

This summary of some relationships between rodents and fleas shows that ecological adaptations which evolved in the parasite-host system are highly diversified.

4.3. Ecological Characteristics of Parasitic Worm (Helminth) Communities

Krystyna KISIELEWSKA

4.3.1. General Characteristics of Helminths in Bank Voles

To date, about 80 species of helminths associated with the bank vole have been recorded in the literature over its geographical range. Recent, comprehensive papers concerning taxonomic revision of helminths (mostly nematods) in rodents introduced significant taxonomic changes. A review of these is beyond the scope of this paper and the numerical data given below on the helminth fauna of the bank vole are therefore approximate:

- 1) 33 species of *Nematoda* (16 genera, 7 families) — 42%
- 2) 21 species of *Cestoda* (7 genera, 3 families) — 26%
- 3) 16 species of *Cestoda*-larvae (6 genera, 1 family) — 20%
- 4) 9 species of *Trematoda* (7 genera, 6 families) — 11%
- 5) 1 species of *Acanthocephala* — 1%

Thus, the helminth fauna of the bank vole is dominated by nematodes, and their dominance would be even higher (52% of the community) if larval forms of nematodes were eliminated from the calculations, though they are only a taxonomic and not an ecological component of the helminth community.

Most frequently noted in bank voles of at least four European countries are:

Trematoda: *Plagiorchis muris* (Tanabo, 1922)

Cestoda: *Catenotaenia pusilla* (Goeze, 1782)

Catenotaenia cricetorum (Kirschenblatt, 1949)

Skrjabinotaenia lobata (Bear, 1925)

Aprostotandrya macrocephala (Douthid, 1915)

Andrya microti (Erhardova, 1956)

Paranoplecephala brevis (Kirschenblatt, 1938)

Hymenolepsis diminuta (Rudolphi, 1819)

- Hymenolepsis horrida* (Linstow, 1901)
Rodentolepsis asymetrica (Janicki, 1904)
- Nematoda: *Syphacia obvelata* (Rudolphi, 1802)
Aspicularis tetraptera (Nitzsch, 1921)
Heligmosomum costellatum (Dujardin, 1845)
Heligmosomum glareoli (Baylis, 1928)
Heligmosomum polygyrum (Dujardin, 1845)
Heligmosomum halli (Schultz, 1926)
Capillaria muris sylvatici (Diesing, 1851)
Trichocephalus muris (Schränk, 1788)
Mastophorus muris (Gmelin, 1870)
- Cestoda (larvae): *Taenia tenuicollis* (Rudolphi, 1819)
Hydatigera taeniaeformis (Batsch, 1758).

These species also occur in other microtins and in murids.

For most of helminths, bank voles are definitive host, being an intermediate host for larval cestodes only. These mature in predatory birds and mammals, the diet of which includes the bank vole.

Developmental cycles of helminths are diversified and include two categories, biohelminths and geohelminths. Biohelminths require at least one intermediate host for the completion of their development, while geohelminths are characterized by so-called "simple" life cycle, that is, without an intermediate host.

Known biohelminth species of the bank vole include: 9 Trematodes, 21 cestodes, 4 nematodes, 1 acanthocephalid, 16 cestode-larvae. The 29 geohelminth species (all *Nematoda*) are: 14 geohelminths (*sensu stricto*), 7 pseudogeohelminths, 8 ageohelminths.

Thus, the helminth fauna of the bank vole is dominated by biohelminths (64%). Then there are geohelminths *s. str.* (17%), ageohelminths (10%), nad pseudogeohelminths (9%).

In this respect, bank voles are closer to insectivorous micromammals than to rodents (Tenora, 1967; Wahl, 1967). The dominance of the parasites reaching the definitive host through the mediation of different invertebrates (myriapods, insects, molluscs) is a good indicator of the richness of the bank vole diet. The helminth fauna of other, more herbaceous, rodents, is dominated by parasites not requiring intermediate hosts.

In bank voles, helminths occupy the stomach, small intestine, large intestine and caecum, while larval nematodes invade the liver, mesentery and body cavity. Gut parasites predominate (64 species, or 80%) for which the bank vole is the definitive host. For larval nematodes (16 species, or 20%), these rodents are intermediate hosts.

Emphasis here is on the ecological (i. e. structural and functional) characteristics of helminthocoenoses living in bank vole populations.

