Occurrence of intermediate hosts and structure of digenean communities of the black-headed gull, *Larus ridibundus* (L.)

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SUMMARY

The factors contributing to the similarity between digenean parasite assemblages parasitizing the black-headed gull were investigated. Thirteen different digenean species from the digestive tract and the bursa of Fabricus were found. We predicted that the structure of parasite communities is not random at either component community or infracommunity levels. We searched for nested patterns in the digenean community, and explored the possible factors contributing to nestedness. We found that digenean species which occupy a narrow range of intermediate hosts are placed out of order in the nested matrix. The influence of several variables related to the water reservoir, geographical distances, and the abundance of intermediate hosts on the species diversity and similarity of parasite communities were tested as well. Because of the complexity in bird digenean life-cycles we supposed that intermediate hosts and ecological characters of their environment could play a major role. We showed that the presence of intermediate hosts is the factor limiting the qualitative and quantitative similarity of parasite communities among different host populations as well as influencing the digenean species diversity in the definitive host. The similarity in abundance of intermediate hosts between different localities was facilitated by the presence of vegetation in water reservoir and more diversified type of water bottom. Digenean species diversity was higher when the water reservoir was exposed to temporal drying. We hypothesized that this factor could facilitate the inclusion of molluscs infected by digeneans in the diet of birds. Both species diversity and dominance were influenced by the bottom type of water reservoir and temporal drying up. Geographical distances between localities influenced the quantitative similarity of digenean communities as well as species richness.

Key words: Digenea, species diversity, intermediate hosts, community similarity.

INTRODUCTION

Patterns of species diversity and/or distribution among islands have been the subject of many ecological studies related mainly to the species–area theory (MacArthur & Wilson, 1967; Connor & McCoy, 1979; Kuris, Blaustein & Alió, 1980; Ricklefs & Lovette, 1999; Morand, 2000). Several factors such as geographical distances between islands, island area and habitat diversity may contribute to the relationship between islands and species richness, or similarity between species communities in terms of species richness (MacArthur & Wilson, 1967; Ricklefs & Lovette, 1999; Morand, 2000).

When the island biogeography theory is applied to parasites, different host populations or different host individuals belonging to one host population could be considered as islands exposed to parasite colonization. One of the aspects related to the island biogeography theory is the search for nested patterns (Patterson & Atmar, 1986; Atmar & Patterson, 1993). On each island, one species is nearest its minimum sustainable population size, and thus at greatest risk of local extinction. If species-extinction order is perfectly replicated on each island of the archipelago, the result would be a set of perfectly nested subsets, when each smaller island would contain only a subset of the species found on all larger islands. However, the extinction order will be perturbed by random processes acting on the individual populations on the islands and may result in species extinction order being not perfectly replicable (Atmar & Patterson, 1993).

Then, nestedness represents a departure from random composition of species in assemblages when species occurring in the species-poor assemblages represent non-random subset patterns of the species-rich assemblages. In recent years, studies investigating this pattern have been carried out predominantly on

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ectoparasites of fish (Guégan & Huguény, 1994; Worthen & Rohde, 1996; Rohde *et al.* 1998; Matejusová, Morand & Gelnar, 2000; Poulin & Guégan, 2000; Poulin & Valtonen, 2001; Šimková, Morand & Gelnar, 2001; Morand, Rohde & Hayward, 2002). Fewer studies have been conducted to investigate the nestedness of endoparasites (Poulin & Valtonen, 2001; Valtonen *et al.* 2001).

However, until now, the nestedness has not been investigated for the parasites with more complex life-cycles than those of fish endoparasites. The increase of life-cycle complexity in bird endoparasites lead us to consider that several local or regional factors may generate the nestedness.

The aims of this study were to investigate the factors contributing to the similarity between parasite assemblages using digenean parasite communities in one bird species *Larus ridibundus*. When considering digeneans of birds, it is important to regard this group as parasites with a complex life-cycle including molluscs as the first intermediate hosts and molluscs, insects or fish as the second intermediate hosts which present the necessary condition for parasite development and successful infection of definitive hosts.

