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AN ATTEMPT AT DETERMINING THE ABSOLUTE POPULATION  
NUMBERS OF *CICADELLA VIRIDIS* L. IN THE LIGHT  
OF ITS LAYER DISTRIBUTION\*

The study was aimed at showing to what extent variations in the number of insects obtained in quantitative samples illustrate the variations in abundance of the whole population living in a meadow habitat, and what the ratio of these two parts of the population is, using a population of *Cicadella viridis* L. (*Auchenorrhyncha* - *Homoptera*) as an example. It was found that the *C. viridis* population is divided into one part living in the grass layer, and one part living in the litter layer. As a result of the vertical movements of the insects the ratio of these two parts of the population varies during the growing season. The following methods, adapted to the conditions of the study population, were used for calculating absolute population numbers: the Lincoln index and the De Lury graphic method. In addition a method based on the vertical movements of the population and extent of reduction among the insects during the growing season was elaborated and used.

CONTENTS

- I. Study area
- II. Methods
- III. Variations in the abundance of *Cicadella viridis*
- IV. An attempt at determining the absolute numbers of a population of *Cicadella viridis*
- V. Discussion of results
- VI. Summary of results

Determination of the abundance of a whole population living in a study habitat has become the fundamental problem of many biological questions. For instance, the problems connected with the productivity of ecosystems,

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forming the centre of interest in contemporary biology, must be based on absolute numbers for calculations.

Methods are used for determining the absolute numbers of insects which, depending on the type of habitat, species of insect, etc., produce more or less real values. The method most often used consists in the capture of all the insects from a given defined area (Remane 1958, Odum 1960, Smalley 1960, Wiegert 1964 and others), or repeated capture of insects from the same area, and in drawing conclusions as to numbers from the curve obtained from the regression of the numbers of the animals caught (De Lury 1947, Hayne 1949, Tanaka 1951, Calhoun and Webb 1953). The methods used to determine absolute numbers of higher animals, chiefly small rodents, based on the "capture - mark - release" method, marking of individuals (Lincoln 1930, Leslie, Chitty 1952, Odum 1960), or calculation of abundance from a "calendar of captures" (Andrzejewski 1962) have also been applied to invertebrate animals (Skuhravý 1957, Chew 1959, Heydemann 1962, Grüm 1965). Generally, however, the above-mentioned methods are applied often mechanically, that is, they do not take into account differences in the behaviour of insects during the growing season.

Insects in a varied natural habitat are distributed more or less unevenly and this distribution varies during the growing season (Andrzejewska 1965). Usually only part of the insects are accessible to observation and conclusions are drawn as to the abundance of the whole population from this part, hence it is essential, when using methods aimed at calculating absolute population numbers, to take into consideration the distribution of the insects in the habitat and the variations in this distribution during the period for which calculations are made.

In the present study calculations of the absolute population numbers were based on the Lincoln (1930) formula and the De Lury (1947) regression curve, the distribution of the population in the layers of meadow plants and variations in this distribution (and accessibility for capture) over the growing season being taken into consideration.

An attempt was also made at obtaining the numbers of the whole population on the basis of the calculated reduction of part of the population caught in samples during the growing season. These calculations were made on the basis of an analysis of the layer movements of the insects during the season. Field experiments were made in order to solve this problem, using a population of *Cicadella viridis* L. (*Auchenorrhyncha* - *Homoptera*) for the investigations. Group marking of individuals made it possible to analyse in detail the vertical movements of *Auchenorrhyncha* during the growing season. The information obtained formed a basis for correcting the method of calculations of the absolute population numbers of this type of insects living in the study habitat and checking the degree of their accuracy by appropriate analysis, in the light of the structure of their vertical distribution.

## I. STUDY AREA

The field experiment was carried out on a meadow in wooded land and on chosen stations on the Strzeleckie Meadows in the Kampinos National Park near Warsaw. Both habitats are covered by plant associations of the *Caricetum elatae* type (W. Koch 1926). Water does not dry up between the high clumps of sedge until July, and in wet years it does not dry up at all. The habitat is eutrophic. There are 34 species of higher plants, but the character of these meadows is determined by the high clumps of sedge, up to 70 cm high. The dominating species is *Carex hudsoni* Bennet (= *Carex elata* Bell.), and in addition the following species are numerous; *C. acutiformis* Ehrh., *C. vesicaria* L., and *C. riparia* Curt. In addition to the sedges the following species occur in far smaller numbers, scattered between the sedge clumps: *Calamagrostis canescens* (Web.) Roth, *Comarum palustre* L., *Lysimachia vulgaris* L., *Caltha palustris* L., *Stachys palustris* L., *Ranunculus repens* L., *Galium palustre* L. (Traczyk in press).

There is a layer of sedge peat between the clumps, which is under water for the greater part of the year. A thick layer of sedge litter with an addition of mosses forms on the sedge clumps. These meadows were not used for farming purposes.

## II. METHODS

The species *Cicadella viridis* chosen for study is the absolutely dominating species in the *Auchenorrhyncha* community in the study habitat, and it was therefore possible to be to a large extent independent of the influence of other populations co-occurring with it (Andrzejewska 1965). The size of individuals of *C. viridis* made it possible to mark the insects and made them relatively easy to see among the plants.

The experiments were initiated by introducing 50 imagines of *C. viridis* on to clumps of sedge of more or less uniform size. As has been mentioned earlier on, the habitat formed by the study meadows has a very well developed litter layer, formed by a thick layer of loosely interwoven live and dead parts of plants, and a certain part of the *C. viridis* population lives in this layer, despite the fact that this insect is a species living chiefly on grasses, and characteristic of the grass layer immediately above the litter (Andrzejewska 1965)<sup>1</sup>.

During the growing season observations of the experiments were made every few days, consisting in counting the number of individuals of *C. viridis* on the given clump in the grass layer only. Results of previous experiments (Andrzejewska 1961) using a similar technique, show that a fairly con-

<sup>1</sup>I have used the term "grass" not in the systematic sense, but merely to indicate the plant layer, i.e. the part of plants above the litter, irrespective of their species composition.

siderable drop in the number of insects in the grass layer takes place within a few days after their introduction on to the spot (post-operational reduction). After this the decrease is more even and far slower (stabilization period). On this account the first observation was made after the post-operational reduction, and all the insects in the grass layer were counted and marked with the first mark (amputation of the end of the right wing). In some of the experiments insects marked with the first mark were introduced. During the next two observations insects were marked which had not hitherto been marked, amputating in turn: the end of the left wing (second mark), then the ends of both wings (third mark). Observations were continued every few days until the autumn disappearance of the insects, the number of unmarked individuals, and the number possessing one or more of the three marks being recorded.

Part of the clumps on which the insects were placed were covered with isolators, which made it impossible for the insects to leave the clump or to enter the clump from a place not included in the observation area. The frame of the isolator, shaped like a cube measuring  $0.5 \times 0.5 \times 0.5$  m, was made of metal rods, the sides being covered with cotton gauze.

Three types of experiments were made: A — on the small meadow in wooded land (8 repeats); B and C — on the Strzeleckie Meadows in the Kampinos National Park (5 repeats each).

Experiment A — 8 isolators were placed on clumps of sedge, and 50 unmarked imagines of *C. viridis* were put under each isolator, first having made repeated and very scrupulous searches for and removal of insects of this species from the grass and litter layers.

Experiment B — marked insects (first mark) were introduced on to clumps of sedge not covered with isolators. All the individuals of the local population of *C. viridis* had previously been removed from grass layer of the clumps, then the 50 insects of this species were introduced. As the clumps of sedge were not covered with isolators in this experiment, while observations, counting and marking were carried out an isolator was placed over the clump in order not to frighten away *Auchenorrhyncha* from the places not included in the observation.

Experiment C — five clumps, not covered with isolators, on to each of which 50 marked (first mark) insects were added to the local *Auchenorrhyncha*. The local population of *C. viridis* was not in any reduced in either the grass or litter layer.

Observations were made every few days in experiments B and C, as they were in A. The results of observations in experiment A are given in Table I, in experiment B in Table II, and in experiment C in Table III.

The marking used made it possible to distinguish 4 groups of insects:

1. The first group consisted of insects marked with the first mark. In experiment A, these are all the insects found in the grass layer during the first observation ( $A_1$ ), whereas in experiments B and C these are introduced insects ( $B_1$  and  $C_1$ ).

2. The second group includes insects marked with the second mark. In experiment A these are insects found in the grass layer on the second day of observations and not as yet marked ( $A_2$ ). In experiments B and C on the first observation day, also as yet unmarked ( $B_2$  and  $C_2$ ).

3. The third group consisted of insects marked with the third mark, caught during successive observation in experiments A, B and C and not as yet marked ( $A_3$ ,  $B_3$ ,  $C_3$ ).

4. The fourth group includes all insects found in the grass layer under the isolators and not marked up to the end of the experiment ( $A_4$ ,  $B_4$ ,  $C_4$ ).

Recapture of marked individuals made it possible to calculate the absolute number of individuals of the *C. viridis* population. The Lincoln (1930) index and the De Lury (1947) graphic method were used for calculations. A more detailed discussion of these methods is given in section IV.

