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METHODS OF INVESTIGATING OF THE PRODUCTIVITY OF ANTS*

(Ekol. Pol. 20: 9-22). Studies on ants concentrate on the estimation of the size, production and food removed by ant populations this enabling the evaluation on the contribution of ants to the total ecosystem standing crop, and their role in ecosystem functioning and dynamics.

Investigations on ants form a part of complex studies on ecosystem productivity now being undertaken at the Institute of Ecology.

Investigations on ecosystem productivity include the estimation of primary production, the production of the dominant herbivorous, carnivorous and saprophytic groups, and the rate of organic matter decomposition.

Studies on ants concentrate on the estimation of the size, production and food removed by ant populations, this enabling the evaluation of the contribution of ants to the total ecosystem standing crop, and their role in ecosystem functioning and dynamics.

All measurements were made systematically during the course of the entire vegetation season, that is from April to November. As far as possible the size

*Proceedings of the IBP (PT Section) Meeting on Methods of Productivity Investigations of Social Insects and their Role in the Ecosystems. Institute of Ecology, Warsaw, June 22-28, 1970. Editors: M. V. Brian, J. Pętał.

of populations was expressed in units of dry weight (mg) and energy (cal), and related either to unit surface area or to the community of an average ant nest.

I. METHODS OF EVALUATION OF ANT POPULATION SIZE

The size of populations is a function of both the density of ant nests in the environment and the number of individuals in a nest. Both parameters undergo distinct changes in the course of the vegetation season. The results given below are for *Myrmica laevinodis* Nyl. the dominant ant species in the habitats studied.

1. The density of ant nests

This was determined by counting the nests on surface areas of particular size distributed uniformly in the study region.

Owing to the contagious, or clumped, distribution of the ant nests it is

difficult to establish the best size and number of sample plots for examination. Four sample plot sizes were used, namely 25 m²–12.5 m², 6.25 m² and 3.125 m², within the same habitat of total area 3,500 m².

In each group of sample plots the frequency of occurrence of ant nests is different (Fig. 1). In the group of sample plots of 25 m² surface area, wide differences in the number of nests was observed, the frequency of occurrence of plots with a large or small number of nests being similar. This is evidence of their contagious distribution (index of dispersion $V = 2.28$).