Characteristics of any ecological unit involve: a) a static description, that is, a synthesis of the structure (Kisielewska, 1970), which provides information on which qualitatively different elements are involved, how many they are and in what proportions; and b) a dynamic description, which shows the variability in these elements. The recurrence of changes in time provides evidence for the reality of a given ecological unit and for its homeostasis.

The structure of helminthocoenoses (multispecies parasite communities) associated with the bank vole is characterized by qualitative, quantitative, and spatial relations. Below, the following types of structures will be discussed: (1) taxonomic, (2) biological, (3) topical, (4) spatial, and (5) quantitative.

4.3.2. Taxonomic Structure

The theoretical maximum of associated parasite species is never attained in real host populations as it is limited by an ecological specificity. This is illustrated in Table 4.4, of the alimentary canal hel-

Table 4.4.

Helminths of the alimentary canal of Polish bank voles (after Kisielewska, 1968).
Number of species is shown

Theoretical maximum for Poland	Helminths	Tape-worms	Nematodes	Trematodes
	19	8	10	1
Białowieża National Park	10	4	5	1 ¹
Leśno	6	3	3	—
Mikołajki	8	4	3	1
Ojców	5	2	3	—

¹ Unknown species.

minths of Polish bank voles (Kisielewska, 1970).

The taxonomic structure of helminths infecting individual bank voles can be largely diversified. All its variants, however, are a combination of the species composition of helminths occurring in a given population of the bank vole (Kisielewska, 1970). The helminthocoenosis of the bank voles in the Białowieża National Park consists of three groups (Table 4.5).

Taxonomic structure involves all the species recorded in the bank voles of the BPN, independent of whether they permanently occur (every month from year to year), or periodically (in some months each year), or sporadically (not every year and in few bank vole individuals).

4.3.3. Biological Structure

Biological structure characterizes a helminthocoenosis with respect to the groups representing various biological and ecological cycles.

Biohelminths. This group comprises *Cestoda* and *Nematoda*. Among *Cestoda* the following species were recorded: 1. *Catenotaenia pusilla* (intermediate hosts: *Tenebrio molitor*, *Gliciphagus domesticus*, *Leptosylla musculi* (Joyeux & Baer, 1936, 1945).

2. *Hymenolepis diminuta* (intermediate hosts: *Coleoptera*, *Lepidoptera*, *Orthoptera*, *Siphonoptera*, *Dermaptera*, and *Myriapoda*, naturally and experimentally, infected (Joyeux & Bear, 1936; Skryabin & Mathevossian, 1948; Yamaguti, 1959).

Table 4.5

Taxonomic structure of the helminth community of the Białowieża National Park bank voles (after Kisielewska, 1970).

	Family	Species
<i>Cestoda</i> ¹	<i>Catenotaeniidae</i> Spassky, 1950	<i>Catenotaenia pusilla</i> (Goeze, 1782)
	<i>Anoplocephalidae</i> Chlodkovsky, 1902	<i>Paranoplocephala brevis</i> Kirschenblatt, 1938
	<i>Hymenolepididae</i> Railliet et Henry, 1909	<i>Hymenolepis diminuta</i> (Rudolphi, 1819) <i>Vampirolepis fraterna</i> (Stiles, 1906)
<i>Nematoda</i>	<i>Heligmosomatidae</i> Cram, 1927	<i>Heligmosomum halli</i> (Szulc, 1928) <i>H. glareoli</i> (Baylis, 1928)
	<i>Capillariidae</i> Neveu-Lemaire, 1936	<i>Capillaria muris sylvatici</i> (Diesing, 1851)
	<i>Syphacidae</i> , Skryabin et Sihobalova, 1951	<i>Syphacia (Syphacia) obvelata</i> (Rudolphi, 1802)
	<i>Spiruridae</i> Oerley, 1885	<i>Mastophorus muris</i> (Gmelin, 1790)
<i>Trematoda</i>		<i>Trematoda spp.</i>

¹ Systematics according to Yamaguti (1959).

3. *Vampirolepis fraterna* (intermediate hosts: *Siphonoptera* and *Coleoptera* (Joyeux & Bear, 1936; Skryabin & Mathevossian, 1948; Yamaguti, 1959).

4. *Paranoplocephala brevis* (intermediate host unknown).

Nematoda are represented by: 1. *Mastophorus muris* (intermediate hosts: *Geotrupes stercorosus*, *Tenebrio molitor*, *Tinca* sp., and *Ceratomyllus fasciatus*).

Each of these helminths occupies only one of several possible intermediate hosts. Their ontogenetic stage occurring in the external environment (eggs) is a possible element of the biocoenosis (it does not feed or move, it is passively transmitted from the environment to the intermediate host). It is subject only to physico-chemical effects of the environment.

