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AN ANALYSIS OF INTERSPECIFIC COMPETITION IN COMMUNITIES OF THE SOIL MACROFAUNA OF SOME HABITATS IN THE KAMPINOS NATIONAL PARK*

Analysis of the influence of habitat factors, food relations and interspecific competition on: 1) number of species, density and activity of individuals, 2) abundance and trappability of the different groups and species of predators and their percentage in the whole macrofauna examined. On the basis of results it is assumed, that: 1) interspecific competition was certainly of fundamental importance in the communities of macrofauna examined, 2) the chief basis of competition in the communities of predators was formed by food relations, 3) the influence of habitat factors on the different predators was connected with their dominance in the community, 4) organisation of the competition systems may be based on the differentiation of the ecological valence of species.

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1. INTRODUCTION

1.1. The problem investigated and the aim of the work

The aim of the work is to estimate the extent and conditions of occurrence of interspecific competition in the communities of soil fauna examined, with particular consideration of competitive relations between predators.

In principle four basic sources of information contribute to the present-day state of our knowledge of interspecific competition:

A) direct observations of the reciprocal elimination of different species in nature,

B) laboratory experiments on competition carried out chiefly on material consisting of *Protozoa* and storage pests,

C) comparative field investigations devoted to the evolutionary significance of competition and

D) hypothetical attempts at connecting defined quantitative relations between species in the biocenoses with competition.

A) Observations of the reciprocal elimination of species in nature are fairly commonly noted within different animal groups and within different habitats (Pearse 1939, Kaškarov 1945, Crombie 1947, Tischler 1956, and others). The following observations of competitive elimination, as connected with our investigations, may be given as examples: *Bembidion lampros* and *Trechus quadristriatus* (Heydemann 1953), *Philonthus quisquiliarius* and *Ph. micans* (Renkonnen 1944), *Myrmica ruginodis* and *Lasius' niger* (Kaczmarek 1953), *Stylothorax agrestis* and *St. retusa*, *Leptyphantes pallidus* and *Porrhomma spp.*, *Meta menardi* and *M. metianae* (Tretzel 1955), *Erigone atra* and *E. dentipalpis* (Knülle 1953) and others.

B) In the second category of information as to interspecific competition is contributed primarily by the laboratory experiments of Gause (1936), Crombie (1947), Park (1948) and others, showing that competition between two species rapidly leads to the complete elimination of one of the competitors (if the habitat is homogeneous), or to a sharp division of zones of influence in the habitat and to ecological separation of species (if the habitat is heterogeneous — imitating natural conditions).

Hutchinson (1948 acc. A l l e e and al. 1949) refers to two situations eliminating the applicability of this model of competition: 1) when density of the population of competitors is considerably reduced as the result of the influence of other factors apart from competition, 2) when the continual fluctuations of habitat variables constantly reverse the direction of competition relationships: now species A eliminates species B, then species B eliminates species A.

C) The third important source of knowledge on interspecific competition is formed by the facts, commonly found in nature, of the ecological (or geographical) isolation of closely related species.

This phenomenon, defined by C r o m b i e (1947) and O d u m (1959) by the name of "Gause's Principle", by P e a r s e (1939) as "Cabrerra's Principle", and by I l l i e s (1952) as "Monardschen Prinzip", was noted as early as 1894 by S t e a r in his work on the birds of the Philippines (acc. Tretzel 1955). C h a n d l e r (1914) expands this observation to take in different species of vertebrates, while M o n a r d (1920) confirms the commonness of this kind of ecological isolation of species in his work on the profundal of Lake Neuchâtel. The first fuller generalisation of this phenomenon is, however, to be found in the work by C a b r e r r a in 1932 (acc. T r e t z e l 1955). Independently of Cabrerra's research work, this subject was taken up in 1946 by E l t o n. Making use of the J a c c a r d[1] generic coefficient, (the ratio of the number of species to the number of genera) he examined 55 animal populations in different geographical latitudes in water and on land, and found that the percentage of genera which are represented in separate biotopes by one species is 86. In the years following this problem was taken up by, inter alia, W i l l i a m s (1947), C r o m b i e (1947), P a r k (1948). A particularly large amount of factual material is supplied by the numerous works by L a c k (1940, 1946) on the isolation between related species of birds. T r e t z e l (1955) in this exhaustive work on competition among spiders demonstrates the importance of the hitherto little-examined form of ecological isolation of related species, such as is the divergence in occurrence during the yearly cycle.

The facts of ecological isolation of species under discussion prove almost indisputably[2], that interspecific competition is of great form-creating importance in speciation processes. Conclusions, however, arising from this on the subject of the current importance of competition in the biocenosis are somewhat scanty. If we go no further than these facts, then it may be assumed, after B o d e n h e i m e r (1955) that competition between species is of very small importance in the biocenosis. Since closely related species are distributed in different biotopes, then competition between them is an exclusively historical phenomenon.

This reasoning does not, of course forejudge an actual lack of interspecific competition in the biocenosis, but only denies that the facts of the intrageneric

[1] Jaccard as early as 1902 applied this coefficient to an analysis of the distribution of Alpine flora.

[2] A different standpoint as far as the evolutionary importance of competition is concerned, cf. L i n d r o t h (1949).

isolation of species which refer to the occurrence of species in different bio-
topes, or even geographical zones, are of adequate evidential value. We have
no proofs that the distribution of competitors in different strata of one biotope
muse lead to a loss of ecological contacts and disappearance of competition.
Neither do we know to what extent evolutionally secondary competition between
more distantly related species is put into action in nature.

D) Finally the fourth category of hypotheses on the subject of competition
between species is connected primarily with the assumptions of Lityński
(1938), Tarwid (1952), Wautier (1952) and certain other ecologists, that
the quantitative predominance, commonly observed in all associations of plants
and animals, characteristic and usually very great, of a small number of domi-
nating species is the result of the competition relationships between species.
Recently Mac Arthur (1960) presented an original form of this assumption,
putting forward the hypothesis that the domination of a species is the express-
ion of its breaking away from the competitive influence of the biocenotic en-
vironment. This specific attempt at therotical connection of the phenomena of
domination of different species of animals with interspecific competition is
also to be encountered in works by Tretzel (1955). Taking, like Litynski,
the well-known statements of Bristowe that abiotic factors determine the number
of species, while biotic factors determine the number of individuals, as his
starting point, Tretzel (1955, p. 86) very skilfully formulates the principle
of research on the domination of species in the sentence: "Wir wollen also
nicht fragen, warum eine bestimmte Art in einem Biotop sehr häufig ist, sonder
warum nur diese Art in ihm so hohe Abundanz erreicht".

Attempts of a different kind at drawing conclusions as to interspecific competition
on the basis of the structure of the community concern the second biocenotic principle
("2. biozönotisches Grundprinzip", Thienemann 1920, acc. 1954) which states,
that together with the increase in the number of species in the habitat the number of
individuals in the different species decreases. The principle referred to was in fact the
source of assumptions as to the competitive elimination of the species putting it (i.e.
this principle) into practice (Gösswald 1932, Tischler 1954, Tretzel 1955 and
others).

These assumptions would not, however, seem to possess much justification until
such time as we have additional information on the variations on the resources of the
habitat and variations in the total abundance of all the species examined. Without
this kind of additional information, the decrease itself in the abundance of each species
together with an increase in the number of species in the habitat may be explained by
the simple decrease in microhabitats inhabitated by separate species. It is a known
fact that the number of species in each community is the function of differentiation
of the habitat ("1. biozönotisches Grundprinzip", Thienemann 1954), while parallel
to the differentiation of the habitat the spatial narrowing of a different type of micro-
habitat inhabitated by each species may and should take place. As a result the relation
referred to between the number of species and number of individuals in each species

may be a simple function of differentiation of the habitat, which of course markedly limits its value as evidence in consideration of competition.

In undertaking an analysis of competition interrelationships in the communities of soil fauna examined an attempt has been made to obtain answers to the following questions.

What was the total intensification of competitive relationships in the communities of fauna examined and what form did the actual contacts between animals take?

Did competition exist between the groups of predatory macrofauna distinguished and what was the fundamental object of this rivalisation?

Did competitive relations within the communities of predators exhibit a definite organisation, i.e. did all the groups of predators distinguished exhibit uniform competitive relations on the principle of "each with each", were these relationships organised and on what principle?

Was the differentiation confirmed in competition relations between predators connected with the character of their ecological specialisation?

What was the relative abundance of ecologically unspecialised predators?

Which groups of the predators examined formed the eliminated party, and which the eliminating?

1.2. Object of the investigations

The object of the investigations was formed by the macrofauna of the litter and the soil layer to a depth of 10 cm.

Fenton (1947) and van der Drift (1957) include in the concept of macrofauna all animals from 2 to 20 mm. in length. This arbitrary principle of dividing macrofaune despite its clarity has, however, two weak points. In the first place in operating exclusively by the criterion of length it does not take into consideration the real dimensions of animals, which affects in particularly the specially elongated forms such as, e.g. *Enchytraeidae* or *Lumbricidae*. In the second place this principle leads to artificial splitting of systematic groups ecologically very uniform (e.g. including in macrofauna part of the species of *Collembola*). These objections incline us to accept the division of soil fauna proposed by Lagerspetz (1953) who includes in the Fenton group of animals corresponding to macrofauna all invertebrates with the exception of *Protozoa, Rotatoria, Nematoda, Acarina, Enchytraeidae* and *Apterygota.* Lagerspetz defines this group by the name of mesofauna, reserving the concept of macrofauna for vertebrates (Fenton's megafauna). This arbitrary shifting of terms can lead only to a confusion of concepts, and therefore despite the fact

that use has been made of Lagerspetz's principle of division, traditional ter-
minology has been adhered to in this work.

Thus the following have been included in macrofauna in this paper: *Lumbri-
cidae*, *Oniscoidea*, *Gastropoda*, *Arachnoidea* (without *Acarina*), *Myriapoda* and
Pterygogenea above 3 mm.

1.3. Description of the habitats examined

Investigations were made in the summer and early autumn in the Kampinos
National Park in the Wydma Dziekanowska area (Laski forest administration
district).

In order to obtain a suitable scale of comparison three habitats were in-
cluded in the investigations, which as far as possible form a distinct series
of development. These habitats were chosen within the pine wood with trees
of the following ages: 10 years – station I, 19 years – station II and 42 years
– station III. In addition use was made in this work of part of the materials
collected, parallel with the forest investigations, from the nearly potato field
(station *P*).

On each of the forest stations the general character of the vegetation and
the more important characters of the soil habitat, i.e. the character of the soil,
its humidity, porosity and humus content, were defined.

Soil on all the forest stations belonged to the scoured soil type on river
sands, with different formation of the organic layer (raw humus).

Humidity was measured throughout the whole study period by means of the
method consisting in comparison of the weight of soil samples before and after
evaporation. The loss in percentage of weight was taken as the index of humid-
ity. In order to define the relative porosity of the soil, a series of samples was
taken for evaporation from places previously extremely abundantly watered
(5 hours previously). Finally the humus contents were defined by the sedi-
mentation method. The sediment of organic particles was treated in this work
as humus, and not humus in the chemical meaning of this word. Figures charac-
terising the humus contents of the soil have similarly an indicative value only
in this work. They reflect the amount of organic sediment obtained after 30 mi-
nutes sedimentation when the soil sample (100 cu. cm. of soil from a depth of
up to 10 cm.) is diluted with 900 ml. of water.

Measurements of moisture, porosity of the soil and humus contents were
made several times during the course of the investigations, taking 10 samples
on each of the stations from different spots in the station. The mean value

was calculated from this material. The results of measurements are given in Table I[3].

Humidity, porosity, humus contents in the investigated soil level
and the lighting of the forest floor of the forest stations

Tab. I

Features of habitat	Stations		
	I	II	III
Average humidity of soil (% water) during the period:			
VI, VII, VIII	10.8	10.9	16.5
VIII	7.6	9.5	15.3
Porosity of soil (% absorbed water)	18.7	13.3	29.3
Index of humus contents (% organic sediments)	17	8	24
Lighting (% sunny spots)	40—50	10—20	30—40

The description of the ground vegetation and shrubs was limited to a general description of the differences in the vegetation cover (Tab. II). It was considered unnecessary to give a list of the flora for the following reasons: in the first place habitat analyses of the occurrence of different systematic groups were concerned exclusively with predators, with reference to which the absence of connections between occurrence and the specific composition of the ground

The structure of vegetation on the investigated stations

Tab. II

Layer	Stations		
	I	II	III
Bryoid stratum	sparse: moss a, lichens	continous: moss (very sparse lichens)	in tufts: moss (very sparse lichens)
Herb stratum	in tufts: Calluna	very sparse: Calluna	discontinous: grasses, Calluna,
Shrub stratum		very sparse: Betula	Vaccinium, Pteridium sparse: Frangula, Betula, Quercus
Tree stratum	Pinus 10 y.old (sparse Betula)	Pinus 19 y.old	Pinus 42 y.old (very sparse Quercus)

[3] In addition, for certain comparative purposes, the humus contents in the soil of field station (P) were also determined. The index of the humus contents was 32% here.

vegetation and shrubs has been confirmed in many works (Kühnelt 1944, Thiele, 1956 and others); in the second analyses of the occurrence of different species was limited to the question of the scope of habitat specialisation only, without deeper penetration into the habitat motivation of the abundance on different stations.

In comparing the data collected on the properties of the habitats examined we note station III (the oldest wood) was characterised by the highest humus contents, porosity and humidity of the soil, and by the greatest differentiation in the vegetation cover, which was expressed in the considerable differentiation of the ground vegetation and shrubs and the very mosaic-like character of the litter (tufts of mosses and grasses intersected by patches devoid of vegetation). Station II (the wood of medium age) represented a transitional habitat from the aspect of soil humidity only. Porosity and humus contents in the soil were lowest here, shade greatest, the vegetation of the forest floor the poorest, not exhibiting practically any vertical differentiation (almost entirely bryoid stratum) and almost no mosaic pattern (uniform moss cushion).

It might therefore seem that the distinct differentness of station II makes it difficult to draw conclusions as to the influence of the development of the forest on the communities of soil fauna examined. In reality, however, this separateness was provoked by an intentional choice of study area. We are of the opinion that the value of the gradient method in ecological field studies lies in its very complexity, as far-reaching as possible. If all the properties analysed above, of the habitat exhibitet agreement with the age gradient of the forest, then drawing conclusions as to the dependence of the biocenotic structures we examined on the age of the forest would be a very problematical matter. Other factors might equally well influence this phenomenon, such as the organic contents of the soil, differentiation of the ground vegetation, mosaic character of the litter etc. If, however, we record the correlation between the community structure and the age of the forest despite the variations, not in accordance with the age of the forest, of the habitat factors mentioned, then our conclusions as to development are far more likely to be correct. As a result it was only owing to the separateness referred to of station II that it proved possible to carry out in this work attempts at distinguishing the influence of biocenotic factors (connected with the development of the community) and of biotope factors, such as the humus contents referred to, the porosity of the soil or absence of herb stratum (and therefore factors in relation to the development of community either secondary or fortuitous).

1.4. Methods

Two capture methods were used, i.e. taking soil samples and using traps.

Soil samples were taken in the following way. The litter (together with the ground layer, if present of vegetation in the form of moss, lichens or short grasses) and a 10 cm. layer of soil from a surface measuring 18 × 18 cm. were removed in turn. The soil (or litter) was then sifted and the macrofauna picked out[4]. Ten litter samples and ten soil samples were taken once only on each station. By means of this method a total number of 1900 samples were taken, and 2380 animals captured.