In elaborating a method adapted to calculations of the absolute numbers of the *C. viridis* population, the layer distribution and variations in it during the growing season were used as a basis (Andrzejewska 1965), and the extent of the reduction of insects in the grass layer also calculated for this period. The degree of reduction was determined by the decrease in the number of insects (their disappearance) during the period between successive observations. Reduction was calculated in percentages for unit of time (one day).

### III. VARIATIONS IN THE ABUNDANCE OF *CICADELLA VIRIDIS*

Variations in the numbers of the insects introduced took similar courses in all three of the experiments made, this applying to that part of the population which occurred in the grass and was counted during successive observations. At first there was a rapid and considerable decrease in the number of *C. viridis* (over a period of about 10 days). Further decrease took place more slowly, and lasted until approximately mid-August. As found in earlier investigations (Andrzejewska 1961) this decrease was similar in character to the natural decrease in the *C. viridis* population under field conditions during this period. Towards the end of August there is a clearly defined increase in the number of *C. viridis*, then the number of insects rapidly decreases and becomes almost nil by the beginning of September (Fig. 1, 2, 3).

In experiment A (Tab. I) — as has been emphasized earlier on — only the introduced insects were to be found under the isolators (before setting up the experiment the local population had been almost completely liquidated). The isolators made contact with the surrounding habitat impossible and hence the August increase in the number of marked insects can be treated only as the movement of the insects to the grass layer from the place not included in the observations, which in this case could only be the litter layer.

In experiments B and C (Tab. II, III) the introduced insects (with marks  $B_1$  and  $C_1$ ) were not isolated by means of isolators and therefore practically speaking it was possible for them to move not only into the litter but also

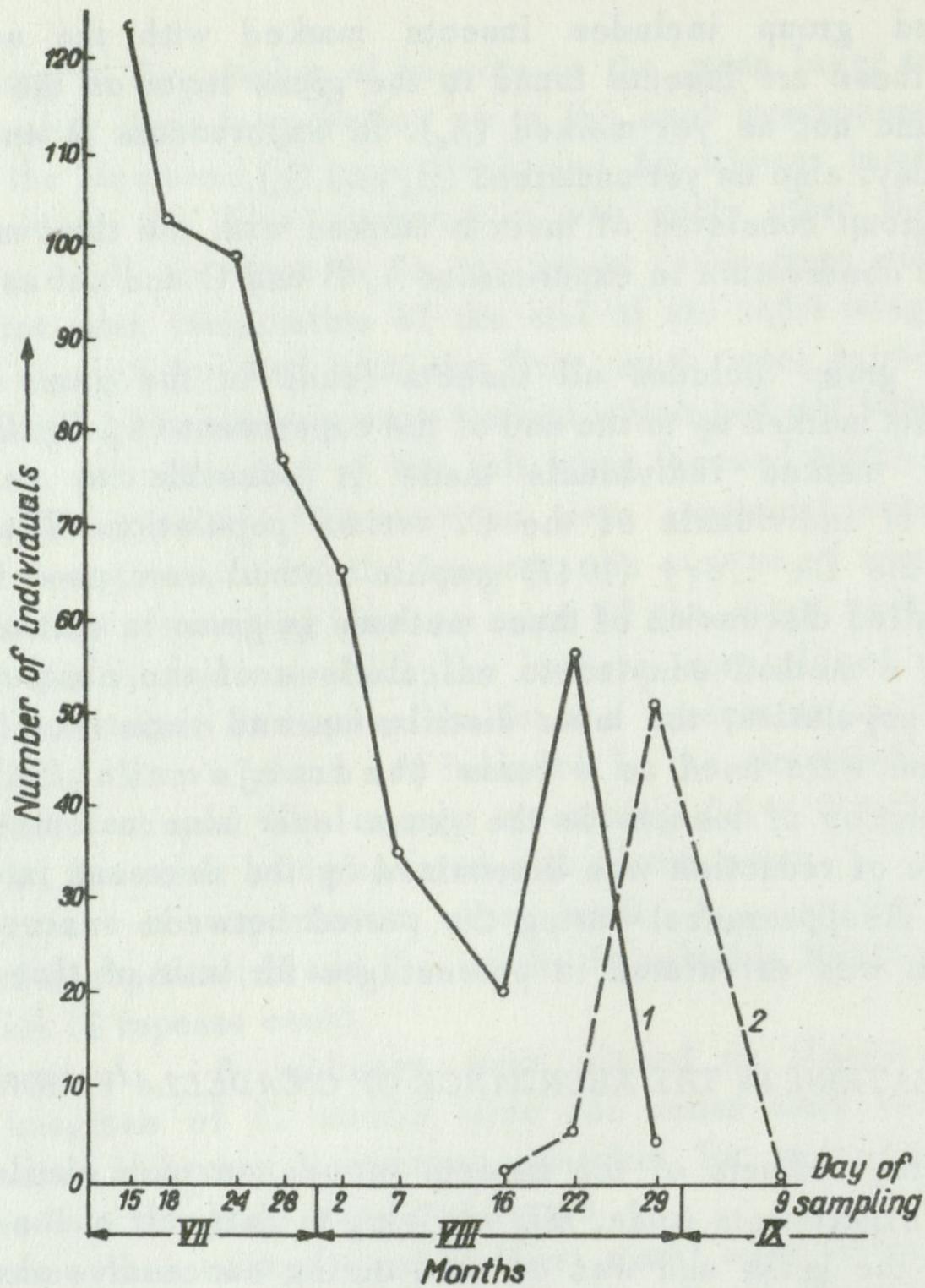


Fig. 1. Variations in numbers of *Cicadella viridis* from the grass layer during the growing season in experiment A  
1 – insects introduced, 2 – second generation

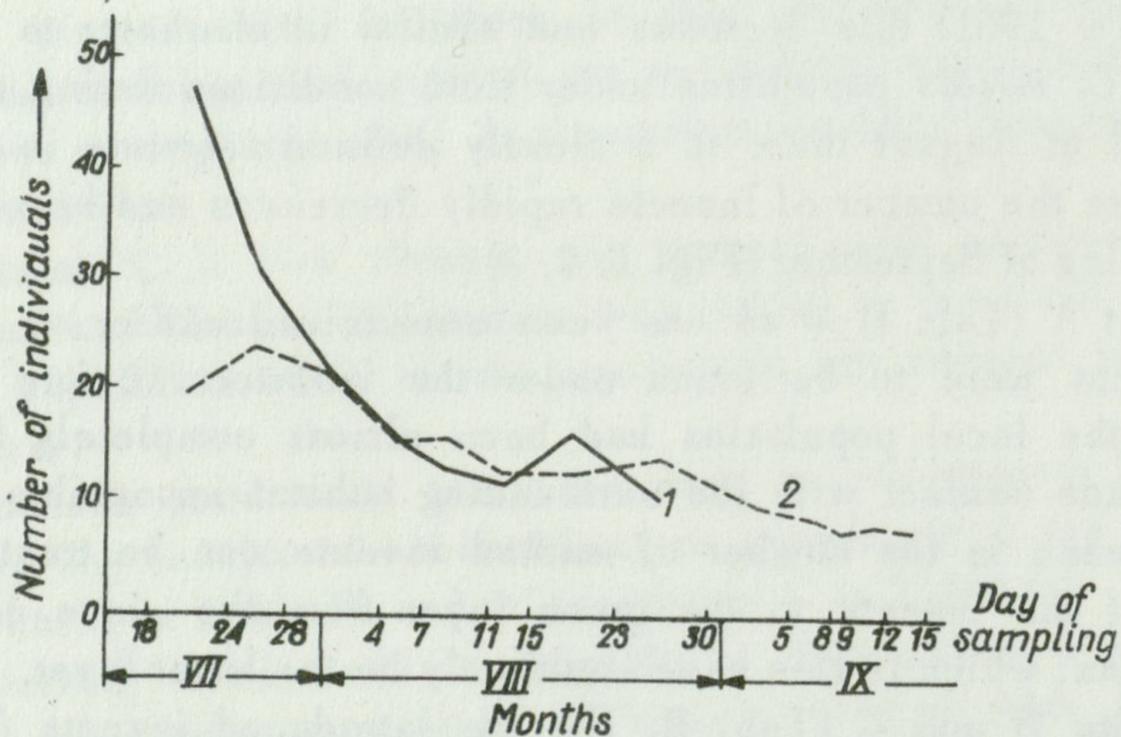


Fig. 2. Variations in numbers of *Cicadella viridis* in the grass layer during the growing season in experiment B  
1 – insects introduced, 2 – local insects

