

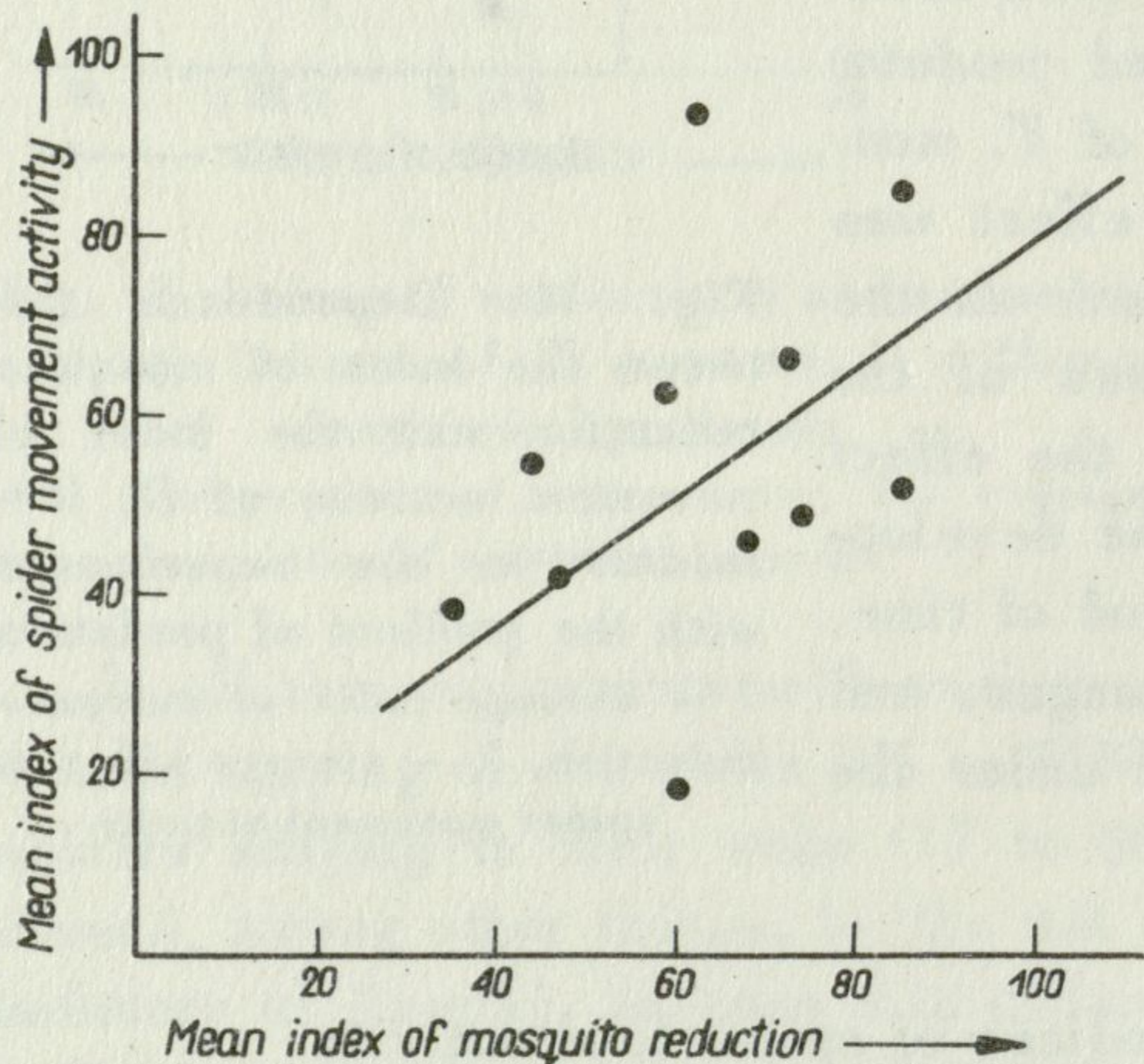


Fig. 15. Value of mosquito reduction index at different values of the movement activity index of *D. fimbriatus* spiders (gradient of preys introduced)

The isolators had rich herb layer, and spiders were trapping their prey both in the vegetation and on the walls, hence there was a weak correlation between the process of reaching the walls and the process of prey reduction.

In the experiments with the gradient of predators we managed to find out a clear dependence between the values of mosquito reduction indices and the values of spider movement activity indices, that is their wanderings all over the isolator. A high index of mosquito reduction was recorded for high indices of spider movement, and a low index for not intensive movement (Fig. 14). *D. fimbriatus* traps only actively,

and thus, differently than *T. montana*, in its case the reduction of mosquitoes depends directly on the activity of spiders. That was evident particularly in the conditions of low poor vegetation in these isolators which neither provided good shelter for the spiders nor conditions for an effective catch in the vegetation.



#### 4.4. Prey reaction to the presence and density of predator

It could be assumed that the mosquito behaviour in the isolators affects their accessibility for the predator, and, as a result of it, their reduction as well. Mosquitoes staying in the vegetation or on the walls without moving are not very accessible for spiders. They reacted, most of all, to the prey moving in their vicinity. In the case of web spiders the activity of prey determined their being trapped in the webs. Similarly changes in the vertical distribution of mosquito populations in the vegetation of the isolators and above it should affect the strength of pressure exerted on the mosquitoes by the spiders.

The investigation concerns two spider species differing in the way of prey trapping and certain reactions to their presence (Chapter 3). Thus we can assume that also the reaction of mosquitoes to these predators expressed by their activity and distribution in the habitat will be different.