In order to obtain data on the activity of fauna within the soil habitat the supplementary method, described previously (M. and W. Kaczmarek 1956), of Barber's plan (Stammer 1948, Tretzel 1955a, Skuhravy 1957) was used in the captures by trap. It consisted in the partial isolation of the jar by means of a Petrie glass (Fig. 1). The litter traps (Fig. 1A) were sunk so as to been level with the surface of the soil and covered with a glass sufficiently large for its edge to rest on the surface of the litter or mosses, lichens etc. surrounding the trap. The soil traps, on the other hand (Fig. 1B) were set on the bottom of a 10 cm. hole covered with a glass in such a way that its edge rested on the surface of the soil round the hole. In this way access to the trap was rendered impossible for animals moving about on the surface of the litter, and was limited exclusively to forms within the litter, while access to the soil traps was limited to forms moving about in the 10 cm. layer of soil under examination.
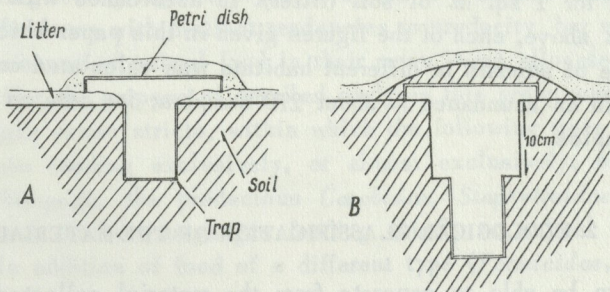

Fig. 1. Plan of trap arrangement.
A — litter trap, *B* — soil trap

A total of 50 soil and 50 litter traps were set on each forest station and 100 soil (litter was absent) on the field station. Soil traps were distributed at

[4] Samples taken at random within an ant's nest were discarded.

intervals of several metres, litter traps — near the soil traps. Both types of trap were distributed as far as possible fortuitously in regard to the mosaic character of the litter (moss, grasses, pine needles etc.) as was the case with the soil samples. With this aim they were placed along a straight line exactly at places separated by a standard number of meters. All the traps functioned throughout the whole study period in the same places in which they had first been placed. They were inspected every 3 days. A total of 6430 inspections (samples) were made, 1799 animals being caught.

During the course of preparation of this paper the results of sifting soil samples were treated as the index of abundance of animals (I shall now use the abbreviation A to indicate this), while the results of trap captures were treated as the index of their trappability (German — Aktivitätsdichte, Heydemann 1956, abbreviation T). When estimating the occurrence of each group use was made of their absolute abundance and trappability and relative abundance and trappability, measured by the ratio to the abundance (trappability) of the whole macrofauna expressed in percentages. In the case of abundance this ratio was defined as dominance (German — Dominanz, abbreviation DA), while there is no English definition of trappability (German — Aktivitätsdominanz, Balogh 1958, abbreviation DT). The ratio of trappability to abundance was taken as the index of the activity of the fauna (abbreviation T/A).

Mean values of all the samples taken throughout the whole study period were used in all the comparisons made. This did not reduce the comparability of material from different habitats, since all the captures were carried out parallel in all the habitats examined.

The mean values for one sifted sample has been given in the comparisons as calculated for 1 sq. m. of soil (litter). In accordance with the number of captures given above, each of the figures given in this paper which characterise the occurrence of animals in different habitats was calculated on the following basis: for data on abundance — about 270 samples; for data on trappability — about 800 samples.

2. ECOLOGICAL CLASSIFICATION OF THE MATERIAL

In order to be able to separate from the material collected the group of predatory forms interesting us in this work it proved necessary to define to some degree the food specialisation of all of the animals caught. This was not an easy task. The difficulties presented were of two kinds. In the first place information on food specialisation of soil forms is somewhat scanty, scattered, and often contradictory. In the second place — and this is probably the most important — the wide food specialisation typical for a soil habitants makes

sharp division into groups difficult. The majority of soil saprophages (*Diplopoda, Lumbricidae,* the larvae of *Tipulidae, Bibionidae* and others) can live on the living tissues of plants (V e r h o e f f 1928, N o s e k 1954, D u n g e r 1958) and many phytophages — on dead organic material (G i l a r o v 1937, 1949). The case is a similar for zoophages. Even the typically predatory species from the *Carabidae* and *Chilopoda* groups can feed on plant tissues (S k u h r a v y 1959, S c h w e r d t f e g e r 1957), not to mention the distinctly twofold character of the menu of larvae of *Asilidae* and *Therevidae* (B r a u n s 1954) or the well-known predaciousness of the otherwise phytophagous wireworms (G ä b l e r 1955). These phenomena are in a certain sense under standable in view of the considerable admixture in the soil habitat of plant particles at different stages of decomposition- from live tissue of fallen leaves to detritus. In habitats above ground the accessibility of a definite type of food is usually connected with the very special peculiarities of the habitat, the utilisation of which must lead to considerable divergency of adaptations and narrower food specialisation. This is the case with the predacity of forms basically phytophagous, which owing to the generally slight activity of soil fauna and the relative abundance in the soil of inactive stages do not have to form special ecological adaptations for obtaining animal food. ·The same adaptations which the necessity for moving about in the soil and biting hard root tissues require from phytophages are sufficient. On the other hand, in habitats above ground, the generally greater activity of the faune requires from predators many special ecological adaptations clearly different from the adaptations of phytophages feeding on immobile food.

Under such circumstances an attempt, even of the most general character, at distinguishing food groups involved solutions to a certain extent conventional. Thus all the forms with distinct tendencies to predacity, but not necessarily with a predominance of animal food in their menu, were allocated to the group of predators. For the purpose of detailed analysis this group was split up into:

1) zoophages sensu stricto, within which the following were distinguished: a) euzoophages feeding exclusively, or almost exclusively, on animal food (*Araneida, Chilopoda,* the predacious *Carabidae, Staphylinidae, ·Heteroptera, Anthicidae* etc.), b) hemizoophages feeding chiefly on animal food, but with a considerable addition of food of a different type (*Formicidae,* pantophagous *Carabidae*).

2) parazoophages feeding primarily on non-animal food (the zoophagous larvae of *Elateridae,* larvae of *Therevidae*) (cf. Fig. 2).

The division made according to these principles of the more abundant groups is illustrated by Table III. The chief sources of information on food requirements are given in the final column of this table. When the source is given in brackets it means that the author has made a statement on the subject of the

food specialisation of a related species, or forms an opinion as to the average properties of the higher taxonomic unit.
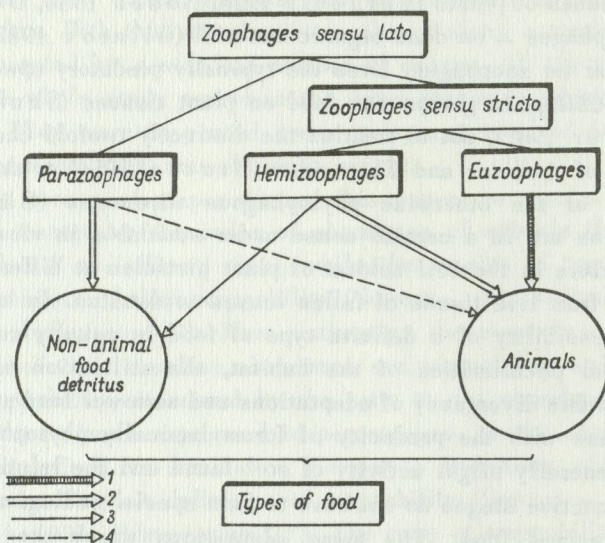

Fig. 2. Plan of the division made of predators into specialisation groups.
1 — exclusive food, 2 — chief food, 3 — frequent food, 4 — occasional food

The larvae of *Carabidae*, not identified as to species, but fairly numerous in the material, were divided according to the proportions of specialisation established among the adult forms.

Classification of the collected animals according to their food specialization

Tab. III

Species	Number of species	Food specializa-tion	Authors of information
1	2	3	4
Araneida	50	Z	
Drassodes umbratilis C.L. Koch			
Drassodes sp.			
Zelotes apicorum (L.Koch)			
Zelotes electus C.L. Koch			
Zelotes petrensis L. Koch			
Zelotes sp.			
Tmarus piger Walck.			
Xysticus pini Hahn			
Zora silvestris Kulcz.			
Zora sp.			

1	2	3	4
Apostenus fascus Westr.			
Agroeca proxima (Cambr.)			
Neon reticulatus Blackw.			
Dendryphantes hastatus Cl.			
Enophrys frontalis Walck.			
Linyphia pusilla Sund.			
Leptyphantes sp.			
Micryphantes rurestris C.L.Koch			
Micryphantes gulosus (L.Koch)			
Macrargus rufus Wid.			
Macrargus herbigradus Blackw.			
Centromerus incilium L.Koch			
Centromerus silvaticus Blackw.			
Centromerus sp.			
Gonatium rubens Blackw.			
Pocadicnemis pumila Blackw. (P)			
Theridion varians Hahn			
Theridion sp.			
Steatoda bipunctata L.			
Robertus lividus Blackw.			
Ero furcata Villys			
Cyclosa conica Pall.			
Mangora acalypha Walck.			
Aranea sturmi Hahn			
Aranea sp.			
Pahygnatha degeeri Sund. (P)			
Tetragnatha pinicola L.Koch			
Hahnia pusilla C.L.Koch			
Hahnia sp.			
Trochoza terricola Thor.			
Tarentula fabrilis Cl.			
Tarentula sp.			
Xerolycosa nemoralis Westr.			
Xerolycosa sp.			
Hygrolycosa sp.			
Lycosa sp.			
Pirata sp.			
Micrommata viridissima (Deg.)			
Philodromus sp.			
Erigone dentipalpis (Wid.) (P)			
Chilopoda	18	Z	
Lithobius erythrocephalus C.Koch			
Lithobius forficatus Linne			
Lithobius agilis C.Koch			
Lithobius piceus Z.Koch			
Lithobius lapidicolla Mein.			
Lithobius nigroculis Folkm.			
Lithobius pelidus Haase			
Lithobius sp. Hsp.			
Lithobius borealis Meinert			
Geophilus flaviolus C.Koch			
Pachymerium ferrugineum C.Koch			
Monotarsobius curtipes C.Koch			

1	2	3	4
Monotarsobius crassipes L.Koch *Photophilus griseus* Folkm. *Monotarsobius aeruginosus* C.Koch *Scolioplanes acuminatus* Leach *Hemicops fulvicornis* Meinert (*P*)			
Diplopoda	?	*PhS*	Verhoeff 1928, Nosek 1954, Dunger 1958
Insecta:			
Blattodea	?	*S*	
Heteroptera	13		
Macrodema micropterum Curt. *Macroparius lineatus* (Costa) *Ischnocoris angustulus* Boh.		*Z*	Schwerdtfeger 1957, Fedorko 1957, (Börner 1933)
Lygus pratensis L. *Lygus* sp. (*pubescens* ?) *Dolycoris baccarum* L. *Eurygaster maura* L. *Eurydema oleracea* L. *Eurydema festiva* L. *Aethus nigrita* (Fabr.) (*P*) *Tyreocoris scarabaeoides* L.		*Ph*	(Börner 1933)
Rhyparochromus lynceus (Fabr.) *Megalonotus chiragra* Fabr.		*PhS*	Schwerdtfeger 1957, Fedorko 1957
Coleoptera			
Carabidae	28		
Cychrus rostratus F. *Leistus ferrugineus* L. *Notiophilus aquaticus* L. *Notiophilus biguttatus* F. *Dyschirus globosus* Herbst. *Clivina collaris* Herbst (*P*) *Clivina fossor* L. (*P*) *Broscus cephalotes* L. *Calathus fuscipes* Goeze (*P*) *Calathus erratus* Schal. *Cal. melanocephalus* L. *Cal. micropterus* Duft. *Stomis pumicatus* Panz. *Masoreus wetterhali* Gyl. *Microlestes minutulus* Goeze *Miscodera arctica* Payk.		*Z*	(Reitter 1908), Reichenbach-Klinke 1938, Burmeister 1939, Schaller 1949, (Davies 1953), Skuhravy 1959, Scherney 1959, Smit 1957, Kühnelt 1958
Epaphius secalis Payk. *Bembidion 4-maculatus* L. (*P*) *Pterostichus niger* Schal. *Pt. oblongopunctatus* F. *Pt. angustatus* Duft. *Pseudophonus pubescens* Müll. (*P*) *Bradycellus collaris* Payk. *Anchus obscurus* Herbst		*H*	

1	2	3	4
Amara communis Panz. (*P*)		*Ph*	
Amara infima Duft.			
Amara brunnea Gyll.			
Amara fulva De Geer			
Staphylinidae	21		(T i s c h l e r 1958)
Bryocharis formosus Graw.		*Z*	
Heterotops dissimilis (*P*)			
Staphylinus erythropterus L.			
Philonthus fuscipennis Mannh.			
Phil. varius Gyll.			
Phil. sanguinolentus			
Phil. nigritulus (*P*)			
Phil. debilis (*P*)			
Xantholinus linearis Ol.			
Xant. tricolor F.			
Xant. elongatus Mannh. (*P*)			
Tachyporus hypnorum F.		*S*	
Tach. solutus Er.			
Tach. chrysomelinus L.			
Lathrobium sp. (*longulum* Graw.?)			
Astenus filiformis Latr.			
Ast. angustatus Payk.			
Oxytelus rugosus F. (*P*)			
Bledius sp. (*P*)			
Atemeles paradoxus Grav.			
Elateridae (larvae)	11		
Melanotus rufipes Obst.		*P*	G ä b l e r 1955, S c h a r-
Dolopius marginatus L.			f e n b e r g e r 1942,
Athous subfuscus Müll.			F r i e d e r i c h s 1951,
Prosternon holosericeum Oliv.			M o c z u l s k i acc.
Selatosomus aeneus L.			G ä b l e r 1955
Cardiophorus ruficollis L.		*PhS*	G i l a r o w 1937
Sericus brunneus L.			
Agriotes sp. (*P*)			
Elater balteatus L.			
Limonius aeruginosus Ol.			
Athous niger L.			
Anthicidae	1		
Notoxus monoceros L.		*Z*	G ä b l e r 1955, S c h w e r d t-
			f e g e r 1957
Cantharidae (larvae)	?	*Z*	S c h w e r d t f e g e r 1957
Coleoptera varia:	?		
Curculionidae (imag.,larv.)		*Ph*	
Melolonthinae (imag.,larv.)			
Chrysomelidae			
Ipidae			

1	2	3	4
Coprinae (imag.,larv.) *Byrrhidae* *Tenebrionidae* *Dermestidae*		S	
Hymenoptera:			
Formicidae	20	H	
Myrmica laevinodis Nyl. *Myrmica rubra* L. *Myrmica rubra* L. var. *microgyna* Brian *Myrmica rugulosa* Nyl. (P) *Myrmica scabrinodis* Nyl. *Myrmica sabuleti* Mein. *Myrmica lobicornis* Nyl. *Myrmica schencki* Em. *Stenamma westwoodi* Arn. *Leptothorax acervorum* Fabr. *Lept. muscorum* Nyl. *Solenopsis fugax* Latr. *Tetramorium caespitum* L. *Lasius flavus* Fabr. *Lasius umbratus* Nyl. *Lasius fuliginosus* Latr. *Lasius niger* L. *Formica sanguinea* Latr. *Formica nigricans* Em. *Formica fusca* L.			
Diptera (larvae):	?		
Therevidae		P	Brauns 1954
Asilidae		PhS	Brauns 1954
Tipulidae			Eglitis 1954,
Bibionidae		S	Brauns 1954
Dolichopodidae		Z	
Oniscoidea	?	PhS	
Oligochaeta:	?		
Lumbricidae		S	

Z — euzoophages, Ph — phytophages, H — hemizoophages, S — saprophages, P — parazoophages, PhS — phyto- or saprophages, (P) — on the station P only.

