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INTERSPECIFIC RELATIONSHIPS OF GAMASOID MITES IN THE NESTS OF CLETHRIONOMYS GLAREOLUS

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Abstract. The interspecific relationships of gamasoid mites from the nests of *Clethrionomys glareolus* have been studied by method of association analysis, in which affinity index derived by Fager (1957) has been used. Other methods of assessment of nidicolous fauna are critically discussed and advantages of the method used are pointed out. In the material from 149 nests containing 42 species of gamasoid mites all pairs of species in each of the four nest variants classed according to biotope and location of the nest have been assessed. The results are expressed by means of matrices and empiric association graphs. The groups of associated mite species and the level of their interrelationships indicating the difference in ecological conditions are defined. The structure of associations is much richer and varied than the mere species composition and therefore well reflects the differences in closely related communities.

The nests of small terrestrial mammals are a clear-cut environment not only for the mammals themselves, but also for a number of invertebrate animals that inhabit the nest and area associated with it to a different degree. If we regard the nest as an environment for these nidicolous organisms, it should be stressed that the nest on one hand represents a closed system separated from the surrounding biotope by space as well as by certain physical factors as has been demonstrated by studies of nest microclimate (Daniel 1970). On the other hand, however, the character of nest environment and its changes are closely dependent on the surrounding nature and this dependence may undergo dynamic changes, e.g. in the course of seasons of the year.

Apart from these abiotic factors the nest conditions are characteristically affected by the mammal inhabitant itself. This may be seen in the selection of nest location (with the same species we find nests built underground, at the ground level and even above the ground — see Daniel, Mrciak and Rosický 1971) and application of diverse material for nest bedding. Both strongly influence the community of nidicolous organisms (Mrciak, Daniel and Rosický 1966). The nest communities are also considerably influenced by direct activities of the mammal — we bear in mind primarily rearing of young, nest pollution by urine and feces, hoarding of remains of food which undergo decomposition etc.

All these factors are reflected in interspecific relationships of nidicolous organisms and to them may be added other dependences resulting from the bionomy of particular nidicolous species which is in many cases known incompletely or not at all.

An important work concerning the statistical evaluation of nest communities is the paper by Nordberg (1936) dealing with avian nests, but the methods used are similar to those applied in solving the problems of nests of small mammals. **Nordberg** revised the previously used methods of analysis and the inaccuracies found caused him to apply the concept of species constancy propagated by phytosociologists of the Zurich-Montpellier school. His classification in categories of dominant, influential and receding species follows up the principles of this school. He proposed a revised classification of **Krogerus** in eucenous, tychocenous and xenocenous species to be applied for the relationship of particular species to nest community. He points out the difficulty in correct listing due to lack of actual knowledge on particular nidicolous species. This situation has remained the same till the present day, although more than thirty years have elapsed since the publication of **Nordberg's** paper.

A marked component of nest communities is represented by mites, especially from the group Gamasoidea, which are a frequent object of research in the nests of most diverse hosts.

Predominant papers are those listing the species found. The mites are classified in them according to food specialization and their relationship to the nest cenosis is expressed by percentage of the total number of nidicolous organisms etc. Against both mentioned views objections should be raised in principle. In most gamasoid mites a strict food specialization is out of the question as their character in this respect is very changeable and therefore cannot be taken as a basis for further analyses. Likewise the mere percentual calculation is too static and does not give a true picture of actual interrelationships in particular species.

The studies on nest communities arouse a special interest also from the aspect of epidemiological practice because a number of nidicolous parasites have been proved or supposed to be vectors in natural foci of diseases. This fact stresses the necessity of searching for a concise expression of results obtained in order to compare them with those obtained by other authors and to retain the possibility of using the published results directly as source data for eventual calculations.

Nidicolous zoocenoses are a suitable object for quantitative ecology and have many common properties which facilitate the creation of a relatively simple theoretical model. This is, for example, a good differentiation of specimens which applies to all zoological objects in contrast to plants. Frequencies may be therefore used which fact, as a rule, leads to more simple statistical methods. On the other hand, the frequent difficulty in animal ecology — the great mobility of objects studied, no longer arises here. The nest microbiotope is strictly limited spatially and ecologically and makes a natural and homogeneous sampling unit. In this way the problems with its size do not arise, either. The ratio between the size of a specimen and the size of the nest is approximately constant and not involving spatial exclusion.

The goal of our paper is not only the presentation of results based on our own material, but also an attempt to create a new method of evaluation of nest materials for a detailed and theoretically well-grounded analysis of relationships in nest communities and for a clear graphical and numerical documentation. For this reason it was necessary to pay attention to the detailed methodical part and to explain in the discussion the advantages of the method preferred.

MATERIAL AND TREATMENT OF SOURCE DATA

The initial material for our analysis were the data published in the paper by **Mrciak, Daniel** and **Rosický** (1966) on gamasoid mites from 149 nests of *Clethrionomys glareolus* collected in all seasons of the year in forest biotopes of Vsetínské Beskydy (northern Moravia). A total of 5,609 gamasoid mites belonging to 42 species were found in these nests. The species with a low frequency of occurrence (i.e. occurrence in less than 5 nests) were eliminated and consequently 25 species given in Table 1 remained to be used in the analysis. A low limit of frequency was chosen because a low total value may be aggregated and thus be significant in any variant.

The collected nests were classed according to biotope, location, season and material used for the nest bedding. However, it was impossible to study all these factors, because classes with expected low frequencies would have arisen in this way. Consequently the influence of biotope and of nest location was chosen as the main object of our studies. The seasonal dynamics would have also to be studied with the regard to these basic categories, but the number of data did not allow that. This is why we present quantitative measures both for individual seasons of the year and always for the whole ecological variant. Total data were used for association analysis. A direct proof on the validity of this step is impossible in most species due to the number of data. Only in several more abundant species the criterion χ^2 could be used. In such cases the distribution of occupied and unoccupied nests changed between seasons only unsignificantly. The material of nest bedding was left unstudied.

The tables are arranged according to biotopes (forest, clearing) and according to nest location in harmony with the classification after Daniel, Mrciak and Rosický (1971). Four basic variants were created: forest – nests situated at the ground level and underground; clearing – nests situated at the ground level and underground. In classifying the data according to the season autumn and winter could not be clearly separated; strict calendar data would not correspond with actual conditions in nature.

METHODS

We used three types of methods describing acarocenosis in quantitative terms. They correspond to three levels of material treatment.

1. Quantitative properties of mites are described by three measures (F, D, A), whose definitions in the application for nest material are expressed by equations:

$$F = \frac{\text{number of nests occupied by a given mite species}}{\text{a total number of nests}}$$

$$D = \frac{\text{a total number of specimens of a given mite species}}{\text{a total number of nests}}$$

$$A = \frac{\text{a total number of specimens of a given mite species}}{\text{number of nests occupied by a given mite species}}$$

and consequently the relation $A \,.\, F = 100\, D$ holds true (Whitford 1949).

The measure F means "frequency", D means density (i.e. the average number of specimens in a unit of area or space, but in our case this unit is the nest). The measure A is close to the concept "abundance" introduced in plant ecology by Whitford (1949). It expresses the density: frequency ratio and may be defined as average density in occupied nests (Greig—Smith 1967). Although we consider this measure to be very useful, it is not currently used in animal ecology and the term abundance is understood rather as a synonymy for density. With regard to this terminological disunity in this paper only symbols for measures are used in the sense of the above equations.

These measures for particular species are given in Tables 1—4. By adding up the values $A + D + F$ a complex measure is created which characterizes the quantitative properties of species by a single value (Figs. 1—2).

2. Association analysis aims to evaluate the relation of each pair of species in the given group. This relation is measured by statistical dependence of both species. (We remind that it is a statistical and not causal dependence. A high statistical dependence of two species may be usually interpreted as a high degree of coincidence in ecological requirements, in other words, both species are equally influenced by environment.)

To assess the statistical dependence the contingency table combined with the criterion χ^2 or Fisher's exact test (Greig—Smith 1967, Vasilevich 1969 et al.) is mostly used. We do not consider this method to be appropriate for the solution of interspecific relationships (see Discussion). Therefore, we used affinity index derived by Fager (1957). It is based on the expected number of joint occurrences which is expressed, under assumption of the statistical independence, by $\frac{n_A n_B}{n_A + n_B}$, while n_A, n_B means the number of occurrences of the species A or B. The author considers only positive associations, consequently does not take any account of cases, when the observed number of joint occurrences I is lower than expected. The positive deviations from the expected value

$$t = \frac{(n_A + n_B)(2\,\mathrm{I} - 1)}{2n_An_B} - 1 \, . \, (n_A + n_B - 1)$$

are significant, if the value exceeds the critical value t at the level of 0.025: 0.005, 0.0005 respectively (one-sided deviation is tested).

All pairs of species in each of the four nest variants are evaluated by this method. For comparison with the method of contingency table we determined by both methods the associations in the whole sample of *C. glareolus* nests before analyzing the particular variants. The results are important only as far as they concern the choice of method of association analysis; particular variants differ from one another so much that their pooling is not warranted.

3. Construction of graphs. For studies of specific interrelationships methods and concepts of graph theory may be used which is a relatively young mathematical discipline. First some basic concepts should be explained. If we have two different elements x, y, then the set containing these two elements –

Table 1. Fundamental characteristics of the occurrence of Parasitiformes mites in the nests of *Clethrionomys glareolus*. (Forest biotope, underground nests.)