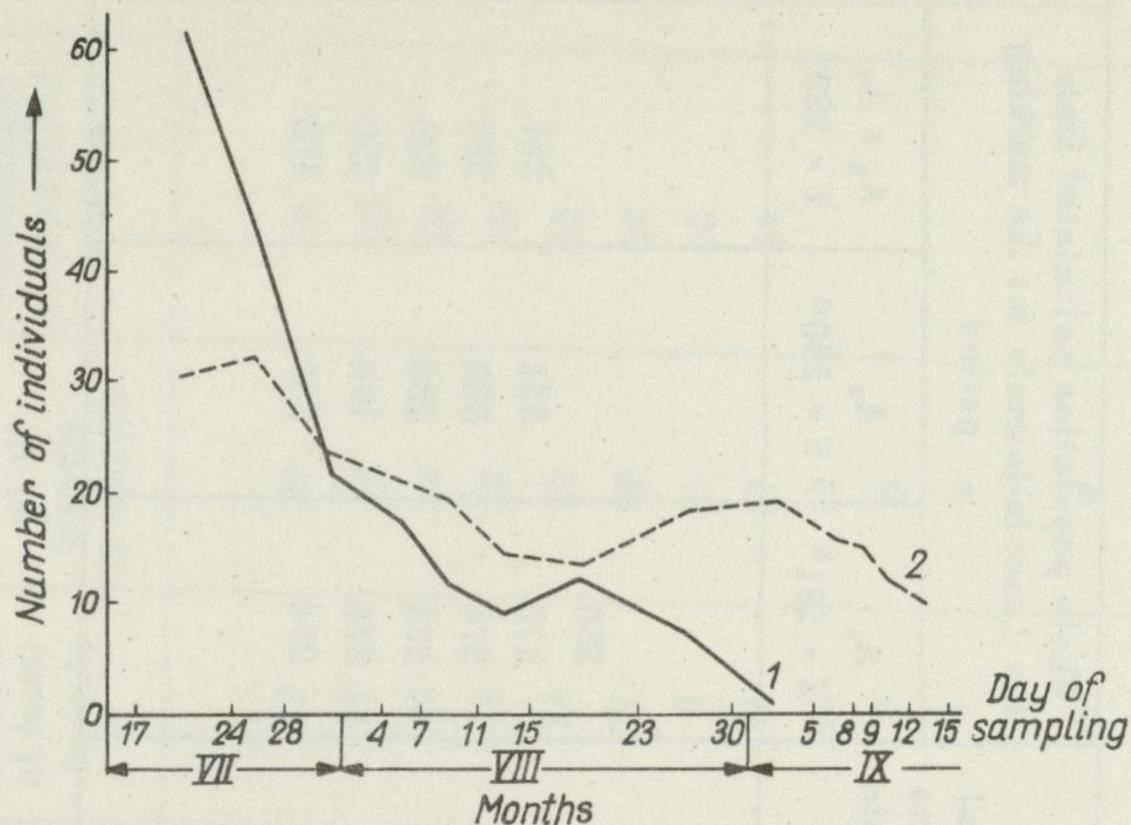


Fig. 3. Variations in numbers of *Cicadella viridis* in the grass layer during the growing season in experiment C  
1 – insects introduced, 2 – local insects

beyond the clump under observation. Regardless of the lack of isolation, variations in the numbers of the introduced insects took place similarly to those in experiment A (Fig. 2, 3). The rate of disappearance of the insects in the grass layer and the degree of reduction is in principle similar in all the experiments. The results of previous experiments showed that horizontal movements of the population are minimum during the period of the experiment (Andrzejewska 1960).

In experiments A, B and C the percentage of reduction was high (post-operational reduction) both after the insects had been placed under isolators and on the uncovered clumps of sedge; later on variations are smaller (experiment A and B). Not until mid-August is there a period of sudden and considerable inhibition of reduction, and there is even an increase in the number of insects. This is the time at which the insects emerge from the litter (Fig. 4, 5, 6). This is clear not only from the analogy to experiment A. An increase in the number of the insects introduced at the beginning of the experiment (marked  $B_1$  and  $C_1$ ) and also of the local insects marked during the first observations ( $B_2$ ,  $C_2$  and  $B_3$ ,  $C_3$ ) takes place during this period (Fig. 1, 2, 3).

The autumn increase in the number of insects, due to emergence from the litter of adult individuals belonging to the first and second generation, occurs in experiments A and B about August 22nd. In experiment C, with an undisturbed local population, it occurs about one week earlier. The increase in the number of insects begins as early as August 15th. After the insects have emerged from the litter there is an increase in reduction liquidating the first generation of *C. viridis* within 7 days. This is expressed by the

Comparison of numerical results obtained in experiment A and calculations from the Lincoln formula of the whole population for three consecutive samples

Tab. I

Consecutive day of sampling	Date	Insects introduced				Sum total of insects in sample	Whole population calculated from the Lincoln formula for the marking period		
		marked with mark:			unmarked A <sub>4</sub>		A <sub>1</sub> $\bar{x} = 281^d$	A <sub>2</sub> $\bar{x} = 240^e$	A <sub>2</sub> + A <sub>3</sub> $\bar{x} = 220^f$
		A <sub>1</sub>	A <sub>2</sub>	A <sub>3</sub>					
0	8. VII				400	400			
1	15. VII	117				117			
2	18. VII	43	60			103	280		
3	24. VII	37	24	38		99	315	231	
4	28. VII	33	12	19	13	77	274	359	
5	2. VIII	28	20	9	8	65	273	182	
6	7. VIII	15	10	3	7	35	274	196	
7	16. VIII <sup>a</sup>	9	5	6	1	21	274	235	
8	22. VIII <sup>a</sup>	38	14	5	5 <sup>b</sup>	62			
9	29. VIII	1	1	2	51 <sup>c</sup>	55			
10	5. IX		—	—	—	—			

<sup>a</sup> Period of emergence of the insects from litter.  
<sup>b</sup> 3 individuals of generation II.  
<sup>c</sup> 2nd generation of *C. viridis*.  
<sup>d</sup> Mean value for the whole population on July 18th.  
<sup>e</sup> Mean value for the whole population on July 24th.  
<sup>f</sup> Mean value for the whole population on July 28th.

Comparison of numerical results obtained in experiment B

Tab. II

Consecutive day of sampling	Date	Insects introduced marked with mark: B <sub>1</sub>	Local insects			Sum total of local insects	Sum total of all insects in sample	Percentages of introduced insects
			marked with mark:		unmarked B <sub>4</sub>			
			B <sub>2</sub>	B <sub>3</sub>				
0	8. VII	250						
1	18. VII	60	19 <sup>a</sup>			19	79	76
2	24. VII	35	9	12 <sup>b</sup>		21	56	62
3	28. VII	27	7	3	17	27	54	50
4	4. VIII	16	1	3	12	16	32	50
5	7. VIII	15	1	—	14	15	30	50
6	11. VIII	11	4	1	12	17	28	39
7	15. VIII	12	1	3	4	8	20	60
8	23. VIII	20	—	—	17	17	37	54
9	30. VIII	—	—	1	11	12	12	
10	5. IX	—	—	—	8	8	8	
11	8. IX	—	—	—	8	8	8	
12	9. IX	—	—	—	7	7	7	
13	12. IX	—	—	—	9	9	9	
14	15. IX	—	—	—	6	6	6	

<sup>a</sup>Insects found unmarked and marked with second mark.

<sup>b</sup>Insects found unmarked and marked with third mark.

## Comparison of numerical results obtained in experiment C

Tab. III

Consecutive day of sampling	Date	Insects introduced marked with mark: C <sub>1</sub>	Local insects			Sum total of local insects	Sum total of all insects in sample	Percentages of introduced insects
			marked with mark:		unmarked C <sub>4</sub>			
			C <sub>2</sub>	C <sub>3</sub>				
0	8. VII	250						
1	17. VII	64	19 <sup>a</sup>			19	83	77
2	24. VII	60	11	33 <sup>b</sup>		44	104	58
3	28. VII	25	—	9	18	27	52	48
4	4. VIII	18	1	1	26	28	46	39
5	7. VIII	17	1	—	18	19	36	47
6	11. VIII	7	1	—	18	19	26	27
7	15. VIII	11	2	3	6	11	22	50
8	23. VIII	14	4	1	11 <sup>c</sup>	16	30	47
9	30. VIII	1	—	1	20	21	22	
10	5. IX	1	—	—	18	18	19	
11	8. IX	—	—	—	15	15	15	
12	9. IX	—	—	2	14	16	16	
13	12. IX	—	—	—	10	10	10	
14	15. IX	—	—	—	10	10	10	

<sup>a</sup>Insects found unmarked and marked with second mark.

<sup>b</sup>Insects found unmarked and marked with third mark.

<sup>c</sup>First individuals of generation II.