3. ANALYSIS OF MATERIAL

3.1. What was the total intensification of the competitive relationships in the communities of fauna examined and what form did the ecological contacts between animals take?

In searching for answers to these questions attempts were made to discover how the faunistic differentiation of the community, and thus probably the intensification of interspecific contacts, affected the abundance and activity of the animals.

Conclusions were drawn as to the faunistic differentiation of the communities from the number of species caught, belonging to the following and more thoroughly examined systematic groups: *Araneida, Chilopoda Carabidae, Staphylinidae, Elateridae, Formicidae* and *Heteroptera* (cf. Tab. III).

The number of species recorded in the soil was lowest on field station (P), and on the forest stations increased with the age of the forest stand (Tab. IV). In the litter this dependence of the number of species on the age of the forest was deflected by the particularly small number of species on station II.

Comparison of the relative number of species, abundance and activity
of individuals in the total macrofauna examined

Tab. IV

Data of species and individuals	Stations			
	P	I	II	III
Soil				
Number of species	32	57	86	100
Number of individuals	148	86	71	50
Activity of individuals	2.0	2.3	2.5	8.4
Litter				
Number of species	—	80	68	100
Number of individuals	—	73	88	62
Activity of individuals	—	3.1	2.1	5.2

The relative number of species: percentage of the number of species collected on III station.

Comparing the results obtained with the differences in the humus contents in the soil and differences in vegetation, we reach the conclusion that the number of species of the macrofauna inhabiting the stations examined was primarily the function of the differentiation of the habitat, and not the function of the food resources of the habitat. This is proved by the two following circumstances:

1) the minimum number of species of the macrofauna on the field station
(Tab. IV) which was characterised by the greatest simplification of the vegeta-
tion cover (potato monoculture) with a high humus content of the soil (index
32% as against 8—24% in the soil on the forest stations),

2) the variations irrespective of the humus content in the number of species
in the soil of the forest stations (minimum number of species on station I,
minimum index of humus contents on station II).

The connection noted between the faunistic differentiation of the com-
munities examined and the differentiation on of the habitat forms yet another
confirmation[5] of the well-known T h i e n e m a n n biocenotic rule (1920 acc.
1954), stating that the more varied the habitat conditions, the greater is the
number of species inhabiting the habitat.

In turn the ratio of number of animals in the trap material to their number
in material obtained by sifting soil and litter (trappability : abundance) was
taken as a measure of the activity of the fauna, as has been mentioned above.

All the figures obtained referring to the abundance and activity of the
animals are set out in Table IV in accordance with the increase in the number
of species in the community. This comparison indicates, that 1) with the in-
crease in the number of species the number of the individuals of the whole
macrofauna decreased, 2) on the other hand the activity of the animals in-
creased.

What conclusions as to the intensity of ecological contacts and possible
competition can be drawn from the relation stated above?

1) Decrease in the density of individuals of the whole macrofauna with an
increase in the number of species was repeated with considerable regularity
(Tab. IV) in both the layers of the soil habitat examined (in the soil and in the
litter[6]. Let us consider the possible causes of this phenomenon.

In principle there are two possibilities: either we were concerned here
with a deterioration, parallel to the increase in the number of species, in the

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[5] From other confirmations of this rule introduced by Thienemann on the basis of
research on water habitats, the results of works by P a l m g r e n (1941) and L a c k
(1951) on birds, D a m m e r m a n n (1948), and D i e r s c h k e (1951) on different in-
vertebrates of forest habitats, S t e b a j e w (1957) on steppe *Orthoptera*, T r e t z e l (1955)
on spiders and others may be referred to.

[6] A similar relation may be read from (using suitable conversions) the material of
J a h n (1950), who examined the fauna of litter in pine woods 14, 46 and 92 years old.
The groups of macrofauna to which she gave quantitative treatment exhibit a distinct
decrease in the number of individuals with the age of the forest stand (this statement
was not included in the conclusions of the work referred to, on account of the more
extensive group of fauna dealt with in this work). From the general qualitative com-
parisons of the material collected by this authoress it may be concluded that the number
of species of the macrofauna increased with the age of the forest.

general living conditions of the macrofauna, some decrease in the capacity of the soil habitat, or various species of the macrofauna reciprocally restricted their occurrence in the habitat.

The first assumption is, however, difficult to accept, since the number of species of the macrofauna was highest, both in the soil and in the litter, in the oldest forest with a high humus content, greatest moisture and porosity of the soil and greatest mass of vegetation cover.

This inclines us to acceptance of the second explanation namely, that the decrease in the abundance of the macrofauna with an increase in the number of species was the effect of reciprocal interference by different species in the full utilisation of the soil habitat and therefore the effect of currently acting interspecific competition.

2) The activity of the fauna exhibited a similarly distinct but opposite to that of abundance, correlation with the faunistic differentiation of the community (soil and litter – Fig. 3, Tab. IV). This correlation would seem to thrown some light on the character interesting us of the ecological contacts between the animals studied, namely it proves that the probable decrease in ecological contacts between the animals accompanying the reduction, referred to above,

Fig. 3. Variations in the activity of macrofauna with the increase in its density.

I, II, III – station, s – soil, l – litter

of the abundance of macrofauna with an increase in the number of species, could to a considerable extent be compensated by the intensified activity of the animals.

In communities poor in species, with a low degres of interspecific competition and great abundance of fauna, the defined level of ecological contacts between animals could be maintained even when the activity of the animals was slight. Together with an increase in the number of species increase of competition and decrease in density of the macrofauna (and certainly also the increase in the ecological isolation of species – see introduction) similar intensification of ecological contacts could be maintained owing to the confirmed correspondingly greater activity of the animals.

In order to obtain a better knowledge of the mechanisms of this phenomenon, an attempt was made at defining in addition the correlation between the activity of the animals and the density of the macrofauna. This is illustrated by Fig. 3. It will be seen that the correlation of activity with abundance of the fauna
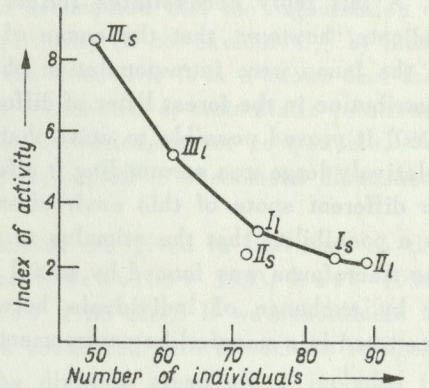
exhibitet great regularity. The only deviation from this regularity was the slight activity of the animals in the soil on station II, justification on for which may, however, be found in the extremely low porosity of the soil on this station (cf. Tab. I).

This outstanding degree of correlation between activity and abundance of the fauna suggests that the compensational variations, discussed above, in the activity of the animals were directly conditioned more by the density of the macrofauna than by its faunistic differentiation (intensity of competition). What were the sources of this correlation?

A full reply necessitates further investigations. A large number of data indicate, however, that the cause of the variations described in the activity of the fauna were intra-population phenomena. In earlier investigations of the distribution in the forest litter of different species of *Collembola* (Kaczmarek 1960) it proved possible to state that the abundance of the species within the relatively large area surrounding it affects the form of aggregation of individuals on different spots of this environment. In the light of this observation there is a possibility that the stimulus to the variations observed in the activity of the macrofauna was formed by social tendencies to intensification of contacts, or by exchange of individuals between aggregations of this same species scattered in a mosaic-like environment[7].

3.2. Did the groups of predatory macrofauna distinguished compete with each other and what was chief object of this competition?

The concept of interspecific competition is connected ex definitione with the phenomenon of quantitative compensation of occurrence of species: with an invariable supply of requisites for competition an increase in the abundance of one of the species leads to a decrease in the abundance of one other, or several other, species connected by competition. Therefore the existence of competition phenomena within a certain group of animals may be concluded, inter alia, on the basis of a defined balance of the total number of individuals of all the species examined. If the abundance of different species varies within wide limits (exhibits considerable variability) and the sum of individuals of all species exhibits relative stabilisation, this means that those variations in the abundance of different species cancel each other out as the result of competition relationships.

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[7] Naumov recored compensational variations of a similar kind in activity with variations in the density of individuals in populations of certain steppe rodents (information given verbally). Ivlev (1954) in experimental research on benthos proved that thinning of the population evokes intensive association of individuals.

It might be assumed, that this kind of quantitative compensation is the function of some undefined properties of the biocenosis not having anything in common with competition; that — in a similar way to that taking place in the organism — the source of compensative phenomens may be, in the biocenosis, some system co-ordinating "from the top" the life functions of the elements of the system.

We known, however, that contrary to the organism, the fundamental basis integrating the biocenosis consists of the different froms of the struggle for existence between each of the elements of the system — the species[8]. The Ockham economy of reasoning induces the assumption that the organisation of the biocenosis is created and maintained primarily (if not exclusively) by inter-specific exploitation and competition. At the same time it is a known fact that exploitation relations (in fact similarly to commensal or mutualistic relations) are characterised by a simple quantitative proportionality of components, and can therefore not form the source of the compensative phenomena discussed. Competition therefore remains.

Two fundamental requisites of competition are given in literature as the foundation of competition: food and space (Nicholson 1953, Lack 1954, Tretzel 1955, Tischler 1956, Naumov 1956 etc.). If we subordinate to the space factor all the habitat requisites connected with it such as refuges, places of reproduction, rest etc, then the division given above includes in principle the whole of the theoretically significant objects of competition between animals. This division is of course, of theoretical importance only. In reality food and space have a complex effect: competition for space implies competition for food and *vice versa* (Tischler 1956, Tretzel 1955). Irre-spective, however, of this complex effect of space and food it is of theoretical importance which of the above requisites forms the chief basis of competition (Tretzel 1955), that is, whether the main basis of competition is space and competition for food is subordinated to competition for space, or whether the main basis of competition is food and competition for space is subordinated to competition for food between the animals examined.

The method for assessing competition given above would appear to make it possible to distinguish to some extent the significance of competition for food and competition for space.

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[8] The basic difference in the system of integration of the organism and the biocenosis perhaps was most neatly put by Tischler (1956, p.26), after Remane in the following comparison:

"Zelle, Vielzeller... Harmonie durch Koordination der Teile. Alle Vorgänge Dienen der Erhaltung des Gesamtsy-stems".

"Lebensgemeinschaften. Harmonie durch Antagonismus der Teile. Gesamt-system erhält sich durch gegenseitige Kompensierung der Kräfte".

For this purpose it is necessary to find out whether the total abundance
of all species (in our case the whole predatory macrofauna) is compensated
with regard to food supplies in the habitat or with regard to space in this
habitat. Do the compensative variations in abundance of each species (or each
group of species) apply to abundance expressed by the relation to abundance
of food, or to abundance expressed by the relation to the space occupied.

In order to distinguish competition for space from competition for food,
the abundance of predators in relation to the space occupied was expressed
by means of a density index per unit of capture (A), and abundance of predators
in relation to abundance of food was expressed by means of their participation
in percentages in the macrofauna (DA).

In order to make an additional check of how these relations were distributed
within the range of variations in trappability, analogical calculations were
made for trap material: the trappability of predators in relation to space (and/or
time) therefore expressed was by the number of animals in trap captures (T),
trappability in relation to food — by the percentage of predators in the whole
of the material obtained by trapping (DT).

Variations in the occurrence of the animals examined were expressed by
using the simplest coefficient of variability:

$$(1) \quad R = \frac{|a_1 - \bar{X}| + |a_2 - \bar{X}| + \dots + |a_n - \bar{X}|}{n\,\bar{X}} \cdot 100$$

where: $a_1, a_2 \dots a_n$ — A (or DA, T, DT) on each of the stations $(1, 2 \dots n)$

n — number of stations

$\bar{x}$ — mean A (or DA, T, DT) on all stations.

Calculation was therefore made of the coefficients of variations in occur-
rence (R) of the total number of predators and of each group of predators (eu-,
hemi-, and parazoophages — cf. section 2 page 000) within the field of:

1) abundance — symbol A (density per 1 sq.m.) and percentage of abundance
in the whole of the macrofauna — symbol DA,

2) trappability — symbol T (number of individuals per trap) and percentage
of trappability in the whole macrofauna — symbol DT.

These calculations were made separately for soil and separately for litter.
The results of the calculations (Tab. V) may be summed up as follows:

1) all categories of zoophages, i.e. eu-, hemi- and parazoophages in all of
the cases analysed (A, DA, T, DT in the soil and in the litter) exhibited
relatively considerable variability of occurrence on the stations investigated,
the corresponding coefficients of variability being as follows: R_A and R_{DA}, R_T
and R_{DT} did not exhibit any regular differences, R_A was not either regularly
higher or regularly lower than R_{DA}. In the same way R_T was not regularly
higher or lower than R_{DT}.

Coefficient of variability (R) of the occurrence of zoophages
in the investigated habitats

Tab. V

Ecological division	R_A	R_{DA}	R_T	R_{DT}
Soil				
Euzoophages	17	29	28	12
Hemizoophages	33	21	59	26
Parazoophages	49	50	84	104
Zoophages total	<u>13</u>	<u>9</u>	<u>39</u>	<u>7</u>
Litter				
Euzoophages	41	26	29	31
Hemizoophages	26	27	36	29
Parazoophages	43	85	89	100
Zoophages total	<u>15</u>	<u>3</u>	<u>17</u>	<u>8</u>

A — abundance, DA — percentage of total macrofauna, T — trappability, DT — percentage of total macrofauna.

2) the sum of the zoophages exhibited less variations on the stations investigated than each group of predators (with the exception of the case of absolute trappability in the soil where R_T for the sum of zoophages was 39%, while R_T for euzoophages — 28%),

3) differences between the variations in the sum of zoophages and variations in each group referred in particular to the fluctuations in the percentage of predators in the macrofauna ($\bar{D}_A$ and D_T). If R_A and R_T for the sum of zoophages were relatively similar to R_A and R_T in each group, then R_{DA} and R_{DT} for the sum of zoophages were very small (3–9%) both in the soil and in the litter. and many times lower than R_{DA} and R_{DT} in each group.

Therefore the percentage of the sum of predators in the macrofauna was very similar on different stations. Ratios between predatory and non-predatory fauna were highly stabilised, despite the considerable fluctuations in the percentage of each group of predators (eu-, hemi- and parazoophages), which indicates that these fluctuations reciprocally compensated each other: increase in the percentage of one group was accompanied by a fall in the percentage of the remaining groups. In other words the predators as a whole exhibited definite compensation of abundance (and trappability) in relation to the abundance (and trappability) of the whole macrofauna.

On the other hand fluctuations in the absolute abundance (number of animals per 1 sq.m.) and absolute trappability (number of animals per trap capture) exhibited this kind of compensative relations to a lesser degree.

In a word distinct compensative relations occurred between the groups of

predators examined only when their abundance was referred to the abundance of potential food forms. On the other hand, when referring the abundance of predators to the space occupied in the habitat this kind of compensative relations were far weaker.