In the experiments carried out the numbers of active (flying) and inactive (sitting on the walls of isolator and on the plants) mosquitoes were observed, as well as the part of the mosquito population staying in the vegetation of the isolator and occurring above it. These observations provide, according to the authors of the present paper, certain characteristics of the behaviour of the prey population in the isolator which may affect the rate of their reduction by the predators. The mosquito population activity in various conditions was described as the index of the "relative activity" of mosquitoes, and it can be expressed by the per cent of flying mosquitoes to the total number of mosquitoes recorded in the isolators (sitting and flying). The vertical distribution of mosquitoes in the isolators was expressed by the per cent of individuals staying above the vegetation in the upper part of the isolator (flying and sitting) in relation to the total number of mosquitoes recorded in the isolator. This index was called the index of the "upward move" of mosquitoes.

Comparing the control experiments carried out in 1965 with the experiments with mosquitoes and spiders it was recorded that predators provoked an increase in the activity of mosquitoes (Dąbrowska-Prot 1966). The author did not have materials that would enable her to draw conclusions on the effect of the two components' density on this phenomenon. She was only in a position to state generally that a simultaneous increase in the prey and predator density resulted in an increase in the activity of mosquitoes. The first conclusion concerning the stimulation of the mosquito activity by the predators was fully supported by the present investigation. The mosquito activity in the control isolators was lower than in the experiments with predators (Tab. VIII). *D. fimbriatus* more strongly stimulated mosquitoes than *T. montana* (Tab. VIII). The values of mosquito activity indices are lower in the experiments with *D. fimbriatus*, but as compared with the control they display a stronger activity of this species. This is probably caused by different periods of the season (ex-

periment with *T. montana* – spring, middle of the summer; experiment with *D. fimbriatus* – second half of the summer, autumn). It is known that the activity of forest mosquitoes decreases in the second half of the summer in natural habitats (Dąbrowska-Prot 1964).

Average values of indices obtained in the experiments with *T. montana* and *D. fimbriatus*, as well as in the control

Tab. VIII

Index of: Experiments	<i>Tetragnatha montana</i>			<i>Dolomedes fimbriatus</i>		
	relative activity	upward move	reduction	relative activity	upward move	reduction
Experiments with 10–180 mosquitoes	26.5	49.9	42.3	20.6	55.3	50.9
Control experiments	22.0	67.2	33.1	14.9	69.3	36.5
Experiments with 6–48 individuals of <i>Tetragnatha montana</i> or with 6–30 individuals of <i>Dolomedes fimbriatus</i>	27.1	76.1	48.2	26.8	85.5	70.6
Control experiments	21.3	80.4	29.5	14.0	95.4	39.2

In the conditions of constant mosquito numbers and variable predator numbers it was recorded, as a general regularity, that the activity of mosquitoes increased together with an increase in the predator density, particularly clearly at higher spider densities, with *D. fimbriatus* in particular (Fig. 16). In the control experiments lower and relatively little variable indices of mosquito activity were obtained. That stressed once again the significance of predators in modifying the activity of mosquitoes.

In the experiments with a variable number of prey introduced and a constant number of predators, mosquitoes behaved differently. It was a general regularity that the higher the initial mosquito numbers were in the isolators, the lower was their activity (Fig. 17). A similar phenomenon was observed in the control experiments, but the level of mosquito activity was then lower at each of the mosquito densities than in the case of the experiments with spiders (Fig. 17). This indicates that a high population density affects the activity of its individuals. Thus the levels of mosquito activity observed are always the resultant of the following two tendencies: the effect of the population density lowering the activity of mosquitoes, and the movements of predators stimulating the activity of mosquitoes.