Mite		Spring (19 nests)			Summer (41 nests)			Autumn-Winter (27 nests)			Total (87nests)		
Symbol	Name	A*)	D	F	A	D	F	A	D	F	A	D	F
1	*Pergamasus* sp.	1.0	+	5	1.0	0.1	9	1.8	0.8	44	1.6	0.3	19
2	*Eugamasus kraepelini*	2.0	0.6	31	2.0	0.3	14	7.0	1.8	25	3.8	0.8	21
3	*Eugamasus remberti*	4.6	2.2	47	3.4	1.5	0.4	3.2	0.7	22	3.7	1.4	37
4	*Eugamasus* sp.	6.4	2.4	36	4.3	2.5	58	3.8	1.1	29	4.6	2.1	44
5	*Euryparasitus emarginatus*	6.9	5.5	78	9.1	7.7	85	6.9	3.6	51	8.1	5.9	73
6	*Cyrtolaelaps mucronatus*	2.7	1.8	68	9.7	3.1	31	3.4	0.6	18	5.7	2.0	35
7	*Cyrtolaelaps minor*	2.0	0.6	31	8.3	3.2	39	4.5	2.2	48	5.8	2.3	40
8	*Gamasellus silvestris*	2.0	0.1	5	0	0	0	1.3	0.2	14	1.4	0.1	5
9	*Veigaia nemorensis*	2.7	1.3	47	1.8	0.6	31	7.2	5.9	81	4.7	2.4	50
10	*Macrocheles pauperior*	1.0	+	+	1.3	0.2	19	2.5	0.7	29	1.8	0.4	19
11	*Geholaspis* sp.	1.0	+	+	0	0	0	1.3	0.1	11	1.3	0.1	+
12	*Proctolaelaps pygmaeus*	0.8	0.4	31	1.0	0.1	10	2.2	0.4	18	1.5	0.3	17
13	*Androlaelaps sardous*	0.8	0.4	31	1.8	0.2	10	2.0	0.2	11	1.6	0.2	14
14	*Hypoaspis heselhausi*	1.6	0.7	42	1.0	+	+	2.7	0.6	22	1.9	0.4	18
15	*Eulaelaps stabularis*	6.6	4.9	73	3.8	1.9	48	2.2	0.8	37	4.3	2.2	50
16	*Haemogamasus horridus*	5.3	2.8	52	4.9	1.9	39	3.5	0.3	7	4.7	1.6	32
17	*Haemogamasus nidi*	25.3	18.6	73	4.1	1.7	41	4.9	1.3	25	12.1	5.3	43
18	*Haemogamasus hirsutus*	10.5	6.1	57	6.1	2.5	41	3.7	0.4	11	7.5	2.7	35
19	*Haemogamasus hirsutosimilis*	5.0	0.8	15	4.4	0.5	12	1.0	0.2	11	3.8	0.5	12
20	*Hirstionyssus isabellinus*	1.0	+	+	0	0	0	1.7	0.2	18	1.0	0.1	6
21	*Myonyssus rossicus*	1.3	0.3	21	3.0	0.1	+	0	0	0	1.8	0.1	6
22	*Pergamasus crassipes*	1.0	+	+	1.0	1.0	+	1.7	0.3	18	1.4	0.1	8
23	*Cyrtolaelaps* sp.	2.8	0.9	31	1.8	0.2	9	0	0	0	2.4	0.3	11
24	*Veigaia kochi*	0	0	0	1.7	0.1	7	1.7	0.2	11	1.7	0.1	6
25	*Geholaspis longispinosus*	2.5	0.3	10	3.0	0.1	+	1.0	0.1	7	2.0	0.1	5

+ Value lower than 0.05 (5 %).

*) For definition of measures A, D, F see p. 69. (Applies also to Tables 2–4.)

(and no others) is designated $\{x, y\}$ and called unordered pair of elements x, y. It does not matter in which order the elements x, y are written and read $\{x, y\} = \{y, x\}$. Both elements in the pair are symmetrical. If a set A is given, then the set containing as elements all pairs of elements from the set A is designated $P_2(A)$. Unoriented finite graph is a structure which is given by the set A having elements called vertices and by some subset $H \leq P_2(A)$ having elements called edges. If the pair x, y is an element of the set H, we say that vertices $\{x, y\}$ are connected in the graph by this edge, or, that $\{x, y\}$ are terminal vertices of edge $\{xy\}$. Graphs are currently depicted by means of figures where the vertices are shown as points in plane or eventually in space and the edges are presented as abscissae connecting the pairs of vertices. In our case the objects of our studies (i.e. species) may be represented as vertices and those pairs of vertices among which significant associations have been found may be connected by edges. Unoriented graphs, as described above, are quite sufficient because significant association as a statistical concept is symmetrical with regard to both objects.

For our purposes it is useful to define the associated set in the group of objects (species) studied as a definite group of elements which are either directly connected by the edge or between each two a way exists connecting them by several edges. Consequently, the biocenosis is an associated set of species relating to a definite group of biotopes. Two methods were used for illustration: initial matrices of associations (Figs. 4—8) on one hand, and graphic diagram used in plant ecology (Figs. 9—14) on the other. The location of vertices in graphs is empirically determined in a way excluding all doubts as to which vertices are connected by particular edges. To make mutual comparison possible the same location of vertices is kept in all figures. The species are arranged and designated by numerical symbols, 1—14 indicating carnivores, sapro-, copro- and necrophagous organisms, while

Table 2. Fundamental characteristics of the occurrence of Parasitiformes mites in the nests of *Clethrionomys glareolus.* (Forest biotope, nests situated at the ground level.)

Mite		Spring (9 nests)			Summer (7 nests)			Autumn-Winter (28 nests)			Total (44 nests)		
Symbol	Name	A	D	F	A	D	F	A	D	F	A	D	F
1	*Pergamasus* sp.	0	0	0	0	0	0	2.0	0.6	28	8.0	0.4	18
2	*Eugamasus kraepelini*	1.3	0.4	33	2.7	1.1	42	4.5	1.1	0.3	3.3	1.0	29
3	*Eugamasus remberti*	1.4	0.8	55	6.5	1.9	28	2.8	0.5	17	2.8	0.8	27
4	*Eugamasus* sp.	4.3	1.4	33	2.3	1.0	42	3.3	0.7	21	3.3	0.9	27
5	*Euryparasitus emarginatus*	3.7	2.9	77	6.7	6.7	100	2.8	1.6	57	3.9	2.7	68
6	*Cyrtolaelaps mucronatus*	5.8	3.9	66	8.3	3.6	42	2.2	0.7	32	3.3	1.4	40
7	*Cyrtolaelaps minor*	2.3	0.8	33	2.0	0.3	14	2.2	0.6	28	2.3	0.6	27
8	*Gamasellus silvestris*	5.0	1.1	22	0	0	0	1.0	—	+	3.7	0.3	6
9	*Veigaia nemorensis*	3.2	2.1	66	3.0	1.3	42	5.2	2.4	0.5	4.4	2.2	50
10	*Macrocheles pauperior*	4.0	0.4	11	0	0	0	1.6	0.4	25	1.9	0.3	18
11	*Geholaspis sp.*	0	0	0	0	0	0	0	0	0	0	0	0
12	*Proctolaelaps pygmaeus*	3.0	0.3	11	0	0	0	2.6	0.5	17	2.7	0.4	13
13	*Androlaelaps sardous*	1.0	0.1	11	0	0	0	3.5	0.3	7	2.7	0.2	6
14	*Hypoaspis heselhausi*	0	0	0	0	0	0	1.5	0.1	7	1.5	0.1	+
15	*Eulaelaps stabularis*	11.9	11.9	100	2.0	1.1	57	3.9	1.0	25	7.1	3.2	45
16	*Haemogamasus horridus*	2.0	0.2	11	1.8	1.0	57	4.0	1.0	25	1.3	0.4	27
17	*Haemogamasus nidi*	2.5	1.7	66	20.5	5.9	28	27.7	6.0	21	15.9	5.0	31
18	*Haemogamasus hirsutus*	3.4	1.9	55	2.3	1.3	57	16.0	3.4	21	4.9	2.8	56
19	*Haemogamasus hirsutosimilis*	1.0	0.1	11	1.0	0.1	14	4.2	0.8	17	3.3	0.5	15
20	*Hirstionyssus isabellinus*	12.0	1.3	11	0	0	0	1.3	0.2	14	3.4	0.4	11
21	*Myonyssus rossicus*	0	0	0	0	0	0	3.0	0.3	10	3.0	0.2	6
22	*Pergamasus crassipes*	0	0	0	0	0	0	1.3	0.1	10	1.3	0.1	6
23	*Cyrtolaelaps* sp.	0	0	0	0	0	0	1.0	0.1	7	1.0	+	+
24	*Veigaia kochi*	0	0	0	0	0	0	0	0	0	0	0	0
25	*Geholaspis longispinosus*	1.0	0.1	11	0	0	0	1.0	+	+	1.0	+	+

+ Value lower than 0.05 (5 %).

15—20 represent species with a differently developed degree of hematophagia. This arrangement facilitated to increase considerably the information value of the documentary material, especially the matrices. The designation of species applies to matrices, all diagrams as well as tables (in which the species 21—25 were added later because they had fulfilled the frequency limit but had not yielded positive results in the association analysis).

RESULTS

I. QUANTITATIVE MEASURES OF MITE OCCURRENCE IN THE NESTS OF *C. GLAREOLUS*

A total of 42 species of gamasoid mites were found in the nests. Tables 1—4 include 25 species whose occurrence frequency is in harmony with the requirement formulated in the methodical part. Out of these 25 species thirteen are associated at a different

Table 3. Fundamental characteristics of the occurrence of Parasitiformes mites in the nests of *Clethrionomys glareolus*. (Forest clearing, underground nests.)