Returning to the questions in the title of this section, the results presented make it possible to assume that:

1) the groups of predators distinquished in the macrofauna: eu-, hemi- and parazoophages exhibited fairly distinct competition relations,

2) the chief basis of this competition was formed by food relations, and not space relations (competition for space itself or for the habitat requisites connected with it such as spaces, of refuge, reproduction etc.); competition for space was to a certain extent subordinated to competition for food.

3.3. Did the competition relations between the groups of predators distinguished exhibit regular differentiation?

In the previous section we stated that the abundance of the whole of the predatory macrofauna was relatively stabilised, despite considerable fluctuations in the occurrence of each group: eu-, para- and hemizoophages. Thus when certain of the predators occurred more abundantly, there was correspondingly less of other predators, the stabilisation of the total abundance of predators referring chiefly to their participation in the macrofauna. These facts gave grounds for the assumption that the groups of predators distinguished reciprocally restricted their occurrence in the habitats examined and that competition between them was concerned primarily with food.

What we are now interested in is whether this kind of competitive elimination applied to a uniform degree to all the groups of predatory macrofauna examined, or whether relations between them were somehow regularly differentiated.

Analysis was made from this aspect of the following:

1) the occurence of eu-, hemi- and parazoophages,

2) occurence of the dominant systematic groups of predatory macrofauna.

1) In the soil the abundance (DA) of hemizoophages was greatest on station I and decreased with the increasing age of the wood the DA of eu- and parazoophages was the reverse — it was lowest on station I and increased with the age of the wood.

In the litter the DA of hemizoophages was lowest on station II, highest on station I. The DA of eu- and parazoophages was the reverse — highest on station II, and lowest on station I.

Finally the percentage of trappability (DT) of hemizoophages both in the
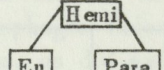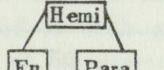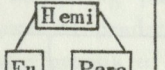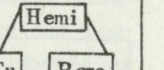
soil and in the litter was lowest on station II, while DT of eu- and parazoopha-
ges exhibited the highest values on this station.

Therefore in all the cases analysed (DA in soil, DA in litter, DT in soil
and DT in litter) eu- and parazoophages exhibited single direction variations
in occurrence, while variations in the occurrence of hemiphages were every-
where the reverse of the occurrence of eu- and parazoophages (Tab. VI).

Changes in the percentage of eu-, hemi-
and parazoophages in total macrofauna

Tab. VI

	DA						DT					
	Soil			Litter			Soil			Litter		
	I	II	III	I	II	III	I	II	III	I	II	III
Euzoophages	−	o	+	−	+	o	−	+	o	−	+	o
Hemizoophages	+	o	−	+	−	o	o	−	+	+	−	o
Parazoophages	−	o	+	−	+	o	−	+	o	−	+	o
Negative relationships	Hemi / Eu Para			Hemi / Eu Para			Hemi / Eu Para			Hemi / Eu Para		

Explanations to tab. VI, VII:
+ : maximum of occurrence, o : middle occurrence, − : minimum of occurrence, DA − percentage of
abundance in total macrofauna, DT — percertage of trappability in total macrofauna, I, II, III —
stations.

From this it follows that the balancing of the participation of predators
in the macrofauna, described in the previous section, may be the result of
competition relations between eu- and hemizoophages and between hemi- and
parazoophages. Eu- and parazoophages did not exhibit any very distinct com-
petition interrelations, or they were not at any rate directly connected. Com-
petition may take place between either of these two groups and hemizoophages
and only hemizoophages could form a link connecting the whole system of com-
petition between the predators examined in the macrofauna.

2) The quantitative relations between dominating groups were also subjected
to a similar analysis, that is: of the euzoophages — *Araneida* and *Chilopoda*,
of the hemizoophages — *Formicidae* and of the parazoophages — the zoophagous
Elateridae. Calculation was made ror these four groups of the mean percentage
(DA and DT) in the soil and litter on each of the forest stations and the maxima
and minima of occurrence of each group compared.

In the soil the percentage of abundance (DA) of *Formicidae* was highest
on station I and decreases with the increase in the age of the wood. Vice versa,
the percentage of abundance of all the remaining groups analysed, that is.

Araneida, Chilopoda and *Elateridae*, was lowest on station I and increased with the increase in age of the wood.

In the litter the percentage of abundance (DA) of *Formicidae* was lowest on station II, while the remainder of the groups analysed exhibited the highest values of DA on this station.

Trappability relations were similar to the above in both habitats. The maximum percentage of trappability DT in the soil and in the litter was attained by *Formicidae* on station I, on which the DT of the all the remaining groups exhibited the lowest values.

Thus in all the cases analysed (DA in the soil, DA in the litter, DT in the soil and DT in the litter) *Araneida, Chilopoda* and *Elateridae* exhibited variations in occurrence similar from the aspect of their direction. Variations in the occurrence of *Formicidae*, however, were everywhere the opposite of the occurrence of the three previously — mentioned groups of predators (Tab. VII).

Changes in the percentage of commonest systematic groups of zoophages
in total macrofauna

Tab. VII

| | DA | | | | | | DT | | | | | |
| | Soil | | | Litter | | | Soil | | | Litter | | |
	I	II	III	I	II	III	I	II	III	I	II	III
Aranea (A)	—	o	+	—	+	o	—	o	+	—	+	o
Chilopoda (Ch)	—	o	+	o	+	—	—	+	o	—	o	+
Formicidae (F)	+	o	—	+	—	o	+	—	o	+	—	o
Elateridae (E) (larvae of zoophagous species)	—	o	+	—	+	o	—	+	o	—	+	o
Negative relationships	A—Ch, A—F, F—E			A—Ch, A—F, F—E			A, Ch—F—E			A, Ch—F—E		

It may therefore be concluded from this, that the competition relations between the four groups of predators examined were fairly regularly differentiated. *Elateridae* did not compete with either *Chilopoda* or *Araneida*. The competion relation between *Elateridae* and the other groups of predators could therefore be of an indirect character only owing to joint competition with *Formicidae*. Similarly *Araneida* and *Chilopoda* did not compete with each other and could be related only indirectly as the result of joint competition with ants. In a word *Formicidae* occupied the special position of a connecting link between the four dominating groups of predators.

Let us now compare the results of both of the comparisons made, that is, comparisons of variations in the occurrence of eu-, hemi- and parazoophages and variations in the occurrence of dominating systematic groups of predators.

Thus the established importance of *Formicidae* in the competitive connection of the remaining dominating systematic groups: *Araneida*, *Chilopoda* and *Elateridae* confirms the role described earlier on, of hemizoophages in integrating the competition system investigated. It gives grounds for assuming that the hemizoophages (*Formicidae*) connected through competition not only the representatives of eu- and parazoophages but also each group of euzoophages: *Araneida* and *Chilopoda*, which — like the representatives of eu- and parazoophages — did not exhibit direct competition relations between each other.

Returning to the question in the title of this section we find that the competitive elimination suggested in the previous part of this paper of different groups of predators exhibited a somewhat characteristic organisation. Competition between different predators could not take place on the principle "each with each", but was played out between definite partners, while competition interrelations did not occur between the remaining partners. Parazoophages and euzoophages belonged to such groups of predators not connected by competition, as did each of the systematic groups of euzoophages analysed: *Araneida* and *Chilopoda*. Parazoophages did not compete with euzoophages. *Araneida* did not compete with *Chilopoda*. This did not, however, mean there were no biocenotic relations of any kind between them. All the groups of predators mentioned were probably connected indirectly by joint competition with hemizoophages, which in the material collected were chiefly represented by *Formicidae*. Hemizoophages could therefore form a central link in the organisation of the groups of predators examined, integrating the group into one system of competition.

3.4. Was the differentiation found in the competitive relations between predators connected with the character of their ecological specialisation

In the previous section we found that competitive elimination of predators could be observed only in the relations between hemizoophages and each of the remaining groups distinguished. The question arises next as to what properties of the hemizoophages were connected with their observed biocenotic importance.

We included with hemizoophages — in accordance with the criteria applied in this paper for the division of predators (cf. Fig. 2) the pantophagous forms in the menu of which the participation of animal and non-animal food is similar.

Thus in comparison with exclusively carnivorous euzoophages and chiefly phyto- or detrito-phagous parazoophages, the hemizoophages formed a group of forms with the most plastic food requirements, with the greatest food valence.

This property of hemizoophages can explain their competition relations both with euzoophages and with parazoophages, in the same way as the difference between the food specialisation of eu- and parazoophages forms a good justification for the proved absence of competition relations between these two groups of predators.

The case is analogical in regard to the habitat plasticity of the groups examined.

When comparing the vertical distribution in the soil of each group of predators it becomes plain that hemizoophages exhibit the greatest range of vertical penetration of the soil habitat (Tab. VIII and IX). Their mean trappability was almost identical in soil and litter (mean ratio of trappability in both these strata was 1.11), while when the trappability of euzoophages was on the average about twice higher in the litter, the trappability of parazoophages was about twice as great in the soil. The corresponding abundance relations were similar. Hemizoophages in the litter, taken on the average, were only twice as abundant as in the soil, while euzoophages were here five times as numerous, and parazoophages were ten times as numerous in the soil.

Stratal specialization of eu-, para- and hemizoophages: ratio of abundance in the litter to the abundance in the soil $(A_l : A_s)$

Tab. VIII

	Stations			Mean
	I	II	III	
Hemizoophages	2.22	1.02	3.32	2.19
Euzoophages	5.94	6.95	3.28	5.39
Parazoophages	0.02	0.17	0.08	0.09

Stratal specialization of eu-, para- and hemizoophages: ratio of trappability in the litter to the trappability in the soil $(T_l : T_s)$

Tab. IX

	Stations			Mean
	I	II	III	
Hemizoophages	0.93	1.59	0.80	1.11
Euzoophages	1.89	2.40	2.68	2.32
Parazoophages	0.29	0.77	0.51	0.52

This special range of vertical penetration of the habitat by hemizoophages may be the second — after their food plasticity — condition of their wide competition relations, since the differing habitat specialisation of euzoophages

concentrating in the litter and parazoophages adapted to the soil may be a further condition limiting competition between these forms.

Finally it would seem that the principle of greater ecological plasticity played a fundamental part in the competition connection of different systematic groups of euzoophages by hemizoophages. It is true that we do not possess more exact information on the subject of differences in the food specialisation of *Chilopoda* and *Araneida,* but the basic differences in body structure and the different ways of penetration of the habitat connected with them suggest considerable differences in the food specialisation of these two groups. *Chilopoda* are adapted to active movement within the soil habitat, while *Araneida* are more adapted to hunting within the natural free spaces in the soil and litter This is confirmed by the differences in abundance of these two groups in the layers referred to. *Chilopoda* occurred in the litter on all the stations on an average twice as abundantly as they did in the soil, while *Araneida* occurred about 16 times more abundantly.

This circumstance indicates the relatively considerable difference between the ecological specialisations of these two groups and may provide the reason for the absence of competition relations between them.

Returning to the question in the title of this section, it may therefore be assumed that the basic properties of hemizoophages, to which their importance in the organisation of the groups of predators examined must be attributed, was their relatively great ecological valence, making possible the connection of the remaining groups of predators, specialising in different directions and therefore not competing with each other.

3.5. What was the absolute abundance of predators not ecologically specialised?

The material discussed above shows that the central position in the organisation of the groups of predators examined is occupied by non — specialised forms with wide ecological valence. We shall deal with the question as to what degree the property of low specialisation was connected with the domination of occurrence of each group and species of predators.

Data on the domination of the group of predators with the least food and habitat specialisation — hemizoophages — may be set out as follows:

1) hemizoophages dominated on all the three forest stations in the material obtained by sifting soil. Their mean participation (from all the stations) was 55% of predators, — 24% of euzoophages and 21% of parazoophages,

2) hemizoophages dominated on two stations (I and III) in material obtained from sifting the litter, their mean participation being 44%, euzoophages forming 50% and parazoophages — 6%.

3) hemizoophages dominated on two stations (I and III) in material from soil traps. Their average participation was 65%, the participation of euzoophages – 13%, and of parazoophages – 22%,

4) finally hemizoophages dominated on all the forest stations in material from litter traps. Their mean participation was 59%, that of euzoophages – 32% and of parazoophages – 9%.

Thus in all the cases examined hemizoophages either dominated over each of the two other groups or were numerically equal partners with them.

Abundance relations between the dominating systematic groups of each of the food groups discussed were similarly in favour of hemizoophages. These relations are illustrated by the diagrams on Fig. 4 and 5. On these diagrams the interrelations found earler (section 3.3) were shown by the interlocking of different wheels, the size of which symbolises the mean (of all the stations) participation of each group in the macrofauna. From this comparison the distinct quantitative domination, connecting the whole system, of the *Formicidae* group can be seen.
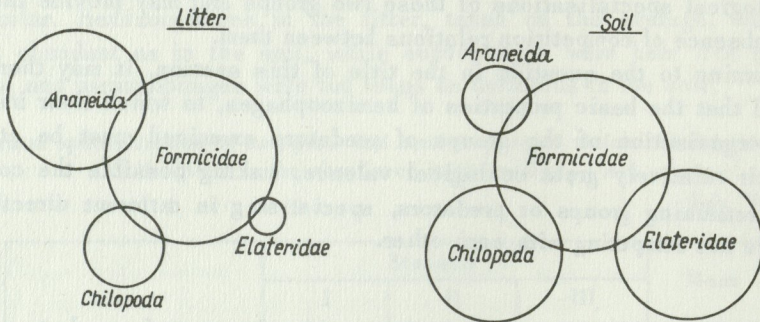

Fig. 4. Diagram illustrating the quantitative relations against the background of competition relations between dominating groups of predators (explanation in text)
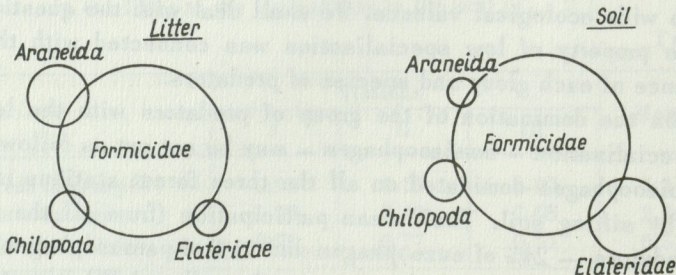

Fig. 5. Diagram illustrating trappability relations (activity) against the background of competition relations between dominating groups of predators (explanation in text)

Thus, as could be foreseen, the influence, determined earlier, of hemi-zoophages on the stabilisation of the total abundance of predators in the macro-fauna is connected not only with their low degree of ecological specialisation (section 3.4.) but also with their great abundance in the habitats examined.

The question then arises as to whether a relation of a similar kind between the ecological valence and participation in the community is a sort of more general phenomenon in the communities studied, whether it applies also to interspecific relations within the various systematic groups of predators.

In the analysis undertaken of the various systematic group their occurrence on many or on all of the stations examined was taken as the exponent of the ecological plasticity of the species investigated. Occurrence exclusively on one of the stations examined was taken as the exponent of stricter special-isation. Comparison of the participation of different species againts the back-ground of differences defined in this way was made separately for all the more abundant groups of predators, as follows:

A. *Araneida* (splitting this group into vagabond and web spiders, and ex-cluding the group of species connected with the layer of vegetation above the ground — Ł u c z a k, 1963),

B. *Chilopoda,*

C. predatory *Carabidae,*

D. predatory *Staphylinidae,*

E. *Formicidae* (splitting this group into three different ecological systems (K a c z m a r e k 1953),

F. predatory *Elateridae.*

A. *Araneida*

A.a. In the community of ground forms three species of spider occurring on all three forest stations clearly dominated: *Leptyphantes kochii, Mangora acaly-pha* and *Linyphia pusilla.* In addition *Robertus lividus* found on stations II and III and *Xysticus pini* found on stations I and II were represented relatively abundantly. The remainder of the species caught were noted only sporadically on the various stations (Tab. X).

