

Research Paper

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Avian trematodes of central European corvids are heterogeneous regarding preferences for host species and age

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Abstract

Corvids are highly adaptive birds that respond well to anthropogenic changes in their environment. Trematode communities of corvids were studied mainly in the 1950s through 1970s in regularly flooded parts of the Volga River delta in Russia; more recent studies and data from other regions where the corvids are in less contact with postflooding habitats are limited. Data for *Corvus corax* were lacking. Using our samples obtained from 1963 to 2023, we performed a large-scale analysis of trematode species composition and community structure in *Corvus frugilegus*, *Corvus cornix*, *C. corax*, *Coloeus monedula*, *Pica pica*, and *Garrulus glandarius*; all originated from the Czech Republic. We identified corvids as hosts of mutually overlapping component communities of only a few species of trematodes (*Brachylecithum lobatum*, *Lyperosomum petiolatum*, *Lyperosomum longicauda*, *Tamerlania zarudnyi*, *Urogonimus macrostomus*), with the presence of many rare and incidental findings of other trematode species. Only a few species used corvids as their core hosts (*L. longicauda* and *B. lobatum*). Trematode component communities in first-year birds included *Prosthogonimus cuneatus*, *Prosthogonimus ovatus*, *Plagiorchis asperus*, and *Morishitium dollfusi* due to an increased share of insects (intermediate hosts of *Prosthogonimus* and *Plagiorchis*) and snails (intermediate hosts of *Morishitium*) in the diet of juveniles. The trematode component communities of corvid species overlapped but were heterogeneous at the level of host individuals, likely reflecting differences in food sources related to the respective host ages and nesting sites.

Introduction

Corvids are highly adaptive birds that respond well to anthropogenic changes in their environment. Some central European corvids are sedentary and do not migrate extensively (*Corvus corax*, *Pica pica*, *Garrulus glandarius*), while others, such as *Corvus frugilegus*, make long migratory movements, and nesting populations are replaced in summer with those nesting in West Russia, Ukraine, and Belarus (Cepák *et al.* 2008). Local populations of other corvid species may also be supplemented in winter by varying numbers of migratory individuals from the northeast. Many corvids are highly opportunistic regarding their diets and consume many anthropogenic food items when such sources are available. Other food items consist of plants, including seeds, and various invertebrates; some predate other birds and mammals and feed on carrion after other predators have exposed the insides or when they have become opened due to roadkill. Although all the species studied herein are omnivorous, they differ in dietary composition, which is directly related to the spectra of immature trematodes that the respective birds can ingest. The diet of *C. frugilegus* is composed mainly of earthworms, insects, snails, small mammals, crustaceans, seeds, fruits, and anthropogenic waste (particularly in winter) (Gromadzka 1980; Orłowski *et al.* 2009; Maciorowski *et al.* 2014; Kitowski *et al.* 2017). The diet of *Corvus cornix* is composed of mollusks, earthworms, insects, and other arthropods, frogs, fish, small birds, and mammals, particularly immature birds, bird eggs, and carrion. The plant part of the diet consists of grain, potatoes, and various fruits and seeds; when occurring close to human settlements, a large part of the diet consists of anthropogenic waste (Berrow *et al.* 1992; Zduniak *et al.* 2008; Annala *et al.* 2012; Goldyn *et al.* 2016). The diet of *C. corax* is composed mainly of vertebrates of small or intermediate size, bird eggs, seeds, carrion, and anthropogenic waste; in some regions, insects are seasonally present in the *C. corax* diet as well (Nogales 1997). The diet of *Coloeus monedula* consists primarily of plant materials (60–84% except in May; can exceed 97% in winter months), mainly grain and other seeds, and less commonly various berries; the diet is also supplemented with insects, particularly beetles, other invertebrates, small mammals, bird eggs, and immature birds (Lockie 1955; Hell and Soviš 1958). As with most other bird species, nestlings consume a higher share of food of animal origin, consisting primarily of adult, larval, and pupal beetles and larval butterflies (Högstedt 1980). The diet of *P. pica* contains mostly insects, mollusks, small mammals, reptiles, immature birds, bird eggs,

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carrion, and, to some extent, seeds and various fruits (Högstedt 1980; Kryštofková *et al.* 2011). When available, a large portion of the diet is composed of anthropogenic waste. The diet of *G. glandarius* is mainly composed of buckeyes and acorns and also contains hazelnuts, grains, berries and seeds, insects, snails and slugs, immature birds and bird eggs, small mammals, reptiles, and carrion; nestlings are fed primarily insects and spiders (Eigelis 1965).

Although corvid populations are being subject to large-scale changes due to synanthropization, and population increases have been recently recorded in most corvid species associated with anthropogenic environments (Keller *et al.* 2020), corvid populations have rarely been studied from the helminthological viewpoint. A series of helminthological studies were conducted in the Volga River delta, Russia, in the 1960s and early 1970s (Lugovoi and Kurochkin 1962; Chernobai 1966, 1969; Budkin 1974). This region has specific properties because the Volga River has strong seasonal dynamics (Gorelits *et al.* 2018); therefore, the study birds had a unique dietary composition following regular flood events. Several large-scale studies were conducted in the 1950s and 1960s in other Eastern and central European countries (Macko 1957; Luft 1960; Stoimenov 1962; Rutkowska 1963; Baruš *et al.* 1972; Koubek and Vojtek 1973). Studies conducted later or in other regions are lacking or include only a few host individuals except for *P. pica* (Davies 1958; Todd 1964; Todd and Worley 1967; Ryšavý *et al.* 1970; Mizuno 1984; Borgsteede *et al.* 2000; Halajian *et al.* 2011; Dipineto *et al.* 2013; Girisgin *et al.* 2019; Yilmaz *et al.* 2020; Sitko and Heneberg 2021) and a recent study on *C. frugilegus* from two cities in Ukraine (Greben *et al.* 2023). A large study of helminths of *Corvus corone orientalis* in Japan lacked data on prevalence and intensity and reported the recorded helminths together with those from *Corvus macrorhynchos japonensis* (Mizuno 1984). An overview of currently available information on the prevalence and infection intensity of trematodes in corvids is provided in Table 1.