Biohelminths also involve trematodes.

Among geohelminths we can distinguish: Geohelminths *sensu stricto*. For some time their larvae are free-living in the external environment: they take food and undergo successive transformations. In a certain stage of their ontogenesis, these parasites are closely related to the external environment both passively (subject to physico-chemical and biotic factors) and actively (as primary consumers). In the Białowieża National Park these are the nematodes *Heligmosomum halli* and *H. glareoli*.

Pseudogeohelminths. Only eggs of these parasite, resembling spores, occur in the external environment. They are subject to ambient temperature, which can delay or accelerate larval development, thus attainment of the invasive stage. In Białowieża National Park they are represented by the nematode *Capillaria muris sylvatici*.

Ageohelminths. Females lay eggs in the perianal region of the host. These eggs have a delicate cover and contain an already developed larva. Infection generally takes place by autoinvasion or by individual contacts between, hosts omitting, in a sense, the external environment. Forms living beyond the host organism, can survive some time in the microclimate of the body surface or nests of the host. In the Białowieża National Park they are represented by the nematode *Syphacia obvelata*.

4.3.4. Topical Structure

In the alimentary canal of the bank vole provides three habitats or zootopes (Petrusewicz, 1938) for helminths: stomach, small intestine, and caecum (Table 4.6). When an animal is heavily infested, parasites characteristic of the small intestine can also occur in the large intestine. No parasite species restricted to the large intestine were recorded. In most heavily infested bank voles no more than five helminth species were recorded (1—2 species on the average). Moreover, the species composition and the number of species can differ for individual bank voles (Table 4.6).

Table 4.6
Topical distribution of the helminth community in bank voles
of Białowieża National Park (after Kisiełewska, 1970).

Stomach	Small intestine	Caecum
<i>Capillaria muris sylvatici</i>	<i>Heligmosomum halli</i>	<i>Syphacia obvelata</i>
<i>Mastophorus muris</i>	<i>Heligmosomum glareoli</i>	<i>Trematoda sp.</i>
	<i>Catenotaenia pusilla</i>	
	<i>Hymenolepis diminuta</i>	
	<i>Vampirolepis fraterna</i>	
	<i>Paranoplocephala brevis</i>	

4.3.5. Spatial Structure

One of the characteristic features of helminth communities in the bank vole is their topical structure (Kisielewska, 1970). This is the spatial distribution of the community components infecting different habitats (zotopes according to Petruszewicz, 1938), within individual hosts (e.g. in the stomach, small intestine, and caecum).

In the biocoenosis, a territorial unit for a helminth community is not an individual host but the whole host population, representing for parasites a mobile mosaic of habitats. The spatial structure of the helminths communities in a host population involves: 1) the proportion of bank voles infested with particular components of the parasite community (incidence of parasite species), 2) the density of parasites in individual hosts (mean intensity of infestation), and 3) the numerical pattern of distribution of parasites in a number of hosts (aggregations of parasites in different groups of hosts).

Distribution of animals in each habitat can be uniform, random, and clumped. This depends on the type of the habitat (heterogeneous or homogeneous) and on the relationships within animal communities (a tendency to aggregation, antagonistic interactions, etc.).

In this paper, the types of spatial structure of helminth will be analysed for the bank vole populations of the Białowieża National Park (BNP) and other forest biocoenoses of Poland (Kisielewska, 1970). Poisson distributions (Oktaba, 1966; Czechowski *et al.*, 1957) for each parasite species of the bank vole, some parasites (dominant species) have a clumped distribution, while the accessory species are randomly distributed. The latter implies that rare parasites are not involved in organized biocoenotic and structural relationships with the host population (Kisielewska, 1970).

Distribution of parasites which are invasive throughout the year (geohelminths) does not vary with season. The species characterized by a seasonal increase in invasion (biohelminths — in relation to the appearance of invertebrate intermediate hosts, and ageohelminths, the appearance of which is related to the period of bank vole reproduction) show a high degree of aggregation during intensified circulation in the biocoenosis. This implies that only certain groups of bank voles are infested. Voles bearing clumped-distribution parasites fall into three groups: a) non-infested bank vole dominated by young individuals not living long enough to be infested. Most will ultimately be parasitized, b) moderately infested bank voles. This is the most abundant group in bank vole populations, and seems to be the most important for the persistence of the parasitic species. They are not free of parasites, which implies they forage in many places and have a diverse diet. But

they are not heavily infested, suggesting a physiological balance in the host-parasite system. The sex ratio and age structure in this group are typical of the whole population. c) heavily infested bank voles (i. e., with a higher intensity of infection than the theoretical maximum). This group involves both young and adult individuals, thus heavy infestation cannot be related to the time of the presence of animals in the biocoenosis. This group seems to consist of the animals most handicapped physiologically or ecologically.