The group of adult forms in this community was characterised by far greater habitat specialisation. No species of spider was found in it which occurred on all the forest stations, never theless here also only the species caught on two stations: *Robertus lividus* and *Leptyphantes kochii* (Tab. XI) attained greater percentages.

A.b. In the group of litter vagabond spiders three species clearly dominated on all the forest stands: *Trochosa terricola, Drassodes umbratilis* and *Tarentula fabrilis,* these three species being the only representatives of the group de-scribed occurring on all the forest stations. The remaining species were either

found on station I (such as, for example, *Xerolycosa nemoralis, Agroeca pigmea* etc.), or on station II only, (*Neon reticulatus, Enophys frontalis*) or occurred on two stations only, II and III, such as *Apostenus fuscus* and *Zora silvestris*, the last two species being characteristically slightly more numerous than the remaining species occurring on one station only (Tab. XII).

Distribution of *Araneida*. Species of the herb and shrub strata:
adults + juvenes

Tab. X

Species	Stations			
	P	I	II	III
Pachygnatha degeeri	0.7			
Dendryphantes pini		+		
Hahnia pusilla		+		
Xysticus pini		+	1.4	
Theridion varians			0.7	
Linyphia pusilla		0.9	+	+
Mangora acalypha		2.3	5.1	3.1
Leptyphantes kochii		+	10.2	0.7
Ero furcata			+	
Robertus lividus			1.5	+
Steatoda bipunctata			+	
Micrommata viridissima			+	
Total	0.7	5.1	25.1	8.2

polyhabitat species

Numbers — percentage of the total fauna of predators collected in the litter and soil strata on station I, ++ — sporadically.
Explanations to tab. X—XX

Distribution of *Araneida*. Species of the herb and shrub strata: adults

Tab. XI

Species	Stations			
	P	I	II	III
Pachygnatha degeeri	0.7			
Dendryphantes pini		+		
Hahnia pusilla		+		
Ero furcata			+	
Theridion varians			+	
Leptyphantes kochii			4.8	+
Robertus lividus			1.5	+
Steatoda bipunctata			+	
Micrommata viridissima			+	
Total	0.7	0.6	8.3	1.0

Distribution of *Araneida*. Species of the litter stratum (vagabond):
adults + juvenes

Tab. XII

Species	Stations			
	P	I	II	III
Zelotes patrensis		+		
Zelotes electus		+		
Agroeca proxima		+		
Xerolycosa nemoralis		+		
Enophys frontalis			+	
Neon reticulatus			+	
*Tarentula fabrilis**		1.0	1.9	+
*Trochosa terricola**		2.6	9.9	7.8
*Drassodes umbratilis**		1.7	1.1	3.1
Apostenus fuscus			1.4	0.7
Zora silvestris			1.7	+
Zelotes apicorum				+
Total	—	5.7	18.9	12.6

* with juvenes *Tarentula* sp., *Trochosa* sp., *Drassodes* sp.

The situation was slightly different after excluding from the group of vaga-
bond spiders the juvenile forms and considering the relations between the
adult forms only. The only species occurring on all the stations and dominating
on all the stations is then *Trochosa terricola*. Each of the remaining species
occurs on one station only and each in very inconsiderable numbers. As a result,
apart from the dominant common to all the stations, each station possesses
a specific group of species (Tab. XIII).

Distribution of *Araneida*. Species of the litter stratum (vagabond): adults only

Tab. XIII

Species	Stations			
	P	I	II	III
Zelotes patrensis		+		
Zelotes electus		+		
Agroeca pigmea		+		
Xerolycosa nemoralis		+		
Tarentula fabrilis		+		
Apostenus fuscus			+	
Enophys frontalis			+	
Neon reticulatus			+	
Trochosa terricola		1.7	2.8	2.1
Zora silvestris				+
Zelotes apicorum				+
Drassodes umbratus				+
Total	—	2.9	3.5	3.1

A.c. A similar phenomenon, but in as even distincter form, occurrs in the group of ground web spiders[9]. This group is represented on all the stations by different species of adult spiders and each station has its own dominants (e.g. *Centromerus silvaticus* on station III, or *Erigone dentipalpis* on the field station — *P*, Tab. XIV).

Distribution of *Araneida*. Species of the litter stratum (netting): adults

Tab. XIV

Species	Stations			
	P	I	II	III
Pocadicnemis pumilla	+			
Erigone dentipalpis	1.4			
Micryphantes rurestris		+		
Centromerus incilium			0.8	
Gonatium rubens				+
Macrargus rufus				+
Micrargus herbivorus				+
Micryphantes gulosus				+
Centromerus silvaticus				1.7
Total	1.5	+	0.8	2.3
Juvenes total	1.4	0.6	8.0	5.8
Adults + juvenes	2.9	0.7	3.8	8.1

The results of all the tables of domination of spiders may be summed up in the following two sentences:

1) in all the spider communities analysed species occurring on several stations dominated numerically over species caught on one station only,

2) mature forms of the spiders examined exhibited greater differences in their occurrence than the juvenile forms; while the juvenile forms of many species occurred on different stations (*Drassodes umbratilis, Trochosa terricola, Tarentula fabrilis, Leptyphantes kochii, Mangora acalypha* and *Linyphia pusilla* on all the forest stations), of the adult forms only *Trochosa terricola* was found on all the forest stations and only *Robertus lividus* and *Leptyphantes kochii* on two stations.

These results indicate that:

1) the domination of the species of *Araneida* examined was connected completely clearly and regularly with their habitat plasticity, and

2) as the individuals matured habitat specialisation and isolation of the

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[9] On account of the difficulties in identifying the juvenile forms in this group it was not possible to draw up complete tables of domination.

species progressed in the associations of *Araneida*, accompanied by habitat dismemberment of the initial large association of juvenile forms into individual groups of adult forms with different dominants, strictly specialised in respect of habitat.

B. *Chilopoda*

An analysis of the *Chilopoda* association similar to that made of the spider material, encounters considerable difficulty on account of the incommensurably weaker habitat specialisation of the species, causing the existing differentiation of the stations examined to yield an inadequate picture of the habitat dismemberment of the association. With the exception of a few species occurring on two stations only, all the other species of *Chilopoda* were found on all the forest stations investigated.

Nevertheless, if all the cases of sporadic occurrence of species are rejected, it is then clear that here as well the two dominating species *Geophilus flaviolus* and *Pachymerium ferrugineum* prove to be the only abundatly represented species on all the forest stations, and are thus the species with the lowest degree of habitat specialisation in the community (Tab. XV).

Distribution of *Chilopoda*

Tab. XV

Species	Stations			
	P	I	II	III
Hemicops fulvicornis	1.8			
Lithobius nigroculis		+	1.1	+
Lithobius agilis		+	2.2	+
Lithobius lapidicolla		+	1.5	+
Monotarsobius crassipes			2.6	+
Lithobius erythrocephalus		1.5	4.0	+
Pachymerium ferrugineum		1.5	8.4	3.3
Geophilus flaviolus		5.8	1.8	6.2
Monotarsobius curtipes		+	2.2	2.6
Lithobius forficatus		+	+	6.2
Lithobius piceus		+		+
Monotarsobius aeruginosus		+		+

C. Predatory *Carabidae*

In this group of predators, contrary to *Chilopoda*, the connection between habitat specialisation and domination of the species is very distinct. The two

interchangeably dominating species: *Calathus micropterus* and *Calathus erratus*, jointly belonged with *Bradycellus collaris* to the only representatives of forms found on all the forest stations. The occurrence of the remaining less numerous species was connected with different stations (Tab. XVI).

Distribution of predacious *Carabidae*

Tab. XVI

Species	Stations			
	P	I	II	III
Clivina collaris	31.2			
Clivina fossor	10.4			
Pseudophonus pubescens	2.8			
Bembidion quadrimaculatus	0.8			
Calathus fuscipes	+			
Miscodera arctica		+		
Microlestes minutulus		1.2	+	
Pterostichus angustatus		0.8	2.0	
Bradycellus collaris		1.6	0.8	0.8	polyhabitat
Calathus erratus		2.8	0.4	1.2	species
Calathus micropterus		1.2	8.4	8.8	
Leistus ferrugineus			1.2	1.2
Cychrus rostratus				+
Stomis punctulatus				+
Notiophilus biguttatus				+
Calathus melanocephalus				+
Pterostichus oblongo-punctatus				0.8
Notiophilus aquaticus				2.0
Mesoreus wetterhalli				2.8
Epaphius secalis				3.2
Anchus obscurus				5.6

A separate group of *Carabidae* with its own dominant — *Clivina collaris* — occurred on the field station. The large number of species caught sporadically in the group of *Carabidae* particularly rich faunistically, on station III, is noteworthy.

D. Predatory *Staphylinidae*

A similar situation was noted in the association of predatory *Staphylinidae*. The dominating species on all the forest stations — *Xantholinus linearis*, here also belongs to the group of species with the least degree of habitat specialisation (occurring on all the forest stations). There is a separate association,

with *Xantholinus elongatus* as dominant, on the field station. The relatively larger number of species caught sporadically on station III, which is the richest in species, is remarkable (Tab. XVII).

Distribution of predacious *Staphylinidae*

Tab. XVII

Species	Stations			
	P	I	II	III
Xantholinus elongatus	5.6			
Philonthus nigritulus	2.7			
Philonthus debilis	1.9			
Heterotops dissimilis	+			
Xantholinus tricolor		2.7	+	+
Xantholinus linearis		10.3	3.7	6.5
Philonthus fuscipennis		+	+	1.9
Astilbus canaliculatus		+	+	+
Bryocharis formosus				+
Philonthus varius				+
Philonthus sanguinolentus				+
Staphylinus erythropterus				1.9

It may be added in passing that in the association of saprophagous *Staphylinidae*, the relation of slight habitat specialisation and domination of species occurred even more distinctly. *Tachyporus hypnorum*, dominating here on all the forest stations, would appear — in view of the fact that it is also found on the field station — to be an undoubtedly eurytopic species (Tab. XVIII).

Distribution of saprophagous *Staphylinidae*

Tab. XVIII

Species	Stations				
	P	I	II	III	
Oxytelus rugosus	5.6				
Bledius sp.	2.8				
Tachyporus chrysomelinus		1.9			
Astenus angustatus		1.9	1.9		
Astenus filiformis		2.8	+	+	
Tachyporus hypnorum	+	4.7	16.7	4.7	eurytopic species
Tachyporus solutus		+			
Lathrobium longulum		3.7			

E. *Formicidae*

As demonstrated in an earlier paper on the associations of pine forest ants (Kaczmarek 1953) *Formicidae* do not constitute a uniform association. The ecological analyses contained in the above paper made it possible to distinguish three groups of ants aggregating forms in different classes of size. In the class of medium forms it proved possible to assign several characters distinguishing this group to the rank of an organised association (the *Lasius niger* group). A characteristic property of this association was the sharp reactions of its structure to the presence of large species of ants of the sub-genus *Formica*. The presence of these species particularly strongly inhibited the occurrence of *Lasius niger*, the dominant of the association. This was probably caused by the fact that *Lasius niger* forms a network of paths, this type of living space being characteristic of the species of the sub-genus *Formica Formica* also, while it does not occur in so distinct a form in other important representatives of the *Lasius niger* association. It is therefore probably that the necessity for the paths to intersect makes joint occupation of the area by species possessing this type of living space impossible, which is the reason why the author almost everywhere found that *Lasius niger* was completely absent in the living space of the colonies of the species *Formica rufa* and *Formica nigricans*.

The materials used in the present paper fully confirm these relations, together with the earlier suggestion as to the universality of the *Lasius niger* association in different habitats in connection with the eurytopis character of this species.

Lasius niger was a dominating species in the field habitat also, as it was in the oldest forest station (station III), its relatively small abundance on stations I and II being undoubtedly connected with the occurrence on these stations of *Formica nigricans* (Tab. XIX). *L. niger* was replaced on these stations by another polyvalential species of the association — *Serviformica fusca*.

A part similar to that played by *L. niger* in the group of medium forms, is played by *Tetramorium caespitum* in the group of small forms. This eurytopic species was distinctly dominant on all the forest stations, the decrease in its abundance with the increase in the age of the wood being accompanied by an increase in the abundance of its partners of the genus *Leptothorax* and the entry into the association on station II of *Stenamma westwoodi* (Tab. XIX).

In the case of the group of large forms, a description of their association would require, on account of the extensiveness of the nesting areas (in particular of species of *Formica*) far larger experimental areas that the study areas on the stations.

Distribution of *Formicidae*

Tab. XIX

Species	Stations				
	P	I	II	III	
Small forms:					
Stenamma westwoodi				+	
Leptothorax acervorum		+		+	
Leptothorax muscorum		+	0.3	2.2	
Tetramorium caespitum	+	28.7	10.5	6.7	eurytopic
Solenopsis fugax		+	+		species
Middle forms:					
Myrmica rugulosa	+				
Myrmica sabuleti			+		
Lasius niger	0.3	0.9	1.0	6.9	eurytopic
Formica fusca		12.1	1.6	0.3	species
Myrmica schencki		+	+	0.6	
Myrmica lobicornis		+	+	0.4	
Myrmica rubra			+	0.6	
Myrmica scabrinodis				0.7	
Myrmica rubra var. microgyna				0.2	
Myrmica laevinodis				0.2	
Large forms:					
Formica sanguinea		3.9	1.4	2.5	
Formica nigricans		0.6	0.6		

F. Predatory *Elateridae*

Finally the small collection of wireworms exhibiting predatory tendencies also exhibited characteristic differences in abundance, consisting in the marked domination of eurytopic species; the eurytopic species *Selatosomus aeneus* dominated on all the stations in the wood, while the second eurytopic species, *Dolopius marginatus*, dominated in the field. *Prosternon holosericeum*, occurring only on forest stations, was clearly less numerous on certain stations, yet more numerous than *Melanotus rufipes*, found only on station III (Tab. XX).

In summing up the results of all above comparisons we find that in all the systematic groups of predators considered, quantitative domination of species was everywhere connected with their large ecological valence, and applied to species distinguished by the least habitat specialisation and greatest plasticity of habitat requirements.

As we stated earlier on — these same two properties would appear to determine the part played by hemizoophages, as a group organising competition

between predators in the field of relations between food groups. We may therefore assume that the wide ecological valence was a common factor in the organisation of the communities of predators examined in the field of interspecific relations within each systematic group also.

Distribution of predacious *Elateridae* (larvae)

Tab. XX

Species	Stations				
	P	I	II	III	
Dolopius marginatus	4.0	+	2.8	2.8	eurytopic
Selatosomus aeneus	0.5	3.0	21.8	8.2	species
Prosternon holosericeum		+	2.3	1.0	
Athous subfuscus			1.0	2.5	
Melanotus rufipes				0.5	

3.6. Which groups of predators formed the eliminated party, and which the eliminating?

During work on this material discovery was made of the phenomenon of quantitative stabilisation of the percentage of predators in the macrofauna, forming evidence of probable competition relations based on food relations. Closer analysis of this phenomenon made it possible to indicate certain of these relations, such as, e.g. the relation between hemizoophages and euzoophages, or between hemizoophages and parazoophages, between *Formicidae* and *Araneida,* or between *Formicidae* and *Chilopoda* etc. In making a closer analysis of these relations, the conclusion was reached that the chief factor responsible for the differences found in competition relations was the ecological plasticity of certain predators. Finally, by correlating this plasticity with the quantitative occurrence of different groups and species it was concluded that the unspecialised forms are of fundamental importance in the organisation of the biocenotic system investigated.