We supposed that parasite species distribution among hosts is not the result of random processes, and that the structure of parasite communities within and between host samples should be repeatable but also influenced by local factors. We predicted that the repeatability in digenean assemblages shows nested patterns among (1) individuals in a local host population and (2) among different host populations. We tried to explain nestedness for bird digeneans using their specificity to intermediate hosts i.e. either digenean species are specific to some intermediate hosts, or digenean species and their intermediate hosts are specific to some locality (local ecological conditions). We also predicted that the similarity of parasite communities could be related to characteristics of the water reservoir, and that the presence of intermediate hosts will be the factor responsible for the similarities among parasite communities, taking into account the influence of geographical distances between host populations.

MATERIALS AND METHODS

A total of 355 individuals of 1 bird species, the black-headed gull (*Larus ridibundus* L., Laridae, Charadriiformes), aged from 21 to 25 days old, were investigated. The black-headed gull is the numerically dominant species living around the water ecosystems and eating the different kinds of vertebrate and invertebrate species (fish, frogs, molluscs, crustaceans, insects) which may represent the intermediate hosts important for digenean life-cycles (Sitko, 1993, 2002). The birds were collected from 8 different localities (10 samples) in the Czech Republic and Poland. Two localities (Ponědraž and Záhlinice) from Czech Republic were sampled for birds twice during different years because ecological conditions in those two localities had changed and we considered their effects on parasite species richness and diversity. All characters related to the different host populations are given in Table 1. Endoparasite species belonging to the Digenea were removed from the digestive tract and bursa of Fabricus. In total 13 digenean species were identified. Other supplementary information concerning the digenean species of the black-headed gull has been published by Sitko (1993, 2002).

The level of parasite infection was assessed according to the method described by Bush *et al.* (1997). Prevalence was calculated as the percentage of hosts infected by a digenean species. Mean intensity of parasite infection is the average intensity of a parasite species in a sample of infected hosts collected at 1 locality. Mean abundance is the average abundance of a parasite species among all host individuals of a host population.

Infracommunity was defined as a community of parasite infrapopulations in an individual host, and component community as all parasite infrapopulations of host individuals belonging to 1 host population (Bush *et al.* 1997). Digenean species richness, Brillouin's diversity index and Simpson's index of dominance were calculated for each component community according to Magurran (1983). Brillouin's index is used for parasite diversity evaluation and calculated also for each infracommunity as $H=1/N\log_e(N!/N1!N2!N3!\ldots NS!)$ where N is the total number of parasite species, $N1, N2, N3 \ldots NS$ are the numbers of parasites of each species 1, 2, 3, … S.

Simpson's index of dominance was calculated as following:

$$D=\sum\left(\frac{n_i(n_i-1)}{N(N-1)}\right)$$

when n_i is the number of species i and N is the total number of individuals.

For qualitative comparison between samples, Jaccard's index of similarity was used $J=100c/(a+b+c)$, where a is the number of parasite species in the first host population, b is the number of species in the second host population, c is the number of parasite species which occur together in both host populations. For quantitative comparison between samples, Steinhaus's coefficient was used as $S=2W^*(A+B)$, where A and B are the sums of the abundances of all species in host individuals of one population, W is the sum of the minimum abundances of different species in host individuals of 1 population (i.e. the sum is calculated using parasite species with the lower abundance on each host individual in 1 population). Both indices were used as described by Legendre & Legendre (1998).

Euclidean distances were used to evaluate similarities between host samples based on the abundance

Table 1. List of localities with the character of host habitat

(Vegetation: 0 – without vegetation, 1 – with vegetation; Intermediate hosts: Molluscs: 1 – absent, 2 – low abundance, 3 – high abundance; Insects: 1 – restricted communities, 2 – natural rich communities; Fish: 1 – restricted communities, 2 – natural rich communities Cypriniformes (*Cyprinus*, *Carrasius*, *Rutilus*, *Scardinius*), 3 – natural rich communities Clupeiformes (*Coregonus*) and Perciformes (*Gymnocephalus*).)