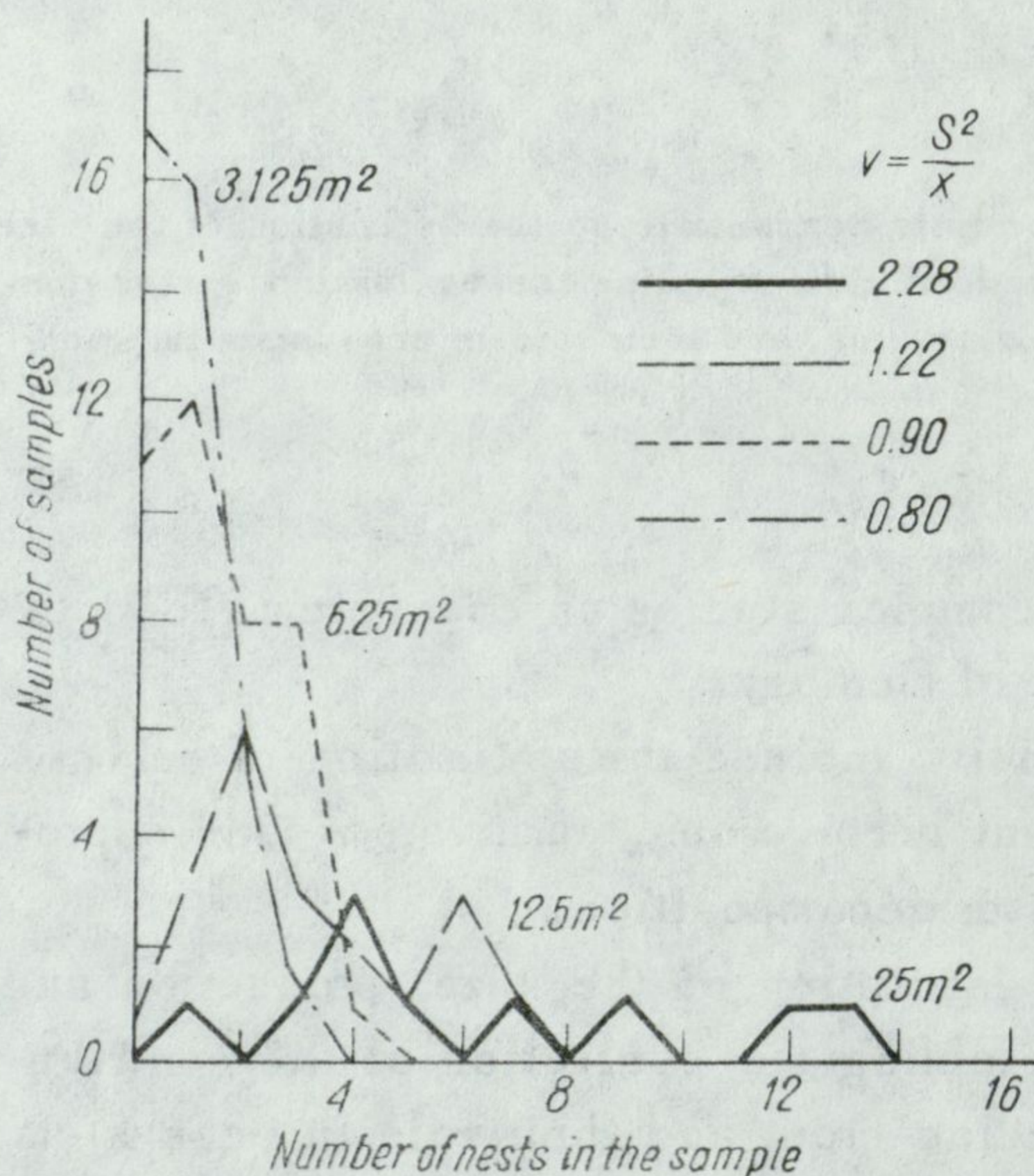


Fig. 1. Distribution of ants nests on surface areas of varying size

of ant nests. Sample plots with a mean number of nests occur more frequently (index of dispersion $V = 1.22$ for plots of 12.5 m² area and $V = 0.93$ for plots of 6.25 m² area). The smallest sample plots of area 3.125 m² show a regular

distribution of ant nests ($V = 0.80$). These values seem to indicate that within a contagious distribution, the nests show a tendency to random or even regular distribution.

The usefulness of sample plots of various sizes and the number necessary for obtaining the required accuracy level, were estimated by the following methods.

Number of sample plots:

a. Graphic method (Fig. 2). This consists of calculating the mean number of ant nests for an increasing number of sample plots. As seen from the graph, the mean varies widely when the number of sample plots is small, whereas when their number is large the differences become slight. For large sample plots (25 m^2) ten is a reasonable number of samples to take. An acceptable number for the middle-sized plots (12.5 m^2) is 13–15, and for the small ones (6.25 m^2) 10–15.