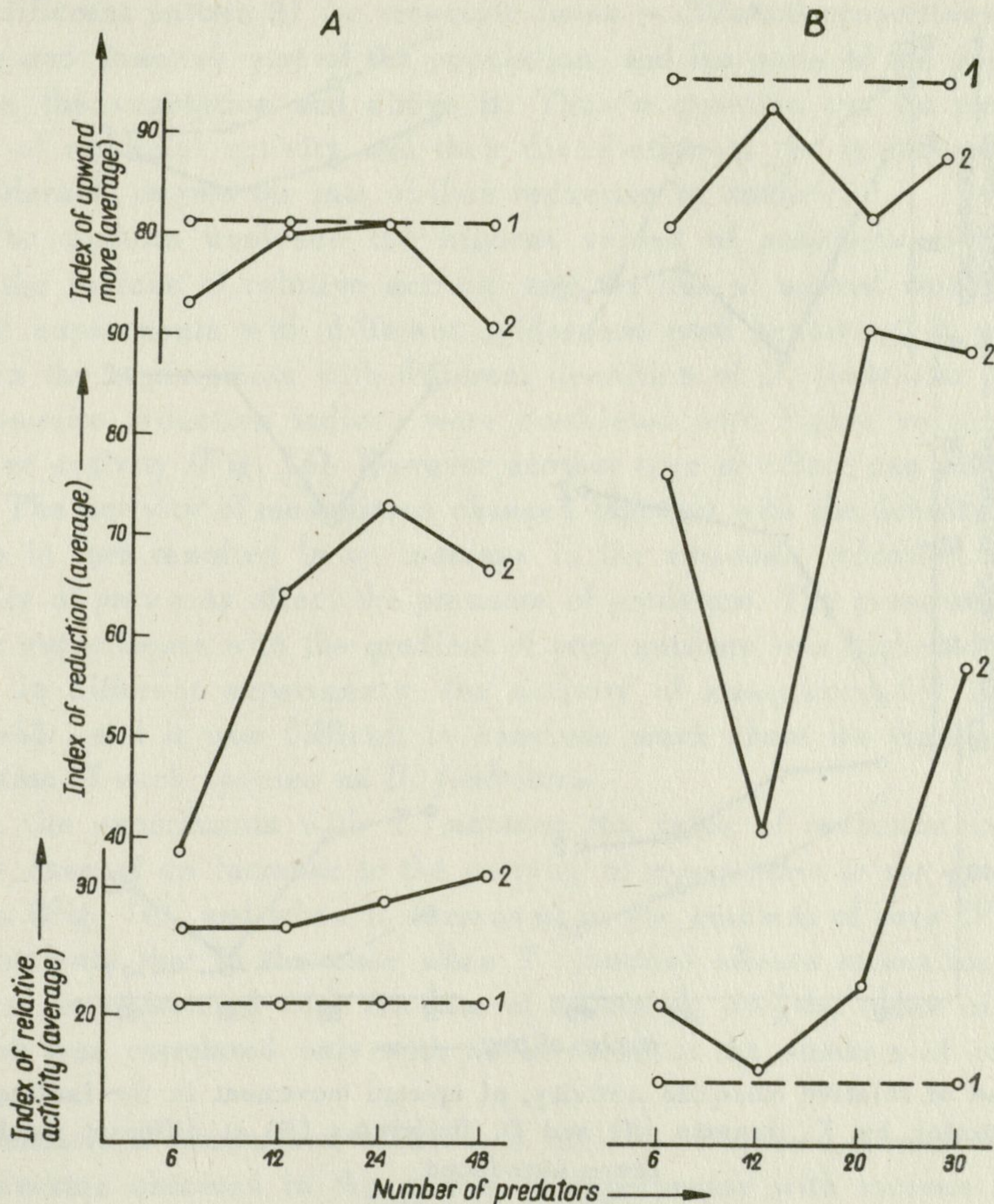


Fig. 16. Value of mosquito relative activity, of upward movement in the isolator, and mosquito reduction by *T. montana* (A) and *D. fimbriatus* (B) at different spider densities  
1 — experiment, 2 — control

It can be assumed that beside the activity of mosquitoes, also the vertical distribution of mosquitoes in the vegetation and above it can be modified by spider species so much differing in their behaviour. It was concluded that mosquitoes in the presence of spiders fly less to the upper part of the isolator than in the control experiments, and they keep rather near the vegetation of the herb layer (Tab. VIII). The index of upward movement, illustrating the differentiation of the mosquito population into the sphere of the vegetation and the space above it, reached higher values in the control than in the experiments with spiders, both *T. montana* and *D. fimbriatus*. A detailed analysis of the experimental results with the gradient of initial mosquito densities supports this conclusion. (Fig. 17). The experiments with the highest initial density of mos-