The final problem to which we shall try to find at least a partial solution, is the question as to "who" was the active side in the competition relations found; "who" eliminated "whom".

The answer to this question may be sought for in the way in which the groups examined reacted to variations in habitat conditions. We shall discuse these in turn.

The relatively simplest picture was that of the variations in the percentage of abundance (*DA*) of predators in the soil. The participation of hemizoophages

decreased here with the age of the wood, while the participation of eu- and parazoophages gradually increased. Similarly the participation of dominating systematic groups (*Formicidae, Chilopoda* and *Elateridae*) varied, each of these dominating groups, judging from the extent of participation, determining the basic direction of variations in the participation of predators of an appropriate food type. Thus variations in DA of *Chilopoda* determined the direction of variations in the DA of euzoophages. Variations in the DA of *Elateridae* — the direction of variations in the DA of parazoophages (Fig. 6).
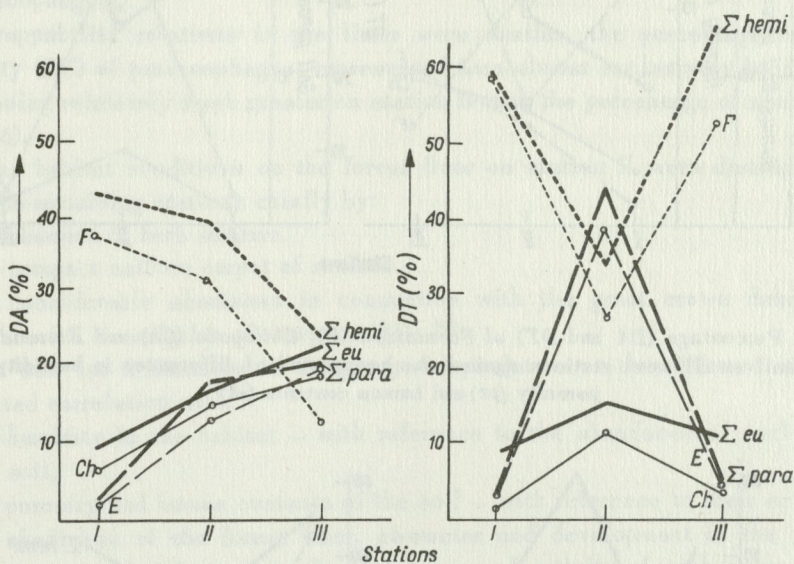
Fig. 6. Percentage (DA and DT) of the sum of hemizoophages (hemi), euzoophages (eu) and parazoophages (para) and *Formicidae* (*F*), *Chilopoda* (*Ch*) and *Elateridae* (*E*) in the soil macrofauna of different stations

Among the basic properties of the soil analysed (cf. Tab. I) variations in the percentage of *Formicidae, Chilopoda* and *Elateridae* were correlated only with variations in humidity, this correlation being most distinct in *Formicidae*, the participation of which in the macrofauna was almost exactly in reverse proportion to soil humidity (Fig. 7).

The percentage of trappability (DT) of predators in the soil was funda-mentally different. *Formicidae* exhibited minimum DT, and therefore the lowest degree of activity on station II, where *Elateridae* and *Chilopoda* exhibited particularly great activity (high values of DT Fig. 7).

The distinct disturbances of the activity of predators on station II were accompanied by particularly small porosity and humus contents in the soil (Fig. 7).
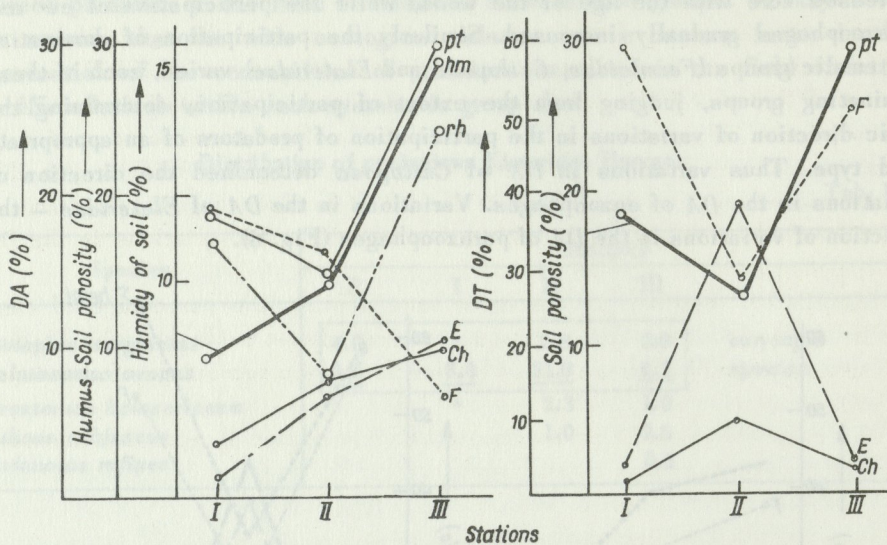
Fig. 7. Percentage (*DA* and *DT*) of *Formicidae* (*F*), *Chilopoda* (*Ch*) and *Elateridae* (*E*) in the soil on different stations against the background of differences in humidity (*hm*), porosity (*pt*) and humus contents (*rh*)
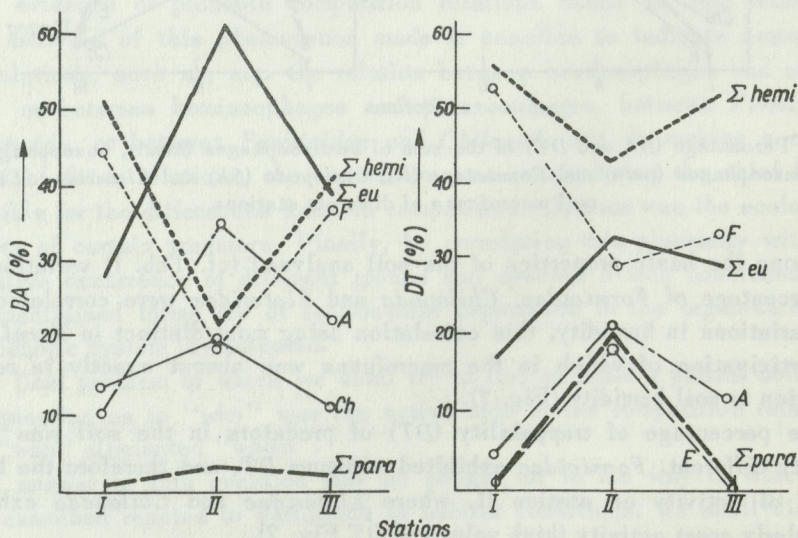

Fig. 8. Percentage (*DA* and *DT*) of the sum of hemizoophages (hemi), euzoophages (eu) and parazoophages (para) and *Formicidae* (*F*), *Chilopoda* (*Ch*), *Araneida* (*A*) and *Elateridae* (*E*) in the litter macrofauna on different stations

In the litter none of the groups of predators examined exhibited distinct trends in the variations of their participation in relation to the age of the wood.

The percentage of abundance (DA) of hemizoophages was decidedly lowest on station II, the DA of euzoophages being highest on this station; the DA of parazoophages, in general small, also exhibited a slight increase on station II, *Formicidae*, as can clearly be seen from the graphs on fig. 8 — being responsible for the course taken by variations in the DA of hemizoophages, and *Araneida* and *Chilopoda* being responsible for the course taken by variations in the DA of euzoophages.

Trappability relations in the litter were similar, the percentage of trappability (DT) of parazoophages, represented here almost exclusively by *Elateridae*, being relatively much greater on station II than the percentage of abundance (Fig. 6).

The habitat conditions on the forest floor on station II were distinguished from the remaining stations chiefly by:

1) absence of herb stratum

2) compact uniform carpet of mosses

3) considerable shadiness in connection with the great crown density of the pines (cf. description of stations, Tab. II).

To sum up, differences in the groups of predators on the different stations exhibited correlation with:

1) humidity in the habitat — with reference to the abundance of each group in the soil,

2) porosity and humus contents of the soil — with reference to their activity,

3) shadiness of the forest floor, character and development of the ground vegetation — with reference to the abundance and activity of each group in the litter.

The results set out in previous sections are evidence that the antithetic variations on abundance and trappability observed cannot be related in their entirety to the habitat reactions of different animals. If, for instance, we observe that the increase in soil moisture is correlated on one hand with a decrease in the abundance of ants, and on the other with an increase in the abundance of *Chilopoda* or *Elateridae* we cannot relate these decreases and increases in abundance in their entirety to the hygrophobia of the first group and the hygrophilia of the remaining groups. Such interpretation is contradicted by the balancing of the participation of predators in the macrofauna, observed in section 3.2, which observation could indicate the fact of the competition influences altering the simple habitat reactions of each group of predators.

On the other hand, however, the fact that the total abundance and trap-

pability of predators are balanced does not exclude the essential influences of the habitat. It only shows that these influences directly affect only definite forms and through their competition relations with the remaining predators can be transmitted to the whole of the community examined.

The aim of the analysis now being mede is not therefore to prove that competition is present, but only to seek out those groups of predators which most directly reacted to variations in habitat conditions, since they must have been the "first link" in the chain of the compensative reactions described earlier on.

Aften this short preliminary explanation we can proceed to an evaluation of the habitat correlations found.

In the first place we must consider the correlation between the abundance of different predators and the soil moisture. *Formicidae* exhibited here a negative correlation, *Chilopoda* and *Elateridae* — a positive one, the correlation of the percentage of *Formicidae* with soil humidity being far more distinct than in the remaining groups; this applied not only to the general direction of variations but also to the measure of reduction of ants with the increase in soil moisture (Fig. 7). This would indicate that — as stated above — direct dependence on soil humidity is exhibited by *Formicidae* only, while variations in the abundance of both the remaining groups were the result of their competition with ants, and hence were only indirectly connected with soil humidity.

Unexpected confirmation of this assumption is supplied by variations in the activity of the groups under discussion, that is, the particularly small activity of *Formicidae* on station II with the particularly high activity on this station of *Chilopoda* and *Elateridae*. This phenomenon is connected in a natural way with the particularly low porosity of the soil[10], which may explain the small activity of *Formicidae*, but cannot explain the particularly high activity of *Elateridae* and *Chilopoda*. It is true that both these groups of animals are perfectly well adapted to active movements in the soil, which adaptation endows them with considerable privilege in relation to *Formicidae* as far as penetration of especially compact soil is concerned, nevertheless it is difficult and even impossible, to hold the opinion that owing to their adaptation *Chilopoda* and *Elateridae* penetrated compact soil more efficiently than porous soil. It should rather be assumed that the low porosity of the soil on station II exerted a stimulating influence indirectly on the activity of *Chilopoda* and *Elateridae*, by limiting the activity of ants. In other words the low porosity of

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[10] It is difficult to assume that the second correlated habitat factor — humus contents — could exert a stronger influence on the activity of macrofauna than the factor considered, i.e. soil porosity.

the soil directly affected the decrease in activity of ants, which in turn through competition relations probably facilitated the increase in activity of *Elateridae* and *Chilopoda* which are better adapted to compact soil.

Let us now turn to relations between predators on the litter.

Here we must consider the correlation between the occurrence of predators and the two properties of the habitat: the character and development of the ground vegetation and shadiness.

The absence of the herb stratum, as a factor responsible for the differences found in the occurrence of litter predators can probably be overlooked, at least as far as *Chilopoda* and *Araneida* are concerned. The first of these live exclusively in the soil and litter, and in the case of the second — particularly in relation to the numerous species found in both litter and ground vegetation — the absence of the herb stratum could at most be a factor limiting abundance, whereas it is on station II, devoid of the herb stratum, that these spiders occurred in the greatest numbers.

Theoretically the absence of the herb stratum might influence the low numbers of *Formicidae* found on station II, by limiting the sources of food in the form of the aphids occurring in this stratum. The low numbers of ants in the litter of this station however, can be adequately explained by the considerable degree of shadiness of the forest floor. The direct and fundamental effect of this factor is indicated by: 1) very distinct correlation between variations in shadiness and abundance of ants with the age of the forest (Fig. 9); 2) earlier observations of the effect of shadiness on the abundance of ants in the pine wood (Kaczmarek 1953).

This would indicate that, as in the soil, in the litter also *Formicidae* formed that group of predators which — according to previous reasonings — was the recipient of habitat influences and transmit-

Fig. 9. Percentage of abundance (*DA*) of *Formicidae* (*F*), *Araneida* (*A*), *Chilopoda* (*Ch*) and *Elateridae* (*E*) in the litter macrofauna on different stations against the background of differences in the lighting of the forest floor

ted them to the remainder of the predators in the whole system, shaping their abundance correspondingly to its own abundance induced by the habitat.

Thus a closer analysis of the material, and in particular a closer analysis of the behaviour of spiders, supplies a large number of confirmatory arguments.
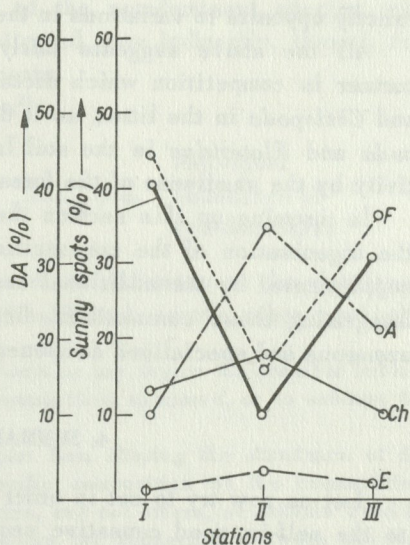
The first argument may be the considerable difficulty in explaining the abundance found in the litter of different groups of euzoophages by variations in shadiness. *Araneida* in particular, at least as far as the species of the families *Lycosidae* or *Linyphidae* dominating on the shadiest station II are concerned, are shadeloving animals. The second argument which suggests that the great abundance of *Araneida* on station II was not connected with the high degree of shadiness of the forest floor lies in the fact that a considerable number of heliophilous species living in the herbal stratum occur here in the litter, such as: *Leptyphantes kochii*, *Mangora acalypha*, *Robertus lividus* and *Xysticus pini* (cf. Tab. X, XI). The third argument suggesting that the particularly great abundance of *Araneida* on station II was connected more with biocenotic than with habitat factors may be fact of the particularly numerous occurrence on this station of juvenile individuals of spiders (Tab. X, XII, XIV). Finally, as shown by Fig. 9, variations in the percentage of spiders were exactly opposite to variations in the percentage of ants.

All the above suggests fairly distinctly that *Formicidae* could be the partner in competition which dictated the abundance and activity of *Araneida* and *Chilopoda* in the litter, as it dictated the activity and abundance of *Chilopoda* and *Elateridae* in the soil layer, itself limited in its occurrence and activity by the shadiness of the forest floor the humidity and porosity of the soil.

In summing up this section the conclusions we have reached so far as to the organisation of the communities of macrofauna examined may therefore be supplemented by the additional assumption that the non-specialised dominants integrating these communities dictated the abundance of the remaining, less numerous and specialised components of the community.

4. SUMMARY OF CONCLUSIONS

Let us now try to set in order the chief conclusions of this work according to the self-imposed causative sequence, that is, starting with the part played by habitat conditions in the chain of the phenomena observed.