Mite		Spring (6 nests)			Autumn-Winter (2 nests)			Total (8 nests)		
Symbol	Name	A	D	F	A	D	F	A	D	F
1	*Pergamasus* sp.	1.0	0.2	16	1.5	1.5	100	1.3	0.5	37
2	*Eugamasus kraepelini*	1.7	0.8	50	0	0	0	1.6	0.6	37
3	*Eugamasus remberti*	5.0	0.8	16	1.0	0.5	50	3.0	0.8	25
4	*Eugamasus* sp.	2.3	1.2	50	8.0	4.0	50	3.8	1.9	50
5	*Euryparasitus emarginatus*	8.7	4.3	100	17.5	17.5	100	7.6	7.6	100
6	*Cyrtolaelaps mucronatus*	1.0	0.5	50	1.0	0.5	50	1.0	0.5	50
7	*Cyrtolaelaps minor*	1.5	0.5	33	4.0	2.0	50	2.3	0.9	37
8	*Gamasellus silvestris*	0	0	0	0	0	0	0	0	0
9	*Veigaia nemorensis*	6.3	3.2	50	3.0	1.5	50	5.5	2.8	50
10	*Macrocheles pauperior*	0	0	0	0	0	0	0	0	0
11	*Geholaspis* sp.	1.0	0.2	16	1.0	0.5	50	1.0	0.3	25
12	*Proctolaelaps pygmaeus*	0	0	0	2.0	1.0	50	2.0	0.3	12
13	*Androlaelaps sardous*	3.0	0.5	16	1.0	0.5	50	1.5	0.4	25
14	*Hypoaspis heselhausi*	0	0	0	0	0	0	0	0	0
15	*Eulaelaps stabularis*	6.7	6.7	100	8.5	8.5	100	7.1	7.1	100
16	*Haemogamasus horridus*	10.0	3.3	33	0	0	0	10.0	2.5	25
17	*Haemogamasus nidi*	42.8	28.5	66	0	0	0	42.7	21.4	50
18	*Haemogamasus hirsutus*	1.5	7.7	66	0	0	0	11.5	5.8	50
19	*Haemogamasus hirsutosimilis*	4.0	0.7	16	0	0	0	4.0	0.5	12
20	*Hirstionyssus isabellinus*	0	0	0	0	0	0	0	0	0
21	*Myonyssus rossicus*	0	0	0	0	0	0	0	0	0
22	*Pergamasus crassipes*	0	0	0	0	0	0	0	0	0
23	*Cyrtolaelaps* sp.	2.0	0.3	16	0	0	0	2.0	0.3	12
24	*Veigaia kochi*	0	0	0	0	0	0	0	0	0
25	*Geholaspis longispinosus*	1.0	0.2	16	0	0	0	1.0	0.1	12

degree and consequently belong to at least one of the four communities studied. Seventeen species which occurred occasionally and could not be therefore included either in tables or in graphs, are as follows: *Veigaia transisalae*, *V. cerva*, *Cyrtolaelaps* sp., *Ologamasus* sp., *Macrocheles punctoscutatus*, *M. montanus*, *Geholaspis mandibularis*, *G. ponticus*, *Eviphis oestrinus*, *Lasioseius remiger*, *Androlaelaps* sp., *Hypoaspis* sp., *Laelaps hilaris*, *L. clethrionomydis*, *Myonyssus ingricus*, *Hirstionyssus musculi* and *H. carnifex*.

In Figs. 1 and 2 quantitative conditions of particular mite species are graphically demonstrated by means of the measure A + D + F for 4 basic nest variants without seasonal differentiation. In all four cases two groups of species with relatively high values are pronounced and the absolute height of columns in graph differs depending on the biotope and nest location. The first group is represented by *Euryparasitus emarginatus* (5) and species closely related to it. The second group is represented by *Eulaelaps stabularis* (15) and members of the genus *Haemogamasus* (16—18), namely *H. nidi* (17).

2. INTERRELATIONSHIPS OF MITES IN THE NESTS OF *C. GLAREOLUS*

The interrelationships following from the association analysis are given in Figs. 3—13. In the first one (Fig. 3) attention is paid only to the species, in the language of the

Table 4. Fundamental characteristics of the occurrence of Parasitiformes mites in the nests of *Clethrionomys glareolus*. (Forest clearing, nests situated at the ground level.)

Mite		Spring (3 nests)			Summer (4 nests)			Autumn-Winter (3 nests)			Total (10 nests)		
Symbol	Name	A	D	F	A	D	F	A	D	F	A	D	F
1	*Pergamasus* sp.	0	0	0	1.0	0.3	25	1.0	0.3	33	1.0	0.2	20
2	*Eugamasus kraepelini*	2.0	0.7	33	0	0	0	2.0	1.3	66	2.0	0.6	30
3	*Eugamasus remberti*	4.5	3.0	66	1.7	1.3	75	6.3	6.3	100	4.1	3.3	80
4	*Eugamasus* sp.	3.0	1.0	33	3.7	2.8	75	10.7	10.7	100	6.6	4.6	70
5	*Euryparasitus emarginatus*	2.0	2.0	100	12.0	9.0	75	11.5	7.7	66	8.1	6.5	80
6	*Cyrtolaelaps mucronatus*	27.5	18.3	66	20.5	10.3	50	7.5	5.0	66	18.5	11.1	60
7	*Cyrtolaelaps minor*	1.0	0.3	33	4.0	2.0	50	11.5	7.7	66	1.0	0.3	33
8	*Gamasellus silvestris*	0	0	0	0	0	0	0	0	0	0	0	0
9	*Veigaia nemorensis*	1.0	0.3	33	1.0	0.5	50	10.3	10.3	100	5.7	3.4	60
10	*Macrocheles pauperior*	1.0	0.3	33	3.0	0.8	25	0	0	0	2.0	0.4	20
11	*Geholaspis* sp.	0	0	0	0	0	0	2.0	1.3	66	2.0	0.4	20
12	*Proctolaelaps pygmaeus*	0	0	0	0	0	0	0	0	0	0	0	0
13	*Androlaelaps sardous*	0	0	0	6.0	1.3	25	0	0	0	6.0	0.6	10
14	*Hypoaspis heselhausi*	0	0	0	2.0	1.0	50	4.7	4.7	100	3.6	1.8	50
15	*Eulaelaps stabularis*	42.3	42.3	100	5.1	5.1	100	4.7	4.7	100	16.2	16.2	100
16	*Haemogamasus horridus*	2.0	1.3	66	17.0	8.5	50	5.0	1.7	33	8.6	4.3	50
17	*Haemogamasus nidi*	93.0	93.0	100	1.5	0.8	50	0	0	0	56.4	28.2	50
18	*Haemogamasus hirsutus*	6.5	4.3	66	5.3	4.0	0.8	4.0	1.3	33	5.5	3.3	60
19	*Haemogamasus hirsutosimilis*	1.0	0.3	33	0	0	0	0	0	0	1.0	0.1	10
20	*Hirstionyssus isabellinus*	13.0	4.3	33	0	0	0	0	0	0	13.0	1.3	10
21	*Myonyssus rossicus*	0	0	0	0	0	0	0	0	0	0	0	0
22	*Pergamasus crassipes*	0	0	0	0	0	0	0	0	0	0	0	0
23	*Cyrtolaelaps* sp.	1.0	0.7	66	0	0	0	0	0		1.0	0.2	20
24	*Veigaia kochi*	0	0	0	0	0	0	0	0	0	0	0	0
25	*Geholaspis longispinosus*	0	0	0	2.0	0.5	25	0	0	0	2.0	0.2	10

graph theory, to vertices. The Fig. 3 therefore can inform about species composition only which is, however, quite uniform in some cases. As in the graphical demonstration of the measure A + A + F, there exist two groups around *E. emarginatus* (5) on one hand and around *E. stabularis* and representatives of the genus *Haemogamasus* (15—18) on the other. The monotony is stressed by the fact that in the main no deviations in the significance levels exist for associations. The information provided by the diagram brings no new results as concerns the previous treatment of material (Mrciak et al. 1966). On its basis it might be ostensibly concluded that there is no difference among the communities of gamasoid mites of the four nest variants studied.

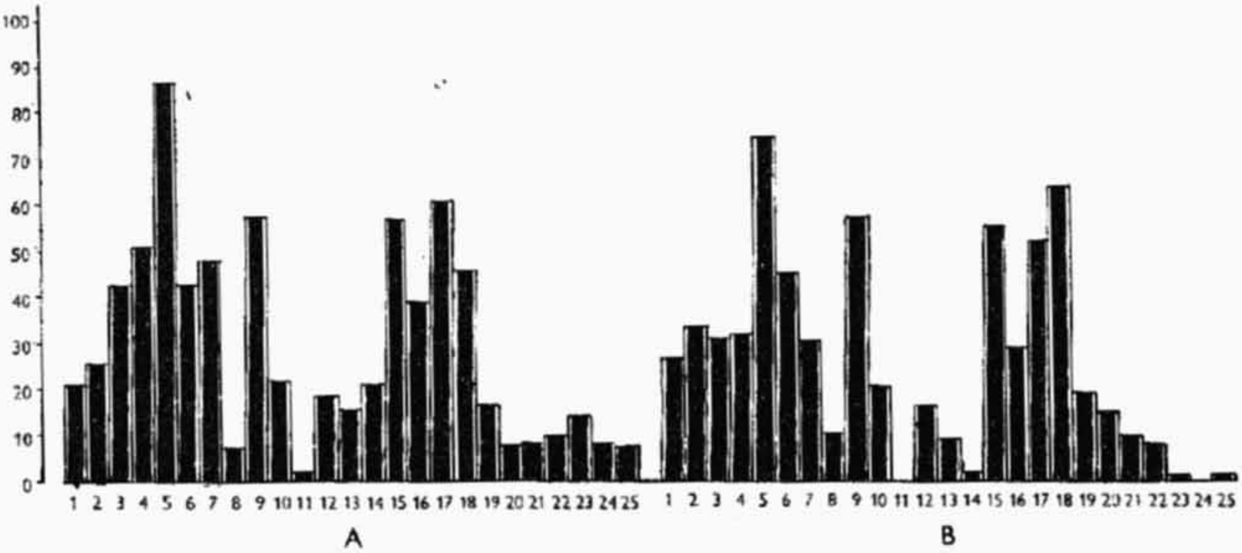


Fig. 1. Derived measure (A + D + F) for particular mite species in the nests of *Clethrionomys glareolus* (forest biotope: A — nests situated underground; B — nests situated on the ground). Vertical axis bears numerical values A + D + F, horizontal axis numerical symbols of particular mite species (in accordance with Tables 1—4).