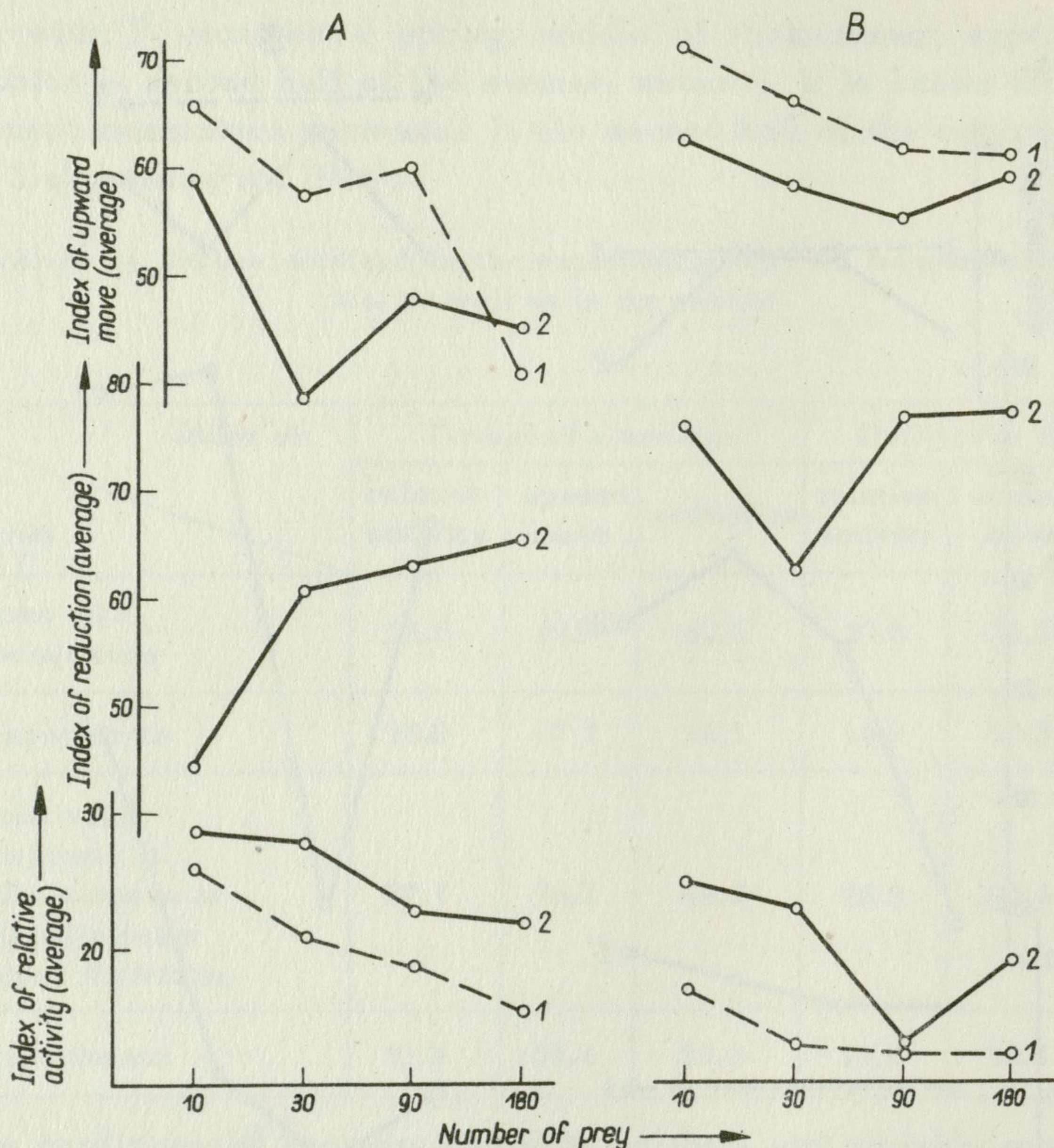


Fig. 17. Value of relative mosquito activity, of upward movement in the isolator, and mosquito reduction by *T. montana* (A) and *D. fimbriatus* (B) at different numbers of preys introduced

1 — experiment, 2 — control

quitoes (180 individuals) were exceptional as the index of upward movement reached slightly lower values in the control than in the experiments with spiders. It can be assumed that similarly as in the case of the relative activity of mosquitoes, outside the influence of predators, the density of mosquitoes itself affects their distribution in the isolator. This is indicated by the values of indices obtained at different mosquito densities in the control experiments: the per cent of individuals staying above the vegetation decreased together with an increase in the density of mosquitoes (Fig. 17). On the other hand the density of predators did not result in any obvious directional changes concerning the values of the index.

Thus it was concluded that both the presence of predators, and their numbers, as well as the density of mosquito populations, affected the level of mosquito activity and their distribution in the isolator. This resulted, in each case,

in a different pattern of the mosquito fauna – different proportions between the flying and inactive part of the population, and the parts of the population staying in the vegetation and above it. Thus a question can be put whether the level of mosquito activity and their distribution in the isolator affects in any considerable degree the rate of their reduction by spiders.

The authors analysed the highest values of mosquito reduction indices with the indices of relative activity and the one of upward movement obtained in the experiments with different spider and prey densities. It was concluded that in the experiments with different densities of *D. fimbriatus* higher values of mosquito reduction indices were correlated with higher values of mosquito relative activity (Fig. 16). However another type of effect can also be recorded here. The activity of mosquitoes changed together with the density of predators, which in turn resulted in an increase in the mosquito reduction. However, the activity of prey may affect the pressure of predators. The pressure of predators in the experiments with the gradient of prey numbers was high and did not differ much in different experiments; the activity of mosquitoes did not differ considerably, and it was difficult to conclude much about its significance for the predation of such species as *D. fimbriatus*.

In the experiments with *T. montana* the index of reduction increased both in the case of an increase in the activity of mosquitoes in the gradient of predators (Fig. 16), and when it decreased in the gradient of prey (Fig. 17). This may indicate that in the case when *T. montana* affects mosquitoes, their activity is not connected with the rate of reduction, and the index of mosquito reduction was correlated only with an increase in the numbers of preys and predators.

Similarly a comparison of average indices of upward movement and indices of reduction obtained in the series of experiments with various mosquito and spider densities did not supply us with an unequivocal answer on the subject of the effect of the mosquito distribution in the isolators on their reduction by spiders. In view of that the authors compared values of reduction indices and their respective indices of activity and upward movement obtained in separate experiments with *T. montana* and *D. fimbriatus* within separate densities of preys and predators. It was concluded that in the experiments with *T. montana* higher values of mosquito activity indices were correlated with lower values of their reduction indices. This was the case both in the experiments with a variable number of preys and predators. On the other hand in the experiments with *D. fimbriatus* a reverse dependence was recorded: high values of mosquito activity indices were correlated with high values of reduction index. In *T. montana* high values of reduction index were correlated with high values of the index of upward movement, while in the experiments with *D. fimbriatus* with lower values of this index.

Summing-up the results on the subject of mosquito reaction to the presence

of predators we can conclude that the activity of mosquitoes and their distribution in the isolators depends on the presence of predators. The activity of mosquitoes can be affected by the density of preys and predators, and the two should be contrasted: an increase in the number of predators stimulates the activity of mosquitoes, while an increase in the density of mosquito populations weakens it.

The spacial distribution of mosquitoes in the isolators depends, to a certain degree, on their density – the higher the density, the smaller per cent of the population remains in the upper part of the isolator. In the presence of predators the mosquitoes keep more to the vegetation.