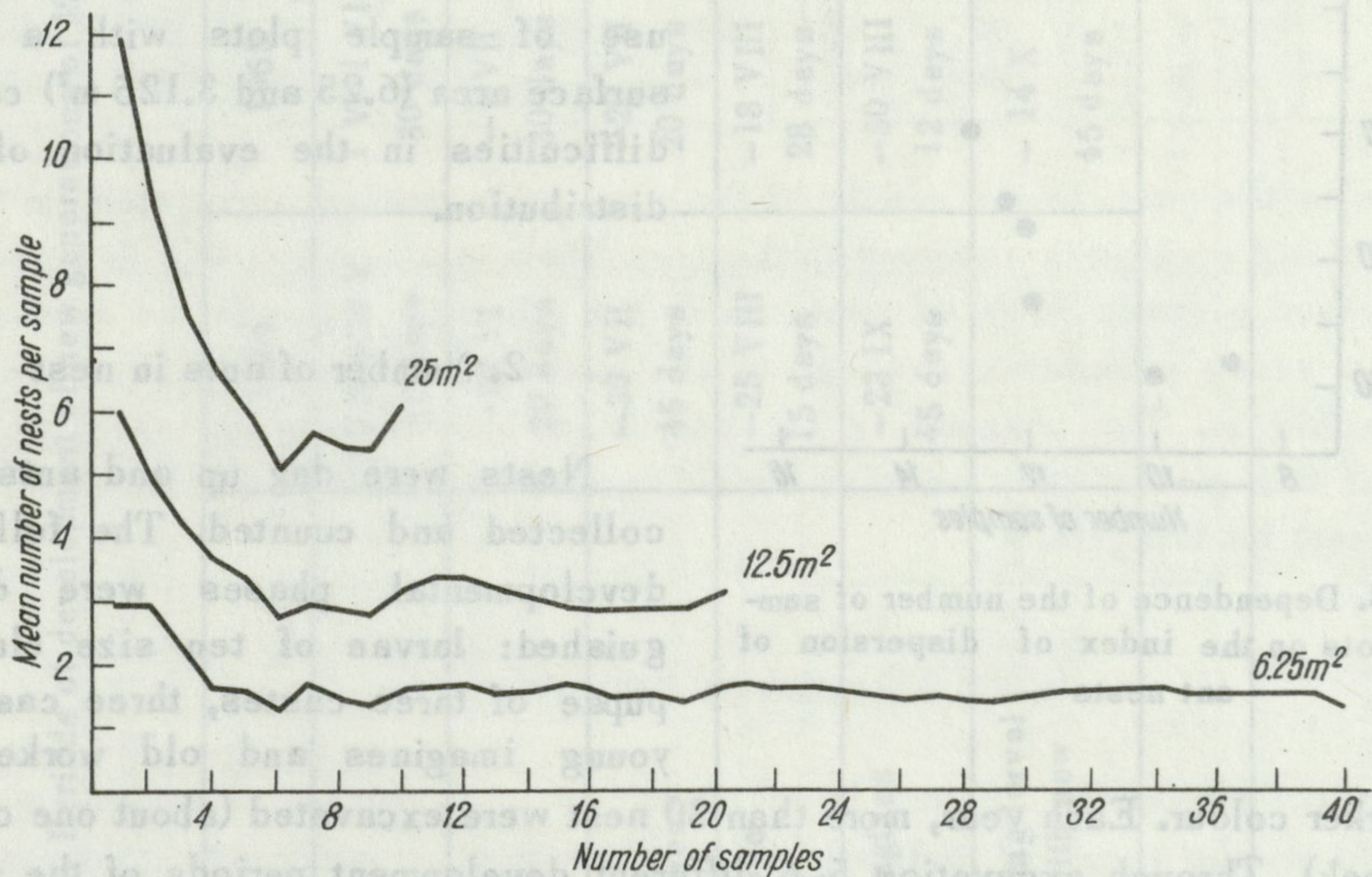


Fig. 2. Estimating of sampling accuracy (mean of first 2, 3 ... 40 samples)

b. Method of calculation (Southwood 1966)

The number of sample plots depends on the degree of accuracy required. In the present investigations a 5% error was adopted. The necessary number of sample plots (N) was determined by means of the formula:

$$N = \frac{t S}{Dx}$$

where S – standard error, D – the required level of accuracy expressed as a decimal, t – a quantity depending on the number of samples obtained from tables.

The necessary number of sample plots estimated by this method is for sample plots of surface area:

$$\begin{aligned} 25 \text{ m}^2, N &= 13,75, \\ 12.5 \text{ m}^2, N &= 13.4, \\ 6.25 \text{ m}^2, N &= 15.43, \\ 3.125 \text{ m}^2, N &= 20.33, \end{aligned}$$

The evaluation of the number of sample plots by this method agrees closely with the results obtained by the graphic method. The optimal number of sample

plots depends on the degree of dispersion, and becomes larger with increase in the index of dispersion (Fig. 3). The use of sample plots with a small surface area (6.25 and 3.125 m²) causes difficulties in the evaluation of nest distribution.