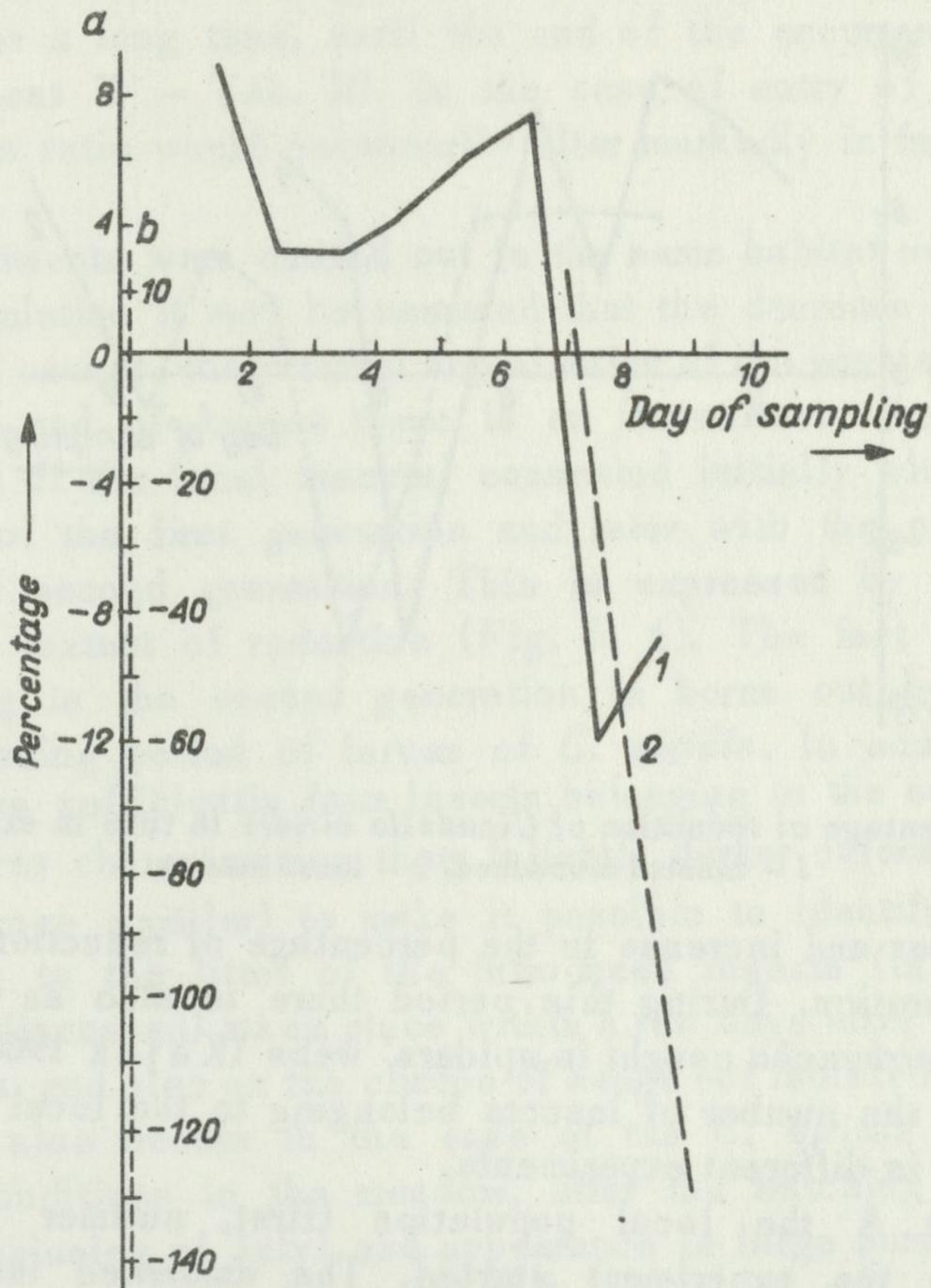


Fig. 4. Percentage of reduction of *Cicadella viridis* in time in experiment A  
1 - insects introduced (scale a), 2 - second generation (scale b)

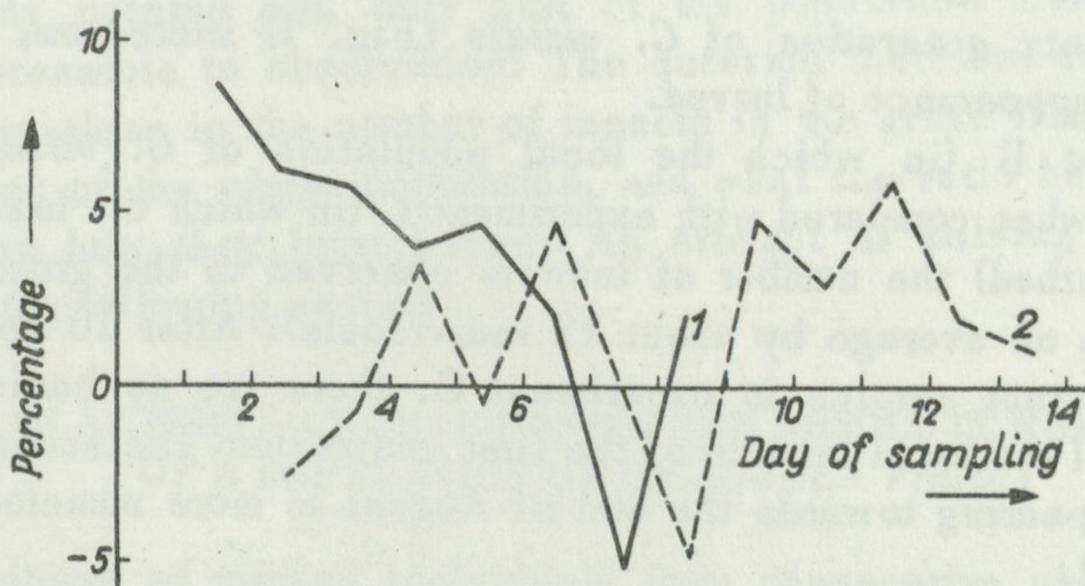


Fig. 5. Percentage of reduction of *Cicadella viridis* in time in experiment B  
1 - insects introduced, 2 - local insects

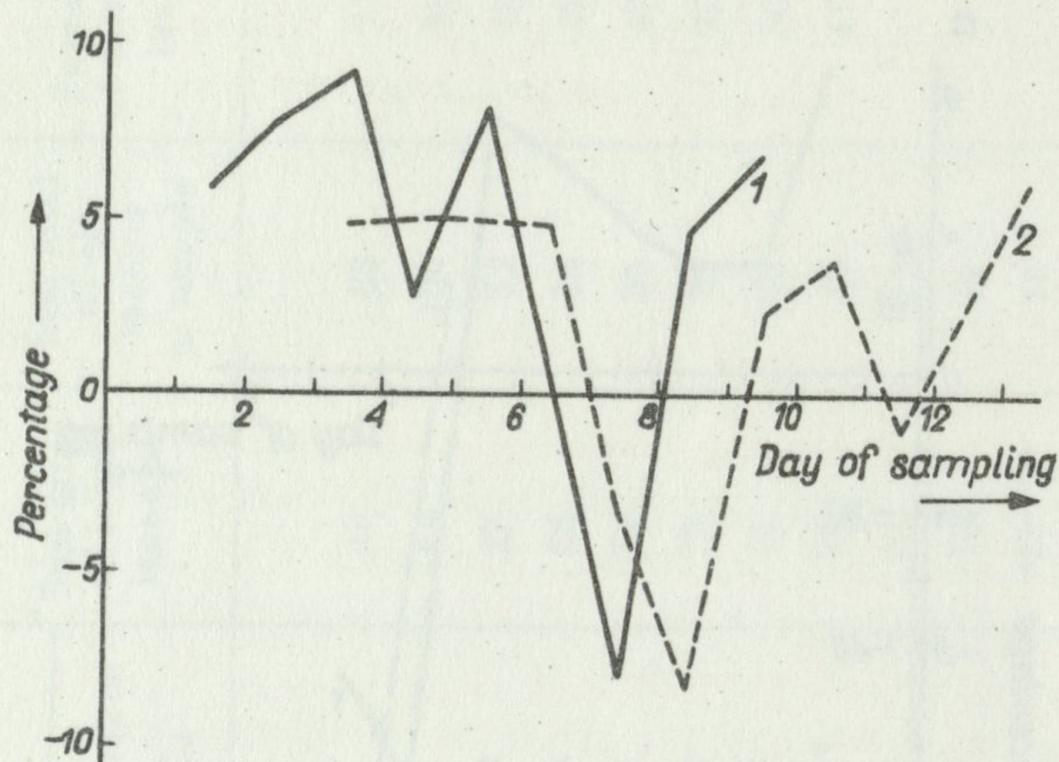


Fig. 6. Percentage of reduction of *Cicadella viridis* in time in experiment C  
1 - insects introduced, 2 - local insects

decrease in number and increase in the percentage of reduction of the insects of the first generation. During this period there is also an increase in the number of *Auchenorrhyncha* caught in spiders' webs (Kajak 1965).

Variations in the number of insects belonging to the local population take a different course in different experiments.

In experiment A the local population (first, summer generation) was liquidated before the experiment started. The unmarked insects appearing during the initial period of the experiment belong to those which entered to the litter after introduction (unmarked insects were placed under isolators in this experiment). Towards the end of August, after the introduced insects had emerged from the litter, the number of unmarked insects belonging to the second and scanty generation of *C. viridis* (Fig. 1) increases, having been preceded by the appearance of larvae.

In experiment B (in which the local population of *C. viridis* had been partly removed) when compared with experiment C (in which the local population was left undisturbed) the number of insects observed in the grass layer is at first smaller (on an average by about 12 individuals). After 10 days, however, despite the constant surplus in experiment C, there are no basic differences in the numbers of the local insects of the first generation. The second generation of *C. viridis* appearing towards the end of August is more numerous in experiment C than in B.