Locality (year of investigation)	Reservoir area (km^2)	Water depth (in m)	Type of water bottom	Temporal drying up	Veg- etation	Influence of sea	Intermediate hosts						
							Molluscs						
							Lithoglyphus naticoides	*Bythinia* sp.	*Valvata* sp.	*Lymnea* sp.	*Planorbis* sp.	Insects	Fish
Strachotín (1963)	5	1·5	Boulder and mud	Yes	1	No	2	3	2	3	3	2	2
Sedlec (1968)	3·15	1·7	Boulder and mud	No	1	No	3	3	3	3	3	2	2
Mušov (1990)	10·34	3·4	Boulder and mud	No	0	No	2	2	3	2	2	2	2
Záhlinice 1 (1963)	1·1	0·7	Boulder and mud	Yes	1	No	1	2	2	3	3	2	2
Záhlinice 2 (1990)	1·1	1·7	Mud	No	0	No	1	1	1	1	1	1	1
Ponědraž 1 (1967)	1·42	1·7	Mud	No	1	No	1	1	1	3	3	2	2
Ponědraž 2 (1990)	1·42	1·7	Mud	No	0	No	1	1	1	1	1	1	1
Zegoty (1993)	0·33	1·2	Boulder and mud	Yes	1	No	2	3	2	3	3	2	3
Kalwa (1963)	5·62	7·0	Boulder and mud	No	1	No	2	2	3	3	3	2	3
Modla (1994)	1·87	1·5	Boulder and mud	No	1	Yes	2	2	3	3	3	2	2

of the intermediate hosts. Presence of each potential intermediate host was recorded and their abundance was coded as 1 – absent, 2 – rare, 3 – high abundance, and included in the matrix to calculate Euclidean distances. Three matrices were calculated: (1) for the potential invertebrate intermediate host, (2) for the potential fish intermediate host, (3) for the all intermediate hosts.

Each locality was classified according to the vegetation presence. The category 'without vegetation' presents the reservoirs which were created from the old pond by removing the bottom and eliminating the littoral zone. As a consequence, the vegetation is presented only in a few places in the maximal depth of 30 cm, the area with the vegetation presents less than 0·5% of the total reservoir area. The category 'with vegetation' presents the reservoirs with intensive vegetation around the whole reservoir.

For fish communities, three categories were used. When fish species of any fish group were found in low abundance, the category 'restricted communities' was used. The category '2 – natural rich communities Cypriniformes' presents the reservoirs with fish communities constituted of mostly Cypriniformes (more than 90%), the fish species different from Cypriniformes were selectively decreased by human activities. The category 'natural rich communities Clupeiformes and Perciformes' presents the reservoirs when the species Clupeiformes and Perciformes were recorded as the numerically dominant group. In those reservoirs Cypriniformes were present as well but did not form the dominant group.

To evaluate the factors determining similarity between locality, parasite diversity and species richness, a correlation using permutation tests on distance matrices was used following the method of Legendre, Lapointe & Casgrain (1994). The coefficient of determination of the multiple regression, as well as the partial regression coefficients, were tested for significance through permutation methods appropriate for each type of dependent-matrix variable. Probabilities were computed after 999 random permutations of the dependent matrix. Backward elimination procedure with Bonferonni correction was used and computed by Permute 3.4 (written by P. Casgrain, available on the internet at http://alize.ere.umontreal.ca/~casgrain/). Nested patterns were investigated using the method proposed by Atmar & Patterson (1993) who used a simple thermodynamic measure of order and disorder to describe nested patterns of presence–absence of species on islands. A matrix temperature of perfect order assumes the attributes of a frozen liquid, and so complete order exists only at 0 °C. As the temperature rises, turbulence is imposed on the system and at 100 °C no discernible extinction order remains. The presence–absence matrix of species has assumed the attributes of a free gas. The temperature of a matrix is dependent on the manner in which species are distributed throughout the matrix.

Elevated temperatures act as an indicator to suggest that these species were disconnected from the biogeographical extinction event of the archipelago. The history of all populations on all islands has become wholly independent of one another and correlatable predictability has disappeared from the matrix.

The majority of datasets associated with this nested temperature calculator have been assembled for a meta-analysis of nested subset distribution patterns and the metrics used to evaluate them. A nested temperature calculator was used in this study following Atmar & Patterson (1995). We calculated probability after 5000 repetitions.