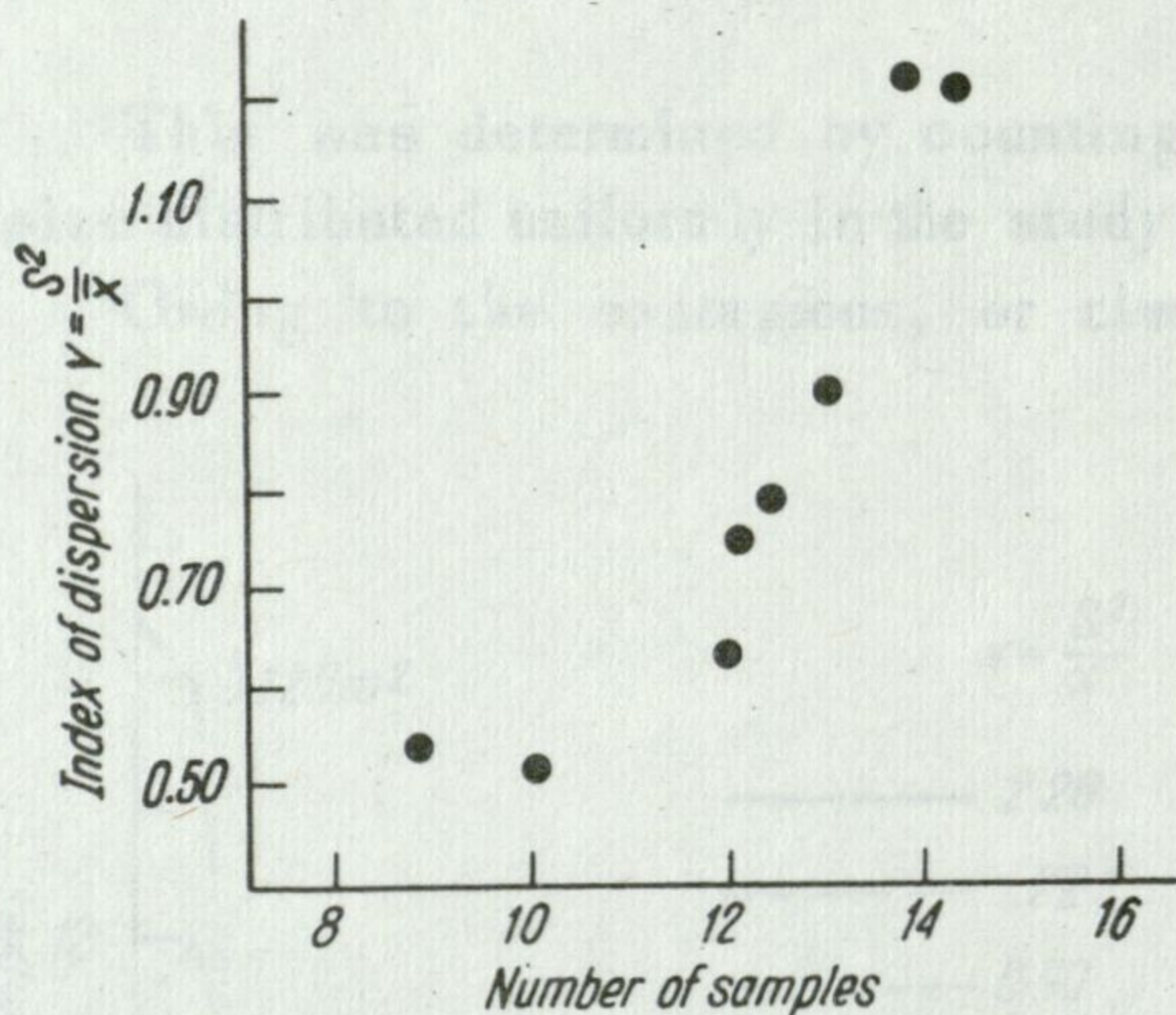


Fig. 3. Dependence of the number of sample plots on the index of dispersion of ant nests

2. Number of ants in nest

Nests were dug up and ants were collected and counted. The following developmental phases were distinguished: larvae of ten size classes, pupae of three castes, three castes of young imagines and old workers of

a darker colour. Each year, more than 30 nest were excavated (about one or two a week). Through excavation 5–6 different development periods of the young generation could be distinguished. Though in various years the timing of these periods may differ slightly and be of unequal duration, it is nevertheless easier to compare them with one another, to view of the same biological and ecological requirements (Pętal 1967). Characteristics of these periods and the time of their duration are given in Table I.

The mean number of individuals in a nest in a particular period, together with statistical evaluation of the data, are shown in Table II.

The range of variability of the number of ants in the nest is rather wide. It is dependent on the age of the nest, on the number of queens, which oscillates from one to a dozen or so, and on the varying rate of development of the new ge-

Periods of development of new generations of *Myrmica laevinodis*

Tab. I

Periods		1964	1965	1966	1967	1968
I	young larvae	13 IV–26 V 40 days	1 V–1 VI 30 days	1 V–24 V 24 days	1 V–23 VI 53 days	12 IV–30 V 48 days
II	appearance of worker pupae	–22 VI 20 days	–1 VII 30 days	–18 VI 25 days	–14 VII 21 days	–4 VII 35 days
III	appearance of new worker imagines	–30 VII 45 days	–20 VII 20 days	–20 VII 32 days	–27 VII 13 days	–18 VII 14 days
IV	occurrence of pupae of sexual castes	–25 VIII 15 days	–18 VIII 28 days	–24 VIII 34 days	–6 IX 40 days	–12 VIII 25 days
V	appearance of imagines of sexual castes	–23 IX 45 days	–30 VIII 12 days	–20 IX 12 days	–27 IX 21 days	–4 IX 23 days
VI	occurrence of young larval stages together with new worker imagines		–14 X 45 days	–14 X 13 days	–14 X 17 days	–24 IX 20 days
				165 days		

- Evaluation of the size of communities in ant nest (P = standard error)

Tab. II

1964 Periods	Number of nest	Larvae		Pupae		Young imagines		Aged imagines	
		\bar{x}	P	\bar{x}	P	\bar{x}	P	\bar{x}	P
<i>I</i>	6	372	63.6					2,016	818.9
<i>II</i>	3	1,042	77.4	5	9.2			1,380	685.1
<i>III</i>	9	459	264.8	409	384.9	802	323.7	1,007	501.1
<i>IV</i>	3	363	59.6	565	248.5	1,385	158.0	1,208	437.7
<i>V</i>	5	348	257.8	188	265.7	1,622	673.6	1,594	562.5
1965									
<i>I</i>	3	215	190.1					2,673	1,682.1
<i>II</i>	2	76	1.4	77	8.5			1,486	493.6
<i>III</i>	4	345	281.6	26	20.4			1,964	531.0
<i>IV</i>	7	285	154.1	310	279.5	276	207.8	864	444.4
<i>V</i>	4	80	48.2	209	259.4	346	66.3	874	394.8
<i>VI</i>	3	606	448.9			974	458.1	1,235	666.4

neration in the nest. In the middle of the vegetation season a reduction in the number of old workers is observed in the nest. Their numbers increase in autumn. The method of excavation of nests does not take into account the foragers, only the young generation confined to the nest and the workers occupied on tasks within it. The changes in the number of old workers recorded on the basis of this method only enables conclusions to be drawn on changes in the requirement for foragers.