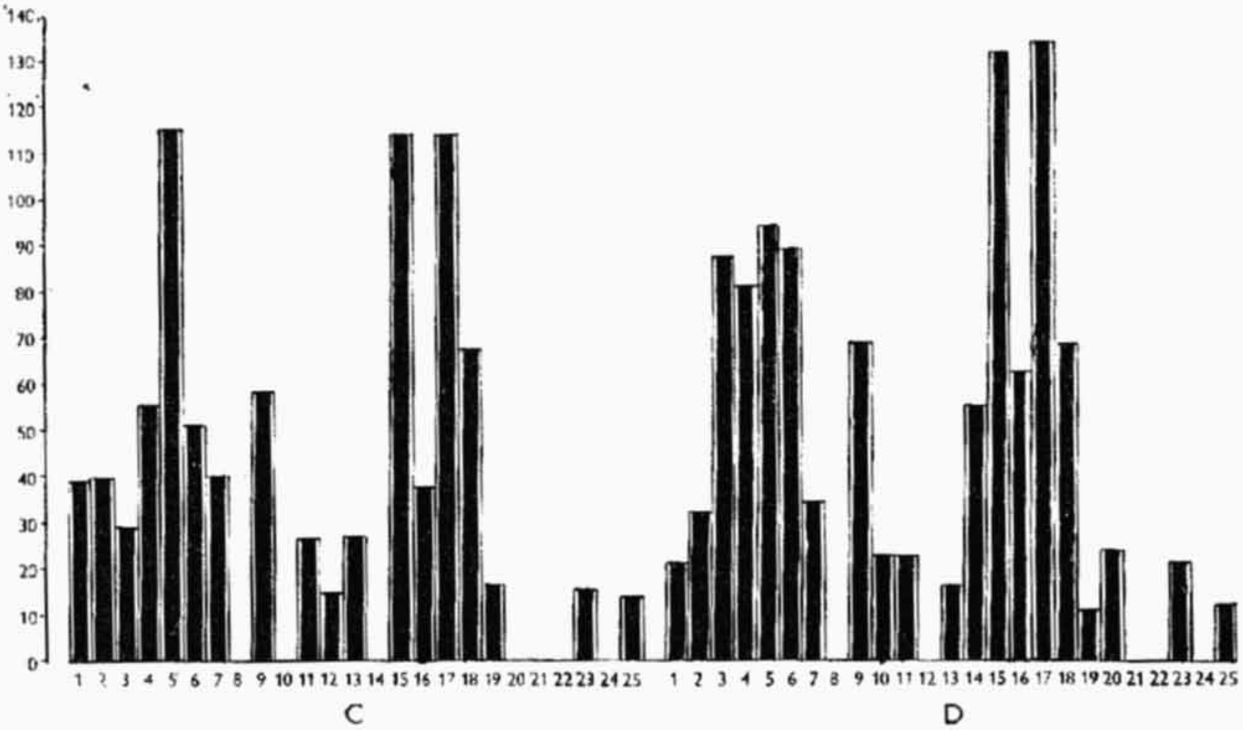
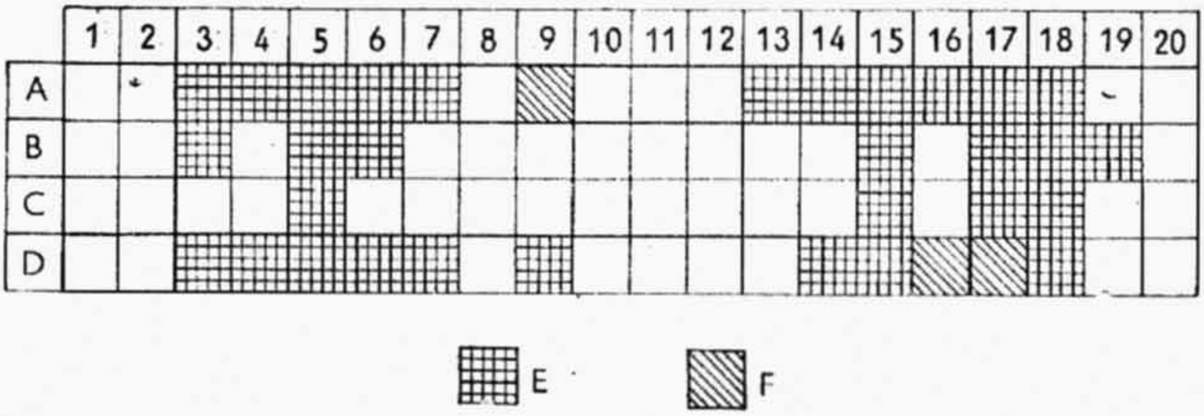


Fig. 2. Derived measure (A + D + F) for particular mite species in the nests of *Clethrionomys glareolus* (clearing biotope: A — nests situated underground; B — nests situated on the ground). Vertical axis bears numerical values A + D + F, horizontal axis numerical symbols of particular mite species (in accordance with Tables 1—4).

A different picture presents itself if attention is directed to edges, i. e. relations (in our case statistically significant associations among species). Figs. 4—7 give this information in the form of matrices for particular nest variants, from which the mutual difference of ecological conditions clearly arises. The order of species in matrices is the same as that in Tables 1—4 and is kept in all cases. It is therefore possible to compare, to subtract the differences and express them in numbers in the table giving a survey of the number of vertices and edges (i.e. species and their relations) in particular nest variants (Table 5).

The number of edges (relations) is certainly a very important indicator because it shows closer relationships of mites among them and the higher degree in the organization of nidocenosis. In our concept analyzed in the Discussion it may be said that at a higher number of edges the ecological space of nidocenosis is more defined.



	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
A			▦	▦	▦	▦	▦		▨				▦	▦	▦	▦	▦	▦		
B			▦		▦	▦									▦		▦	▦	▦	
C					▦										▦		▦	▦		
D			▦	▦	▦	▦	▦		▦					▦	▦	▨	▨	▦		

▦ E ▨ F

Fig. 3. Species composition of Gamasoidea mites in the nests of *Clethrionomys glareolus*. Four variants according to biotope and nest location: A — forest (underground nests); B — forest (nests at the ground level); C — clearing (nests at the ground level); D — clearing (underground nests). Numerical symbols of particular mite species are in accordance with Tables 1—4. E — significance level of association 0.05; F — significance level 0.10.

If we compare the forest nests having different location, we see clearly that the nests situated underground predominate as concerns the number of vertices and edges; it is especially apparent in edges with a high association level. In nests from the clearing (situated underground) no comparison is possible because the nests from the summer season (see Table 3) are missing. The clearing variant (at the ground level) also contains a small number of nests. The size of the group is certainly important and cannot be overlooked, but this variant with relatively small nest group still has a large number of associations. While studying the matrices in detail we see that there are differences not only in numbers, but also in the quality of vertices and edges. There are relatively

Table 5. A survey of numbers of vertices and edges in graphs illustrating particular nest variants of *C. glareolus*

Biotope – nest location	Number of nests investigated	Number of vertices investigated	Number of edges at the level of	
			0.001–0.05	0.10
Forest – underground	87	10	17	3
Forest – at the ground level	44	7	8	2
Clearing – underground	8	4	2	—
Clearing – at the ground level	10	11	16	9

few vertices in particular variants, but plenty of different edges. In other words, the identical mite species under varied conditions of biotope and nest location differ in their interrelationships.

The nests of the forest (underground) variant (Fig. 4) reveal three pronounced groups of edges (i.e. positive associations) at the highest level 0.001. The first group connects species 3—6 (i.e. *Eugamasus remberti*, *Eugamasus* sp., *Euryparasitus emarginatus* and *Cyrtolaelaps mucronatus*). The second group includes species 15—18 (i.e. *Eulaelaps stabularis*, *Haemogamasus horridus*, *H. nidi* and *H. hirsutus*). The third group of associations connects the first and second group and namely the species *E. emarginatus* and *Eugamasus* sp. on one hand and *E. stabularis* on the other.

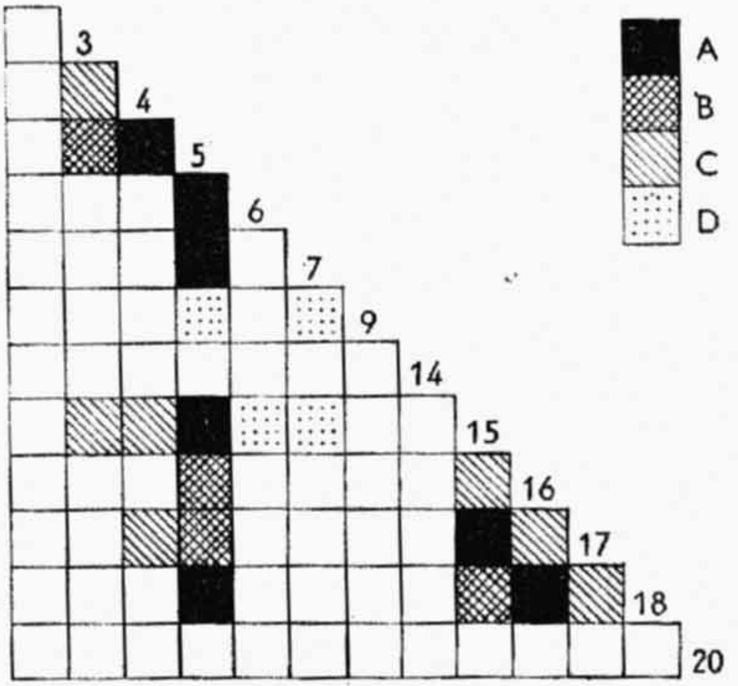


Fig. 4. Matrix of interspecific associations of gamasoid mites in the nests of *Clethrionomys glareolus* (forest — underground nests). Numerical symbols of particular mite species are in accordance with Tables 1—4. A — association on level of 0.001; B — association on level of 0.01; C — association on level of 0.05; D — association on level 0.10. This legend also applies to Figs. 5—8.

In nests of the forest (at the ground level) variant (Fig. 5) there are hints of all three groups, but they are very attenuate both as for the number of edges and for the significance level of their associations. In the clearing (at the ground level) variant the positive associations are numerous, but at a low level, diffusely dispersed all over the matrix. No groups come into consideration. The species designated by lower numeral symbols are associated with one another rather than the nest parasites themselves. The results obtained in both biotopes correspond partly with the fact that *C. glareolus* is primarily a forest animal and partly that the nests situated on the ground have less definitely formed conditions of environment and are more exposed to the contact with the surrounding mite fauna in the leaf litter. This influence is more apparent in the nests from the clearing (at the ground level).