4.3.6. Quantitative Structure

This structure characterizes the quantitative relations among the components (individuals, groups) of a collective unit either by means of absolute values or indices. In a sense, this structure is superior to

Table 4.7

Synthesis of the helminth community in the bank vole population of Białowieża National Park (after Kisielewska, 1970).

No. of helminth species	Taxonomical groups	Biological groups	Topical groups
10	<i>Cestoda</i>	4 bichelminths	6 stomach
	<i>Nematoda</i>	5 geohelminths	2 small intestine
	<i>Trematoda</i>	1 pseudogeohelminths	1 caecum
		1 agehelminths	2

Table 4.8

Incidence of intestinal parasite species in the bank vole population of Białowieża National Park (after Kisielewska, 1970).

Parasite species	1953	1954	1955	1956	1957	1958	1961	Total
<i>Catenotaenia pusilla</i>	28.3	28.0	34.4	46.6	27.2	31.8	18.5	30.9
<i>Paranoplocephala brevis</i>	0.3	0.7	2.6	0.9	1.5	—	1.3	1.3
<i>Hymenolepis diminuta</i>	0.9	0.3	0.8	—	—	—	—	0.5
<i>Vampirolepis fraterna</i>	0.3	0.5	1.1	1.9	—	—	—	0.7
<i>Heligmosomum halli</i>	65.8	42.4	65.3	52.3	51.5	63.6	40.9	56.6
<i>Heligmosomum glareoli</i>	1.7	1.2	1.3	0.9	—	—	—	1.2
<i>Capillaria muris sylvatici</i>	30.9	21.4	32.2	17.1	18.8	18.7	19.7	26.4
<i>Mastophorus muris</i>	14.1	3.2	24.9	8.5	9.0	13.6	3.7	13.3
<i>Syphacia obvelata</i>	2.0	10.3	4.4	5.7	4.5	4.5	2.4	4.8
<i>Trematoda spp.</i>	1.4	0.2	0.2	0.9	—	—	—	0.5

the qualitative structure which provides description of the set of components of a collective unit. Numerical approaches allow analysis of community structure and dynamics, since numerical relationships are likely to be the most important indication of parasite community inte-

gration. Numerical structure of helminth communities is characterized by:

a) Quantitative composition of its structural elements, as expressed in absolute numbers (Table 4.7),

b) Frequency of the degree of infestation of the host population (extent of invasion, Table 4.8),

c) The size of the parasite community or the number of individuals (intensity of invasion, for individual hosts),

d) Density or the number of parasites per unit of space, that is, per individual host within the vole population (Table 4.9),

Table 4.9
Concentration of intestinal parasite species in the bank vole population of Białowieża National Park (after Kisielevska, 1970).

Parasite species and years							For all the years, mean	
1953	1954	1955	1956	1957	1958	1961	Concentration	Intensity
			<i>Catenotaenia pusilla</i>					
0.7	0.8	1.0	1.0	0.9	1.0	0.4	0.8	2.7
			<i>Paranoplocephala brevis</i>					
0.003	0.009	0.03	0.04	0.02	—	0.01	0.02	1.4
			<i>Hymenolepis diminuta</i>					
0.01	0.003	0.01	—	—	—	—	0.008	1.3
			<i>Vampirolepis fraterna</i>					
0.003	0.007	0.01	0.03	—	—	—	0.009	1.3
			<i>Heligmosomum halli</i>					
2.2	1.1	2.0	2.8	2.4	2.7	3.2	2.4	3.7
			<i>Heligmosomum glareoli</i>					
0.02	0.02	0.01	0.03	—	—	—	0.02	1.3
			<i>Capillaria muris sylvatici</i>					
5.5	2.1	2.9	8.8	2.3	2.1	1.0	3.5	12.9
			<i>Mastophorus muris</i>					
0.4	0.07	0.7	1.8	0.3	0.2	0.1	0.5	3.7
			<i>Syphacia obvelata</i>					
1.9	8.2	3.2	4.3	3.2	3.2	0.5	4.1	81.7
			<i>Trematoda spp.</i>					
0.001	0.0003	0.0001	0.0005	—	—	—	0.0008	1.5

e) Mean size of parasite aggregations in individual hosts, number of parasites per infested bank voles (Table 4.9).