The following were analysed in this paper:
1) the influences of the more important habitat factors:
a) different habitat factors
b) abundant food supply
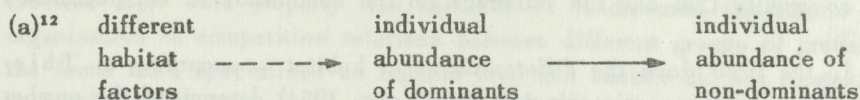2) the influence of differentiation of the habitat.

1a) As indicated by the results of section 3.6., the different, habitat factors analysed (humidity, soil porosity, shadiness of the litter) provided a good explanation of the abundance and activity of the dominating group of predators — *Formicidae* (hemizoophages). The abundance of the remaining groups, repre-

sented by smaller numbers of individuals, was not directly dependent on the habitat factors analysed, but on biocenotic factors, that is, the abundance and activity of *Formicidae* – imposed by the above habitat factors – would seem in turn to define the abundance and activity of *Elateridae* (parazoophages) *Chilopoda* and *Araneida* (euzoophages).

Relations were – as it seems – similar in the case of the habitat within each of the groups of predators. This problem, on account of the lack of suitably detailed material, was not closely analysed in this paper. Nevertheless even these very general data on the occurrence of each species, combined with earlier analyses (Kaczmarek 1953) make it possible to assume that, for example, in the communities of *Formicidae* the dominating species transmitted the habitat influences to the remaining, less numerous species of the community (section 3.5., p. 458).

Thus each habitat factor influences – as it seems – the abundance of the dominating forms. Abundance and activity of the non-dominant species was connected with the habitat properties investigated more indirectly, through the competitive limitations imposed by the dominants.

This relation may be presented as follows[11]

(a)[12]   different   individual   individual
           habitat   – – – – →   abundance   ————→   abundance of
           factors   of dominants   non-dominants

lb) An abundance of food did not extert a direct influence on the abundance of any of the predator groups considered. It affected, on the other hand, the

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[11] The enclosed plan does not pretend to exhaust to any degree the possible habitat influences on the structure of the biocenotic communities examined, or to exhaust the factors influencing the abundance of dominants.

The complex of defined habitat factors, apart from shaping the abundance of dominants, also undoubtedly conditions the specific composition of the communities examined and determined that certain such species, and not others, of animals lived in the habitat. Tretzel (1955) perhaps best renders the connection between the two regularities discussed in hi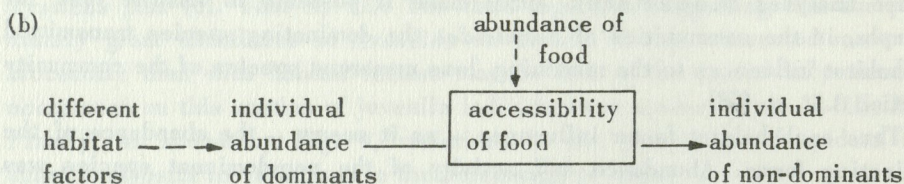s work on competition among spiders, when he writes: "Ist eine Konstellation abiotischer Faktoren Voraussetzung für das Vorkommen einer Art überhaupt ("Verteilung")..., so dürfte die Stärke der Entfaltung ("Produktion") durch Konkurrenzfaktoren bestimmt und reguliert werden" (p. 87).

On the other hand the abundance of the dominant may be, and undoubtedly is, controlled in addition by several other factors apart from habitat ones, such as, for instance, predators of a higher order, parasites, intrapopulation limitations etc. For example, in the case of *Formicidae* dominating in the communities examined it would seem that an important factor regulating their occurrence is formed by – according to Paczoski's assumptions (1925) – strictly defined intrapopulation relations.

[12] In plans from (a) to (d) the relations based on the relation organism-habitat were denoted: – – →, resulting from interpopulation relations: ————→, resulting from intrapopulation relations: ·······→.

total number of all predators through the medium of competition relations between their different groups (species), that is, the dominating forms of predators limited the abundance of the remaining predators to a degree highly proportional to the abundance of the whole macrofauna, and therefore to the potential abundance of the common food. This was expressed by the considerable evenness, described in section 3.2, of the percentage of the total number of predators in the macrofauna of different stations with simultaneous very great fluctuations in the percentage of each of the groups of predators distinguished.

This relation — supplementing plan (a) — may be represented as follows:

(b)   abundance of
                                             food

different   individual   accessibility   individual
habitat — — →   abundance ————   of food   ————→   abundance
factors   of dominants   of non-dominants

2) The role of differentiation of the habitat in the sequence of relations described applied to two questions: its influence on the faunistic differentiation of the community (2a) and the influence on the domination of non-pecialised forms (2b).

2a) In the first place the differentiation of habitat — according to Thienemann's first biocenotic principle (1920 acc. 1954) determined the number of species in the community, as is indicated by the results described in section 3.1, p. 438.

The biocenotic consequence of this relation was the decrease, observed with the increase in the number of species, of the total number of individuals in the community (section 3.1, Tab. IV). This phenomenon was evidence — in accordance with the discussion made (p. 438) — that the effects of the competitive struggle analysed between different species of the macrofauna were not limited to division on the existing habitat requisites between competitors. In addition the competing species hampered each other in the collective utilisation of the habitat. Competition limited the accessibility of habitat requisites to a degree in proportion to the number of competing species, and therefore in proportion to the number of competitive contacts between different populations.

Finally, the decrease, caused by intensified competition, in the number of individuals in the macrofauna was distinctly correlated with the increase in activity of the animals (Fig. 3), which phenomenon, most probably resulting from intrapopulation relations (tendencies to maintain contacts between individuals in a thinned population) must at the same time have led to an increase in contacts between species reduced as a result of competitive isolation of species.

The whole of the phenomena mentioned under 2a) may therefore in the sequence of relations described be noted as follows:
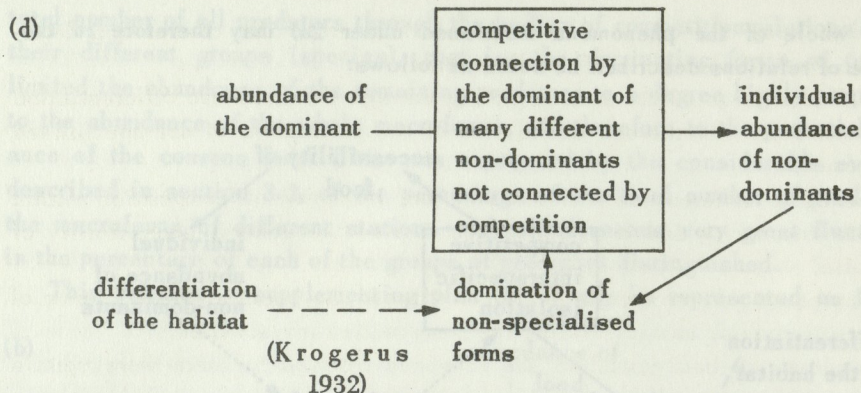
(c)
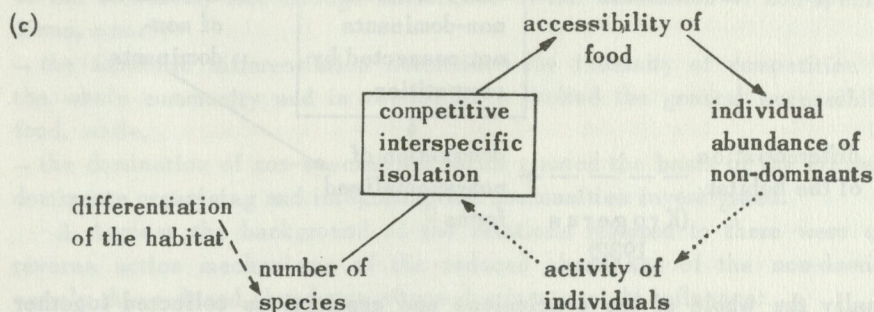
2b) the second property of the communities examined probably to some extent connected with differentiation of the habitat was the common domination, indisputably confirmed in this work, of ecologically non-specialised predators[13] (section 3.5). This property was certainly of fundamental importance in the organisation of competition relations between different groups of predators — the forms more specialised as regards food and habitat did not compete with each other but competed with the non-specialised dominating forms. As a result of this the dominating forms could form the central link integrating the competition systems of predators investigated, a sort of centre forming the structural units in the communities of predatory macrofauna examined.

Since simultaneously — as is shown by earlier discussion — the biocenotic relations between the predators examined were so formed as to sugest that the non-specialised dominants eliminated the less numerous specialised forms, the effect of this competition might be the intensification of the numerical predominance of the dominants; the initial numerical predomination — caused by differentiation of the habitat — of the non-specialised forms might be increased a second time as a result of the competitive elimination of specialised forms by the dominants.

Representing this in the categories of the developed plan of relations we obtain the following picture:

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[13] According to K r o g e r u s rule of domination (1932) the individual abundance of species ecologically non-specialised increases with the differentiation of the habitat, while that of specialised species decreases.

(d)

abundance of
the dominant ——

competitive
connection by
the dominant of
many different
non-dominants
not connected by
competition

individual
abundance
of non-
dominants

differentiation
of the habitat

domination of
non-specialised
forms

(K r o g e r u s
1932)

Finally the whole of the conclusions and assumptions collected together
here (Fig. 10) make it possible to conclude the following:

1. The basic trend of the biocenotic relations observed ran from the influence
of different habitat factors on the individual abundance of dominants — through
the competitive limitation by dominants of accessibility of food the remaining
forms — to compensative variations in the abundance of non-dominants.

2) Abundance
of food

Specific composition
of community

1) Different
habitat factors

Individual abundance
of dominants

Inter-specific
competition

Accessibility
of food

Individual
abundance
of non-dominants

Intensity
of competition

Intensity
of contacts

Number of species
in community

Organisation
of competition

Activity
of individuals

3) Differentiation
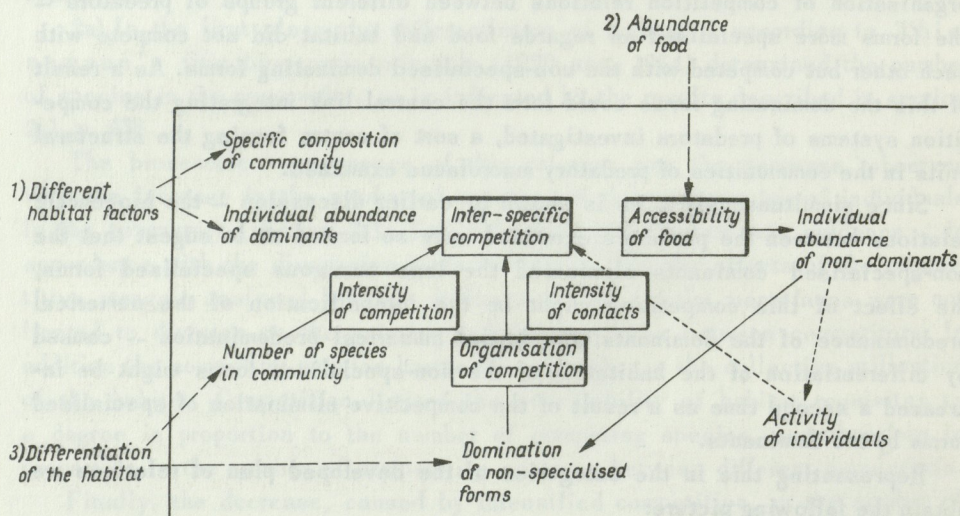of the habitat

Domination
of non-specialised
forms

Fig. 10. Plan illustrating the results of the work in regard to habitat influences on the
organisation of competition in the communities of predacious soil fauna examined

2. The following had a modifying influence on the given sequence of re-
lations and its effects:

A) abundance of food, in relation to which interspecific competition determined the level of abundance of non-dominants;

B) differentiation of the habitat acting through the faunistic differentiation of the community and through stimulation of the domination of non-specialised forms, namely:

– the faunistic differentiation determined the intensity of competition within the whole community and in consequence limited the general accessibility of food, while,

– the domination of non-specialised forms created the basis of the influence of dominants organising and integrating the communities investigated.

3. Against the background of the relations referred to there were certain reverse action mechanisms of the reduced abundance of the non-dominants, namely this reduced abundance of non-dominants might influence:

A) competitive interspecific isolation trought variations in the activity of individuals,

B) the organisation of competition through intensifying the numerical predomination of dominants

5. DISCUSSION OF RESULTS IN THE LIGHT OF RELEVANT LITERATURE

The results obtained in this work correspond in particular with those considerations of competition which are concerned with the formation of defined quantitative relations between species in the biocenosis (cf. introduction 1.1., p. 424).

Descriptions of the participation of different species (% Abundanz – Oekland 1930, Dominanz – Palmgren 1930) form the basic and oldest method of quantitative description of animal communities. This method, like the majority of methods describing the structure of animal communities, was taken from phytosociology and was at first used solely for comparison of different communities and definition of the differences between them (Nefedov 1929, Oekland 1930, Palmgren 1930, Krogerus 1932, Brundin 1934). To facilitate such comparisons the species were divided into several classes of relative abundance: dominants and non-dominants, or dominants, influents and recendents. The Polish terminology used in this classification was introduced by Petrusewicz (1938).

At first the divisions into the classes of abundance mentioned above were conventional, for instance, Oekland took as his criterion of domination a percentage of species above 50%, Palmgren a percentage over 5%, Brundin was of the opinion that arbitrary criteria were unacceptable and that the criterion of domination should be defined separately for each community depending on the total number of species forming it.

A fundamentally new element was introduced to this problem in the work by Gause in 1936. Gause, in summing up the results of his varied experimental researches, supplemented them by a description of the domination relations which he succeeded in calculating for the abundant material of the entomofauna collected in 1932 by Beklemišev and his co-workers. By drawing the curve of domination so that he placed on one axis the percentage of the species in -the community and on the other axis the number of species with this percentage, he obtained a detailed picture. The curve exhibited the characteristic inconsecutiveness appearing in the form of the absence of species with a certain transitional participation in the community. There was a extremely distinct gap in the form of absence of species of a transitional character between the class of greatest abundance and the class of lowest abundance (Fig. 11).
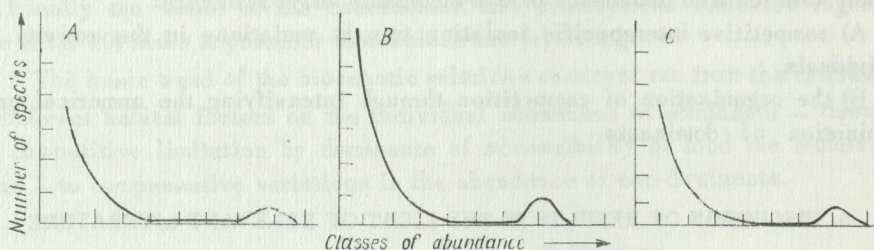

Fig. 11. Curves of distribution of species in classes of abundance acc. to Gause, from data given by Beklemišev (A) and Duplakov (B), and acc. to Lityński (C)

Together with the discovery of this inconsecutiveness the category of dominants obtained for the first time in zoocenotic research a naturally real criterion of differentiation, while the concept of domination structure (in German — Abundanzstaffelung, Tretzel 1955) took on a new significance in ecological investigation[14]. The inconsecutiveness of domination structure,

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[14]In the research initiated by Gause on domination structure, a separate place is occupied by analyses of the causes of the phenomenon itself of the decrease in the number of species represented by an increasingly large number of individuals, that is, analyses of the causes of the total formation of the domination curve without entering into the moments of its inconsecutiveness. In the light of research (Margalef 1958, Wiliams 1944 and others) this kind of hyperbolic distribution of frequency (cf. Fig. 11) refers literally to all phenomena and objects on the face of the earth (including, e. g. surnames in a telephone directory) and thus would seem to refer to some kind of purely fortuitous regularity. It would therefore follow that the hyperbolic formula of domination structure is the result of the imposition of the abundance of each species by fortuitous differentiation of the habitat, and can therefore only be a module, a point of reference for more exact biocenotic research. It is the deviations from this module, and therefore the inconsecutiveness of domination structure, which can provide information on the biocenotic arrangement of relations between species.

hitherto overlooked, began to be generally noticed and recorded in research work. Petrusewicz (1938) found it in investigations of spider communities, concluding that he never encountered difficulties in distinguishing dominating species, since their abundance always clearly predominated over the abundance of the remaining species, Lityński (1938) confirms the universality of this inconsecutiveness of domination structure in different plankton and benthos communities of lake and river fauna. Further, he succeeded in proving that this inconsecutiveness is gradually formed in the community. It is correlated with the development of the community in the yearly cycle and with the increase in density of the fauna. At first the species do not exhibit such great differences in abundance and it is not until the community develops further that the phenomenon of distinct predominance of dominating species over the abundance of the basic mass of the remaining species begins to occur.