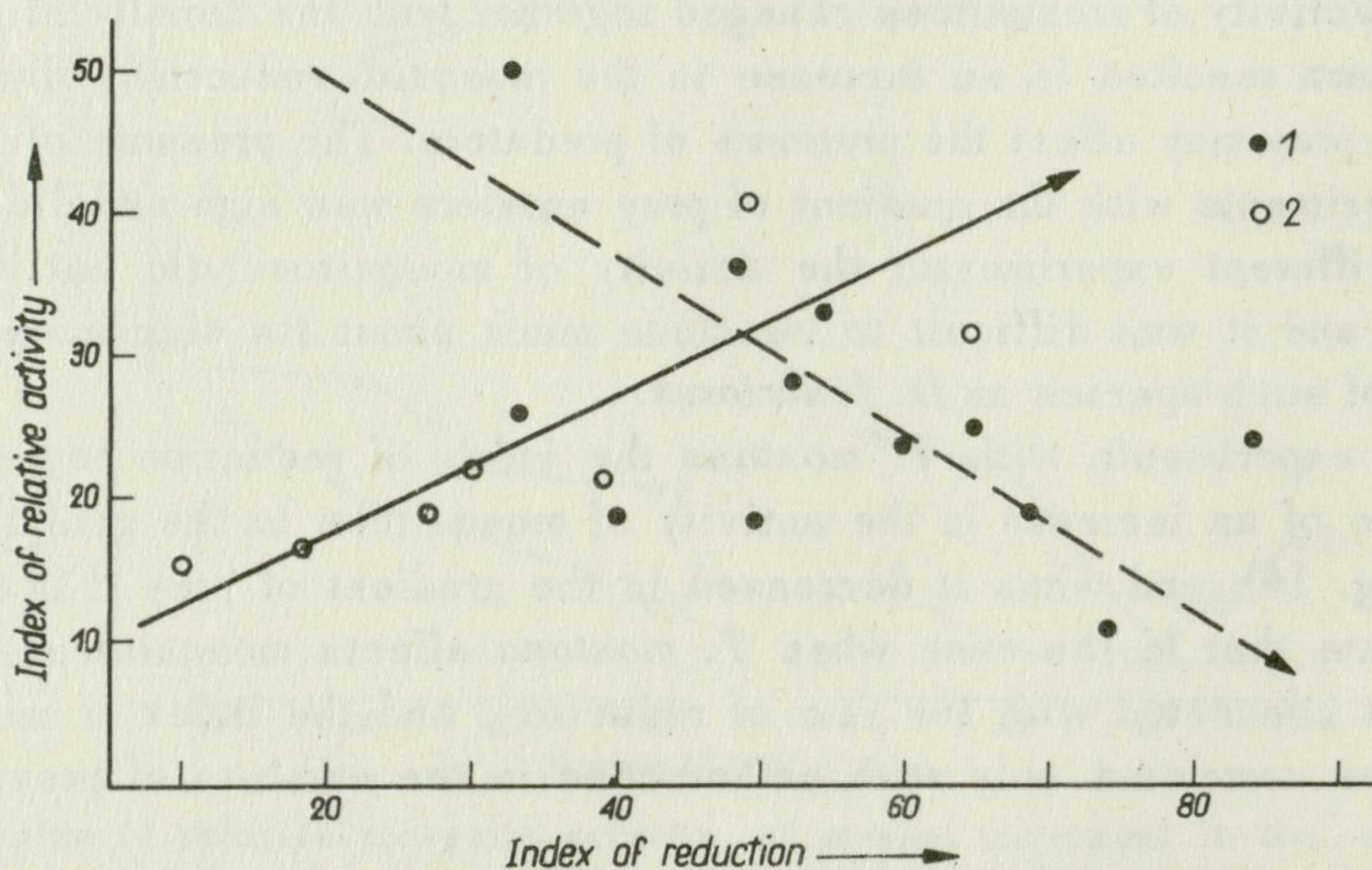


Fig. 18. Dependence of mosquito reduction by *T. montana* (1) and *L. triangularis* (2) on the activity of mosquitoes

The effect of the two indices on the reduction of mosquitoes undoubtedly exists, but it is also very much complicated by the prevailing effect of the density of preys and predators. Hence with the material at the authors' disposal it was only possible to determine certain tendencies concerning the effect of the mosquito population behaviour on their reduction. The results obtained are to a certain extent connected with the character of predators, that is the way in which they move and capture their prey. This is well born out by a comparison between *T. montana* and *L. triangularis* (Fig. 18), as in such a case in similar environmental conditions mosquito reduction by the web species *L. triangularis* increased together with an increase in the mosquito activity, and it decreased in the experiments with *T. montana* which behaved in the isolators as a web-wandering species.

## 5. SUMMING-UP AND DISCUSSION OF RESULTS

The reduction of mosquitoes by spiders in the conditions of the isolators, where the mosquitoes are reduced by the predator without an influx of other individuals during the experiment, can be expressed with the help of the following function:  $N_t = N_0 e^{-\mu t}$ . Thus we can assume that it does not depend on the density of prey. This function indicates the settlement in the experiment of a constant rate of reduction in spite of a progressive decrease in the density of prey. This function refers to a predominant number of experimental data obtained in the investigation. This means a random character of prey and predator meeting in specified ecological conditions. Such a type of reduction is not the only one in the ecological literature. We can mention here the reduction according to a logistical curve both in view of its significance in theoretical ecology and because such a character of reduction in natural insect populations was recorded. It can be exemplified by Varley's investigation on the oak pest, caterpillars of *Operoptera brumata*. He concluded that only in a certain period of life of the population the reduction of the caterpillars, depended on the density of their population and occurred according to the course of the logistic function.

In the present investigation, in spite of the fact that the rate of prey reduction had a tendency to get stabilized in each separate experiment, we could observe a variety of reduction rates in various experiments, and sometimes changes in the rate of reduction in the course of one experiment. This indicated the effect of a number of factors on the process of reduction.