II. EVALUATION OF PRODUCTION

The net production of ants is taken as the total amount of organic matter produced as the result of multiplication of the average community in the nest. The difficulty in evaluation of the net production lies in: a) the widely varying, but continuous fertility of the queens throughout the season, b) the highly variable rate of development of the young individuals in the nest, c) the auto-regulation of the number of young larvae within the population; under unfavourable conditions, these are eaten by the workers. Evaluation is made easier by the fact that young individuals do not go foraging. Thus evaluation of the production could be based on an analysis of the dynamics of the numbers of the young generation in the nest and the changes in biomass. This method follows the work of Nees, Dugdale (1959), Greze (1965), Winberg, Pečen, Šuškina (1965), Petruszewicz, Macfadyen 1970.

Evaluation of production of average nest

Tab. III

1964 Periods	Developmental stage						State of biomass of young generation dry biomass mg	Production for the period dry biomass mg	Index of productivity mg/24 hr
	larvae		pupae		imagines				
	N	mg	N	mg	N	mg			
I	313	93.5					93.5		
II	1,042	687.7	5	4.6			692.3	598.8	29.9
III	459	356.3	409	368.1	802	641.6	1,366.0	673.7	14.9
IV	363	195.5	566	529.2	1,385	1,186.0	1,910.7	544.7	36.3
V	348	60.8	188	173.0	1,622	1,550.1	1,783.9 +234.0*	107.2	2.4
							T	1,924.4	11.6
1965									
I	215	125.8					125.8		
II	76	27.3	77	53.9			81.2	-44.6	-6.71
III	347.1	520.2	26.2	18.3			538.5	457.3	22.9
IV	285	352.2	310	244.8	214	171.2	768.2	229.7	8.2
V	80.1	61.7	233.7	1,723.4	344.2	275.4	509.4 + 352.0*	93.2	7.7
VI	605.2	253.9	0		972	776.6	1,031.5	522.1	11.6
							T	1,346.9	8.2

*Biomass of sexuals which left the nest in this period.

The size of the community in the nest and the state of the biomass of the young generation relate to the period of biological development of the latter (Tab. I and III). For each particular period production was calculated using the biomass increment. By taking only short time intervals between calculations, the accuracy of evaluation was increased. By this procedure it is possible to establish the timing of the diminution in the number of individuals and in biomass (period II in 1965 and periods V in both the quoted years). Analysis of the caste structure, the larvae of older stages pupae and adult forms, enabled evaluation of their numbers and hence calculation of the biomass. The production of an average community in a nest in the course of the vegetation season was calculated from the sum of biomass increments (ΔB) and losses (E) of the young generation during particular time periods. Thus $P = \Delta B + E$. The index of production expressed as dry weight (mg) per 24 hr shows a high variability of production during the course of the season and in corresponding periods in various years (Tab. III).

III. ELIMINATION

Elimination within the ant nest involves both young individuals (larvae, adult individuals or sexuals) and old workers. Analysis of the dynamics of the number of individuals in the community during the course of the vegetation season permits evaluation of the number eliminated. Changes in the number of old workers in the nest are due to their absence when foraging as well to mortality. It is therefore difficult to draw conclusions on mortality in the course of the season on the basis of their number in the nest. Total mortality may only be evaluated from the difference between their number at the beginning and at the end of the season. In the years of the study elimination of old workers varied widely, ranging between 20–50%. Differences in temperature and precipitation distribution in particular years, as well as in food abundance in the environment and of autoregulation within the population, are important influences on worker mortality.

IV. METHODS OF EVALUATION OF FOOD REMOVED FROM THE HABITAT BY ANTS POPULATION

Material removed (MR) was estimated from data on the number of foragers the seasonal and diel dynamics of their numbers (Pełal and Pisarski 1966), and the amount of food supplied by them to nest.

1. Number of foragers

The number of foragers was evaluated by recording the ants returning to the nest within a certain time period (5 min.). Observations were always made in the morning and afternoon on a group of 3–5 nests, two to three times weekly over the entire vegetation season. The dynamics of the number of foragers and statistical evaluation of the data are presented in Table IV.