Frequency, size, and density can be related either to the community as a whole (community indices) or to particular components (indices for particular species of parasites).

These quantitative features of the relations among parasite species (or communities) express: statistically, the probability of the encounter of a parasitized individual per definite number of individuals examined, ecologically, the degree of the infestation of the host population. The sum of the incidence of infestation for particular parasite species in a com-

Table 4.10

Quantitative structure of the helminth community in the bank vole population of Białowieża National Park (after Kisielewska, 1970).

Incidence	Intensity		
	Low	Average	High
Low	<i>Heligmosomum glareoli</i> <i>Paranoplocephala brevis</i> <i>Hymenolepis diminuta</i> <i>Vampirolepis fraterna</i>		<i>Syphacia obvelata</i>
Moderate		<i>Catenotaenia pusilla</i> <i>Mastophorus muris</i> <i>Capillaria muris sylvatici</i>	
High		<i>Heligmosomum halli</i>	

munity is not equal to 100 because the same individual host can be counted several times if it has more than one parasite species.

In the topocoenosis of the bank vole helminths, three numerical categories of components have been distinguished; dominant, influent, and accessory species (Dobrowolski, 1963). BPN is known to carry five rare (extensity 0.5—1.3%) and nonabundant (density 0.008—0.02; mean intensity 1.3—1.5) species. They are considered accessory species. Moreover, one species was frequent and moderately abundant (extensity 56.6%, density 2.4, mean intensity 3.7), one species rather rare and very

Table 4.11

Index of infection calculated for helminth species occurring in the bank vole population of Białowieża National Park (after Kisielewska, 1970).

1953	1954	1955	1956	1957	1958	1961	Total
1.5	0.7	1.3	<i>Heligmosomum halli</i> 1.6	1.2	1.7	1.6	1.2
1.7	0.5	0.9	<i>Capillaria muris sylvatici</i> 1.3	0.4	0.4	0.2	1.0
0.2	0.2	0.3	<i>Catenotaenia pusilla</i> 0.4	0.2	0.4	0.07	0.2
0.05	0.002	0.2	<i>Mastophorus muris</i> 0.1	0.02	0.03	0.004	0.06
0.04	0.8	0.1	<i>Syphacia obvelata</i> 0.2	0.1	0.2	0.01	0.2
0.0003	0.0002	0.0002	<i>Heligmosomum glareoli</i> 0.0003	—	—	—	0.0001
0.000008	0.0001	0.0008	<i>Paranoplocephala brevis</i> 0.0009	0.0007	—	0.0001	0.0003
0.0001	0.000006	0.00009	<i>Hymenolepis diminuta</i> —	—	—	—	0.00004
0.000008	0.00004	0.0001	<i>Vampirolepis fraterna</i> 0.0003	—	—	—	0.00005

abundant (extensity 2.5%, density 4.1, mean intensity 81.7), and three species moderately frequent and moderately abundant (extensity 13.3—30.9%, density 0.5—3.5, mean intensity 2.7—12.9) (Table 4.10) (Kisielewska, 1970). Lack of a close correlation between the frequency and abundance of these species made it difficult to determine their dominance position. Therefore, the infestation index used by Janion (1968) to estimate the infestation of rodents with fleas was calculated. This index is a product of extensity and intensity. It yields: one dominant, (permanent) component of the community and has the highest infestation index (1.3), three influent species, having an average infestation index (0.2—0.9) and permanently occurring in the community, one seasonal influent species (index 0.1), which appears in the community only during the bank vole breeding season; and five accessory species, with a very low infestation index (0.00009—0.0008), appearing sporadically and irregularly (Table 4.11).

On the basis of the results obtained for the biocoenoses in Poland (Kisielewska, 1970), and using the data of other authors (Rupeš, 1964; Sharpe, 1964; Erhardova, 1958; Mozgovej *et al.*, 1966; Tenora, 1967a, b), it has been found that the helminth communities living in the alimentary canal have the same general model of the quantitative structure (Table 4.12). This model is characterized by: a) one dominant nematode species of the genus *Heligmosomum*, b) one subdominant species of cestode (most frequently *Catenotaenia pusilla*), and c) accessory species, of the genus *Heligmosomum*, other species of nematodes, and of trematodes. Influent species show the least regularities, especially in their taxonomy.