The investigation proved that the course of reduction depends on the numbers of predators introduced into the isolator and the initial number of prey. It was concluded that the rate of reduction is higher in the experiments with a higher number of predators if always the same number of prey are introduced. The rate of reduction was also higher in the experiments with larger numbers of prey and a constant number of *T. montana* predators. Such a strong predator as *D. fimbriatus* did not react with an increase of reduction to larger numbers of prey used in our experiments. It was always a species strongly reducing its prey in these conditions.

When we take into account not only the number of preys and predators introduced into the isolator but also the number of preys per one predator, then we can obtain a regular picture of the dependence of the reduction rate on the size of this relation. At its small values the index of reduction is low and then it increases together with an increase in this relation, and it decreases in turn when there is a large number of preys per one predator. The highest indices of reduction were obtained when there were one to three mosquito individuals per one predator. In the case of the wandering species *D. fimbriatus* the difference between the highest values of reduction indices and the smallest ones

was more considerable than in the case of the web-wandering species *T. montana*.

As a reaction connected with the prey-predator density relation we also observed a change in the rate of prey reduction in the course of the given experiment. Changes in the rate of reduction in separate experiments occurred most frequently at a large number of preys introduced and a small number of predators. Besides they were more frequent in the experiment with *T. montana* than with *D. fimbriatus*. In the case of the latter, changes in the rate of reduction usually meant its increase.

All the dependences discussed above were not very strong in our experiments, and sometimes they were only tendencies. Hence it can be concluded that dependences being a result of the density relation of the components in the prey-predator system were also modified by other type of factors.

It was found out that both the presence of the second component in the habitat, and the numbers of both the components affected the behaviour of preys and predators. Mosquitoes displayed an increase in their activity in the presence of predators, the stronger, the larger the numbers of predators occurring in the habitat. On the other hand an increase in the density of prey weakened their activity. Mosquitoes in the presence of predators keep more to the bottom of the isolator and to its vegetation.

Spiders also reacted to the presence and numbers of mosquitoes. It was concluded that spiders increase their web activity after the introduction of mosquitoes into the habitat which was previously devoid of prey. *T. montana* reacted to larger numbers of preys introduced into the isolators by a decrease in the per cent of individuals spinning their webs, but it increased the per cent of individuals moving to the walls of the isolator in pursuit of their prey. Similarly *D. fimbriatus* was more active at higher initial prey densities. The density of predators also modified their behaviour. In the case of *T. montana* an increase in the density of the population weakened the movement of this species in the isolator.

The correlation of indices characterizing the behaviour of prey and predator populations with the indices of prey reduction showed the occurrence of certain dependences. It seems that *T. montana* reduced more intensively mosquitoes when their activity was lower, and when they actively passed into the upper part of the isolator. *D. fimbriatus* was a more effective predator in such a case when mosquitoes kept to the vegetation and were more active. The reduction of mosquitoes was affected both by the movement of *T. montana* spiders in the isolator, and by the per cent of individuals spinning their webs, which changed according to the season and was dependent on the density of prey. In the case of *D. fimbriatus* its predation activity was correlated with the movement of this species. The more intensive the movement of spiders on the walls, the higher was the reduction of mosquitoes. A similar dependence, although less clearly



expressed, was displayed by *T. montana*. The explanation seems to be the following: both types of food activity in the case of this species – web activity and their movements on the walls – affect the rate of prey reduction.

The mechanism of predation, in the case of our experiments, was the result of a combination between the initial density of the components and their behaviour in various ecological conditions. The different reactions of mosquitoes – resting, flying and hiding in the vegetation – and different types of spider food activity in specified conditions of prey and predator density determine the type of contacts between the two components. Within these relations the meetings of preys and predators occurred at random and this results in the reduction of prey determined by the exponential function given above. A change in the relations between preys and predators results in a change in the rate of mosquito reduction adapted to the new ecological situation. To put it differently – the initial density of prey and the density of predators determine the behaviour of the two components, and the four factors described (density of the two components and their behaviour) determine the rate of reduction. In certain conditions this rate is maintained until there are no more mosquitoes in the isolator, while in other conditions (usually a high density of prey and a low density of predators) it is changed after some time – either weakened or strengthened.

The reduction of prey is also modified (but not determined) by other factors, such as for example environmental. So the course of reduction is affected by the vegetation structure. Scarce and low vegetation in the isolator resulted in an increase in the reduction of mosquitoes, probably in view of the lack of hiding places. Long spells of bad weather weakened the activity of spiders and mosquitoes and probably affected the mosquito reduction. The period of the season affected the intensity of food activity displayed by the spider population.

The authors found out considerable specific differences in the way, type, and rate of prey reduction in the two predator species investigated; that was proved sufficiently in the paper.

The variability of mosquito reduction indices occurring in the course of one experiment, and when different experiments were compared, indicated that the process of spider predation, although based on the regularity of random meetings between preys and predators, depends on a number of factors: environmental (e.g. vegetation structure), which may be different in different isolators, on factors being the result of the predator population structure (e.g. different spacial distribution of *T. montana* spiders – in their webs or on the walls of the isolator without any web), and those being the result of the prey population structure (e.g. different mosquito distribution in the isolator being the result of the cycle of their 24-hours activity was affected by the presence of predators), as well as on the number of preys introduced. All these factors,

sometimes together and sometimes separately, as the strongest stimulus, which depends on the ecological conditions, affect the rate of prey reduction.