When doing the nested analysis, the presence–absence matrix is constructed, the matrix specified which species occur in which sites, and reflects the relative hospitability of sites to the species. The matrix has been packed to a state of maximal nestedness. The island positioned on the top of matrix is considered as the most hospitable island. The species positioned in the left corner of the matrix presents a species for which niche requirements are most common and prevalent, this species is more resistant to extinction. In the perfectly nested matrix (the matrix which is created by packing to maximal nestedness), the set of species on any island is the subset of all species on the islands preceding in the matrix. The hypothetical boundary line separates the occupied area from the unoccupied and is specified by the matrix's rank and fill (how many presences it contains). To calculate the matrix temperature, the distribution of 'unexpected species' presences and absences is used. At low temperature (i.e. the nestedness system), unexpected presences and absences cluster near the line. When the temperature increased (the system of randomness is increased), unexpected presences and absences extend further into the matrix. The probability that any distribution pattern might be randomly produced can be estimated using Monte Carlo simulations. To assess the probability, the matrix is generated wholly at random (the temperature equating to 100 °C). The extent to which the temperature of the matrix deviates from 100 °C depends on the degree of fill of the matrix. For more information see Atmar & Patterson (1995). The nestedness temperature calculator is available on the internet at http://aics-research.com/nestedness/tempcalc.html.

RESULTS

Component communities

A total of 13 digenean species was found in the present study (Table 2). When considering separate host populations the number of digenean species ranged from 2 (in Ponědraž 2 and Záhlinice 2) to 8 (in Strachotín and Zegoty). When considering all digenean species the total prevalence of infection was high for all host populations (more than 65% for each of them) except in Záhlinice 2 where the prevalence was lower (35%). The maximum value of prevalence was reached in Strachotín, Kalwa and Modla (Table 3). The most prevalent species were *Diplostomum* spp. and *Plagiorchis laricola*. *Diplostomum* spp. was considered as a species with high prevalence in 6 of 10 host populations (the values about or more than 50%); its highest prevalence was found in Kalwa. *Plagiorchis laricola* was considered as a species with the high abundance and prevalence in 8 of 10 host populations; and its highest values of prevalence were found in Kalwa and Modla. This last species had low values of prevalence only in Záhlinice 2. *Prosthogonimus ovatus* and *Echinoparyphium recurvatum* could be considered as the species with high prevalence only in 1 host population (Table 2). The most abundant species was *P. laricola* with the highest mean abundance in Kalwa. *Diplostomum* spp. was the second most abundant species and *E. recurvatum* reached the highest value of mean abundance in Strachotín.

Digenean species richness, species diversity (Brillouin's index diversity) and dominance (Simpson's index), and mean abundance at the component community level are given in Table 4. The highest species diversities were reached in Strachotín and Zegoty, and the lowest dominance indices were found for Strachotín, Záhlinice 1 and Zegoty. Digenean communities in Ponědraž 1 and Ponědraž 2 (the same locality investigated at different times) had different indices of diversity but they showed similar dominance indices. Digenean communities in Záhlinice 1 and Záhlinice 2 (also the same locality investigated at different times) differed by both diversity and dominance indices. Qualitative similarity of parasite communities between host populations was evaluated using Jaccard's index (Table 4). The same digenean species were present in Ponědraž 2 and Záhlinice 2. A high level of qualitative similarity was reached between Strachotín and both Záhlinice 1 and Zegoty. Quantitative similarity of parasite communities between host populations was evaluated using Steinhaus's index (Table 4). The highest values of Steinhaus's index were found between pairs of localities Záhlinice 1, Sedlec, Zegoty and Modla.

Nested patterns

Nested patterns were observed when different host samples presenting different host populations isolated in space or time were analysed (Tables 5 and 6). When analysing the matrix of presence/absence data of digenean species from different host populations, we found that parasite species with close affinity to some intermediate hosts (i.e. using a narrow host range either as first or second intermediate hosts) are placed as outliers in the matrix even if *Ichthyocotylurus platycephalus* restricted to *Valvata* sp. as

Table 2. Prevalence of infection and abundance (mean ± S.D.) for 13 digenean species in the host populations

(DS, *Diplostomum* spp.; IP, *Ichthyocotylurus platycephalus*; IE, *I. erraticus*; AM, *Apophallus muehlingi*; SD, *Stephanoprora denticulata*; CC, *Cryptocotyle concavum*; PL, *Plagiorchis laricola*; PM, *P. moravicus*; PO, *Prosthogonimus ovatus*; ER, *Echinostoma revolutum*; EN, *E. nordiana*; ECR, *Echinoparyphium recurvatum*; LP, *Leucochloridium perturbatum*.)

