CESTODE COMMUNITIES IN NON-BREEDING POPULATIONS OF FOUR GREBE SPECIES (AVES: PODICIPEDIDAE) FROM THE BULGARIAN BLACK SEA COAST

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Summary :

Cestode communities in *Podiceps cristatus*, *P. grisegena*, *P. nigricollis* and *Tachybaptus ruficollis* during their migrations and overwintering are studied at the Bulgarian Black Sea coast. The infracommunities exhibit high richness, abundance and dominance, and low diversity and similarity. The component communities have a similar taxonomic structure at the levels higher than species, a small number of core species and a high portion of grebe specialists in the richness and abundance. The comparison with cestode communities in grebes from Canada (Stock & Holmes, 1987) reveals several differences and similarities. The higher richness and abundance of the infracommunities in Canada are explained by the constant conditions of breeding habitats enhancing higher transmission rates. At the component community level, there is a significant difference between the two species lists. The degree of parasite exchange among the grebe species in Bulgaria is lower. Several characters of cestode component communities in grebes do not depend on either historical factors or different habitats. These are the similar patterns of the taxonomic structure at the levels higher than species, almost the same list of generalists, the participation of specialists of anatids, and the leading role of grebe specialists in the structure.

KEY WORDS : parasite ecology, communities, cestodes, Podicipedidae, Bulgaria.

Résumé : LES COMMUNAUTÉS DE CESTODES DANS LES POPULATIONS NON REPRODUCTRICES DE QUATRE ESPÈCES DE GRÈBE (AVES: PODICIPEDIDAE) DE LA CÔTE BULGARE DE LA MER NOIRE

Cette étude porte sur les communautés de cestodes de *Podiceps cristatus*, *P. grisegena*, *P. nigricollis*, *Tachybaptus ruficollis* pendant leurs migrations et leur hibernage sur la côte bulgare de la Mer Noire. Les infracommunautés montrent une grande richesse, abondance et dominance, une faible diversité et une faible similarité. Les xénocommunautés ont une structure taxonomique semblable pour les niveaux supérieurs aux espèces, un petit nombre d'espèces cores et une grande proportion de spécialistes des grèbes en richesse et en abondance. La comparaison avec les communautés de cestodes des grèbes du Canada (Stock & Holmes, 1987) révèle plusieurs différences et similitudes. Les plus grandes richesses et abondances des infracommunautés au Canada sont expliquées par la constance des conditions dans les habitats de reproduction qui favorise un taux de transmission plus élevé. Au niveau de la xénocommunauté, il y a une différence significative entre les deux listes d'espèces. Le degré d'échange de parasites est plus bas parmi les espèces de grèbes de Bulgarie. Plusieurs caractères des xénocommunautés de cestodes chez les grèbes ne dépendent ni des facteurs historiques ni des différences d'habitat. Ceux-ci sont les patrons similaires des structures taxonomiques de niveaux supérieurs aux espèces, la liste pratiquement identique des généralistes, la participation de spécialistes des anatides et le rôle majeur des spécialistes des grèbes dans la structure.

MOTS CLÉS : écologie parasitaire, communautés, cestodes, Podicipedidae, Bulgarie.

INTRODUCTION

One of the classical studies on the helminth communities in avian hosts is the survey by Stock & Holmes (1987, 1988) on intestinal helminth parasites in four grebe species from fresh-water breeding habitats in Alberta, Canada. It revealed large and complex helminth communities. A large number of core and secondary species, primarily cestodes, which exhibited a consistent pattern of co-

occurrence, was identified. Stock & Holmes (1987) indicated that the level of the host specificity and the food habits of the host are important determinants of the structure of helminth communities in grebes.

There are numerous faunistic and taxonomic studies on cestode parasites from grebes in the Palaearctic (reviewed by Ryzhikov *et al.*, 1985). They show that this specialised group of aquatic birds supports a species-rich cestode fauna. However, no studies on cestode communities in Palaearctic grebes have been carried out. The aim of the present article is to describe the cestode communities in Palaearctic grebes and to identify the main factors determining their structure. Since the breeding populations are highly protected in Bulgaria, the samples were collected from migrating and overwintering birds along the Bulgarian Black Sea coast.

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MATERIALS AND METHODS

A total of 44 birds belonging to four grebe species were collected under a license of the Ministry of Environment of the Republic of Bulgaria during 1983-1994. These were 12 *Podiceps cristatus* (L.), 21 *P. nigricollis* Brehm, four *P. grisegena* (Boddaert) and seven *Tachybaptus ruficollis* (Pallas). The birds were captured from three localities along the Bulgarian Black Sea coast (Lake Durankulak, Lake Pomorie and Burgas) in January, March-April and September-October. Representative samples of cestodes were isolated alive from the intestines, relaxed in tap water, fixed in 10 % formalin and preserved in 70 % ethanol. Subsequently, they were stained in iron acetocarmine, dehydrated in an ascending alcohol series, cleared in eugenol and mounted in Canada balsam, or mounted in Berlese's medium, for the purposes of adequate morphological and taxonomic studies. All remaining gut contents including cestodes were fixed in 4 % formalin for subsequent examination. All the cestode specimens were identified and counted.