Number of foragers

Tab. IV

Year		Period	II	III	IV	V	VI
		1964	n	12.00	50.00		34.00
	\bar{x}	16.17	11.84		5.56		
	S	4.96	5.70		4.79		
1965	n	29.00	56.00	66.00	32.00	65.00	
	\bar{x}	49.76	36.07	29.20	40.00	23.48	
	S	26.86	13.74	12.42	12.37	11.69	

Activity within the 24-hr cycle was investigated by Barber's trap method. The traps were emptied four times within the 24-hr period at 10-day intervals over the entire season. On the basis of catches in the course of daylight, twilight, night and dawn, indices of 24-hr activity were calculated, the number of catches during daylight being assumed as unity (Tab. V).

Indices of forager activity in the 24-hr cycle

Tab. V

Periods	I	II	III	IV	V
Daylight (10 hr)	10.0	10.0	10.0	10.0	10.0
Twilight (4 hr)	1.2	2.4	2.0	0.4	1.6
Night (8 hr)	2.4	15.2	2.4	1.1	2.9
Dawn (4 hr)	2.0	3.2	1.6	0.4	1.0
Σ 24 hr	15.6	30.8	16.0	11.9	15.5

On the basis of the data on the number of ants returning from foraging in the course of 5 min. and the changes in activity of the ants over 24 hr, their number was calculated for 24 hr, for any given period, and also for the entire season.

2. Food supplied to the nest

It was calculated on the basis of the amount of food brought to the nest in one unit of time. Both diurnal and seasonal patterns of activity of the foragers was taken into account. The ants returning after foraging bring food to the nest in the maxillae or in the crop. The food from the maxillae, mainly young *Araneida*, *Auchenorrhyncha*, *Diptera* and *Heteroptera*, was removed, identified and weighed.

Most of the foragers, about 90%, bring food to the nest in the crop. The contents of the crop were evaluated on the basis of the difference in weight between the groups of workers returning and those leaving the nest:

$$Nr \frac{w}{d} - Nd \frac{w}{d}$$

where Nr – number of returning foragers, Nd – number of foragers leaving the nest, w – fresh weight biomass, d – dry weight.

The weight of the contents of the crop calculated in this way amount at times to 10% of the total weight of the forager (Tab. VI).

Evaluation of weight of crop contents (biomass in mg)

Tab. VI

Year \ Periods		II	III	V	Season
1964	n	23	4	6	33
	\bar{x}	0.158	0.128	0.143	0.151
	S	0.141	0.074	0.120	0.12736
1965	n	10	19	15	44
	\bar{x}	0.152	0.184	0.251	0.199
	S	0.1336	0.1096	0.1554	0.13866

The total amount of forage brought to the nest, i.e. the sum of the food in the crop and in the maxillae, is shown in Table VII.

The production yield, calculated as the ratio of production to material removed (PT/MR) for the season, varies slightly from year to year and ranges between 1.65–2.58%.

This figure may, therefore, be taken as a measure of the contribution of ants to the flow of energy and reduction of organic matter in the ecosystem.

Food removed by a community of average nest (biomass in mg)

Tab. VII

Periods	1964	1965
	mg	mg
I	57,600.0	69,465.6
II	44,352.0	23,754.4
III	91,712.0	23,065.2
IV	17,950.0	8,739.4
V	19,251.0	35,154.0
VI		
T	230,965.0	160,178.6

V. METHOD OF EVALUATION OF THE ROLE OF ANTS AS PREDATORS

As mentioned above, ants draw enormous quantities of organic matter from the environment. Only a small part of this, about 2%, is involved in production. The remains of unconsumed food and faeces remain in the nest and undergo further decomposition by animal and plant saprophages. This results in changes in the soil and the succession of vascular vegetation (Pętal, Jakubczyk, Wójcik 1967). The major part of the energy used is expended for the costs of maintenance (respiration metabolism) of the community. Ants, which are extremely numerous in the environment (ca 200–300 individuals per 1 m²), are therefore major element of energy dispersion in the ecosystem, and may moreover significantly affect the sources from which they draw energy.

Reduction due to ants (number of specimens /m²)

Tab. VIII

Year	1964	1965
<i>Araneida</i>	4,035.8	2,675.3
<i>Diptera</i>	1,796.7	476.2
<i>Auchenorrhyncha</i>	3,470.0	2,379.0

Observation of the foragers returning to the nest indicates that the main nutrition base of *Myrmica rubra* are young forms of *Araneida*, *Auchenorrhyncha*, *Diptera* and *Heteroptera*. Taking into account seasonal changes in the amount of prey brought to the nest and the 24-hr activity of the foragers, the reduction of the above mentioned groups in the course of the vegetation seasons was calculated per 1 m² of the environment (Tab. VIII).