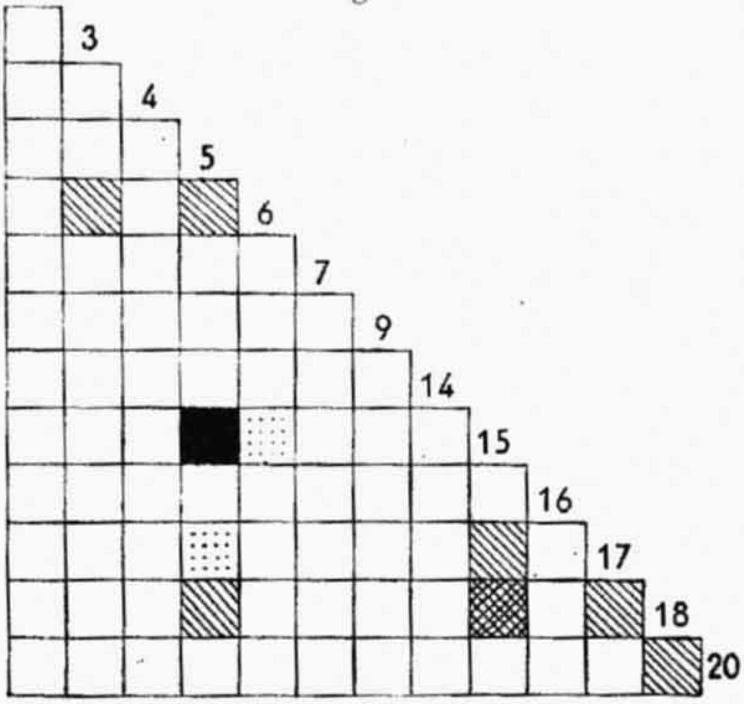


Fig. 5. Matrix of interspecific associations of gamasoid mites in the nests of *Clethrionomys glareolus* (forest — nests situated at the ground level). For explanations see Fig. 4.

The nature of material did not allow to study by this method the influence of season, which will certainly supplement previous conclusions in treatment of other materials. Also further information included in matrices will be able to be used after comparison with other material (e.g. the nests of some other forest animals, nests from other biotopes etc.).

Although we are well aware on the basis of the conclusions presented that the nests from different variants cannot be pooled and evaluated as a whole, we did so in Fig. 8 which gives a matrix for the whole group studied aiming especially to illustrate the difference in results based on the assessment of pairs of species by means of contingency table (the right hand upper half) and by method of Fager's affinity index (the left hand bottom half). The relation of these two methods is discussed in detail below. As for the result proper, it may be stated that all edges of the total matrix are contained in some partial matrix of particular variants. An exception is the edge 1—9 which is not included in any partial diagram, but in both variants of forest nests reaches the affinity index of values which are close to the significance limit. (The diagrams 13 and 14 correspond to the total matrix.)

The results presented lead to the following conclusion: if we regard the biocenosis as a group of species directly or indirectly associated, only 13 species included in matrices and diagrams make the nest community of gamasoid mites in the particular case studied. Although other species (29 in number) occurred in the nests, they were virtually a part of different communities (free-living edaphic ones on one hand or parasitic somatic (hair) mites on the other). Such an analysis consequently leads to a precise delimitation of the concept of nest community and its actual contents, which may be of practical importance in possible epidemiological considerations, when a large initial number of species found is necessary for the assessment.

Another form of demonstrating the groups of associated species is the empirically derived association diagram where vertices are depicted in the way close to a layman's idea

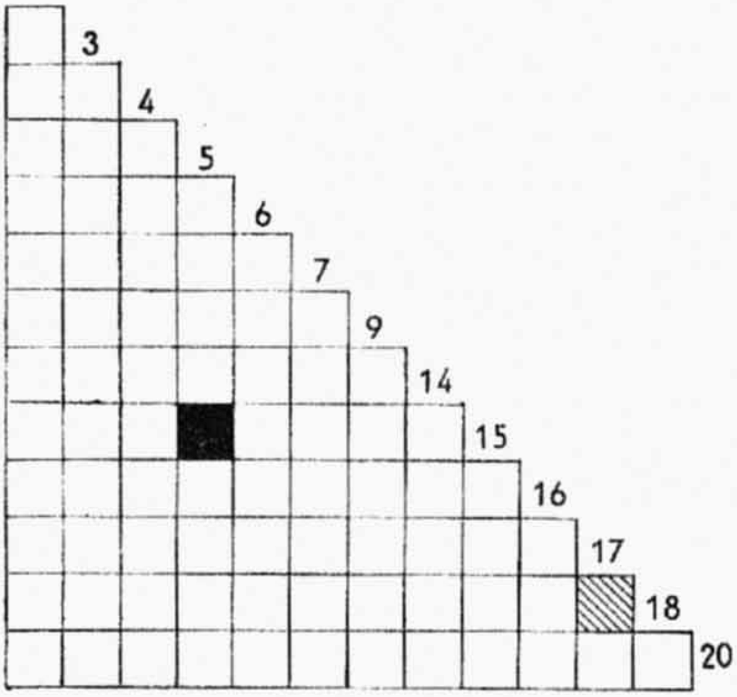


Fig. 6. Matrix of interspecific associations of gamasoid mites in the nests of *Clethrionomys glareolus* (clearing — underground nests). For explanations see Fig. 4.

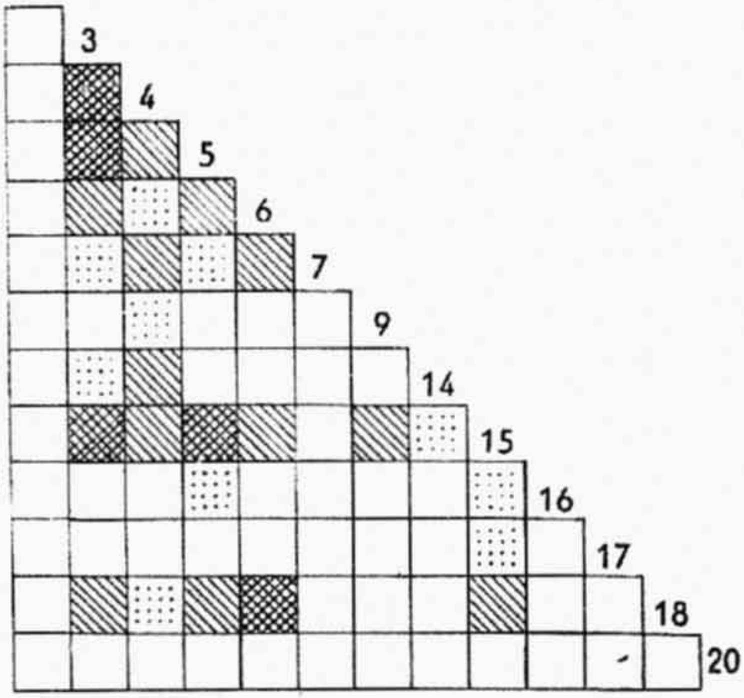


Fig. 7. Matrix of interspecific associations of gamasoid mites in the nests of *Clethrionomys glareolus* (clearing — nests situated at the ground level). For explanations see Fig. 4.

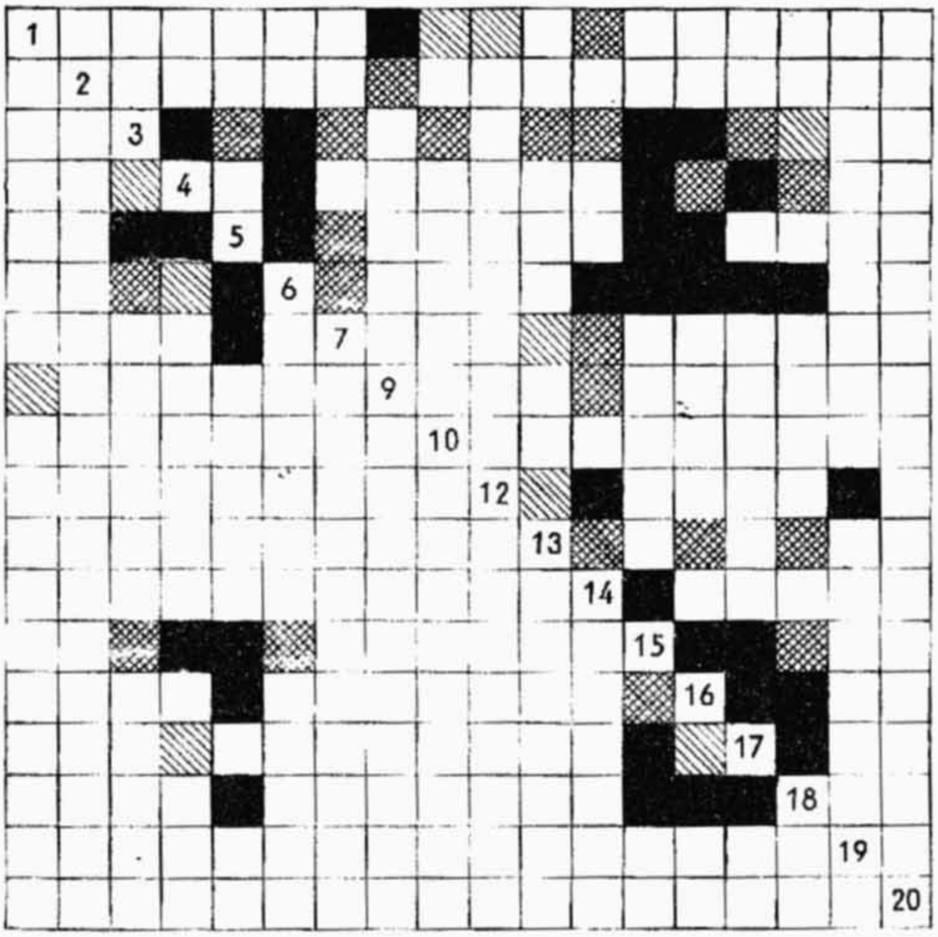


Fig. 8. Matrix of interspecific associations of gamasoid mites in the nests of *Clethrionomys glareolus* (total group studied). The right-hand upper half — results based on the evaluation of pairs of species by contingency table. The left-hand bottom half — results based on Fager's affinity index. For further explanations see Fig. 4.