The cestode identification was based on the following works: Baer (1954), Dubinina (1966), Temirova & Skryabin (1978), Ryzhikov & Tolkacheva (1981), Ryzhikov *et al.* (1985), Gulyaev (1990, 1992) and Vasileva *et al.* (1996a, b, 1998, 1999a-c).

The terminology used in the description of helminth communities follows Bush *et al.* (1997).

For consistency of the comparisons, the prevalence criteria of 40 % and 70 % were adopted for the identification of satellite, secondary and core species (as applied by Stock & Holmes, 1987). The following parameters of community structure were calculated at the infracommunity level: the mean number of cestode species and individuals, the mean Brillouin's Index (HB), the mean index PIE' and the mean Berger-Parker Dominance Index (d) (see Magurran, 1988; Krebs, 1989; Baev & Penev, 1995). The participation of the specific parasites of the Podicipedidae (= grebe specialists) in the infracommunity abundance is characterised by the modified Berger-Parker Dominance Index ($d' = N_{\text{spec}}/N$, where N_{spec} is the total number of individuals of grebe specialists, and N is the total number of cestode individuals in the sample), as applied by Kostadinova (1993) for trematode communities. The similarity was measured using Jaccard Coefficient (SJ) for qualitative data and the Percent Similarity Index (PS) for quantitative data (Krebs, 1989). Medians, mean values and SD of the similarity of each infracommunity sample sets (corresponding to each of the four component communities studied) was calculated on the basis of the comparisons between all possible pairs of infracommunities within each grebe species.

The random distribution of cestode species in each of the four infracommunity sample sets was tested by the Index of Dispersion Test (IDT) (Krebs, 1989).

The prevalence and mean intensity data presented by Stock & Holmes (1987) have been used to calculate: 1) the total number of individuals of each cestode species in a certain grebe species (= prevalence $\times$ number of examined birds $\times$ mean intensity); 2) mean number of cestode species in a certain grebe species (= sum of prevalences/100) (see Holmes, 1990). The former has been used to calculate the mean number of individuals in each host species as well as the parameters of diversity (HB, PIE', d) and similarity (SJ and PS) at the component community level.

All diversity and similarity measures were calculated by the program BIODIV (Baev & Penev, 1995). Standard non parametric Kruskal-Wallis (K-W) and Mann-Whitney (M-W) tests were used for hypothesis testing (Sokal & Rohlf, 1981).

RESULTS

Cestode communities of grebes examined along the Bulgarian Black Sea coast were characterised by a high species richness and abundance. Out of 44 birds, 43 were infected with cestodes and only one specimen of *P. cristatus* was uninfected. Infected individual birds harboured one to six cestode species. A total of 27 cestode species was found (Table I). The parameters of the cestode communities are given in Table II.

CESTODE COMPONENT COMMUNITIES

Species richness and abundance

Although the cestode species diversity was high (Table I), the four host species had similar component community taxonomic structure at the level of the family. The families Hymenolepididae and Amabiliidae exhibited the highest species richness and abundance. The majority of the recorded species belonging to these families were grebe specialists (see Spasskaya, 1966; Ryzhikov & Tolkacheva, 1981; Ryzhikov *et al.*, 1985; Galkin, 1986). The remaining species, belonging to the families Diphyllbothriidae, Tetrabothriidae and Dilepididae, showed considerably lower richness and abundance.

The component cestode community in *P. nigricollis* demonstrated the highest species richness and abundance. 43 % of individual *P. nigricollis* had more than four cestode species and 43 % had infection of more than 300 tapeworms. The family Hymenolepididae had the highest species richness (53.3 %); among them, *Confluaria furcifera* and *C. podicipina* were the most frequent and abundant (Table I). Amabiliids had