Host population	DS	IP	IE	AM	SD	CC	PL	PM	PO	ER	EN	ECR	LP
Strachotín	57·9% 40·61±92·35	5·3% 0·05±0·23	—	2·6% 0·05±0·32	—	—	76·3% 48·89±88·62	10·5% 1·97±7·95	23·7% 0·82±1·74	44·7% 2·76±6·74	—	73·7% 63·63+142·43	—
Sedlec	50% 10·43±16·86	22·5% 0·35±1·17	—	35% 12·35±26·9	—	—	97·5% 21·25±16·29	—	2·5% 0·08±0·47	—	2·5% 0·35+2·19	12·5% 0·25+0·86	—
Mušov	14·63% 1·56+7·28	17·1% 1·29+4·12	—	2·4% 0·10+0·62	—	—	78·1% 16·51+41·2	—	—	4·9% 0·07+0·35	—	—	2·4% 0·02+0·16
Záhlinice 1	45·7% 8·71±17·57	2·9% 0·03±0·17	—	—	—	—	37·1% 10·69±18·0	5·7% 0·17±0·75	5·7% 0·06+0·24	11·4% 0·57+1·99	—	17·1% 3·17±9·12	—
Záhlinice 2	32·5% 1·03±2·06	—	—	—	—	—	5% 0·05+0·22	—	—	—	—	—	—
Ponědraž 1	22% 1·63±6·36	—	—	—	—	—	90·2% 45·78±90·54	—	—	2·4% 0·02±0·16	—	2·4% 0·68+4·37	—
Ponědraž 2	12·2% 0·17±0·50	—	—	—	—	—	75·6% 4·73±6·14	—	—	—	—	—	—
Zegoty	63·2% 10·18±22·79	13·2% 0·29±0·87	7·9% 0·34±1·65	2·6% 0·03±0·16	—	—	81·6% 14·42±21·40	—	13·2% 0·37±1·17	39·5% 3·74±11·02	—	26·3% 2·18+7·85	—
Kalwa	86·7% 22·27±25·14	6·7% 0·13±0·52	13·3% 0·27±0·80	—	—	—	100% 316·13±146·47	—	86·7% 3·93±6·63	6·7% 0·07±0·26	—	—	—
Modla	69·2% 5·92±13·48	11·5% 0·31±1·05	—	7·7% 0·08±0·27	38·5% 1·58±3·81	7·7% 1·04±5·09	100% 14·46±3·55	—	11·5% 0·31±1·19	—	—	—	—

Table 3. Digenean component communities (parasite abundance, prevalence, species richness, Brillouin's diversity index and Simpson's index of dominance) for each host population

Host population	Number of hosts in the population	Parasite abundance mean ± S.D.	Prevalence (%)	Species richness	Brillouin's index	Simpson's index of dominance
Strachotín	38	158·89±168·57	100	8	1·232	0·401
Sedlec	40	45·00±42·32	97·50	7	1·154	0·427
Mušov	41	19·56±41·71	82·90	6	0·568	0·844
Záhlinice 1	35	23·40±32·79	65·70	7	1·13	0·457
Záhlinice 2	40	1·10±2·12	35·00	2	0·158	0·954
Ponědraž 1	41	48·12±93·43	95·10	4	0·223	0·951
Ponědraž 2	41	4·90±6·44	75·60	2	0·142	0·965
Zegoty	38	31·47±38·49	92·10	8	1·296	0·457
Kalwa	15	342·53±156·24	100	6	0·312	0·922
Modla	26	23·73±20·25	100	7	1·074	0·61

Table 4. Values of Jaccard's index for qualitative similarity (up to diagonal) and Steinhaus's index for quantitative similarity (down to diagonal) between host populations