It is clear from this that initially the reduction in the local insects in experiment B is smaller than in experiment C (Fig. 5, 6). The evening up of numbers of the local population (in the grass layer) was due to the decrease

in reduction of the temporarily destroyed population which was removed (which rebuilt the grass-living part of its population from the litter-living part), and not to entry of insects from clumps not included in the observations. This is borne out by the almost constant ratio of introduced to local insects which is maintained for a long time, until the end of the occurrence of introduced insects (experiment B - Tab. II). In the case of entry of *Auchenorrhyncha* from outside, this ratio would necessarily alter markedly in favour of the local insects.

As the experiments were carried out in the same habitat and on individuals of the same population it may be assumed that the decrease in reduction was due to ecological causes, the internal organization of the population.

Towards the end of August there is an increase in the numbers of the grass-living part of the local insects, connected initially with the emergence from the litter of the first generation and later with the appearance of the imagines of the second generation. This is expressed by the considerable decrease in the extent of reduction (Fig. 5, 6). The fact that the insects appearing belong to the second generation is borne out by the occurrence during the preceding period of larvae of *C. viridis*. In addition the autumn generation differs sufficiently from insects belonging to the summer generation as to the features characterizing them (slightly darker coloration; the insects are on the average smaller) to make it possible to identify them correctly.

The entering to the litter of the introduced insects (in the case of all the experiments discussed) takes place within a few days after their introduction into the isolators, and also on the clumps of sedge not isolated from the habitat. This movement also occurs in the case of the *C. viridis* population living under natural conditions in the meadow, after the hatching of the imagines (end of June, beginning of July) and appearance in large numbers of the adult insects. The rapid drop in the number of insects in the grass layer, apart from mortality, is due to the insects entering the litter. For this reason the insects living in the grass, recorded during the various observations, do not form the whole of the population occurring in this habitat.

As already pointed out, only part of the population living in the grass layer was accessible to observation. The question therefore arises as to what extent the variations in the number of insects in the grass illustrate variations in the numbers of the whole population, and what the ratio between these two groups is and how they interchange? An attempt at solving this problem is presented in the following section.

#### IV. AN ATTEMPT AT DETERMINING THE ABSOLUTE NUMBERS OF A POPULATION OF *CICADELLA VIRIDIS*

The recaptures of marked individuals from consecutive observations made it possible to apply the Lincoln (1930) index and to calculate on the basis of this index all the individuals of *C. viridis* living under the isolators -

in both the grass and litter layers. Calculation was made according to the formula  $x = \frac{Z \cdot N}{Z_1}$ ; where  $Z_1$  – number of recaptured insects, previously marked

with a given mark;  $Z$  – all insects marked with a second mark;  $N$  – number of insects in a sample;  $x$  – number of all insects in the study population living in the section of the habitat covered by the isolator.

In addition, the De Lury (1947) graphic method was used to determine the absolute numbers of insects. This method necessitates several quantitative samples (capturing insects until no more are found) being taken in the same section of the habitat. The samples are taken at fairly close intervals of time on the same day. As a result we obtain several figures of decreasing value describing the number of insects in each sample, and on this basis calculation is made of the absolute number of animals in the study area<sup>2</sup>.

The material obtained by means of the marking used made it possible to draw a De Lury curve. It must, however, be pointed out that samples in the experiments discussed were taken at intervals of several days and therefore the curve obtained describes the size of the population, not at a definite moment, but as a certain average value for the sampling period. The figure obtained for the size of the population is burdened with an error resulting from the insects' mortality during the period from the first to last samples, from which the numbers of insects were taken as a basis for calculations, not having been taken into consideration.

Use of one-day data to draw the De Lury curve would be burdened by a greater and significant error in the case of the study population of *C. viridis*. If we bear in mind the data from the previous section on the distribution of the population in several parts of its niche and the rate of interchange between them, then it must be assumed that samples taken during one day only, only reflect the numbers of part of the population. This will be that part of the population living in that part of the niche from which the samples were taken, in this case from the grass layer only. It may therefore be assumed that drawing a curve from a longer period (and not from one day) gives a better chance of grasping the size (the sum total of parts) of the whole population living in a given section of the habitat under conditions when there is interchange of individuals between parts of the population.

In experiment A successive marking with three marks enabled four groups of *Auchenorrhyncha* to be distinguished,  $A_1$ ,  $A_2$ ,  $A_3$ ,  $A_4$ , and therefore we obtain values for three consecutive observations from calculations made using

<sup>2</sup>The first point of the diagram is marked on axis  $y$  at the place corresponding to the numbers of insects in the first sample. Next, by intercepting on axis  $y$  the number of insects in consecutive samples and on axis  $x$  the sum total of insects caught in this and in previous samples, we obtain a curve from several points which we extend to intersection with axis  $x$ . The place of intersection indicates the absolute numbers of animals living in that habitat.

Indices of layer differentiation and of absolute value of population abundance  
in consecutive control periods in experiment A (under isolators)

Tab. IV

Consecutive day of sampling		0	1	2	3	4	5	6	7	8	9	
Date of sampling		8. VII	15. VII	18. VII	24. VII	28. VII	2. VIII	7. VIII	16. VIII	22. VIII	29. VIII	
Number of insects in the grass layer per sample	d		117	103	99	77	65	35	21	59	4	
Abundance of whole population	e*	W		L	L	L	P	P	P	K		
	f	400		281	240	220	173	93	56	59		
Number of insects in litter layer (f - d)	g			178	141	143	108	58	35			
Percentage of insects	in grass layer $\left(\frac{d}{f} \cdot 100\right)$	h		36,6	41,1	35,0	$\bar{x} = 37,5^{**}$		37,5	37,5	37,5	100
	in litter layer $\left(\frac{g}{f} \cdot 100\right)$	i		63,4	58,9	65,0	62,5	62,5	62,5	62,5	0	

\* Method of calculating the size of whole population:

W – insects introduced at the start of the experiment,

L – value obtained from calculations acc. to Lincoln's formula,

P – value calculated on the basis of percentage of insects in the grass layer (37.5%) from previous three observations,

K – number of insects in the grass layer characterizing the whole population during the period of emergence from the litter.

\*\* Mean for three samples.

the Lincoln formula. These figures show (Tab. IV) that there is a certain part of the population outside the part of the habitat, in this case the grass layer from which the insects were taken. During this period on an average only 37.5% of the whole population (mean value from three first observations) was living in the grass and was accessible to captures (Tab. IV). As the first observations and calculations were made after the period of maximum reduction (post-operational) it may be taken that this percentage (37.5%) is more or less constant and the same for further observations during the period of relatively even decrease in numbers in the stabilization period. This was also shown in earlier investigations (Andrzejewska 1961). In such case the size of the whole population may be calculated for each number of insects of the given population in the grass obtained from the successive samples (Tab. IV).

A knowledge of the variations in the vertical movement of the *C. viridis* population (described in section III) enables us to check the correctness

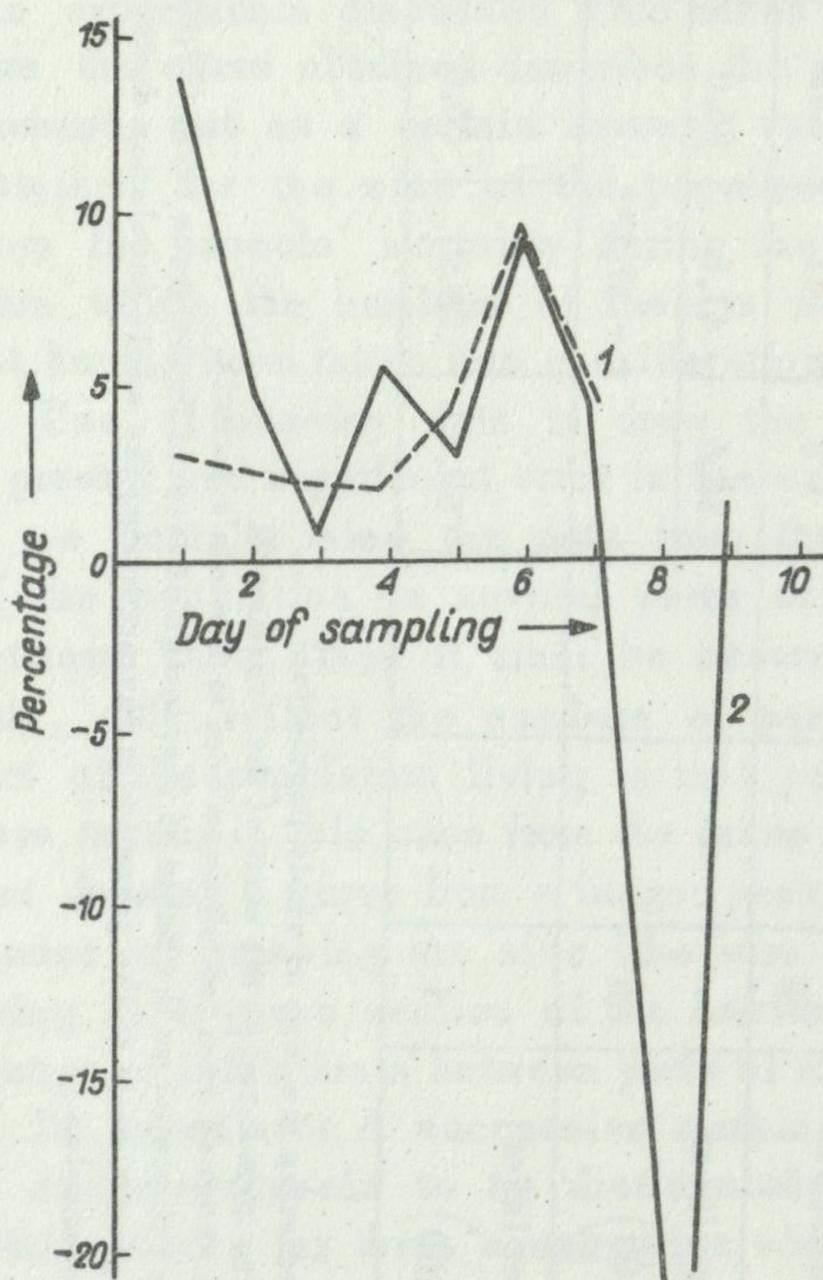


Fig. 7. Percentage of reduction of *Cicadella viridis* in time in experiment A

1 — percentage of reduction of the whole population calculated for 1 day, 2 — percentage of reduction of insects observed in the grass calculated for 1 day