Taxa	Speci- ficity	<i>Podiceps cristatus</i>				<i>Podiceps nigricollis</i>				<i>Podiceps grisegena</i>				<i>Tachybaptus ruficollis</i>			
		P%	MI	MA	S	P%	MI	MA	S	P%	MI	MA	S	P%	MI	MA	S
Diphyllbothriidae																	
<i>Ligula intestinalis</i> (L., 1758)	G	16.7	3.0	0.5	Sat	—	—	—	—	—	—	—	—	—	—	—	—
Tetrabothriidae																	
<i>Tetrabothrius macrocephalus</i> (Rud., 1810)	G	33.3	3.5	1.2	Sat	4.8	163.0	7.8	Sat	50.0	76.0	38.0	Sec	—	—	—	—
Dilepididae																	
<i>Paricterotaenia porosa</i> (Rud., 1810)	A	—	—	—	—	14.3	23.3	3.3	Sat	—	—	—	—	—	—	—	—
Amabiliidae																	
<i>Ryjkovilepis dubininae</i> (Ryzhikov & Tolkacheva, 1981)	X	—	—	—	—	28.6	11.2	3.2	Sat	—	—	—	—	—	—	—	—
<i>Schistotaenia macrorhyncha</i> (?) (Rud., 1810)	X	—	—	—	—	4.8	1.0	0.05	Sat	—	—	—	—	14.3	1.0	0.1	Sat
<i>S. rufi</i> (Sulgostowska & Korpaczewska, 1969)	X	—	—	—	—	—	—	—	—	—	—	—	—	14.3	1.0	0.1	Sat
<i>Schistotaenia</i> sp.	X	8.3	1.0	0.1	Sat	—	—	—	—	—	—	—	—	—	—	—	—
<i>Tatria acanthorhyncha</i> (Wedl, 1855)	X	—	—	—	—	—	—	—	—	—	—	—	—	71.4	10.6	7.6	C
<i>T. biremis</i> Kowalewski, 1904	X	16.7	207.5	34.6	Sat	76.2	173.3	132.0	C	75.0	114.3	85.8	C	28.6	7.5	2.1	Sat
<i>T. biuncinata</i> (Joyeux & Baer, 1943)	X	—	—	—	—	—	—	—	—	—	—	—	—	14.3	259.0	37.0	Sat
<i>T. minor</i> Korpaczewska & Sulgostowska, 1974	X	8.3	11.0	0.9	Sat	33.3	744.6	248.2	Sat	—	—	—	—	—	—	—	—
<i>T. mircia</i> (Gulyaev, 1990)	X	33.3	53.5	17.8	Sat	14.3	165.7	23.7	Sat	25.0	4.0	1.0	Sat	—	—	—	—
<i>T. octacantha</i> Rees, 1973	X	—	—	—	—	—	—	—	—	—	—	—	—	14.3	1.0	0.1	Sat
<i>T. pilatus</i> (Borgarenko & Gulyaev, 1991)	X	—	—	—	—	—	—	—	—	—	—	—	—	28.6	1.5	0.4	Sat
<i>Tatria</i> sp.	X	—	—	—	—	—	—	—	—	—	—	—	—	14.3	4.0	0.6	Sat
Hymenolepididae																	
<i>Confluaria capillaris</i> (Rud., 1810)	X	8.3	105.0	8.8	Sat	—	—	—	—	75.0	32.7	24.5	C	—	—	—	—
<i>C. furcifera</i> (Krabbe, 1869)	X	—	—	—	—	66.7	27.4	18.2	Sec	75.0	175.0	131.3	C	14.3	3.0	0.4	Sat
<i>C. multistriata</i> (Rud., 1810)	X	—	—	—	—	4.8	1.0	0.05	Sat	—	—	—	—	42.9	39.7	17.0	Sec
<i>C. podicipina</i> (Szymanski, 1905)	X	—	—	—	—	47.6	68.2	32.5	Sec	—	—	—	—	28.6	33.0	9.4	Sat
<i>C. pseudofurcifera</i> Vasileva et al., 1999	X	50.0	8.2	4.1	Sec	—	—	—	—	—	—	—	—	—	—	—	—
<i>Confluaria</i> sp.	X	—	—	—	—	19.0	15.5	3.0	Sat	—	—	—	—	14.3	1.0	0.1	Sat
<i>Dollfusilepis hoploporus</i> (Dollfus, 1951)	X	33.3	2.8	0.9	Sat	—	—	—	—	—	—	—	—	—	—	—	—
<i>Fimbriarioides</i> sp.	A	—	—	—	—	—	—	—	—	25.0	4.0	1.0	Sat	—	—	—	—
<i>Mackoja podirufi</i> (Macko, 1962)	X	—	—	—	—	4.8	1.0	0.05	Sat	—	—	—	—	42.9	19.7	8.4	Sec
<i>Microsomacanthus</i> sp. 1	A	—	—	—	—	4.8	2.0	0.1	Sat	—	—	—	—	—	—	—	—
<i>Microsomacanthus</i> sp. 2	A	—	—	—	—	4.8	14.0	0.7	Sat	—	—	—	—	—	—	—	—
<i>Pararetinometra lateralacantha</i> Stock & Holmes, 1981	X	—	—	—	—	4.8	25.0	1.2	Sat	—	—	—	—	—	—	—	—

Abbreviations: G: generalists; X: grebe specialist; A: accidental species (specialists of other hosts group); C: core species; Sec: secondary species; Sat: satellite species.

Table I. – Prevalences (P%), mean intensities (MI), mean abundances (MA) and status (S) of cestode species found in four grebe species from Bulgarian Black Sea coast.

the major portion of the total component community abundance (85.9 %) due to the high values of prevalence and/or mean abundance of *Tatria* spp. and *Ryjkovilepis dubininae*.