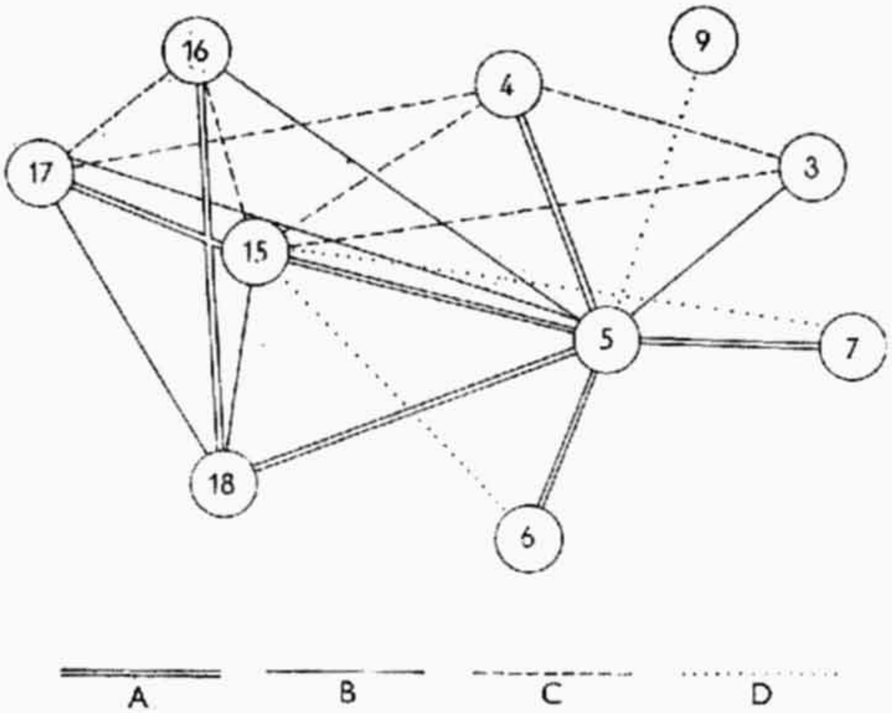


Fig. 9. Association diagram of gamasoid mites in the nests of *Clethrionomys glareolus* (forest — underground nests). Vertices include numerical symbols of particular mite species in accordance with Tables 1—4. A — edges on the level of 0.001; B — edges on the level of 0.01; C — edges on the level of 0.05; D — edges on the level of 0.10. This legend also applies to Figs. 10—14.

of knots in a net and lines representing edges (Figs. 9—14). These association diagrams may be well used for considerations about the circulation of pathogenous agent in the nest community etc.

If we assess the results from the aspect of particular mite species, their biocenotic characteristics is given in Table 6. It shows that the most associated species was *Eulaelaps stabularis* which fact is in full harmony with the results of a field experiment (Daniel 1970) in which its dependence on the nest as well

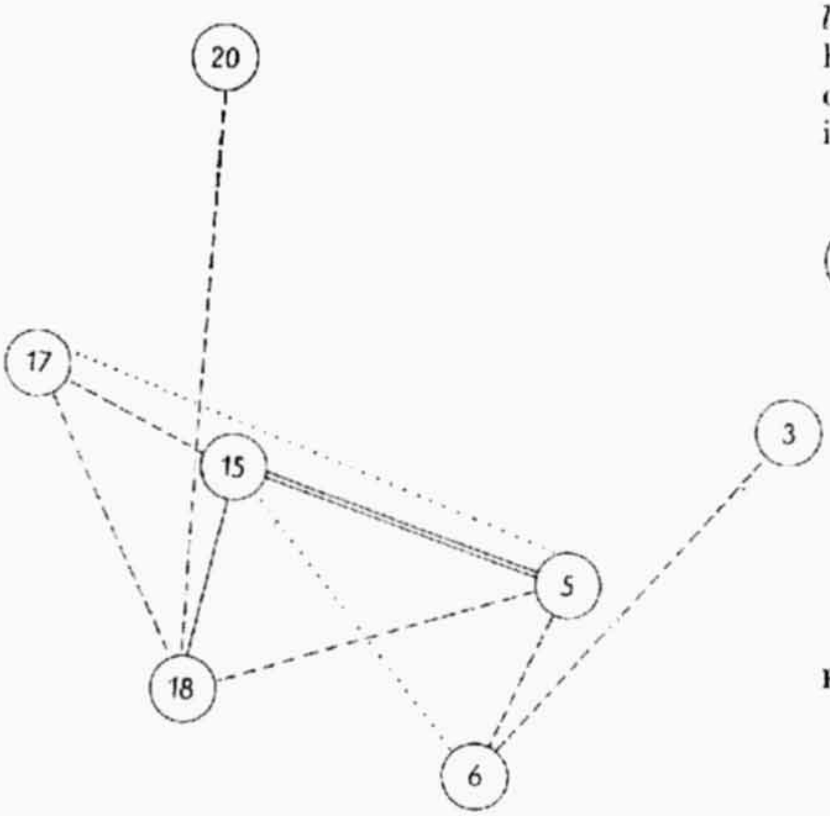


Fig. 10. Association diagram of gamasoid mites in the nests of *Clethrionomys gareolus* (forest — nests situated at the ground level). For further explanations see Fig. 9.

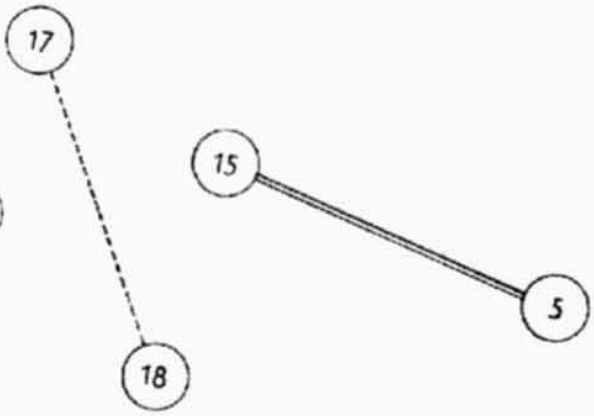


Fig. 11. Association diagram of gamasoid mites in the nests of *Clethrionomys glareolus* (clearing — underground nests). For further explanations see Fig. 9.

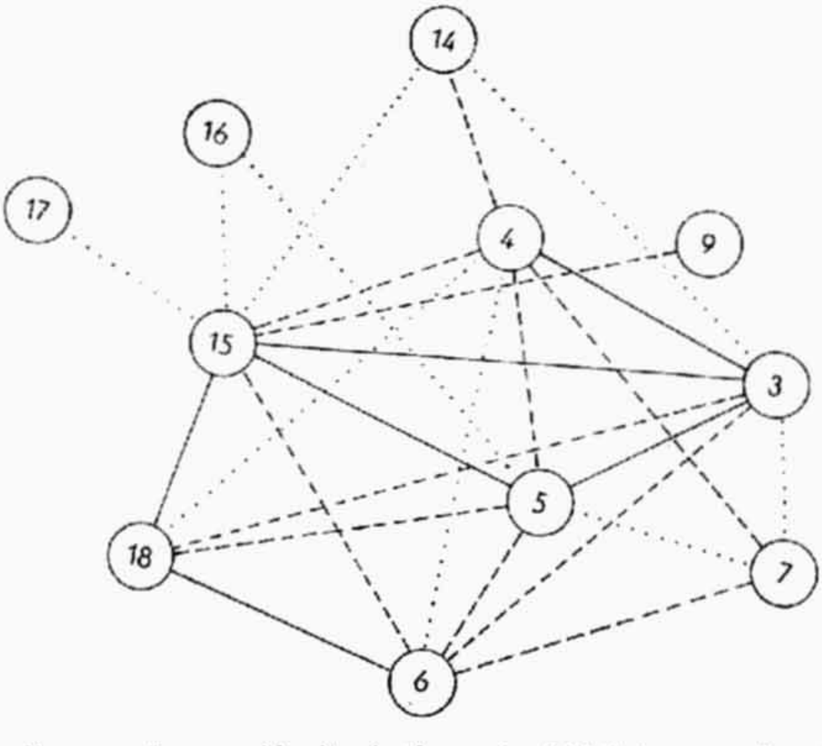


Fig. 12. Association diagram of gamasoid mites in the nests of *Clethrionomys glareolus* (clearing — nests situated at the ground level). For further explanations see Fig. 9.

Table 6. Biocenological characteristics of associated species of gamasoid mites from nests of *C. glareolus* (Digits indicate a total number of positive associations at the level of 0.001, 0.01, 0.05. Digits in brackets indicate number of positive associations at the level of 0.10)

Biotope – nest location	Numerical symbols of particular mite species *Gamasoidea*											
	3	4	5	6	7	9	14	15	16	17	18	20
Forest underground	3	4	8 (1)	1 (1)	1 (2)	(2)		6 (2)	4	5	4	
Forest – at the ground level	1		3 (1)	2 (1)				3 (1)		2 (1)	4	1
Clearing – underground			1					1		1	1	
Clearing at the ground level	5 (2)	5 (3)	5 (2)	5 (1)	2 (2)	1 (1)	1 (2)	6 (3)	0 (2)	0 (1)	4 (1)	

as its wide ecological amplitude was demonstrated. According to the number of associations *Euryparasitus emarginatus*, *Eugamasus* sp., *Haemogamasus hirsutus*, *H. nidi* and *H. horridus* followed next.

DISCUSSION

Methods used in this work have not been so far applied in the studies of nidocenoses. We therefore consider it expedient to discuss some questions connected with their utilization in this respect.