Host populations	Strachotín	Sedlec	Mušov	Záhlinice 1	Záhlinice 2	Ponědraž 1	Ponědraž 2	Zegoty	Kalwa	Modla
Strachotín		0·667	0·556	0·875	0·25	0·5	0·25	0·778	0·556	0·5
Sedlec	0·328		0·444	0·556	0·286	0·375	0·286	0·667	0·444	0·556
Mušov	0·219	0·583		0·444	0·333	0·429	0·333	0·556	0·5	0·444
Záhlinice 1	0·337	0·528	0·545		0·286	0·571	0·286	0·667	0·625	0·4
Záhlinice 2	0·014	0·047	0·102	0·1		0·5	1	0·25	0·333	0·286
Ponědraž 1	0·488	0·491	0·535	0·337	0·1		0·5	0·5	0·429	0·222
Ponědraž 2	0·065	0·201	0·401	0·394	0·074	0·394		0·25	0·333	0·286
Zegoty	0·315	0·64	0·627	0·778	0·069	0·315	0·287		0·756	0·5
Kalwa	0·398	0·343	0·25	0·229	0·017	0·547	0·075	0·285		0·444
Modla	0·163	0·449	0·635	0·74	0·131	0·342	0·492	0·603	0·188	

the first intermediate host is placed in the matrix order. *Stephanoprora denticulata* and *Cryptocotyle concavum*, that utilize many different species of snails as first intermediate host, but are restricted to sea-living fish as the second intermediate hosts. *Leucochloridium perturbatum* is restricted to *Succinea* sp. as the one intermediate host and the presence of *Apophallus muehlingi* is associated only with the distribution of the molluscs *Lithoglyphus naticoides*. *Ichthyocotylurus erraticus* is present only in cold waters when the fish communities of *Coregonus* and *Gymnocephalus* species occur. *Prosthogonimus ovatus* had a wider first intermediate host range i.e. was restricted to either *Bithynia* species or dragonfly. Other digenean species used a wide range of intermediate hosts.

Nested patterns were also found when the analysis was done for digenean assemblages in separated host populations (2 host populations were excluded from the analysis because only 2 species were present).

Factors determining the similarity among host populations

The influence of the water reservoir factors (reservoir area, water depth, vegetation of water reservoir, temporal drying up, bottom type of water reservoir, influence of sea) and the geographical distances between localities was tested on the similarity in the abundance of intermediate hosts. When the matrix based on Euclidean distances only for the invertebrate intermediate hosts was considered, we found that the bottom type of water reservoir and the vegetation in the reservoir were the factors influencing the similarity in abundance of intermediate hosts (for bottom type: $b=0{\cdot}646$, $P=0{\cdot}001$, for vegetation: $b=0{\cdot}436$, $P=0{\cdot}008$; $r^2=0{\cdot}768$, $P=0{\cdot}001$). When the matrix based on Euclidean distances only for the vertebrate host species i.e. fish was considered, no variable of water reservoirs was related to the similarity in abundance of intermediate host. The similarity in abundance for all potential intermediate hosts was related to the bottom type of water reservoir ($b=0{\cdot}625$, $P=0{\cdot}002$), the vegetation in the reservoir ($b=0{\cdot}467$, $P=0{\cdot}014$) and area of water reservoir ($b=-0{\cdot}112$, $P=0{\cdot}021$) with $r^2=0{\cdot}788$, $P=0{\cdot}010$.

The variables related to water reservoir, the geographical distances between localities and the abundance of intermediate hosts were tested as potential factors determining similarity of parasite component communities (Table 7). Qualitative similarity of parasite communities was higher between host populations living in the localities not influenced by the sea. Bird host populations living in a habitat

Table 5. Nested analyses using nestedness temperature metric

(*P* was calculated after 5000 repetitions.)

Nested analysis	Host population	Matrix temperature (°C)	Fill (%)	Random ± S.D.	*P* (T < Trandom)
Among host populations		18·16	39·1	46·88 ± 9·52	0·001
In host population	Strachotín	17·74	36·8	52·69 ± 6·41	< 0·0001
	Sedlec	7·37	31·5	48·62 ± 7·38	< 0·0001
	Mušov	2·38	24·0	40·77 ± 8·62	< 0·0001
	Záhlinice 1	14·66	27·3	46·37 ± 7·06	0·001
	Ponědraž 1	5·12	30·7	44·25 ± 9·65	< 0·0001
	Zegoty	14·93	33·5	51·4 ± 7·1	< 0·0001
	Kalwa	15·18	50·0	40·7 ± 8·98	0·002
	Modla	12·24	35·1	47·04 ± 8·08	< 0·0001

Table 6. Matrix of digenean species composition in the different host population

(See Table 2 for species abbreviations. Species in bold are species using a narrow host range as the first or second intermediate host, more precise data concerning the intermediate hosts on *Plagiorchis moravicus* (PM) were not available because of its rare occurrence.)