Tachybaptus ruficollis had also a species-rich and abundant component community. Only amabiliids and hymenolepidids were found in this host. The former had the highest species richness and abundance. In addition to the common grebe specialist *Tatria biremis*,

the component community of *T. ruficollis* comprised six other amabiliids recovered only in this host. Among hymenolepidids, *Confluaria multistriata*, *Mackoja podirufi* and *C. podicipina* showed the highest values of prevalence and mean abundance (Table I).

The component cestode community in *P. cristatus* comprised nine species. The Amabiliidae prevailed in this host in both richness and abundance (44.4 % and 77.6 %, respectively). The species with the highest pre-

Locality	Alberta (Canada)				Black Sea Coast (Bulgaria)			
	AO	PG	PN	PA	PC	PN	PG	TR
Birds examined	20	33	31	7	12	21	4	7
Cestode species number	10	13	19	11	9	15	6	13
Infracommunities								
Mean number of species per bird	3.9	6.2	7.6	4.7	2.1	3.3	3.3	3.4
SD	–	–	–	–	1.2	1.5	1.7	1.7
Median	–	–	–	–	2.0	3.0	3.5	3.0
Range	–	–	–	–	0-4	1-6	1-5	1-6
Mean number of individuals per bird	336.3	1475.5	6135.5	1858.4	68.8	473.9	281.5	83.6
SD	–	–	–	–	117.3	501.6	426.8	100.2
Median	–	–	–	–	7.5	257.0	104.5	35.0
Range	–	–	–	–	0-368	19-1865	4-913	5-294
Brillouin's Index (HB)								
Mean	–	–	–	–	0.339	0.527	0.695	0.497
SD	–	–	–	–	0.37	0.44	0.53	0.25
Median	–	–	–	–	0.357	0.423	0.760	0.648
Diversity Index (PIE')								
Mean	–	–	–	–	0.261	0.299	0.403	0.320
Berger-Parker Index (d)								
Mean	–	–	–	–	0.726	0.790	0.690	0.785
SD	–	–	–	–	0.29	0.19	0.27	0.13
Median	–	–	–	–	0.784	0.860	0.685	0.762
Jaccard similarity (SJ)								
Mean	–	–	–	–	0.165	0.289	0.358	0.172
SD	–	–	–	–	0.211	0.202	0.398	0.153
Median	–	–	–	–	0.000	0.250	0.300	0.167
Percent similarity								
Mean	–	–	–	–	0.113	0.355	0.197	0.169
SD	–	–	–	–	0.18	0.32	0.24	0.23
Median	–	–	–	–	0.000	0.290	0.095	0.048
Component communities (estimated on summed data)								
Brillouin's Index (HB)	0.470	1.190	1.610	0.462	1.330	1.350	1.230	1.570
Diversity Index (PIE')	0.205	0.579	0.755	0.231	0.660	0.639	0.664	0.731
Berger-Parker Index (d)	0.888	0.603	0.342	0.870	0.502	0.524	0.466	0.443
Dominant structure								
Core species number	3	6	6	2	0	1	3	1
Secondary species number	0	0	2	4	1	2	1	2
Satellite species number	7	7	11	5	8	12	2	10

Abbreviations: AO: *Aechmophorus occidentalis*; PG: *Podiceps grisegena*; PN: *P. nigricollis*; PA: *P. auritus*; PC: *P. cristatus*; TR: *Tachybaptus ruficollis*.

Table II. – Parameters of the cestode communities in grebes from Alberta (from Stock & Holmes, 1987, or based on their data after recalculation) and Bulgaria (present study).

valence and abundance were *Tatria mircia* and *T. biremis*. In the second position of species richness and abundance was the family Hymenolepididae. Two of the three hymenolepidids found in *P. cristatus* (*Confluaria pseudofurcifera* and *Dollfusilepis hoploporus*) occurred in this grebe only. The other two cestode families were represented each by a single species.

P. grisegena had the lowest total species richness of the component community. The cestode species belonged to three families. Among them, the Hymenolepididae had the highest richness (50 %) and abundance (55.7 %), the latter due to the high prevalence and abundance of *C. capillaris* and *C. furcifera*.

Similarity

Out of 27 cestode species recovered, only one, *Tatria biremis*, was shared by the four grebe species. The qualitative similarity between the four component communities was low to moderate (Table III). The highest values of SJ were between the communities in *P. cristatus* and *P. grisegena*, and in *P. nigricollis* and *T. ruficollis*. The values of PS between component communities of *P. cristatus*, *P. nigricollis* and *P. grisegena* were moderate; in contrast, these values were considerably lower between *T. ruficollis* and each of the other three species (Table III).

Dominant structure

All the cestode component communities were characterised by a high number of satellite species and a low number of core species (Table I). This in *P. grisegena* had three, and those in *P. nigricollis* and *T. ruficollis* had only one core species. No core species was found in *P. cristatus*.

Four species (15 % of the total species richness) were identified as core in at least one component community. Six species (22 %) were recognised as secondary. The satellite species contributed to the high richness of the component communities in *P. cristatus*, *P. nigri-*

collis and *T. ruficollis* (89 %, 80 % and 77 % of their species richness, respectively).