of calculations made in this way. We can compare the numbers of insects in the grass towards the end of the season, at the time they emerge from the litter, assuming that all the individuals of *C. viridis* emerged (22nd Aug. — 59 individuals) with the theoretically calculated population as a whole for the period immediately preceding the time of emergence (16th Aug. — 56 individuals). During the six-day period (from 16th-22nd August) a certain part of the insects was reduced by mortality and therefore there should be more than 59 during the period preceding the emergence of the insects from the litter. From theoretical calculation of the whole population we obtain a figure of 56 insects, and thus a figure reduced in relation to their real numbers in the habitat. As the ratio of insects in the grass is constant in relation to the number in the litter, then it is clear that the degree of reduction of insects in the litter is slightly smaller than in the grass.

The figures obtained exhibit considerable agreement, and they may therefore be taken as reliable, as may the calculated value of the whole population living in the given section of the habitat.

For determination of the size of the whole population it might have been accepted in the above calculations that reduction of the insects in the grass and litter layers, despite the slight differences (during the stabilization period) is similar. This is also shown by comparison of reduction of the whole population with the reduction of individuals living in the grass. This reduction was calculated in percentages for unit of time (Fig. 7). During the first period, after the experiment had been set up, a considerable difference occurs between the size of the reduction in the grass and reduction of the whole population (sum total from grass and litter). This is due to the movement of the insects from the grass to the litter.

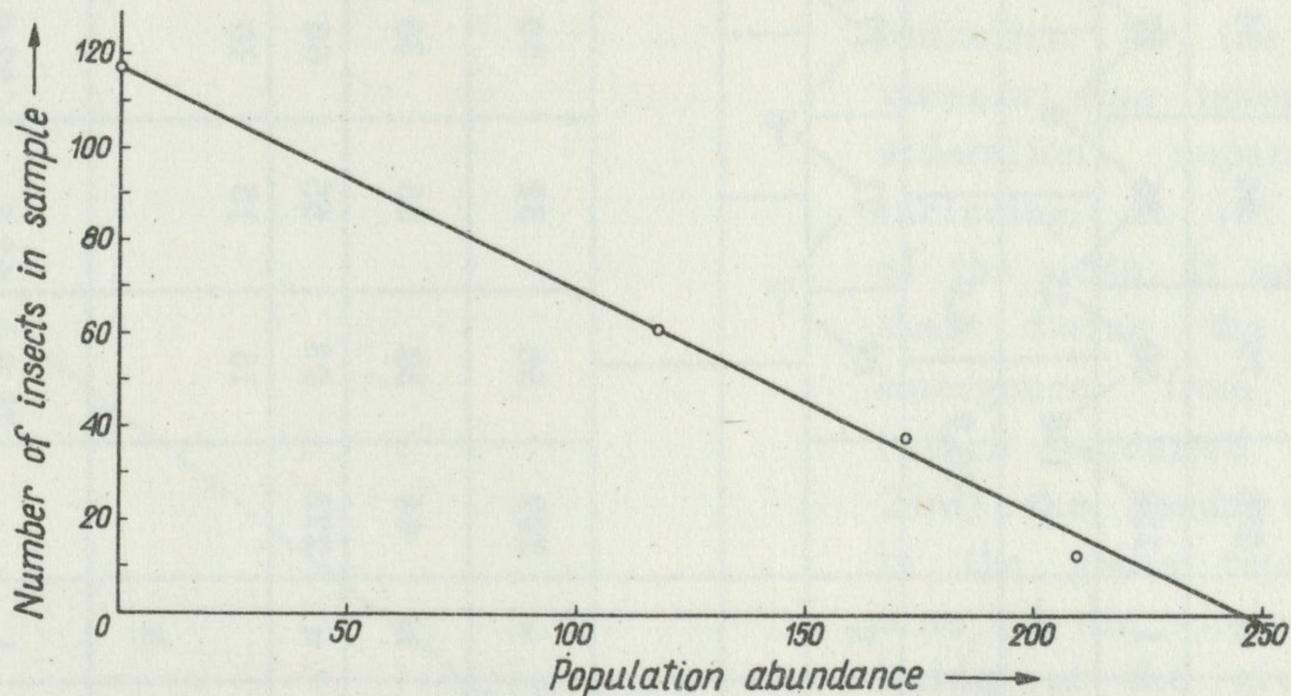


Fig. 8. Determination of population abundance by the De Lury graphic method in experiment A

Using the De Lury graphic method of calculation we obtain similar figures for the size of the whole population living under isolators. In experiment A we obtain values within limits of 240–250 individuals for the period from July 8th – 24th (Fig. 8). Approximately for the same period we obtain 240–281 individuals from the Lincoln formula.

In experiment B marked individuals were introduced into a certain litter part of the local population, the numbers of insects in this part being unknown. Determination of its value by the method used in experiment A would not produce results. The insects introduced had already been marked with mark B<sub>1</sub>, and the first of two successive observations had been made during the period of increased post-operational reduction. The insects introduced exhibited greater activity; part entered into the litter and initially they were subject to more reduction than individuals belonging to the local population. It is known that under the conditions when the introduced, marked insects are not incorporated in the local population, that they do not behave in the same

Consecutive day of sampling		0	1	2	3	4	5	6	7	8	
Date of sampling		8. VII	18. VII	24. VII	28. VII	4. VIII	7. VIII	11. VIII	15. VIII	23. VIII	
Sum total of local and introduced insects from the grass layer per sample (f + g)		d	250	79	56	54	32	30	28	20	37
Introduced insects	number in grass layer	f	250	60	35	27	16	15	11	12	20
	number of reduced insects		190	25	8	11	1	4	-1	-8	
	percentage of reduction for one day		10.9	6.9	$\bar{x} = 1.6$						
Local insects	number in grass layer	g		19	21	27	16	15	17	8	17
	number of reduced insects			-2	-6	11	1	-2	9	-9	
	mean percentage of reduction for one day calculated from period July 18th-Aug. 23rd			$\bar{x} = 2$							
Number of introduced insects in grass and litter layers calculated by the reduction estimate method		w	229	55	32	30	27	26	24	23	20*
Number of local insects in grass and litter layers calculated by the reduction estimate method		m	44	38	33	30	26	24	22	20	17*
Abundance of whole population (w + m)		e	273	93	65	60	53	50	46	43	37
Percentage of whole population living in litter layer $\left(\frac{d}{e} \cdot 100\right)$		h		15	13	10	40	40	39	53	0
				$\bar{x} = 43$							
Percentage of introduced insects calculated from sum total of introduced and local insects in grass layer $\left(\frac{f}{d} \cdot 100\right)$		i		75.9	62.5	50.0	50.0	50.0	39.3	60.0	54.0

\* Number of introduced and local insects in grass layer during the period of emergence from litter.

way as the insects of this population and it is then impossible to obtain reliable results when calculating the whole of the population by using the Lincoln formula (Leslie and Chitty 1952).

Making use of the information obtained from experiment A, however, it is possible to calculate the local population in another way.