These observations — in Lityński's opinion — indicate the connection between an inconsecutive domination structure and competition relations. As justification for this view Lityński cites as an additional argument the known commonness of a similar type of domination in the balanced "closed associations" of vascular plants, where the fundamental role of competition would seem to be for him a proved fact. Wautier (1952) reaches similar conclusions, mentioning in addition to that referred to above, a large amount of new material forming evidence of the commonness of the inconsecutive domination structure in heretogeneous animal communities.

A further stage of studies on domination structure would be attempts at connecting this structure with suppositions as to the elementary structural units within the biocenosis.

It is obvious that the associations of vascular plants, from investigation of which Lityński drew his supposition as to the competition sources domination structure, cannot be directly compared with the animal communities analysed by him and by Gause. These communities, as asserted by, inter alia, Wautier (1952) and Chodorowski (1959) are composed, contrary to the associations of vascular plants, of representatives of different groups and food types, between which there are exploitation relations excluding competition. The pictures of domination structures noted by Gause and Lityński can only be connected with competition by assuming that they were the effect of the simple superimposition of similar structures of many elementary biocenotic systems grouping forms with potential capacity for competition, and therefore of a similar way of life — with a similar function in the biocenosis.

Such systems have long since been distinguished in ecology under the following terms:

second degree synusiae (Gams 1918)

Lebensformen (Warming 1884, Remane 1943, Kühnelt 1944, Akimov 1954, Tischler 1956)

Syntrophien (Balogh 1958, Schelenyj 1955)

Synurien (Tischler 1951, Strencke 1952)

Lebensgruppen (Schwenke 1953)

competitive associations (Tarwid 1952)

Probably the first attempt at connecting the theory of elementary zoocenotic systems with an analysis of domination structure is to be found in the work by Balogh (1938), who in his paper on the zoocenosis of an alfalfa field writes "zu einem gegebenen Zeitpunkt innerhalb eines Ernährungstypus (syntrophium) meistens eine einzige dominante Art nachweisbar ist. Die Kondominanz ... innerhalb eine Synusie kommt gerade dadurch zustande, dass die Mitglieder der Synusie von einander stark abweichende Ernährungstypen angehören" (1956, p. 25). In accordance with this hypothesis the number of condominant species, shown by Lityński and in particular by Gause, small in comparison with the number of non-dominants, although fairly considerable in absolute figures, would reflect the plurality of heterogeneous syntrophia composing the communities examined by these authors.

A different, programmed attempt at connecting the elementary matters of biocenotic systems with domination structure is to be found in the paper by Tarwid (1952) on mosquito populations and in several related works devoted to spider communities (Łuczak 1953, 1954) and ant communities (Kaczmarek 1953).

Passing to the results of the present paper, they would appear to correspond fairly well to the facts and suppositions presented referring to the causes of the formation by animal communities of the domination structure described. In particular they would appear to be useful when interpreting such questions, still open, as, for example:

1) In what exact way is the inconsecutiveness of domination structure connected with interspecific competition?

2) On what principle can a large number of different non-dominants be subordinated in elementary biocenotic systems to one dominant?

3) What can the relation of elementary competitive systems be to the general structure of the biocenosis and therefore what is their relation to the structure of circulation of matter (conversion of energy) in the biocenosis and what can the character of reciprocal relations between different elementary groups of species be within the extent of one food level?

1) Connection to inconsecutive domination structure with interspecific competition.

In the light of our results, the genesis of an inconsecutive domination structure, and therefore the genesis of this unproportional preponderance of the

dominant over the abundance of the remaining species, may consist in the single – direction character of competition relations, that is, in the directional elimination of less numerous species by the dominating species. A permanent relation of this type should in principle alter the initial quantitative relations between species and therefore the relations imposed by fortuitous differentiation of the habitat (cf. p. 469), causing this characteristic gap in the domination structure.

This assumption corresponds well with the two hypotheses discussed in the introduction to this paper: that of Mac Arthur (1961) assuming the breaking away of dominating species from the controlling influence of competitors and Gause's (1936) model of competition, according to which in all cases of interspecific competition there is always a victor and a vanquished, the victorious species being better adapted to the prevailing habitat conditions and therefore a more numerous species (dominating).

In accepting the above explanantion of the sources of inconsecutive domination structure it must be pointed out that absolute value of the quantitative preponderance of the dominant may be – in the light of our materials – the result of the fact that the eliminated species isolate themselves from the dominant by means of the margins of the unutilised habitat. This isolation may be explained by the formation, noted in literature (Ivlev 1954, Kaczmarek W. 1955, 1960, Kaczmarek M. 1961), by the thinned specific populations of a distinctly gregarious structure.

The whole of the assumptions contained here may then be illustrated by means of a simple diagram (Fig. 12).

2) The role of dominants in integrating competition systems

The second of the questions raised is connected with the difficult problem of the organisation of competition systems.

The heterogeneity of the ecological specialisation of species, the heterogeneity of ecological niches of these species causes the relations within the competition systems to be highly varied. In each group, even those apparently the most uniform ecologically, in addition to forms with wery similar ecological requirements there are always forms with requirements sufficiently divergent to make competition between them difficult to imagine. The second circumstance, which must affect the differentiation of competition relations between species is the heterogeneity of their ecological valence (Hesse 1924, Thienemann 1926).
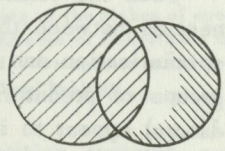

Fig. 12. Circles — extents of the niches of two competing species. Lined areas — actual extents of the occurrence of these species as the result of competition

Thus a general theory may put forward that the probability of the actual interlocking of the niches of different species is increasingly smaller, with the increasingly narrow ecological specialisation of the species. This theory results from the fact that with an increase in specialisation, its heterogeneity in the community must automatically increase, and therefore also the differences in the specialisation of different species. The correctness of this theory is in addition indicated by the fact that together with the narrowing of the ecological valence of competitors the evolutionary success of interspecific ecological isolation increases — the chances of this evolutionary isolation becoming permanent in the requirements and behaviour of individuals increase to an extent leading to the disappearance of all ecological contacts. This takes place as a result of the obligatory character of the ecological contacts of such strictly specialised species. A relation of this type clearly results from the extensive research, discussed at the beginning of this paper (section 1.1. p. 423), on the evolutionary isolation of related species (Elton 1946, Wiliams 1947, Lack 1954 and others).

On the other hand low ecological specialisation of species provokes a reverse relation: a greater probability of niches interlocking with other, even the most narrowly specialised species and lesser success of evolutionary interspecific isolation, since contact between non-specialised and specialised species can be of a facultative character only.

Thus the relations found in the work (in the form of: A) a distinct connection between the domination of the species examined and their ecological specialisation and B) an absence of competition relations between specialised groups of predators when their abundance is limited by non-specialised predators) appear to indicate that the source of the role of dominants, suggested in literature as organising competition systems, is their relatively wide ecological valence, as a rule wider than the valence of non-dominants. At the same time it would seem that this initial quantitative predominance, preceding the formation of competition, of forms less specialised, grows from the fact that the less specialised forms are better adapted to habitat differences than more specialised forms (Krogerus 1932).

Finally therefore the motivation, suggested by our materials, of the integrating action of dominants on the competition system may be shown in the diagram form presented on Fig. 13.

3) The relation of elementary competition systems to the general structure of the biocenosis

The last question in the field of the theory of elementary biocenotic systems to which the certain of results of this work refer, is the place of these systems in the general structure of the biocenosis.

The basis of competition is of primary importance in this question. The majority of authors in considering the basis of competition at the level of general deliberations, hold the view that food competition dominates in the biocenosis. Lityński, Balogh and Tretzel concur with the widely cited statements made by Bristowe (acc 1941, p. 508): "The climate of countries and of habitats' limits the number of species, and food supply the number of individuals which can inhabit them". A natural supporter of the hegemony of food relations in biocenotic relations is Elton. Lack (1954) in his monograph on the phenomena of quantitative regulation endeavours, through food relations, to interpret all the manifestations of variations in the abundance of species.
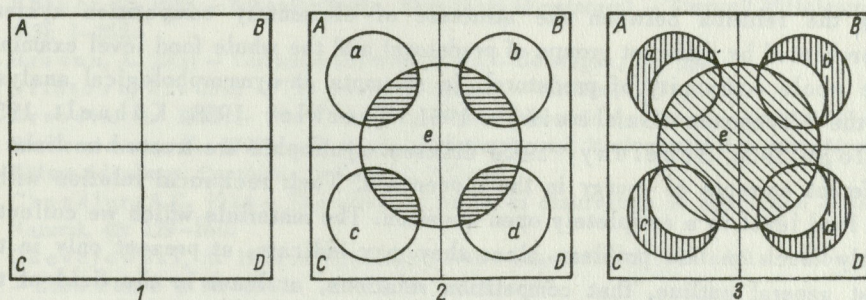

Fig. 13. Plan of the discussed course of competition in multispecies systems.
1 — Habitat differentiation in microhabitats *A*, *B*, *C* and *D*. 2 — Overlapping of the niches of spesialised species *a*, *b*, *c* and *d* and of non-specialised species *e*. 3 — Effects of competition in process of formation in the form of elimination of species *a*, *b*, *c* and *d* by species *e* and the separation of the eliminated species by the margins of the unutilised habitat

Actually the biological sense of the elementary competition systems, as a "brick" in the structure of the biocenosis, would seem to a very considerable degree to depend on dominance in these systems of competition for food or to avoid a common enemy (predators). This results from the fact that it is the food relations which constitute the basis of biocenosis metabolism and therefore of the basic processes of integration of biocenoses (Elton 1927, Allee et al. 1949, Odum 1959, Schmalhausen 1961 and others).

This theoretical structure, however, hides a relatively scanty supply of factual evidence with a simultaneous abundance of facts apparently contradicting the conception of food competition. In the first place mention may be made of the generally known fact that food by itself does not limit the abundance of animals — there is always a great over-abundance of food. Further there is the undisputable fact of competition between different species of animals for such spatial habitat requisites as places for nesting, reproduction, shelter from unfavourable habitat conditions etc.

How far food competition is here as element ordering other kinds of competition and what is the scope of the action of food competition itself and what the scope of competition for avoiding a common enemy remains in principle an open question. The results obtained in the present work would seem to indicate that at least in the field of relations between the groups of soil predators examined, the model of food competition is the valid one.

A second little-investigated problem, of the organisation of food levels, is connected with the place of elementary biocenotic systems in the structure of the biocenosis. If the community of predators of the macrofauna examined in this work is to be treated as representative of a defined food level in the biocenosis of the habitats investigated, then the question arises as to what was the relation between the structure of elementary competition systems (represented by different groups of predators) and the whole food level examined (the whole community of predators). In attempts at synmorphological analysis of the biocenoses (Beklemišev 1951, Tischler 1958, Kühnelt 1958, Balogh 1956, Schelenyj 1955) different syntrophia are treated as links in different currents of energy in the biocenosis. Their reciprocal relation within the food level is a completely open question. The materials which we collected partly touch on this problem, since they may indicate, at present only in the most general outline, that competition relations, at least in the field of the communities of the macrofauna examined, included the whole of the food level investigated. In addition they may indicate that competition connected different elementary systems (different groups of predators) with each other, on similar principles to those on which the interspecific relations were formed within these elementary systems.

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ANALIZA KONKURENCJI MIĘDZYGATUNKOWEJ W ZGRUPOWANIACH
MAKROFAUNY GLEBY KILKU ŚRODOWISK
KAMPINOSKIEGO PARKU NARODOWEGO

Streszczenie

Praca oparta jest na materiałach makrofauny gleby zbieranych w sezonie letnim
i jesiennym w trzech środowiskach leśnych (las sosnowy w wieku 10, 19 i 42 lat) oraz
na sąsiadującym polu ziemniaczanym. Stosowano przesiewanie gleby i ściółki (à 1900
prób) oraz odpowiednie połowy pułapkowe (6430 prób).

Badane środowiska opisane zostały pod względem typu gleby, jej wilgotności
i porowatości, zawartości próchnicy, oświetlenia, mozaikowatości ściółki i zróżnico-
wania szaty roślinnej. Przeanalizowano wpływ tych czynników na liczbę gatunków,
zagęszczenie i ruchliwość osobników całej makrofauny oraz na liczebność i łowność
poszczególnych grup ekologicznych i gatunków drapieżców.

Zagęszczenie i ruchliwość makrofauny były kształtowane w pierwszym rzędzie
przez bogactwo gatunkowe zgrupowania, nie zaś przez zasobność pokarmową, czy inne
analizowane czynniki środowiska. Ze wzrostem liczby gatunków regularnie malało za-
gęszczenie a wzrastała ruchliwość całej makrofauny, co w świetle przeprowadzonej
analizy środowiskowej wskazywało na znaczne nasilenie oddziaływań konkurencyjnych
między gatunkami. W badanych bliżej zgrupowaniach drapieżców jedynie liczebność
form dominujących była podporządkowana czynnikom siedliskowym. Liczebność pozo-
stałych form nie wykazywała bezpośrednich zależności od warunków środowiska.
Kształtowała się ona głównie pod wpływem liczebności form dominujących, w ten spo-
sób, że sumaryczna liczebność całego zgrupowania była skompensowana względem
obfitości potencjalnego pokarmu. Przy czym dominujące formy drapieżców rekrutowały
się spośród gatunków nie wyspecjalizowanych ekologicznie, dzięki czemu zapewne
mogły one wykazywać wspomniane reakcje kompensacyjne w stosunku do różnych,
różnokierunkowo wyspecjalizowanych form drapieżnych i wiążąc je w jeden układ
konkurencyjny.

Na podstawie uzyskanych wyników wyprowadzono model zależności konkurencyj-
nych uwzględniający bezpośrednie i pośrednie wpływy czynników środowiska na li-
czebność badanych zwierząt oraz wysunięto ogólną hipotezę organizacji wielogatunko-
wych systemów konkurencyjnych opartą na zróżnicowaniu ekologicznej walencji kom-
ponentów. Hipoteza ta jest konfrontowana z wynikami eksperymentalnych badań nad
konkurencją między gatunkami oraz badań nad strukturą dominacji w zespołach zwie-
rzęcych.

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