CESTODE INFRACOMMUNITIES

The distribution of cestode species among the host samples suggested a random pattern in all grebe species (IDT, Chi-Square 8.118, 13.998, 2.692 and 5.1666; $dF = 11, 20, 3$ and 6 for *P. cristatus*, *P. nigricollis*, *P. grisegena* and *T. ruficollis*, respectively; $P > 0.05$). The cestode specimens, however, showed aggregated distributions for all four grebe species (variance/mean ratio 199.9, 530.9, 647.2 and 120.2 for *P. cristatus*, *P. nigricollis*, *P. grisegena* and *T. ruficollis*, respectively). The distribution of individuals was significantly different among the four sample sets (K-W $H = 15.81$, $p = 0.0012$); however, the differences in the distribution of cestode species were not significant (K-W $H = 5.52$, $p = 0.1375$). The infracommunity diversity was low, as estimated by both diversity indices (Table II). The values of d were high for all samples. No significant differences between the values of the diversity and dominance parameters were found when the four sample sets were compared. The qualitative and quantitative similarity among the infracommunities in each grebe species was low, rarely moderate (Table II). There were significant differences between the values of the similarity when comparisons were made among the four sample sets (K-W: SJ, $H = 19.9888$, $p = 0.0002$; PS, $H = 38.8772$, $p = 0.0000$). This was due to the significantly higher homogeneity of the infracommunities in *P. nigricollis* relative to those in *P. cristatus* (M-W: SJ, $U = 3702.5$, $p = 0.0000$; PS, $U = 2844.5$, $p = 0.0000$) and in *T. ruficollis* (M-W: SJ, $U = 1543.5$, $p = 0.0236$; PS, $U = 1409.5$, $p = 0.0065$).

PARTICIPATION OF GREBE SPECIALISTS IN THE CESTODE COMMUNITIES

Out of the 27 cestode species found, 21 (78 %) are grebe specialists (Table I). They represented 66.7-

Jaccard similarity (SJ)								
	AO-C	PG-C	PN-C	PA-C	PC-B	PN-B	PG-B	TR-B
AO-C		0.533	0.450	0.615	0.188	0.250	0.231	0.150
PG-C	0.162		0.391	0.500	0.158	0.167	0.188	0.083
PN-C	0.087	0.256		0.500	0.077	0.133	0.087	0.103
PA-C	0.093	0.303	0.291		0.176	0.182	0.214	0.143
PC-B	0.018	0.224	0.169	0.503		0.200	0.364	0.048
PN-B	0.051	0.259	0.188	0.259	0.358		0.235	0.333
PG-B	0.477	0.289	0.173	0.315	0.412	0.337		0.118
TR-B	0.013	0.031	0.044	0.031	0.026	0.101	0.031	

Percent similarity (PS)								
AO-C		0.533	0.450	0.615	0.188	0.250	0.231	0.150
PG-C	0.162		0.391	0.500	0.158	0.167	0.188	0.083
PN-C	0.087	0.256		0.500	0.077	0.133	0.087	0.103
PA-C	0.093	0.303	0.291		0.176	0.182	0.214	0.143
PC-B	0.018	0.224	0.169	0.503		0.200	0.364	0.048
PN-B	0.051	0.259	0.188	0.259	0.358		0.235	0.333
PG-B	0.477	0.289	0.173	0.315	0.412	0.337		0.118
TR-B	0.013	0.031	0.044	0.031	0.026	0.101	0.031	

Abbreviations: Grebes from Canada: AO-C, *Aechmophorus occidentalis*; PG-C, *Podiceps grisegena*; PN-C, *P. nigricollis*; PA-C, *P. auritus*. Grebes from the Bulgarian Black Sea coast: PC-B, *P. cristatus*; PN-B, *P. nigricollis*; PG-B, *P. grisegena*; TR-B, *Tachybaptus ruficollis*.

Table III. – Similarity values (SJ and PS) between cestode component communities in grebes from Bulgaria (present study) and Alberta (Stock & Holmes, 1987).

100 % of the species richness and 86.1-100 % of the abundance in each component community. These species had also substantial role at the infracommunity level: the mean values of d' for each of the four infracommunity sample sets ranged between 0.4 and 1.0. The distributions of the species number and the abundance of grebe specialists, as well as d' , were significantly different among the infracommunities in the four hosts (K-W: number of species, $H = 8.54$, $p = 0.0361$; number of individuals, $H = 15.84$, $p = 0.0012$; d' , $H = 13.18$, $p = 0.0043$). The number of grebe specialist species in the infracommunities in *P. cristatus* was significantly lower compared to *P. nigricollis* (M-W $U = 56.5$, $p = 0.0098$) and *T. ruficollis* (M-W $U = 15.5$, $p = 0.0111$). Concerning the abundance of grebe specialists, it was significantly higher in the infracommunities in *P. nigricollis* compared to *P. cristatus* (M-W $U = 32.0$, $p = 0.0005$) and *T. ruficollis* (M-W $U = 25.0$, $p = 0.0109$). The communities in *P. nigricollis* had a significantly higher dominance of grebe specialists compared to *P. cristatus* (M-W $U = 70.0$, $p = 0.0378$) and *P. grisegena* (M-W $U = 13.5$, $p = 0.0153$). Grebe specialists exhibited also higher dominance in *T. ruficollis* compared to *P. cristatus* (M-W $U = 17.5$, $p = 0.0182$) and *P. grisegena* (M-W $U = 3.5$, $p = 0.0212$).