During the autumn emergence from the litter, for a short time practically all the individuals of the first generation of *C. viridis* are present in the grass. At the same time it is known that reduction during the stabilization period takes a similar course in both the grass and litter, and the percentage of reduction for all the local and introduced insects of the first generation is uniform (during this period the percentage of introduced insects is practically constant, being about 50% — Tab. II). We can therefore calculate the mean percentage of reduction for unit of time (one day) from variations in the number of *C. viridis* present in the grass. The initial high percentage of post-operational

reduction for the introduced insects was taken into consideration separately, not including it in calculation of the mean. It may be taken that during the period of emergence from the litter (which occurred on August 23rd) the number of insects in the grass represents the size of the whole population living at the given moment in the section of the meadow covered by the experiment (this was checked in experiment A). Knowing the percentage of reduction in numbers of that part of the population living in the grass, from the time the experiment was set up up to the emergence of

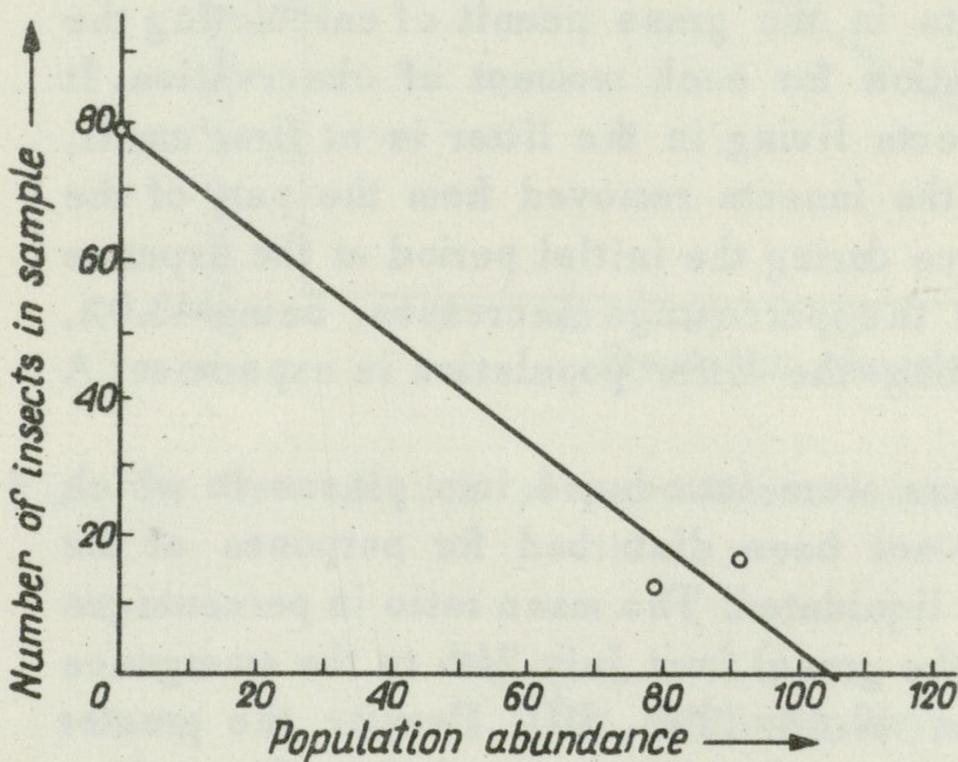


Fig. 9. Determination of population abundance by the De Lury graphic method in experiment B

the insects from the litter, it is possible to define its numbers during the various observations, both for the introduced and local individuals of *C. viridis* (Tab. V).

Calculations were made in the following way: for introduced insects  $B_1$ , mean reduction during one day (in the grass) during the stabilization period is 1.6%. During the time of emergence from the litter, on August 23rd there were 20 individuals with mark  $B_1$ . This is a number of insects reduced in relation to the number in the previous observation (August 15th) by 12.8% ( $1.6\% \times 8$  days). This means that on August 15th, taken jointly for grass and

litter, there were 23 introduced insects  $\left(\frac{20 \cdot 100}{87.2} = 22.9\right)$ . Twenty-three again is a value reduced in relation to the previous observation, etc. Values for the local insects were calculated in the same way.

Calculations indicate that at the time the experiment was set up 229 insects were introduced. The actual number introduced was 250, and the error is therefore only 8.6%. Similar calculations were made for the local population, and it was calculated that 44 individuals formed the remaining local litter population of *C. viridis*. If it is assumed that the figure of 44 obtained is burdened by the same error (8.6%) then the figure for the local population must be corrected from 44 to 48 insects.

Data referring to the population as a whole show that on July 18th there were 93 individuals of *C. viridis* on the clumps included in observations (in both grass and litter). The value obtained by the De Lury graphic method for a similar period varies within limits of 100–110 individuals (Fig. 9).

The values calculated for the whole population and data from the various observations of the number of insects in the grass permit of calculating the size of the litter part of the population for each moment of observation. It was found that the percentage of insects living in the litter is at first small, which indicates that replacement of the insects removed from the part of the population living in the grass took place during the initial period at the expense of the insects in the litter. Later the percentage increases, being 43.0%, and is similar to the value describing the litter population in experiment A (37.5% – Tab. IV, V).

In experiment C the marked insects were introduced into places in which the local *C. viridis* population had not been disturbed for purposes of the experiment, and was not to any extent liquidated. The mean ratio in percentages of the introduced to local insects (in the grass) from July 24th to the emergence of the insects from the litter was 49.4% (Tab. III). Despite the greater variability of the ratio of introduced to local insects during the various observations, this result is similar to the proportions obtained in experiment B (50.2% – Tab. II).

As mentioned in the descriptive section, emergence of the insects from the litter in experiment C began slightly earlier (about August 15th) than in experiment A and B (about August 23rd). During the next observation, made on August 23rd, only part of the insects were observed, immediately after their emergence from the litter, during the course of their rapid autumn liquidation. It did not prove possible in this experiment to grasp the moment at which all the insects from the litter are present in the grass and not yet in course of the autumn liquidation, and it was therefore not possible to calculate the value of the litter part, the grass-living part and the absolute numbers of the whole *C. viridis* population by the method used in experiment B.

It is possible that the presence of the local undisturbed population of *C. viridis* affected the different behaviour of *Auchenorrhyncha* in experiment C (considerable variations in the ratio of introduced to local insects in the grass, earlier emergence of the insects from the litter).

The results obtained in experiment C made it possible, however, to draw a curve by the De Lury method for calculation of the whole population. Thus during the period from July 17th to July 24th there was a total number for both grass and litter of from 140–150 individuals (Fig. 10).

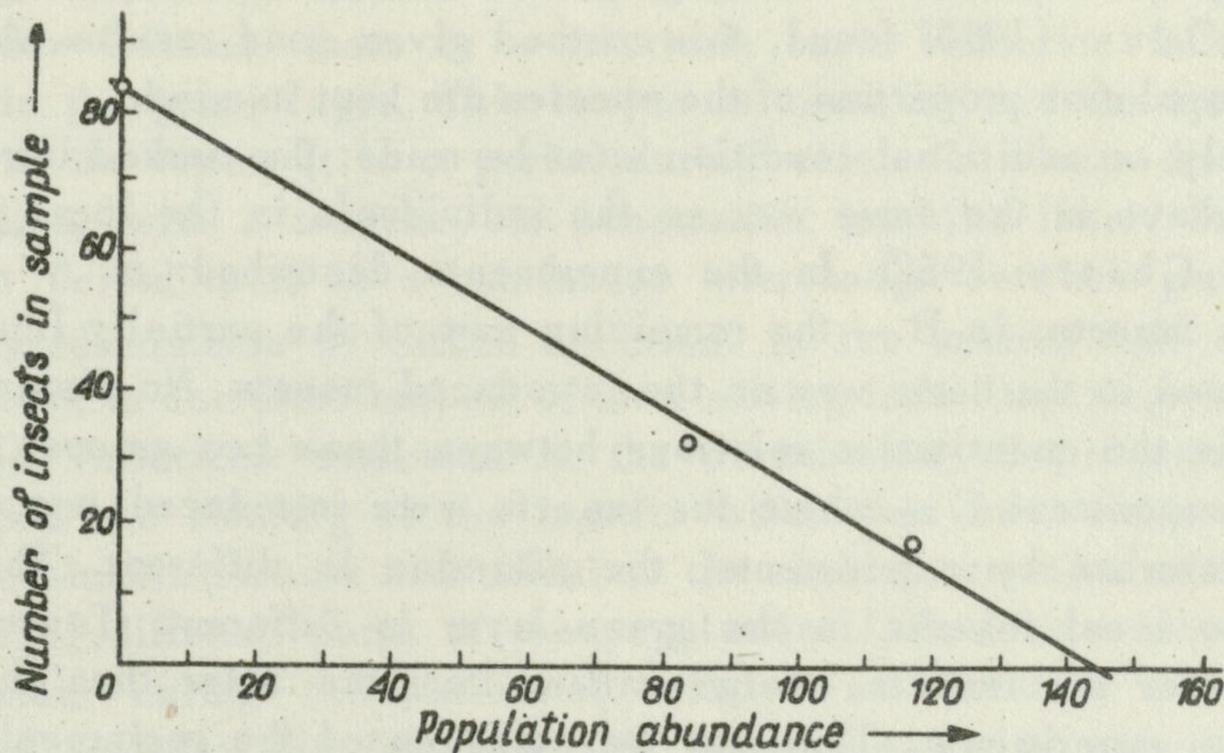


Fig. 10. Determination of population abundance by the De Lury graphic method in experiment C

## V. DISCUSSION OF RESULTS

The considerable degree of agreement obtained in the results of calculations made by different methods is not only a criterion of the correctness of the figures obtained, but also proves that the reasonings made during the course of the study are also correct.

In the light of the material elaborated in the present study, the methods used for calculation of absolute numbers of populations examined must be applied on the basis of a thorough knowledge of the life cycle of the population, its dynamics and distribution in space, also the variations in this distribution. The method of capturing all insects from a given area, in fairly general use permits of defining the numbers of a population only when captures are carried out for a sufficient period of time. It is not enough to make a single search for and capture of the animals, even a very scrupulous one, to ensure that the population has been completely removed from a given habitat. For instance: it was only after 8 days of daily and thorough removal

of *C. viridis* from the grass layer that their number (in the grass) decreased and only single individuals remained (Andrzejewska 1960).