Host populations	DS	PL	**IP**	PO	ER	ECR	**AM**	**PM***	**IE**	**SD**	**CC**	EN	**LP**
Strachotín	x	x	x	x	x	x	x	x					
Zegoty	x	x	x	x	x	x	x		x				
Záhlinice 1	x	x	x	x	x	x		x					
Kalwa	x	x	x	x	x				x				
Modla	x	x	x	x			x			x	x		
Sedlec	x	x	x	x		x	x					x	
Mušov	x	x	x		x		x						x
Ponědraž 1	x	x											
Záhlinice 2	x	x											
Ponědraž 2	x	x											

sustaining similar intermediate hosts, had similar parasite communities. Quantitative similarity of parasite communities between host populations was related to geographical distances between localities and fish intermediate hosts. Digenean species diversity was higher in the host populations living around the water reservoir with temporal drying up and in the water reservoir with both boulder and mud bottom. Species dominance was related to the same variables. Parasite species richness was related to the same characters of reservoir as was found for both diversity and dominance. Moreover, parasite species richness was increased with increase of distances between abundance of intermediate hosts. The similarity in species richness increased with the increase of geographical distances.

DISCUSSION

Structure of gastrointestinal parasite communities

Kennedy, Bush & Aho (1986) showed that the helminth communities of birds are species rich compared to other vertebrate hosts, in particular fish. Helminth communities of birds appear to be interactive when interspecific interactions are induced by high abundance and limited niche space offered by definitive hosts (Bush & Holmes, 1986; Stock & Holmes, 1988) whilst helminth communities of fish show low population density and diversity and are considered to be isolationists (Kennedy, 1995; Rohde, 1991). Nevertheless, in the case of bird endoparasites, which include parasites with more complex life-cycles than fish endoparasites, the relation of the environment to the parasite life-cycles, i.e. allochtonous cycles, and the necessity for all components for successful development of parasites should be considered as the basic factor influencing the helminth community structure.

Nested patterns

The structures of parasite communities generally show a departure from a random pattern. Nestedness of ectoparasites and endoparasites has previously been investigated in fish species (see many conclusions in the Introduction section). However, until

Table 7. Results of multiple regressions on distance matrices to explain the effect of variables related to the water reservoir on the similarity of parasite communities

(Independent variables considered in the model were reservoir area, vegetation of water reservoir, water depth of reservoir, temporal drying up, bottom type of water reservoir, influence of sea, geographical distances between host populations, distances between all intermediate hosts, distances between invertebrate intermediate hosts, distances between vertebrate intermediate hosts. Values *b* present partial regression coefficient for each variable, r^2 presents the coefficient of determination, the significance given in parentheses is derived from 999 random permutations.)

Dependent variable	Independent variables	*b*	*P*	r^2 (*P*)
Qualitative similarity of between component communities (Jaccard's index)	All intermediate hosts	−0·864	0·001	0·750 (0·001)
	Influence of sea	−0·35	0·001	
Quantitative similarity of between component communities (Steinhaus's coefficient)	Geographical distances	0·32	0·028	0·306 (0·026)
	Fish intermediate hosts	−0·55	0·019	
Brillouin's index diversity	Bottom of water reservoir	0·554	0·001	0·407 (0·001)
	Temporal drying up	0·358	0·017	
Simpson's index of dominance	Bottom of water reservoir	0·415	0·003	0·381 (0·001)
	Temporal drying up	0·487	0·001	
Parasite species richness	Temporal drying up	0·193	0·014	0·907 (0·001)
	Geographical distances	−0·118	0·012	
	Invertebrate intermediate hosts	0·247	0·011	
	Fish intermediate hosts	0·3	0·007	
	Bottom of water reservoir	0·545	0·004	

now no attention has been paid to the case of endoparasites of birds which represent the definitive hosts for parasites with a complex life-cycle (i.e. including 2 intermediate hosts in many cases). When considering the bird endoparasite communities, it seems that there are also other factors which could play a role in nestedness generation because of high complexity of parasite life-cycle. Among those factors, the occurrence of intermediate hosts and environmental conditions facilitating their successful development should be taken into consideration. The analysis of the structure of bird digenean communities in the present study confirms that a nested pattern occurs at both interpopulation and intrapopulation levels. For the case of fish ectoparasite communities, the nested pattern was found to occur more at the host interpopulation level than at the intrapopulation level (Šimková *et al*. 2001). Nestedness of bird endoparasites seems to be determined by a similar structure of intermediate host communities (maybe also nested among the different localities). Moreover, for some digenean species, their occurrences are connected with the restricted range of first or second intermediate hosts, which are generally connected to the several particular environmental conditions of localities. Then, digenean species with narrow intermediate host range are positioned out of the matrix order, and therefore those species should be less resistant to extinction.