DISCUSSION

COMPONENT COMMUNITIES

Taxonomic structure

The present results demonstrate a similar pattern of the cestode component community structure in the four grebe species. The main element of the richness and abundance is the group of grebe specialists (21 species) belonging to the Hymenolepididae (nine species of *Confluaria*, *Dollfusilepis*, *Pararetinometra* and *Mackoja*) and Amabiliidae (12 species of *Tatria*, *Schistotaenia* and *Ryzikovilepis*). In the case of *T. ruficollis*, they are the only component. In addition to the grebe specialists, the cestode communities in *P. cristatus*, *P. grisegena* and *P. nigricollis* include cestodes, which are generalists or specialists of other groups of aquatic birds. They have a minor role relative to the component community richness and abundance.

The group of the specialists of other aquatic birds includes four species. Three species of the hymenolepidid genera *Fimbriarioides* Fuhrmann, 1932 and *Microsomacanthus* Lopez-Neyra, 1942, recorded in *P. grisegena* and *P. nigricollis*, respectively, are parasites of anatid and larid birds (Spasskaya, 1966; Ryzhikov *et al.*, 1985; Hoberg, 1996). The fourth species, *Paricterotaenia porosa*, is a common parasite of gulls (Laridae) (Ryzhikov *et al.*, 1985; Hoberg, 1996). It has

been found in *P. nigricollis* in Ukraine (Sergienko, 1972) and recorded in the same host by us. The most probable reasons for these records are the habitats and foods common to grebes and other aquatic birds. In particular, *P. nigricollis* associates with gulls and other aquatic birds outside the breeding season (B.B. Georgiev, personal observations).

The group of generalists contains two species. The record of *Ligula intestinalis* (Diphylobothriidae) in *P. cristatus* is anticipated because this host is more piscivorous than the other Palaearctic grebes (Cramp & Simmons, 1977; Simeonov *et al.*, 1990). It should be mentioned that *Ligula* spp. exhibit low specificity to the definitive hosts (various piscivorous birds) and high specificity to the second intermediate host (fishes) (Dubinina, 1966). The second generalist is *Tetrabothrius macrocephalus* (Tetrabothriidae), a parasite of various marine birds (Temirova & Skryabin, 1978). We have recorded it in the three larger grebe species, which tolerate more diverse habitats outside breeding season, i.e., coastal waters, saltwater lakes and lagoons (Cramp & Simmons, 1977). However, it has not been found in *T. ruficollis* whose nesting and non-breeding habitats are almost entirely restricted to fresh waters (Cramp & Simmons, 1977; Simeonov *et al.*, 1990).

Stock & Holmes (1987) recovered a total of 23 cestode species in four grebes (*Aechmophorus occidentalis*, *P. grisegena*, *P. nigricollis* and *P. auritus*) in Alberta. There are only six species occurring in both component communities in grebes from Alberta and Bulgaria. However, similarly to our results, the cestode component communities described by Stock & Holmes (1987) are characterised by a high richness and abundance. In addition to the five families recorded by us, they also found a species of the family Dioecocestidae. In Alberta, 15 cestode species are grebe specialists. These were members of the families Hymenolepididae (nine out of 13 hymenolepidid species) and Amabiliidae (five species) which prevailed relative to the richness and abundance in all four component communities. Another grebe specialist, the dioecocestid *Dioecocestus asper* (Mehlis, 1831), occurred at low abundance in *P. grisegena*. The generalists were three species with a comparatively low abundance, two diphylobothriids and one tetrabothriid (*T. macrocephalus*, syn. *T. immerinus*, see Temirova & Skryabin, 1978). Two of these are the same as recorded in Bulgaria, plus *Schistocephalus solidus* (Muller, 1776). Specialists for other aquatic bird groups are five species (hymenolepidids and a dilepidid from anatids), all recorded in *P. nigricollis* only.