4.3.7. Seasonal Dynamics of Helminth Community

The preceding data concerned the total sample taken from the field (pooled for several years or seasons). They are static and can be called a synthesis of the community in a biocoenosis (Fig. 4.10). Community dynamics are equally important and may indicate some underlying population control mechanisms.

The structural criterion of each mature community is the balance in proportions among dominant, influent and accessory species. This balance is not static, however. It undergoes changes, but these changes follow some patterns — seasonal cycles correlated with phenological changes in the biocoenosis and with the host population dynamics. A chaotic variability would imply that the community is not an integrated unit.

Structural variability in the parasitocoenoses of the bank vole has

Table 4.12
Frequency of helminths in different bank vole populations
(after Kisilewska, 1970).

Present paper 1953—1961. Białowieża National Park	Rupeš (1964), Krčky les 1959—1960	Rupeš (1964), Šarka 1959—1960	Mozgovoj <i>et al.</i> (1966), Karelia	Tenora (1967a), Slovakia
76.4%	60%	General incidence 63%		75%
10	9	No. of species found 6		9
Dominant species				
<i>Heligmosomum halli</i> (N) 57%	<i>Heligmosomum costellatum</i> (N) 17%	<i>Heligmosomum skrjabini</i> (N) 24% <i>Heligmosomum polygyrum</i> (N) 18%	<i>Heligmosomum costellatum</i> (N) 44%	<i>Heligmosomum costellatum</i> (N) 42% <i>Hymenolepis horrida</i> (C) 44%
Influent species				
<i>Catenotaenia pusilla</i> (C) 31%	<i>Catenotaenia pusilla</i> (C) 10%	<i>Paranoplocephala omphalodes</i> (C) 7%	<i>Aprostotandria macrocephala</i> (C) 7%	<i>Catenotaenia cricetorum</i> (C) 8%
<i>Capillaria muris sylvatici</i> (N) 26% <i>Mastophorus muris</i> (N) 13% <i>Syphacia obvelata</i> (N) 3%	<i>Syphacia obvelata</i> (N) 8% <i>Paranoplocephala omphalodes</i> (C) 8% <i>Heligmosomum skrjabini</i> (N) 8%	<i>Syphacia obvelata</i> (N) 7% <i>Heligmosomum costellatum</i> (N) 6%		<i>Aprostotandria macrocephala</i> (C) 6%
Accessory species				
<i>Hymenolepis diminuta</i> (C) 0.5% <i>Vampirolepis fraterna</i> (C) 0.7% <i>Paranoplocephala brevis</i> (C) 1.3% <i>Heligmosomum glareoli</i> (N) 1.2% <i>Trematoda spp.</i> 0.5%	<i>Heligmosomum polygyrum</i> (N) 3% <i>Capillaria muris sylvatici</i> (N) 3% <i>Rodentolepis straminea</i> (C) 2% <i>Skrjabinotania lobata</i> (C) 2%	<i>Capillaria muris sylvatici</i> (N) 2%	<i>Paranoplocephala omphalodes</i> (C) 2% <i>Catenotaenia pusilla</i> (C) 2% <i>Hymenolepis horrida</i> (C) 2% <i>Rodentolepis straminea</i> (C) 1% <i>Syphacia spp.</i> (N) 2% <i>Heligmosomum glareolis</i> (N) 0.4% <i>Trichocephalus muris</i> (N) 0.4%	<i>Mastophorus muris</i> (N) 3% <i>Rodentolepis ampla</i> (C) 3% <i>Paranoplocephala dentata</i> (C) 2% <i>Heligmosomum polygyrum</i> (N) 0.3% <i>Rictularia sp.</i> (N) 0.3%