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One of the basic problems of the paper is the quantitative expression of the spider pressure on the mosquito population. In the arachnological literature there are papers suggesting methods of calculating the indices of predation intensity. The behaviour of predators when trapping their prey, the timing of their attack after letting in the prey, and the time of its consumption have been discussed in the papers by Gardner (1964, 1965), as well as Haynes and Sisojevič (1966). Different preys in the diet of separate spider species have been discussed by Kajak (1965a, b), Turnbull (1960), and Pötzsch (1966). The problem of the effect of spiders as predators on selected prey groups or species has been analysed in the field research using diversified technics by Whitcomb and his collaborators (1963, 1964), Loughton and others (1963), Dempster (1966), Warren and others (1967), Gałęcka (1966), and others.

The problem of the quantitative expression of spider food activity has already cropped up in the arachnological literature. And so Kajak (1965a, b) introduced the index of spider food activity (corresponding to our index of web activity) mainly to determine the web trappability of two *Argiopidae* meadow species. She recorded that the web activity of the two different spider populations varied in the course of the season. In the case of *Araneus cornutus* this was correlated with the air temperature. In the case of *Araneus quadratus* the web activity was not correlated with meteorological factors and was highest in the period of the most intensive web trappability of this spider occurring in the period preceding the egg-laying. In our experiments we have investigated mainly the effect of the presence of prey and the effect of different numbers of preys introduced into the isolator on the web activity of *T. montana* populations. Beside of the effect of the initial prey density we could also record seasonal variations in the web activity of *T. montana*. However this was not correlated with meteorological data and should be attributed to the effect of the spider population development stage.

There are various ways of expressing quantitatively the intensity of predation. Most of the investigators understand this as the number of prey consumed by the predator. E. g. Kajak (1965a, b) determined the intensity of spider population predation by the numerical index being the quotient of the average number of preys trapped in the course of 24 hours by one spider of the population investigated and the number of spiders in an area of 5 m<sup>2</sup>. In our paper the index of predation intensity described the pressure of spiders on the prey population, and was determined indirectly by the rate of mosquito reduction in

the isolators with spiders, and directly by a comparison between the rate of mosquito reduction in the control and in the experiment with predators.

A very important problem in the investigation on predation is the problem of predator hunger or satiation. An interesting attempt at analysing the behaviour of spiders in relation to their food in laboratory conditions are efforts of Haynes and Sisojevič (1966) who endeavoured to estimate different reactions of hungry and satiated *Philodromus rufus* (*Thomisidae*) individuals to their prey. They investigated changes in the intensity of attacks (number of fruit flies killed in the course of one day) directed by spiders depending on the length of time they suffered hunger. Experimenting in laboratory conditions they were able to calculate the number of preys killed by separate individuals. This was impossible in our conditions. We could only record that at large numbers of preys some spiders trapped them intensively and collected entire "bunches" of them in their webs, while others situated less advantageously and probably less stimulated by their prey, were satisfied with sucking for a long time, only one of the mosquitoes trapped. In our investigation on the reaction of spider populations to their prey as contrasted with the investigation on the reaction of separate individuals, it was impossible to study the effect of spider hunger on the strength of their attacks on the prey because each population, disregarding the number of preys introduced, included some more and some less hungry or satiated individuals. Their different attitudes towards the prey were compensated though they must have had an effect on the result of the populational reaction of spiders to their food. The effect of biological development stages (moult, cocoon-laying), and physiological phases of separate individuals (degree of the satiation of spiders) are already included in the reaction displayed by the spider population investigated.

The two authors cited above recorded, similarly as the authors of the present paper, a very important phenomenon. Spiders transferred from one habitat to another behave at the beginning differently than later on, and they need a certain period of time to adapt their predation functions to the new habitat. This can be applied particularly to *T. montana* in the conditions of our investigation. Both the web activity of these spider populations, and the pressure of their populations on the prey increased clearly 10–12 days after the moment of their introduction into the isolators.

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ROLA ZAGĘSZCZENIA DRAPIEŻCY I OFIARY ORAZ ICH ZACHOWANIA SIĘ  
WZGLĘDEM SIEBIE W PROCESIE REDUKCJI KOMARÓW PRZEZ PAJĄKI  
W WARUNKACH EKSPERYMENTU TERENOWEGO

Streszczenie

Redukcję komarów przez pająki zachodzącą w warunkach izolatorów, gdzie wprowadzona porcja komarów jest zredukowana przez drapieżcę bez dokładania, w czasie trwania eksperymentu, nowych osobników, można określić funkcją  $N_t = N_0 e^{-\mu t}$ . Mówi ona o ustaleniu się stałego tempa w procesie redukcji, mimo postępującego spadku zagęszczenia ofiar w ciągu trwania eksperymentu. Funkcja ta odnosi się do przeważającej liczby danych uzyskanych w naszych badaniach. Oznacza to losowy charakter spotkań drapieżców i ich ofiar w określonych warunkach ekologicznych.

Mimo ustalenia się określonego tempa redukcji ofiar w każdym eksperymencie, obserwowano wielką różnorodność tempa redukcji w różnych eksperymentach oraz wy-

stępowanie zmiany tempa redukcji w czasie trwania niektórych eksperymentów. Świadczy to o oddziaływaniu na proces redukcji szeregu czynników.