The comparison between the taxonomic structures of the cestode component communities in grebes from freshwater lakes in Alberta and from the Bulgarian Black Sea coast reveals several common features: 1) The

main component of the cestode communities in Alberta and Bulgaria are the grebe specialists of the Hymenolepididae and Amabiliidae. 2) The range of the generalists includes almost the same taxa. 3) The range of the cestodes, which are specialists of other avian groups, includes mainly species parasitising anatids. In the context of the same comparison, the principal differences are as follows: 1) Though hymenolepidid and amabiliid grebe specialists are the major part of the component lists (21 species, or 77.8 % for Bulgaria and 14 species, or 60.9 % for Alberta), there are only four species in common for the two studies among them (*Tatria biremis*, *Confluaria furcifera*, *C. podicipina* and *Pararetinometra lateralacantha*). The considerable differences between the two species lists could be explained with their affiliation to different faunistic complexes (Palearctic and Nearctic). 2) Some species recorded in both studies may have a different participation in the abundance of the component communities. The higher mean intensity of the marine species *Tetrahobrius macrocephalus* and the lower mean intensity of the freshwater species *Ligula intestinalis* in Bulgarian material in comparison to those in Canada could be explained by the coastal habitats where the Bulgarian samples were collected. *L. intestinalis* has a short life span in the final host (c. five days, see Dubinina, 1966) and, therefore, it could be expected to be a permanent and abundant component of the cestode communities in grebes in constant freshwater conditions only. The low abundance of *Pararetinometra lateralacantha* in Bulgaria could be explained by its apparent circumboreal distribution (Vasileva *et al.*, 1996a); this species could be expected in Bulgaria in severe winters only when the northern populations of *P. nigricollis* migrate to the Black Sea (Simeonov *et al.*, 1990). 3) The marine habitats of grebes examined in Bulgaria facilitate a restricted amount of transfer of cestodes from larids to *P. nigricollis*.

Similarity and diversity

The four grebe species examined in Bulgaria exhibit relatively low qualitative and quantitative similarity among the component communities (Table III). On the basis of their qualitative similarity, two groups of cestode component communities are outlined: 1) in small-sized grebe species, *P. nigricollis* and *T. ruficollis*, possessing 2 amabiliid and 5 hymenolepidid grebe specialists in common; 2) in large-sized grebe species, *P. cristatus* and *P. grisegeta*, having 2 amabiliid and 1 hymenolepidid grebe specialists, and 1 generalist in common. This may be an indication for the partial dietary overlap of grebe species in each of both groups. The quantitative similarity analysis reveals that the component community in *T. ruficollis* is essentially different from those in the remaining three grebes studied. This may be interpreted as a reflection of both

its ecological specialisation (e.g., the restriction to freshwater habitats and the lesser degree of dietary overlap with other grebes) and the evolutionary determined higher level of specificity of its cestodes (see the discussion on the host specificity below).

The qualitative similarity among cestode component communities in the four grebes from Alberta, calculated on the basis of the data of Stock & Holmes (1987), is considerably higher as compared to our data (Table III). This is mainly due to the fact that 13 cestode species (52.2 %) are common for three or four host species in Alberta. In contrast, only four species (14.8 %) occur in three or four component cestode communities in grebes from Bulgaria. This difference suggests a lower degree of parasite exchange among the grebe species studied in Bulgaria than among the nesting populations in Alberta. It could be speculated that the main reason for this difference is the homogeneity of the freshwater nesting habitats in Alberta. The continued presence of various nesting grebe species on the same lakes may result into more efficient parasite cycling which increases cestode local populations. The trophic overlap in freshwater habitats, which is due to the ability of grebes for opportunistic feeding depending on the season and the available food resources (Cramp & Simmons, 1977; Stock & Holmes, 1987; Storer & Nuechterlein, 1992), provides a common parasite pool for all the grebe species and can explain the higher extend of parasite exchange there.

In spite of the obvious differences of the qualitative similarity, the quantitative similarity calculated for the cestode component communities in Canadian grebes are almost within the same range compared to those in Bulgarian grebes (Table III). This indicates the similar patterns of the grebe species unequal contribution in maintaining the populations of certain cestode species. Stock & Holmes (1987) considered that, though many parasites are shared among the grebe species, the major portion of each parasite population is concentrated in «the main host» species. The same is the case with the component communities studied in Bulgaria.

The present study and the survey of Stock & Holmes (1987) provide comparable-sized samples of *P. nigricollis*. The component communities of this host from Alberta and Bulgaria contain only four species in common and exhibit very low qualitative and quantitative similarity (Table III). Applying the similarity as a criterion for the component community predictability (Holmes, 1990), this indicates the low predictability of the cestode component community in this host on a coarse geographical scale.

The comparison between the diversity measures based on summed data (HB, PIE' and d, see Table II) shows a considerably higher variability of the values for the

component communities in Alberta and narrower ranges for those from Bulgaria. These results demonstrate a rather uneven distribution of cestode species among Canadian grebe populations.