It is clear from this that in order to determine the absolute numbers of a population living in a natural habitat, captures must be continued for as long as the cycle of interchange between the majority of individuals occupying different parts of the population area continues.

The use made in this study of calculations according to the Lincoln formula for determining the absolute numbers of a population would seem justified, since under the conditions of the study population of *C. viridis* a relatively rapid interchange of individuals takes place between different parts of this population. As Odum (1963) found, this method gives good results when the biological and population properties of the species are kept in mind.

Simultaneously an additional condition must be made: the marked introduced insects must behave in the same way as the individuals in the local population (Leslie, Chitty 1952). In the experiments described: in A – there were only local insects; in B – the remaining part of the partially liquidated population behaved in the same way as the introduced insects. No disturbances were observed in the quantitative relations between these two groups. On the other hand, in experiment C – where the insects were introduced into a local population undisturbed by experiments, the situation is different. The ratio of introduced to local insects in the grass layer is different. Towards the end of the summer the insects emerge earlier from the litter than they did in the other two experiments. This may be evidence of the reciprocal effect of the local undisturbed population and the insects introduced there<sup>3</sup>.

Under such conditions, when the introduced marked individuals are not incorporated with the local population in the rhythm of interchange between different parts of this population, it is incorrect to apply the Lincoln formula to determine the absolute numbers of the population.

The De Lury graphic method also used for calculation of the absolute numbers of the population required the introduction of a change, consisting in taking into consideration during calculations the number of insects obtained from samples taken from the same area at intervals of several days. This was necessitated by the fact that the cycle of interchange between parts of the population lasts for considerably longer than the time taken to make the captures. The use of repeated captures during the course of one day enabled the absolute numbers to be determined, but only of that part of the population within the range of the method used.

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<sup>3</sup>Łomnicki (1964) observed a local population to exert a similar effect. Under the conditions of the experiment, in which the local population of the snail *Helix pomatia* L. was subjected to different degrees of liquidation on different study areas, he introduced a certain number of individuals of this species on to these areas. In the areas in which the population had been left undisturbed the introduced snails did not look for hiding places, but remained closed up in their shells and after a short time left the area occupied by the local population.

## VI. SUMMARY OF RESULTS

1. The population of *Cicadella viridis* living in a varied meadow habitat is divided into a part living in the grass layer and a part living in the litter.

2. These two parts of the population are not isolated from each other, and interchange of individuals takes place between them, varying as to intensity and direction, over the period from spring to autumn. After the period of mass hatching of the imagines (end of June, beginning of July) and also under the conditions created by experimental introduction of *C. viridis* into the meadow habitat, there is a relatively rapid reduction in the number of insects in the grass layer. This is due to mortality and the movement of the insects to the litter. It is a period during which *C. viridis* distributes itself in the area, with a tendency to penetration into the litter. During the stabilization period there is a continuous interchange between grass and litter, without predominance of either direction. In the second half of August the insects move in one direction, all of them moving from litter to grass.

3. The variations examined in the distribution of the population in the habitat and the marking of the insects which was used made it possible to apply the Lincoln formula and calculate the absolute numbers of the population, and also of different parts of the population. Calculations show that during the summer, during the period of relative stabilization of the *C. viridis* population, despite the fact that this is a grass-living species, only about 40% of the insects live in the whole grass layer. The remainder, about 60% lives in the litter. Towards the end of August, after the insects have emerged from the litter, 100% of the population is present in the grass.

4. Correct interpretation of results giving absolute population numbers of *C. viridis*, obtained by the De Lury graphic method, and also the values obtained by the Lincoln formula, required the introduction of certain additions resulting from an analysis of the layer distribution of the population and changes in this distribution in time.

5. Analysis of the vertical structure of the population and recording of the insects' movements in the layers of meadow plants made it possible to elaborate a method of calculating the absolute numbers of the population. The basis of calculations was formed by determination of the extent of reduction of the insects in the grass-living part of the population.

6. Reduction of insects due to mortality took a similar course in both the grass- and litter-living parts of the population. When the grass-living part of the population was destroyed, however, rebuilding of this part of the population took place by means of reduction of mortality in the litter layer and movement of part of the insects to the grass.

7. Variations in the vertical distribution of the population over the growing season form evidence that the index values obtained by using the quantitative methods of capture are not proportional to the variations in the absolute num-

bers of the population. This is due to the fact that the degree of accessibility of the population to the methods used varies over a period of time.

8. Under the conditions created by the experiment the local undisturbed population of *C. viridis* and the introduced individuals of the same species mutually influence one another.

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## PRÓBA WYZNACZENIA BEZWZGLĘDNEJ LICZEBNOŚCI POPULACJI *CICADELLA VIRIDIS* L. NA TLE JEJ PIĘTROWEGO ROZMIESZCZENIA

### Streszczenie

Tematem pracy jest analiza zmian w pionowym rozmieszczeniu populacji *Cicadella viridis* L. (*Auchenorrhyncha* – *Homoptera*) w środowisku łąkowym oraz próba obliczenia bezwzględnej liczebności populacji tych owadów.

Dla rozwiązania powyższego zagadnienia przeprowadzono w roku 1961 eksperyment terenowy na łąkach Kampinoskiego Parku Narodowego pod Warszawą. Do badań wybrano płaty roślinności turzycowej (zespół *Caricetum elatae*), w których badany gatunek skoczka był bardzo licznie reprezentowany.

Wykonano trzy typy eksperymentów:

A – pod osiem izolatorów z gazy (po uprzednim kilkakrotnym wyłowieniu miejscowych skoczków z warstwy trawy i ściółki) wprowadzono po 50 osobników *C. viridis*.

B – po wyłowieniu osobników badanej populacji (tylko z warstwy trawy) wprowadzono na 5 kęp po 50 osobników *C. viridis*.

C – na pięciu kępach turzycy umieszczono po 50 osobników *C. viridis*. Miejscowa populacja tego gatunku nie była w jakimkolwiek stopniu usuwana.

Kępy turzycy w eksperymencie B i C nie były osłaniane izolatorami.

Co kilka dni przeprowadzano obserwacje polegające na przeliczaniu wszystkich osobników *C. viridis* znajdujących się w warstwie trawy. Zastosowano grupowe znakowanie osobników, obcinając im końce pierwszej pary skrzydeł. Do obliczeń bezwzględnej liczebności populacji zastosowano wzór Lincolna (1930) oraz metodę graficzną De Lury (1947), przystosowując te metody do warunków ekologicznych badanej populacji. Zastosowano również metodę opartą na redukcji części populacji przebywającej w warstwie trawy oraz na zmianach w piętrowym rozmieszczeniu tej populacji w ciągu sezonu wegetacyjnego.

Na podstawie przeprowadzonych eksperymentów stwierdzono, że:

Populacja *C. viridis*, żyjąca w środowisku badanych łąk, dzieli się na część zajmującą warstwę trawy i część zasiedlającą ściółkę. Te dwa fragmenty populacji nie są od siebie izolowane; zachodzi między nimi wymiana osobników. Nasilenie i kierunek tej wymiany ulega jednak zmianie w ciągu okresu wegetacyjnego. Po okresie masowego wylęgu imagines (koniec czerwca, początek lipca), a także w warunkach eksperymentalnego wprowadzania *C. viridis* w środowisko łąkowe, następuje szybka redukcja ilości owadów w warstwie trawy, spowodowana śmiertelnością oraz przejściem owadów do ściółki. Jest to okres rozmieszczania się *C. viridis* z przeważającą tendencją do wnikania do ściółki. W okresie stabilizacji (lipiec, sierpień) zachodzi natomiast ciągła wymiana owadów w warstwach trawy i ściółki bez wyraźnego uprzywilejowania któregoś kierunku. W drugiej połowie sierpnia owady przemieszczają się w jednym kierunku; wszystkie przechodzą ze ściółki do trawy.

Przebadana zmienność piętrowego rozmieszczenia populacji *C. viridis* w środowisku łąkowym i zastosowane znakowanie owadów dało również podstawę do wyznacze-

nia liczebności całej populacji oraz poszczególnych jej fragmentów. Z obliczeń wynika, że w ciągu lata, w okresie względnej stabilizacji populacji *C. viridis* (mimo, iż zalicza się *C. viridis* do gatunków natrawnych), tylko około 40% owadów przebywa w warstwie trawy. Reszta, około 60%, znajduje się w ściółce. Pod koniec sierpnia owady wychodzą ze ściółki i w trawie znajduje się 100% osobników populacji. Zmienność piętrowego rozmieszczenia skoczków wskazuje, że wnioskowanie o liczebności całej populacji na podstawie oceny liczebności osobników w warstwie trawy, jest prawidłowe tylko dla końca sezonu wegetacyjnego, w którym cała populacja znajduje się w tym piętrze roślinności.

Bezwzględne liczebności populacji *C. viridis*, uzyskane przy zastosowaniu wymienionych metod, uwzględniających różne informacje, wykazują dużą zbieżność. Wskazuje to na przydatność stosowania każdej z tych metod (po uwzględnieniu zachowania się owadów w środowisku) dla oceny bezwzględnej liczebności *Auchenorrhyncha* — *Homoptera*.

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