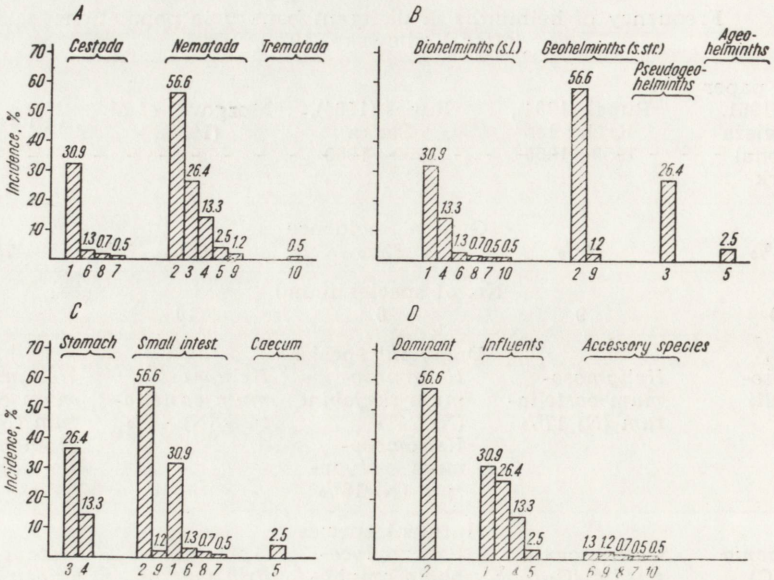


Fig. 4.10. Structure of the intestinal helminth community in the bank vole population of the Białowieża National Park.

1 — *Catenotaenia pusilla*, 2 — *Heligmosomum halli*, 3 — *Capillaria muris sylvatici*, 4 — *Mastophorus muris*, 5 — *Syphacia obvelata*, 6 — *Paranoplocephala brevis*, 7 — *Hymenolepis diminuta*, 8 — *Vampirolepis fraterna*, 9 — *Heligmosomum glareoli*, 10 — *Trematoda* spp. A — taxonomic structure, B — biological structure, C — topical structure, D — quantitative structure.

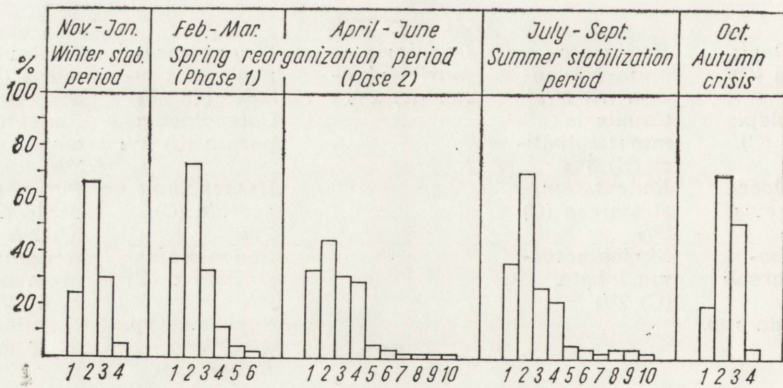


Fig. 4.11. Seasonal changes in the structure of a helminth community of bank vole in the Białowieża National Park.

Explanation see Fig. 4.10.

been analysed from the materials collected in the Białowieża National Park (Kisielewska, 1970). Five periods are distinguished in which helminth communities of the bank vole differ in structure over the annual cycle (Fig. 4.11).

Winter Balance (November-January)

In this period helminth communities consist of one dominant and three influent species; there are no seasonal influents and accessory species; and the dominant is much more abundant than influent species. The bank vole population is stable except for random mortality, which approximates one third of the summer mortality (Gliwicz *et al.*, 1968).

Spring Reorganization (Phase 1: February-March)

The acute differentiation in numbers between the dominant and influent species continues. A seasonal influent appears as a result of intensified sexual contacts among individual bank voles. Also accessory species, mostly biohelminths, appear. Bank voles switch to low energy content diet (Górecki & Gębczyńska, 1962), resulting in drastic increases of their daily activity (Grodziński, 1963). Sexual maturity intensifies this activity (Kubik, 1965). Invertebrates appear and become the prey of these actively foraging rodents.

Spring Reorganization (Phase 2: April-June)

The number of accessory species increases, and seasonal influents become more abundant. At the same time, the difference in abundance between dominant and influent species is reduced. Young voles appear en masse and become infested as a result of their contacts with the biocoenosis. The new generation of bank voles disturbs the numerical structure of the population, thus the structure of the parasite community.

Summer Balance (July-September)

The parasite community in the Białowieża National Park attains its theoretical maximum and comprises one dominant, four influent, and five accessory species, each with clear differences in abundance. Young bank vole mass abundance cease to disturb the numerical relations in the parasite community.

Autumn Begins (October)

Accessory species and the seasonal influents disappear, leaving only the four most abundant species, one of which predominates. Autumnal helminth community changes relate to bank vole population shifts (Kubik, 1965) as overwintered individuals and some current adults die out. This results in drasting decline in species and abundance of helminths

previously occupying the oldest voles. These observations at BNP compare favourably with data from other places (Kisielewska, 1970b).