Dominant structure

The dominant structure of the four cestode component communities in Bulgaria is characterised by a small number of core species (0-3). *T. biremis* is the only cestode, which is core in two grebe species (Table I). Each cestode component community is characterised by a distinct list of secondary species (Table I) or, in other words, each grebe species has a host-specific group of common cestode species. In contrast, the component communities in Canadian grebes exhibit a different dominant structure (Stock & Holmes, 1987). It is characterised by a higher number of core species (2-6) (Table II). Four species attain core status in at least two component communities (out of 10 cestode species recognised as core). Since the prevalence criteria have been used for the identification of the dominant status of the cestode species, the observed difference can be explained by the more intense parasite cycling, respectively more abundant local populations, in the freshwater habitats.

Host specificity

The host specificity is usually defined as the extent to which a parasite taxon is restricted in the number of host species used at a given stage in the life cycle (e.g., Poulin, 1998). In relation to the specificity to their final host, the species recorded have to be regarded as generalists ("eurixene" parasites of Combes, 1995), grebe specialists ("stenoxene" and "oiioxene" parasites of Combes, 1995) and accidental parasites (specialists of other groups of aquatic birds occurring in grebes with low prevalence and abundance). The grebe specialists are the main element of the richness and abundance of the cestode communities both in Bulgaria (present results) and in Alberta (Stock & Holmes, 1987). Nine out of the 10 cestode core species from Canada and all core species from Bulgaria are grebe specialists. Therefore, host specificity seems to be the main factor determining the structure of the cestode communities in grebes.

The extent of the host specificity revealed by Stock & Holmes (1987) differs from that in our results. The only cestode species restricted to a single host (an "oiioxene" parasite) in Alberta is *Dioecocestus asper*. Almost all the other grebe specialists share two or more hosts; this low extent of specificity allows exchange among related host species (Stock & Holmes, 1987). In our results there are four species restricted to a single host species (*S. rufi*, *T. octacantha*, *C. pseudofurcifera* and *D. hoploporus*). Their narrow specificity is confirmed by data on their previous host records (Sulgostowska

& Korpaczewska, 1969; Rees, 1973; Vasileva *et al.*, 1998; 1999c). In addition to them, there is an intermediate group between the typical "stenoxene" and "oiioxene" parasites, which includes *C. multistriata* and *M. podirufi*. The bulk of their abundance is in *T. ruficollis* ("main or required host", a term proposed by Holmes *et al.*, 1977); we found only single immature specimens of them in *P. nigricollis*. The previous records of these cestodes are also mainly from *T. ruficollis* (see Vasileva *et al.*, 1996b, 1999b). These results indicate that the degree of interspecific cestode exchange is considerably lower in grebes at the Black Sea coast than in those from freshwater habitats in Canada.

INFRACOMMUNITIES

The infracommunities in the four host sample sets have a similar pattern of structure. All the infracommunities exhibit a low degree of diversity, a high dominance and a low similarity. There are no differences among the infracommunities in the grebe species examined relative to the distributions of species and the diversity parameters. Compared with our results, the species richness and abundance of the cestode infracommunities in breeding grebes in Canada (Stock & Holmes, 1987) are higher (Table II). Probably, the almost constant conditions of breeding habitats enhance the higher cestode infestation. The decrease of the helminth infection parameters during migrations has been widely discussed by many authors (e.g., Dubinina, 1950; Dogel, 1962; Esch *et al.*, 1990; Bush, 1990). The present results, obtained on the basis of host samples representing birds of migratory and overwintering populations, agree with the assumption that the same phenomenon may also have a major impact at the infracommunity level. However, since the infracommunities in grebes from Canada and Bulgaria are samples of different faunistic complexes (Nearctic and Palearctic), the differences between them may also be determined by historical factors.

CONCLUSIONS

Our results and their comparison with the previous study on the helminth communities in grebes (Stock & Holmes, 1987) exhibit several important differences and similarities.

The main distinctions between the results of the two investigations at the infracommunity level concern the higher species richness and abundance of the cestode infracommunities in breeding grebes in Canada. The most possible explanation is the almost constant conditions of breeding habitats enhancing the higher cestode transmission rates.

At the component community level, there are several main differences. There is a significant difference between the two species lists, which could be explained by historical factors (their affiliation to different faunistic complexes). Other distinctions are the lower degree of the parasite exchange among the grebe species in Bulgaria and the different abundance of some common species (e.g., *L. intestinalis* and *T. macrocephalus*). These and the occurrence of specialists of larids in grebes from the Bulgarian coast can be explained mainly by habitat differences.

The following similar characters at the component community level are revealed: 1) the same pattern of the taxonomic structure at the generic and family levels which is characterised by the dominance of the grebe specialists of the families Hymenolepididae and Amabiliidae, almost the same species list of generalists, and the slight participation of hymenolepidid genera containing specialists of anatids; 2) close ranges of the quantitative similarity indicating a common pattern of an unequal contribution of the host species in the support of the cestode species populations; 3) the important role of the grebe specialists in cestode communities (i.e., the host specificity is the main factor for the determination of the community structure and the species richness in grebes). Evidently, these features of component communities of grebes do not depend on either historical (zoogeographical) factors or the different habitats utilised by grebes during the breeding season and during migration and overwintering.

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