Badania wykazywały, że przebieg redukcji uzależniony jest od liczebności wprowadzonych do izolatora drapieżców i początkowej liczby ofiar. Stwierdzono, że tempo redukcji jest większe w eksperymentach z większą liczbą drapieżców przy stałej liczbie ofiar. Tempo redukcji było również większe w eksperymentach z większą liczbą ofiar, a stałą liczbą drapieżców *T. montana*. *D. fimbriatus* nie reagował na ogół zwiększeniem tempa redukcji na większe liczebności ofiar stosowane w naszych eksperymentach. Był on w tych warunkach gatunkiem zawsze intensywnie redukującym swoje ofiary.

Jeśli weźmiemy pod uwagę nie samą liczebność wprowadzonych do izolatora ofiar i drapieżców, a liczbę ofiar przypadającą w momencie ich wprowadzania do izolatora na jednego drapieżcę, to uzyskujemy bardzo prawidłowy obraz zależności tempa redukcji od wielkości tego stosunku. Przy bardzo małych wartościach wskaźnik redukcji jest niski, wzrasta przy wzroście liczby ofiar na jednego drapieżcę i z kolei spada, gdy liczba ofiar przypadająca na jednego drapieżcę znacznie wzrasta. Najwyższe wskaźniki redukcji uzyskano w eksperymentach, gdzie 1–3 komarów przypadało na jednego drapieżcę.

Jako reakcję na liczebność komponentów układu drapieżca-ofiara obserwowano również zmiany tempa redukcji ofiar, jakie w poszczególnych eksperymentach zachodziły najczęściej przy dużej liczbie wprowadzonych ofiar a małej liczbie drapieżców. Zachodziły one ponadto częściej w eksperymentach z *T. montana* niż *D. fimbriatus*, u którego zmiany tempa redukcji polegały na jego przyspieszeniu.

Wszystkie omówione wyżej zależności wystąpiły w naszych eksperymentach niezbyt silnie, czasami występowały tylko jako pewna tendencja. Nasuwa się stąd wniosek, że zależności wynikające z wpływu zagęszczenia komponentów w układzie drapieżca-ofiara były modyfikowane działaniem jeszcze innego typu czynników.

Stwierdzono, że zarówno sama obecność w środowisku drugiego komponenta układu drapieżca-ofiara jak i liczebność jednego i drugiego wpływa na zachowanie się drapieżcy i ofiary. Komary wykazywały wzrost aktywności w obecności drapieżcy i to tym silniejszy, im większa była liczebność drapieżców występujących w środowisku. Wzrost zagęszczenia komarów natomiast osłabiał ich aktywność. Ponadto komary w obecności drapieżcy silniej trzymały się dna izolatora i jego roślinności.

Pająki również zmieniały swoje zachowanie w obecności komarów i w zależności od ich liczebności. Stwierdzono, że u pajaków wzrasta aktywność sieciowa po wprowadzeniu komarów do środowiska uprzednio pozbawionego ofiar. *T. montana* reagowała na większe liczebności wprowadzanych do izolatorów ofiar zmniejszeniem udziału w populacji osobników budujących sieci; zwiększał się natomiast udział osobników przemieszczających się na ściany izolatora w pogoni za ofiarami. Podobnie *D. fimbriatus* był bardziej aktywny ruchowo przy większych zagęszczeniach ofiar. Zagęszczenie własnej populacji także modyfikowało jego zachowanie się. U *T. montana* wzrost zagęszczenia jej populacji osłabiał przemieszczanie się tego gatunku w izolatorze.

Korelacja wskaźników charakteryzujących zachowanie się ofiar i drapieżców ze wskaźnikami redukcji ofiar wykazała istnienie pewnych zależności. Wydaje się, że *T. montana* bardziej gwałtownie redukuje komary przy mniejszej ich aktywności, a intensywniejszym przechodzeniu ich w górne strefy izolatora. *D. fimbriatus* był z kolei skuteczniejszym drapieżcą w przypadku, gdy komary trzymały się raczej warstwy roślinności i wykazywały większą aktywność ruchową. W redukcji komarów odgrywało rolę zarówno przemieszczanie się w izolatorze pajaków *T. montana*, jak i zmienny w sezonie i zależny od gęstości ofiar udział w populacji osobników budujących sieci.

U *D. fimbriatus* aktywność drapieżnicza była skorelowana z przemieszczeniem się w izolatorze osobników populacji tego gatunku; im większe było to przemieszczanie się, tym większa była redukcja komarów. Podobną zależność, choć znacznie słabiej wyrażoną, wykazywała *T. montana*. Wydaje się, że spowodowane to jest faktem, że u tego ostatniego gatunku oba typy aktywności pokarmowej – sieciowa i ruchowa (przemieszczanie się w izolatorze) – wpływają na wielkość redukcji ofiar.

Przebieg redukcji ofiar określony wyżej wymienionymi czynnikami modyfikują (ale nie determinują) również inne czynniki np. środowiskowe. Tak na przykład stwierdzono, że na przebieg redukcji wpływa struktura roślinności. Rzadka i niska roślinność w izolatorze wpływa na zwiększenie redukcji komarów, zapewne ze względu na brak kryjówek, w których mogłyby być zabezpieczone przed drapieżcą. Zła, długotrwała pogoda osłabiała aktywność pajaków i komarów i wpływała na przebieg redukcji komarów. Stwierdzono również różną intensywność aktywności pokarmowej populacji pajaków w różnych okresach sezonu.

Tak więc mechanizm drapieżnictwa, którego wynikiem jest określone tempo redukcji ofiar, polegałby na działaniu zagęszczenia ofiar i drapieżców oraz ich reakcji względem siebie w różnych warunkach ekologicznych – w sprzężeniu zwrotnym.

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