Nestedness for ectoparasites and endoparasites of fish was explained by variation in fish size (Guégan & Hugueny, 1994; Hugueny & Guégan, 1997; Poulin & Valtonen, 2001). Those findings confirm the prediction of island biogeography theory when host individuals are considered as islands, with smaller parasite communities considered as subsets of the larger ones. Nested patterns occur in endoparasite communities of fish in a predictable fashion proportional to host size related to accumulation of parasite species by feeding fish hosts (Poulin & Valtonen, 2001). However, when investigating the host of the same size, it is not host size but local availability of parasite species and their probability of colonization which may lead to nestedness (Rohde *et al*. 1998). Host size is not found to be the case for bird digeneans, as birds of the same age were taken into account in the present study.

Several studies suggested that interspecific interaction could have contributed to nestedness. However, no study either on ecto- or endoparasites confirms this prediction and, as was suggested by Morand *et al*. (2002), interspecific competition is not necessary for explaining nestedness.

Some studies have explained the nested pattern in relation to host specificity (Poulin, 1996; Matejusová *et al.* 2000; Valtonen *et al.* 2001). Valtonen *et al.* (2001) suggested that nested patterns in parasite communities are related to the fact that host species harbouring few parasite species would harbour mainly generalists, and that specialist parasites would occur mainly in host species harbouring species-rich parasite communities. Nevertheless, Poulin & Valtonen (2001) suggested that not only host size but also host specificity could be important for endoparasite communities.

We found that the presence of generalist species, from the view of specificity to the intermediate host, is repeated among the component communities and the position of specialists with close affinity to their intermediate hosts presents departure from nested pattern i.e. in the matrix of presence of endoparasite species in the different hosts, specialists seem to be positioned out of a completely nested matrix.

Similarity between parasite communities

Two hypotheses explaining the similarity of animal species richness among the different islands applied to different groups of free-living animals as well as parasites arise from an island biogeography background. Here, there are species–area relationships applied to the relationship between abundance and host size (Guégan *et al.* 1992; Guégan & Hugueny, 1994) or to the relationship between parasite species richness and host habitat area (for instance lake surface area and parasite species richness in fish: Kennedy, 1978; Hartvigsen & Halvorsen, 1993; Poulin & Morand, 1999). In our study, we found no relationships between water reservoir area and parasite community similarity, species richness or diversity. However, the similarity based on abundance of potential intermediate hosts was related to water area, suggesting that more diversified intermediate host fauna occurs in the water reservoirs with greater area. Conversely, our analyses showed that intermediate hosts and digenean parasites were mainly influenced by local ecological characters. A more diversified type of water bottom and the presence of vegetation facilitated the presence of many intermediate hosts and increased their abundance as well. Parasite species richness, diversity and dominance were also influenced by the bottom type of the water reservoir, and temporal drying seems to be a factor which could facilitate the inclusion of molluscs infected by digeneans in the diet of birds. We suggested that ecological factors of habitat around which a definitive host is living, present important determinants for both intermediate host species and parasite species.

Patterns of species diversity and similarity would also be influenced by the geographical distances between islands (Morand, 2000). This hypothesis was confirmed for the parasite species of conspecific fish populations (Poulin & Morand, 1999) when predicting that low geographical distances among hosts facilitate parasite species colonization and then hosts of geographically adjacent populations would harbour similar parasite fauna. Rigby *et al.* (1997) concluded that the endoparasite communities among hosts from the same island are similar but the differences among endoparasite communities from the hosts living in different islands may be due to potential host species and distances among the islands. However, Kennedy (2001) did not confirm the prediction that the similarity of endoparasite fish communities is influenced by decreasing distances among host populations. We do not confirm the influence of geographical distances on the qualitative similarity between bird digenean community but we found that quantitative similarity as well as species richness were influenced by the geographical distances.

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