The quantitative properties of mites in nests are sufficiently described by three measures (F, D, A). Their choice is determined by the character of the data studied. Most species have a markedly contagious distribution. Some nests reveal very high

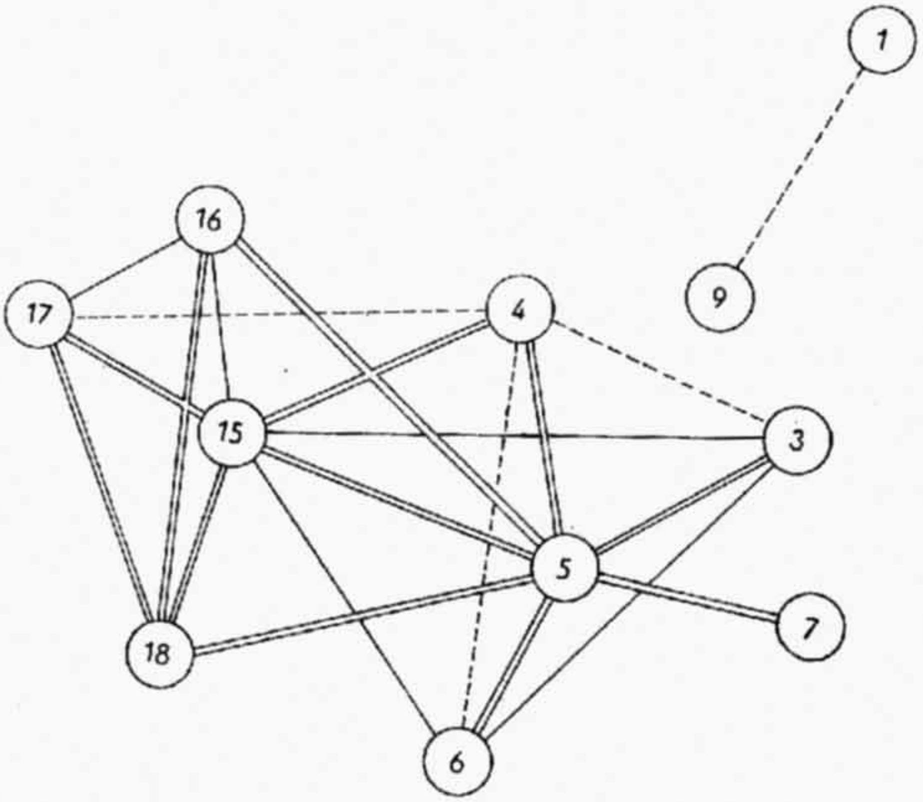


Fig. 13. Association diagram of gamasoid mites in the nests of *Clethrionomys glareolus* (total group studied). Results are based on the evaluation of pairs of species by Fager's affinity index. For further explanations see Fig. 9.

frequencies, which do not correspond with the assumption that the probability of mite occurrence in nests is the same. Also the mean: variance ratio highly exceeds the value 1. Only in one or two cases the whole group could be differentiated in two parts, the empty and non-empty, which follows Poisson distribution.

Under such conditions a mere perfunctory comparison of these three measures offers a clear view not only of the quantity of the species, but also of the degree of aggregation. For the convenience of prompt information three different values may be disadvantageous. That is why we tried to form the derived measure obtained by adding up the values A + D + F (Figs. 1—2). This measure is similar to Curtis's "importance value" (Greig—Smith 1967). It differs partly by using density instead of the so-called dominance, but especially in the fact that the values calculated for particular species were used without transformation to the percentual total value of all species. The derived measure of this type is quite arbitrary and therefore suitable only for illustrating data and offering prompt information about the nature of the species. A more serious assessment and comparison of particular nest variants should result from quantitative analysis for which suitable methods must be found.

Analysis of interspecific relationships in larger groups of species usually found in nests is a considerably complicated case. As a rule, the quantitative data must be reduced to qualitative ones (presence—absence) as a large number of zero values prevents the calculation of correlation coefficient. However, even if qualitative data are used, there are many difficulties of theoretical character.

Most frequently 2×2 contingency table is used, having the following categories: *a* — both species present; *b* — the first species present, the second one absent; *c* — the

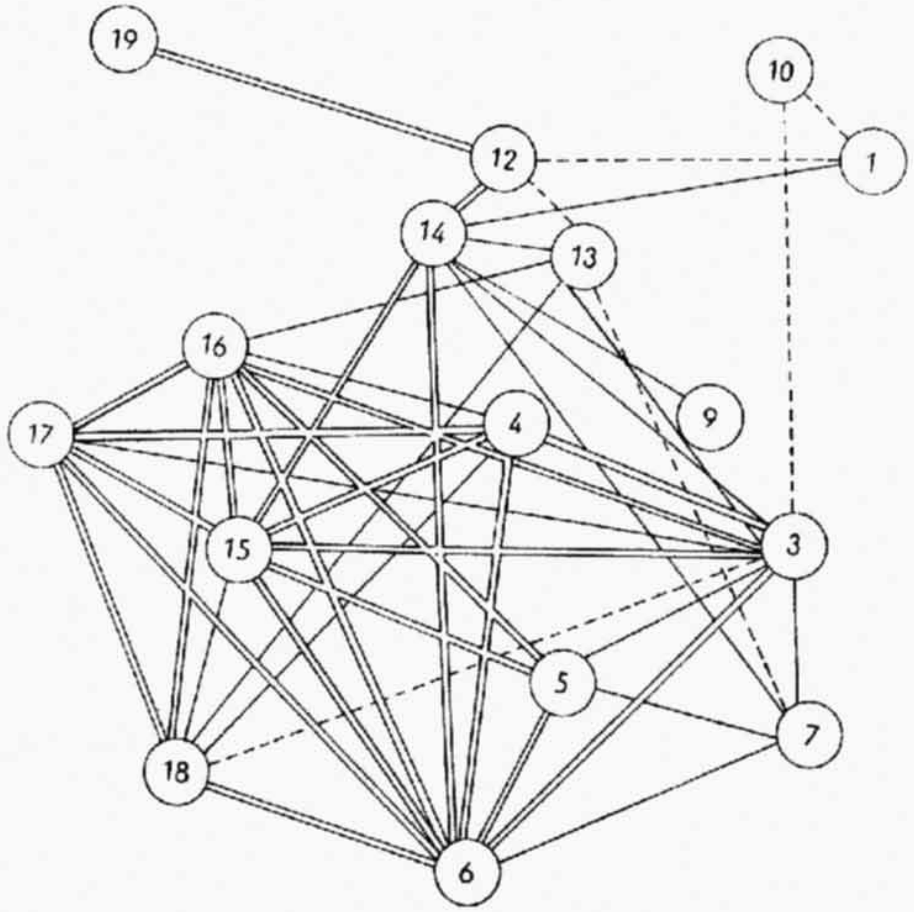


Fig. 14. Association diagram of gamasoid mites in the nests of *Clethrionomys glareolus* (total group studied). Results are based on the evaluation of pairs of species by contingency table. For further explanations see Fig. 9.

first species absent, the second one present; d — both species absent. These data are evaluated by the criterion χ^2 or Fisher's exact test. The results are not always satisfactory. The concept of independence included in this method is rather different from the intuitive notion employed by ecologists. Undesirable above all is a strong influence exerted upon the result by the quantity in the fourth cell (both species absent). If both species are frequent and present in almost all sampling units (a value in cell d is very low), these species appear to be quite independent. Vice versa, in rare species the cell d contains a large number of basic units and the dependence is too high to be true. These phenomena were met with during our studies and also in papers of different authors. The first case is quite frequent in the studies of e.g. interspecific relationships in plants: the dominant species cannot be assessed because the method of contingency table leads to unacceptable conclusion about mutual independence of dominants and other species. The second of the mentioned cases became markedly manifest in our material. This is why the diagram of interspecific relationships based on the contingency table (Fig. 8) reveals a high number of associations, of which many are unlikely. They are, for example, the pairs 12—15 and 12—20, where 115 (121) nests respectively out of the total number 150 goes to cell d. The resulting positive association is caused by the high value in cell d.

These reasons induced us to choose a method in which the category d is not considered. Strictly speaking, this is not the case of association in the original sense. Some authors (Bray 1956, Morisita 1959) therefore designate the indicator of this type as "index of interspecific overlapping". In the present paper the term association sensu lato is used including all these indicators. Among various "indices of interspecific overlapping" Fager's index is of great priority in the fact that it can be statistically evaluated by t-test. Approximation to normal distribution is the best if both species have equal number of occurrences. Fager (1957) considers it to be sufficient even in case that the occurrence number of one of both species is double value of the other. In our material this ratio was exceeded only exceptionally and mostly in cases when the insignificance of interspecific association was apparent. Approximation also deviates from the actual value when the total number of occurrences is low. This situation could arise in the nests in clearings when one sample included 8 and the other 10 nests. In order to apply this method more widely it will be necessary to find a method for small samples, too.

We consider the testing of one-sided deviation to be the advantage of Fager's coefficient. The difficult interpretation of negative associations which usually appear in graphs no longer arises. While using the χ^2 method our material revealed three negatively associated pairs: 2—13, 4—14 and 10—18. All their vertices were incidental with a large number of edges, optimal paths between both members of the negatively associated pair were very short, mostly consisting of two edges and one vertex only. Sometimes there are more than one of these short paths (e.g. the pair 4—14). The determination of negative associations itself brings a valuable information: the species which "repell" one another can have, for example, a different ecology which limits or eliminates their joint occurrence. However, it is difficult to imagine that there exist two negatively associated (and consequently ecologically very different) species and along with them others, which are positively associated with the both mutually different species. Apparently negative associations should be interpreted in some other way than the positive ones.

The application of correlation or association analysis in the studies of interspecific relationships in biocenosis or in some of its part as well as the presentation of results in the form of graphs is not quite new. These methods serve to define the group of mutually associated species ("ecological group", "recurrent group" etc.). The information obtained is then used in a different way: for example, to define the controlling ecological factors in biocenosis, to make indirect classification or ordination of the cenose etc. This concept is met with less in animal than in plant ecology where the recent works depict the group of associated species by means of empirically derived diagram (**Hopkins** 1957, **Agnew** 1961). Details on these works are reported by **Greig—Smith** (1967) and **Vasilevich** (1969). The diagram of specific interrelationships is very objective, but the total information is presented without any possibility of further utilization.

As mentioned above for the investigation of these problems the knowledge on graph theory is most useful. A graph is a set of objects and a set of relations at the same time. In biocenological studies the objects are species, the relations are statistically significant associations among them. The graphs published mostly in ecological papers are intuitively close to the mentioned concept, but are neither defined theoretically nor formally exactly described. This is apparently the reason why many possibilities provided by this method remain unused. Mostly a part of information contained in the graph is used only, namely the information on the set of vertices. Ecologists in this way define the species composition of biocenosis in the sense very close to our definition on associated set of species. However, a species may be defined also by its distribution area or by a complex of ecological conditions. This concept is often met with in ecology. In this connection the knowledge on the set of edges is also important for the understanding of biocenosis or its part. In the intuitive approach to assessment, however, this is mostly missing.