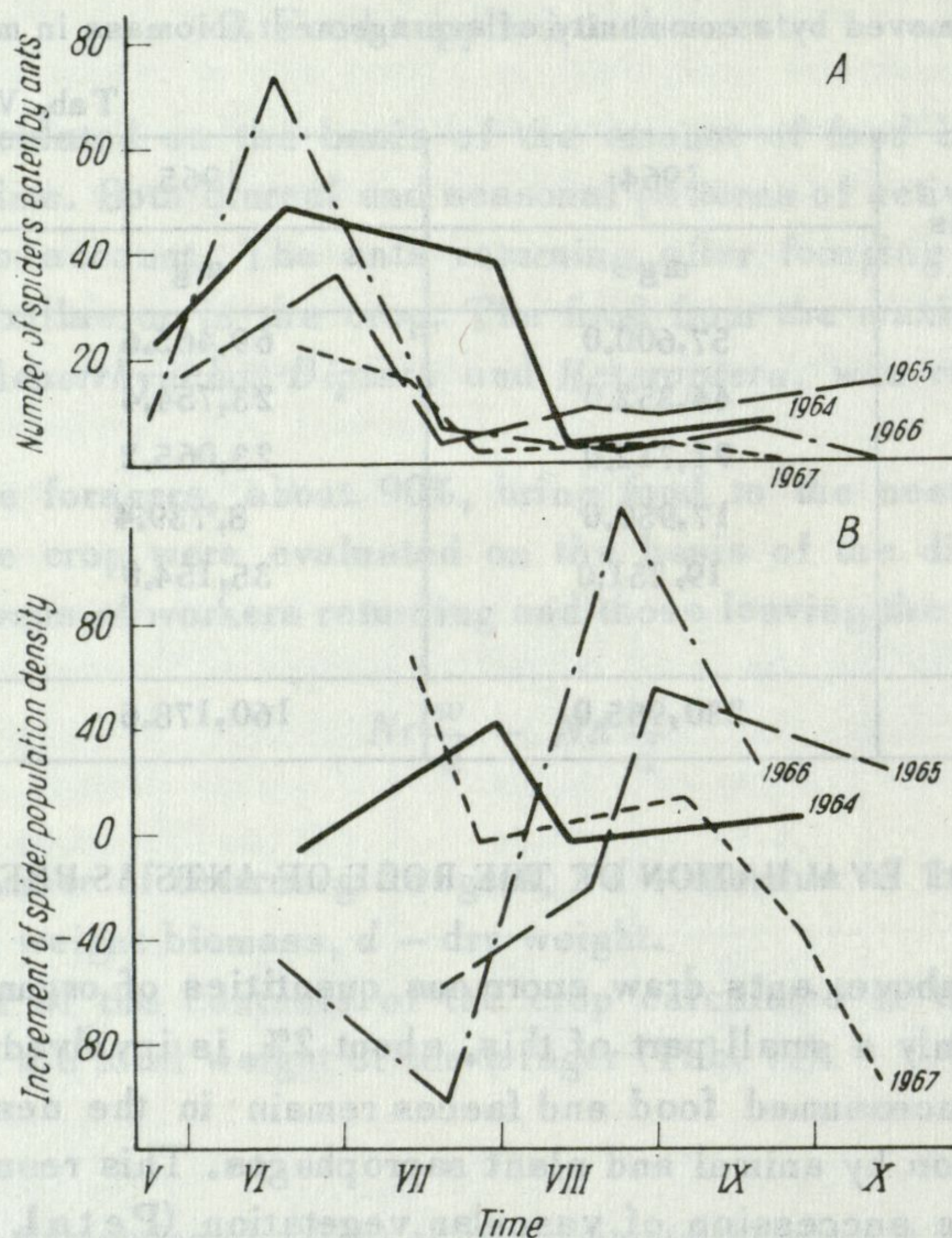


Fig. 4. Relation between consumption of *Araneida* by ants and density increment of *Araneida* (after Pętal, Andrzejewska, Breymeyer, Olechowicz 1971)

A – density increments of *Araneida*, B – number of *Araneida* devoured per 1 m² per 24 hrs

In order to establish the influence of this reduction on the size of the prey population, it was compared (1) with the changes in the density of the prey, and (2) with the production of the prey.

1. The role of ants can be evaluated on the basis of changes in the density of the prey populations (Pętal, Breymeyer 1968). This method was applied for several species of wandering spiders dominant in the food consumed by ants. Changes in the increment of spider density were calculated as:

$$\frac{B - A}{\frac{A + B}{2}} \times 100$$

where *A* and *B* are successively observed densities in the season. These values, when compared with reduction of spiders by ants, show an inverse relation during the course of the vegetative season (Fig. 4). This indicates an influence of ants on the size of the spider population. It does not, however, determine the degree of this effect.