	Dominants	Influents	Accessory species
Spring			
Białowieża National Park	3	2	5
Mikołajki	2	1	5
Summer			
Białowieża National Park	1	4	5
Leśno	1	4	1
Autumn			
Białowieża National Park	1	3	—
Ojców	1	3	—

Mechanisms Organizing Helminth Communities

In each ecological unit there are direct processes and interactions (among individuals) and indirect ones (environmental), which together determine the structure and function of a community.

If a species can exist in a given biocoenosis, its numbers are determined by environmental and intrabiocoenotic mechanisms. And so, individual bank voles, particularly those moderately infested, never have all the niches within the biotope (alimentary canal) saturated with parasites. Co-occurrence of parasite species in single hosts has been analysed (Tarwid, 1960, Kisielewska, 1970). Three groups of parasites have been distinguished: a) co-occurring more frequently than indicated by the random distribution (protective species), b) indifferent to each other (random co-occurrence), and c) avoiding each other (antagonistic species). Two species illustrate the interacting complexities possible: *Heligmosomum halli* (a nematode) and *Catenotaenia pusilla* (a tape-worm), both within the small intestine. In all the biocoenoses studied these two species showed suggested mutually protective relationships. At the same time, correlation tables suggest inverse numerical occurrences such that the more the nematodes, the fewer the tape-worms, and conversely. Thus, the index of co-occurrence shows that these are concurrent species, while the correlation of numbers says that they are antagonistic, or, at least, that they limit numbers of each other. This apparent inconsistency is a result of two mechanisms determining numbers of the two species. One mechanism acts within individual hosts (in an idiohostal community), and is competition. Both species occupy the same habitat, though their ecological niches are not identical. *H. halli* feed on erythrocytes, while *C. pusilla* on the intestinal content. They may compete, however, for space. The other mechanism acts within

the whole biocoenosis. The common source of infection with the two species is plant litter and low vegetation, where occur free-living nematode larvae and also acarids — the intermediate hosts of *C. pusilla*. Hence, the chance of bank vole infestation with the two parasites simultaneously is greater than random. Two mechanisms clash here: intracoenotic antagonism and biocoenotic convergence, the latter being more effective.

Clumped distribution of the bank vole parasite in population can be explained by physiologically or ecologically. Physiological reasons involve, e. g. individual differences in the host resistance to the infection with various parasites. Due to these differences, some individuals are not parasitized as a result of an inherited or acquired resistance, while other individuals are more heavily infested than at random, though the chances of infestation are presumably equal for all individuals. Ecological reasons lie in uneven chances of contact with the source of infection for different groups of population members. This may be due to differences in lifestyle; differential foraging positions or times. Different voles may occupy different ecological niches, or have different search ranges. It seems that ecological relationships are ultimately of basic importance, though the role of individual resistance cannot be excluded (there are no data available for the bank vole resistance).

Thus, the mechanisms determining the clumped distribution of parasites in the host population are contained in the structure of this population, and indirectly in environmental interactions.

The mechanism shaping numerical relations in parasite community is intracoenotic selfregulation and biocoenotic regulation.

The dominance of individual species in parasite communities is determined by: a) ecological valence of the species in a biocoenosis, the "efficiency" of the ways of circulation, determining the chances of encounter with a host, and b) its physiological vitality due to which it could eliminate or reduce the abundance of competing species during the community formation.

Related species have the same integration plane, or largely overlapping niches. They do not tolerate each other, though the same type of their circulation in the biocoenosis theoretically creates identical chances of the host infection. For example, among nematodes of the genus *Heligmosomum* only one species becomes dominant in a community. The other members of this genus are reduced to the role of accessory species (Kisielewska, in press.). The dominance structure is the result of a scramble competition (for space, food, etc).

Unrelated species but living in the same biotopes (but occupying

different niches) can be dominants or influents in a synthostal community, but they limit numbers of each other in individual hosts (e. g. the already quoted nematode *H. halli* and the tape-worm *C. pusilla*).

The abundance of the species that have no competitors in their tope is maintained at the level determined by environmental conditions of the biocoenosis (e. g. the nematode *Syphacia obvelata*, which is a seasonal influent with a highly clumped distribution, living in the caecum) strongly depends on the dynamics of the host population.

Among the accessory species, some belong to this group as a result of heavy competition with related species, and other because the ways of their circulation in the biocoenosis do not coincide with typical foraging sites and the diet of the host species (casual accessory species). In the former case, intrabiocoenotic competition is the regulatory mechanism, while in the latter case regulation goes through the biocoenosis.