The use of species as indicators of environment is well known in ecology. This idea is included, for example, in some concept of the Zurich-Montpellier phytosociological school (characteristic combination of species, differentiating species or differentiating combinations etc.). By means of ecological amplitude of species the biotopes may be described or compared even when no direct data on ecological factors are at our disposal. The species in this method "substitutes" the complex of ecological conditions existing in all sites of its occurrence. If this complex is briefly called "ecological space", then a species is the reflection of its ecological space, i.e. the set of its occurrences (in nests where the species has been found). The ecological space of biocenosis is then composed of ecological spaces of species of which it consists.

The association analysis appears to be a suitable method even in tasks of this type, because it introduces an objective criterion in deciding which species create the ecological space of biocenosis. The relationship between the ecological space of species associated in the group and the ecological space of the group (biocenosis) as a whole is depending on the concept of biocenosis. If we proceed from the concept of biocenosis as a set of species, of which each is at the same time a set of locations, then the ecological space of

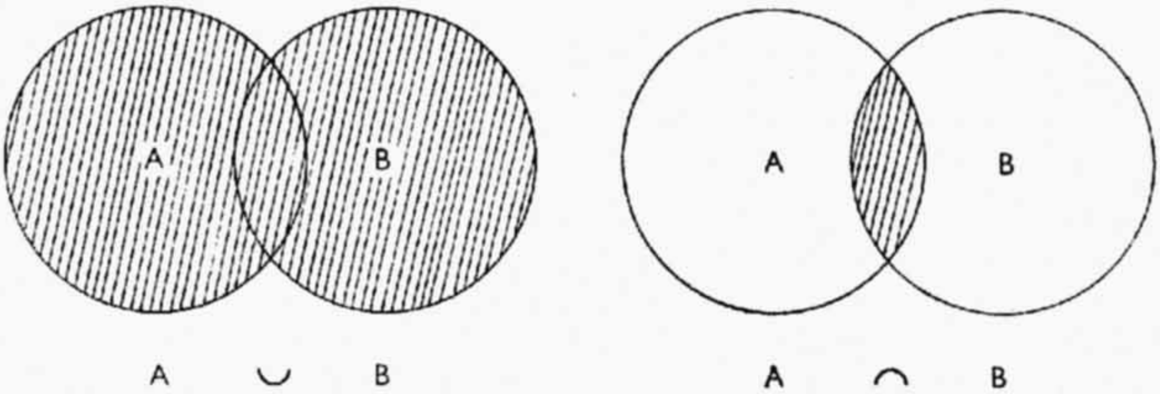


Fig. 15. Schematic illustration of ecological space of biocenosis based on the concept of biocenosis as a set of species (left) and the concept of biocenosis as a set of relations (right). Union of sets A and B (indicated as $A \cup B$) and intersection of sets A and B (indicated as $A \cap B$) is shaded.

biocenosis is defined as the union of these sets of locations. In this concept the ecological space of biocenosis is considerably wide, because it includes whole ecological spaces of species associated in biocenosis (Fig. 15).

On the other hand, the ecological space of biocenosis following from the concept of biocenosis as a set of relations has a more strict sense. The contents of the relation between two species is a statistically significant association which is resulting from the number of common occurrences. If the species is defined by a set of locations, then the relation between two species is an intersection of these sets and the ecological space of biocenosis is defined as union of intersections of the mentioned sets of locations. The ecological space of biocenosis includes only parts of ecological spaces of particular species; it is always the part common to two or more species in biocenosis. The difference between both concepts is formally expressed in the example of nests of the forest (at the ground level) variant. The ecological space is defined

1. from the concept of nidocenosis as a set of species:

$$E = S_3 \cup S_5 \cup S_6 \cup S_{15} \cup S_{17} \cup S_{18} \cup S_{20}$$

2. from the concept of nidocenosis as a set of relations:

$$E = (S_3 \cap S_6) \cup (S_5 \cap S_6) \cup (S_5 \cap S_{15}) \cup (S_5 \cap S_{18}) \cup (S_{15} \cap S_{17}) \cup$$
$$\cup (S_{15} \cap S_{18}) \cup (S_{17} \cap S_{18}) \cup (S_{18} \cap S_{20})$$

[E = ecological space; S_i ... species of forest nidocenosis (at the ground level). The concepts union and intersection are schematically illustrated in Fig. 16.]

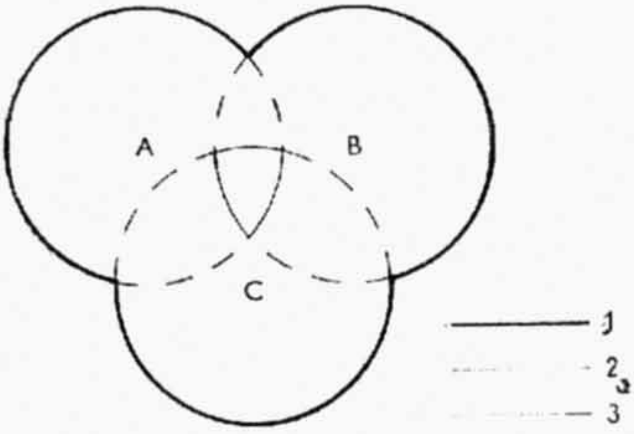


Fig. 16. Schematic illustration of ecological space of biocenosis. Area limited by particular lines represents: 1 — union of sets A, B, C (A ∪ B ∪ C); 2 — intersection of sets A, B, C (A ∩ B ∩ C); 3 — union of intersections of all pairs from the sets A, B, C — (A ∩ B) ∪ (A ∩ C) ∪ (B ∩ C).

A more strict definition of ecological space based on the set of associations is suitable for mutual comparison. The structure of associations is much richer and more varied than the structure of species and well reflects the differences even in closely related biocenoses. On the other hand, the species composition following from the concept of a set of species is less variable. It appears to be rather appropriate for the definition of a higher category which connects several closely related cenoses. It is also apparent from our material, especially in comparison with the data published by **Mrciak** et al. (1966).

However, also other reasons speak for the differentiation of both concepts. In studies of this type only samples are used. The result is an estimate of actual conditions and is subject to random deviation. The null hypothesis could be formulated, but cannot be tested. The deviations can be assessed only subjectively. Under these conditions those methods are preferable which cause large differences, because they reduce the risk of an error in any subjective evaluation.

CONCLUSIONS

The material of gamasoid mites collected from 149 nests of *Clethrionomys glareolus*, which had been evaluated in a previous paper (**Mrciak, Daniel** and **Rosický** 1966) by traditional method was re-evaluated from new aspects introduced and modified primarily from the field of plant ecology. Earlier methods used in analyses of nest communities have been scrutinized and the reasons for the choice of newly applied methods have been given in the Discussion.

The following general conclusions may be drawn:

1. Distribution of mites in nests corresponds to the contagious type and this fact plays an important role in the possibility of using statistical methods.

2. In order to describe quantitative properties of mites in nests three measures are defined; for a prompt and especially clear visual information which can be expressed in simple graphs, their total sum (A + D + F) is used.

3. Interrelationships of mites are solved by association analysis based on the evaluation of pairs of species, with application of Fager's affinity index. The results obtained may be evaluated and compared by matrices, or be presented in the form of empirically derived association diagrams. They reveal the difference between specific relationships of gamasoids in particular nest variants, help define the groups of associated mite species and the level of their interrelationships which indicate the difference of ecological conditions. The structure of associations is much richer and varied than the mere species composition and well reflects the differences in closely related communities.

4. Out of the total number of 42 species of gamasoids found only 13 were associated at a different degree. If we understand the nidocenosis as a directly or indirectly associated group of species in which mutual causal relationships exist, the nest community of gamasoid mites under conditions studied is composed of these 13 species only. Other species also occurred in the nests, but they are actually members of different communities. Such an analysis leads to a precise delimitation of the nest community which may be of practical importance in epidemiological considerations.

5. The comparison of results concerning the core proper of the nest community of gamasoid mites fully corresponds to the conclusions based on field experiments and aimed to determine the effects of microclimate of *C. glareolus* nests on the development of nest parasites (Daniel 1970) and clearly confirms the solidity of interrelationships of species, namely of *Haemogamasus nidi*, *H. hirsutus* and *Eulaelaps stabularis* as well as their dominance in *C. glareolus* nests under our natural conditions. In the field experiment conducted under conditions of south-Moravian inundated forest also *Haemolaelaps fahrenholzi* was present, but the explanation of its absence in the material of Vsetínské Beskydy should be sought after in other causes irrelevant to the nests of *C. glareolus*.

6. The comparison of results presented and those obtained by traditional method of evaluation of the material from Vsetínské Beskydy clearly demonstrates the simplicity, lucidity and easy comparability of the presented results as well as a wider and more profound assessment and consequently provides further detailed information. We therefore propose to accept this method as a part of standard evaluation of extensive groups of nest organisms.

МЕЖВИДОВЫЕ СООТНОШЕНИЯ ГАМАЗОВЫХ КЛЕЩЕЙ В ГНЕЗДАХ ЕВРОПЕЙСКОЙ РЫЖЕЙ ПОЛЕВКИ

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Резюме. Межвидовые соотношения гамазовых клещей из гнезд *Clethrionomys glareolus* решались путем анализа сопряженности при применении индекса аффинности, выведенного Фагером (1957). Критически обсуждаются другие способы оценки фауны нидикольных организмов и аргументируются преимущества примененного метода. В материале из

149 гнезд, в которых обнаружено 42 видов гамазовых клещей, дана оценка всем парам видов в каждой из четырех вариант гнезд, группированных по биотопу и размещению гнезда. Результаты выражены с помощью матриц и эмпирических ассоциационных графов. Определены группы ассоциированных видов клещей и уровень их взаимоотношений, указывающих различие экологических условий. Структура ассоциаций гораздо богаче и более разнообразна чем сам видовой состав и ясно отражает разности между близкими сообществами.

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