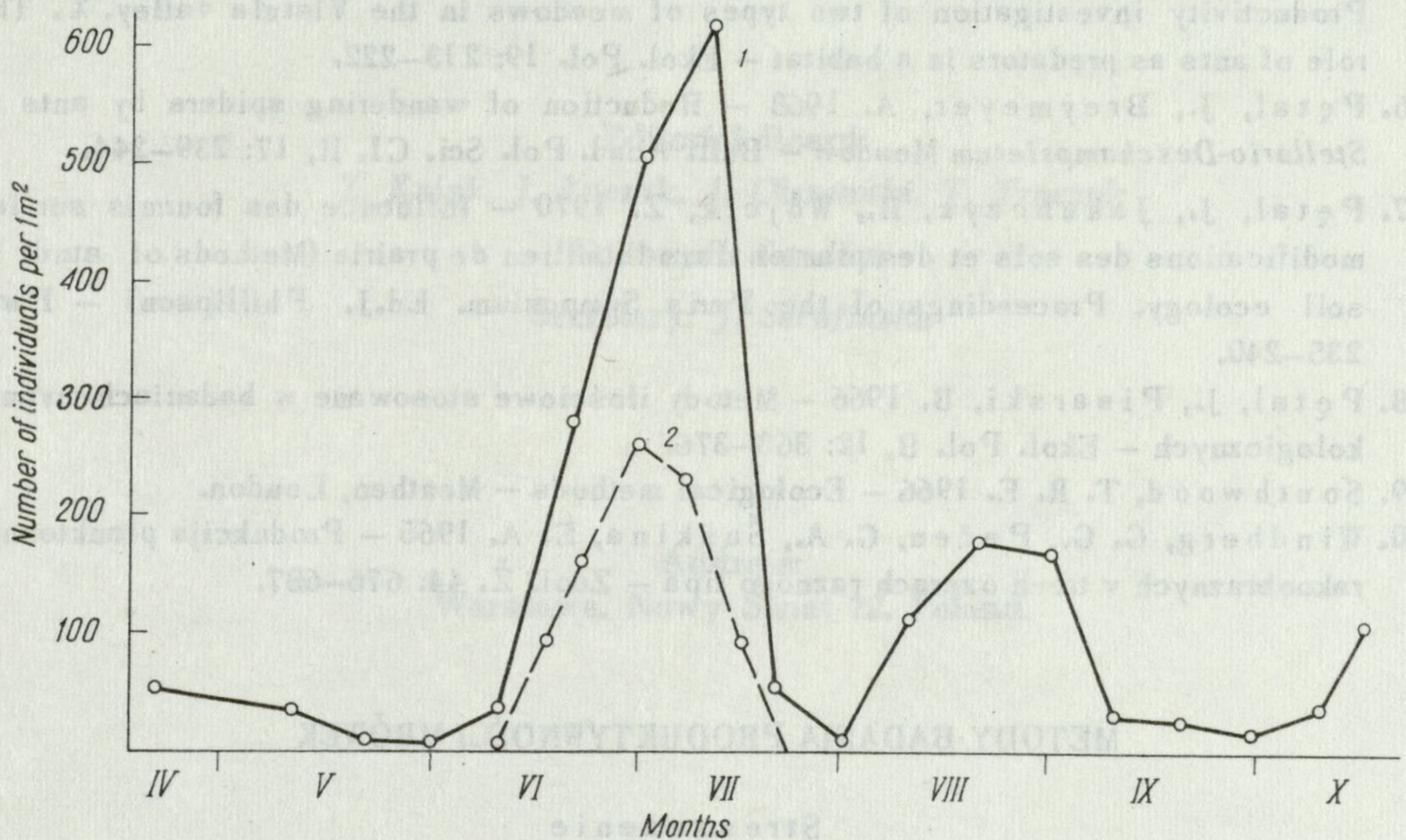


Fig. 5. Comparison of *Auchenorrhyncha* production and their consumption by ants (after Pętal, Andrzejewska, Breymeyer, Olechowicz 1971)

1 - production of *Auchenorrhyncha*, 2 - reduction by ants

2. A closer evaluation of the role of ants may be obtained by comparing reduction of prey with the size and production of the prey population (Fig. 5), (Pętal, Andrzejewska, Breymeyer, Olechowicz 1971).

It results from our data that predator ants can considerably limit the population size of other invertebrates. Devouring mainly the young forms at the moment of their appearance in a habitat they can be important factor preventing a mass outbreak. This method is a good measure of ecological pressure of the predatory population on the population preyed upon.

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METODY BADANIA PRODUKTYWNOŚCI MRÓWEK

Streszczenie

Przedstawione metody badań wchodzą w skład kompleksowych badań produktywności ekosystemów trawiastych. Dotyczą one metod oceny wielkości populacji mrówek, tj. liczebności gniazd i osobników w gnieździe, produkcji populacji oraz ilości pobieranego przez nią ze środowiska pokarmu.

Jako metodę oceny roli mrówek jako drapieżców zaproponowano porównanie liczby zredukowanych ofiar z ich produkcją lub ze średnimi przyrostami ich zagęszczenia w ciągu sezonu.

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