Prior studies of corvid trematodes have provided highly heterogeneous data, reporting the component communities of *P. pica* (21 trematode species), *C. cornix*, and *C. frugilegus* (16 trematode species each) to be the most diverse. In contrast, those of *C. monedula*, *G. glandarius*, and *Nucifraga caryocatactes* contained only three to six species. Those of *C. corone* contained a single species, and there were no trematodes reported for *C. corax* (see Table 1 for more details). Some additional host-species records were reported in national checklists without any detail regarding the respective findings (Bykhovskaya-Pavlovskaya 1962; Sulgostowska and Czaplinska 1987; Iskova *et al.* 1995; Sitko *et al.* 2006). In the present study, we aimed to analyze the species composition and community structure of trematodes parasitizing central European corvids. We examined a large series of host individuals of six corvid species (*C. frugilegus*, *C. cornix*, *C. corax*, *C. monedula*, *P. pica*, and *G. glandarius*), focusing on those living in rural environments outside large cities and large municipal waste dumps, thereby avoiding those who feed mainly on anthropogenic waste. As the dietary composition of adults and nestlings differ, we analyzed the component communities of first-year birds and those of adult females or males separately.

Materials and Methods

Using data we obtained from 1963 to 2023, we examined 206 specimens of *C. frugilegus*, consisting of 105 adult males, 85 adult

females, and 16 birds in the first calendar year (1Y). We further examined 39 specimens of *C. cornix*. The dataset included 20 adult males, 13 adult females, and six 1Y birds. We examined 17 specimens of *C. corax*, specifically, 3 adult males, 7 adult females, and seven 1Y birds. We examined 44 specimens of *C. monedula*, including 22 adult males, 15 adult females, and seven 1Y birds. We examined 169 specimens of *P. pica*, specifically, 98 adult males, 59 adult females, and 12 1Y birds. We also examined 120 specimens of *G. glandarius*, including 59 adult males, 46 adult females, and 15 1Y birds. Note that the same dataset of *P. pica* was analyzed by Sitko and Heneberg in their study of longitudinal trends among farmland birds (Sitko and Heneberg 2021).

We assigned the examined birds to three age and sex categories: 1Y birds (born in the calendar year when they were examined), adult females, and adult males (we considered birds in their second calendar year of life or older as adults). All the examined birds originated from the eastern and central Czech Republic (48.7°N–49.80°N, 13.3°E–18°30'E). We obtained the dead birds when they were provided to the Comenius Museum collection (Přerov, Czech Republic). The birds were wounded and injured individuals sacrificed in rescue stations due to untreatable wounds, and as some corvid species are legally hunted in Czechia, some of the examined birds were also provided by licensed hunters. Birds provided by the rescue stations included only those untreated with antihelminthic agents before being sacrificed. Governmental and local authorities authorized our long-term research; the Ministry of the Environment of the Czech Republic issued our most recent permit on August 3, 2009 (No. 11171/ENV/09-747/620/09-ZS 25).

We performed full-body necropsies, fixed the trematodes in 70% ethanol, stained them with borax carmine, transferred them through an alcohol series to xylene, and mounted them in Canada balsam, as described by Sitko and Heneberg (2015). We recorded the infection intensities and species richness of trematodes in each examined host individual. We stored representative specimens in the Comenius Museum collections (Přerov, Czechia). We published some of the host–parasite records from the examined datasets in revisions of specific trematode taxa and previously used some of the analyzed helminths for molecular analyses (Heneberg *et al.* 2015, 2016, 2018); data obtained until 2006 were also used in the checklist of Czech trematodes (Sitko *et al.* 2006). The nomenclature used follows the Fauna Europaea database (de Jong *et al.* 2014) and recently published reclassifications (Heneberg and Sitko 2023). For details concerning the life cycles of the examined helminths, refer to Sitko *et al.* (2006).

We calculated the mean frequency of infection and trematode load, trematode species-specific mean relative prevalence (the proportion of host individuals infected by the respective trematode species), and mean intensity of infection (the number of trematode specimens per host calculated over all hosts that were positive for the respective trematode). We computed rarefaction curves to interpolate the trematode species richness (Willis 2019). We calculated the Chao-1 estimator corrected for unseen helminth species to estimate the true trematode species richness. Additionally, we compared helminth species richness using the presence/absence-based Sørensen similarity index and the abundance-based Bray-Curtis similarity index. We tested for differences in helminth diversity among the analyzed component communities using the Shannon diversity *t*-test (comparing values of the Shannon H index with a Poole's bias correction term of two abundance datasets while assuming equal sampling conditions). Further, we calculated Gini-Simpson's dominance, evenness, equitability, Fisher's alpha, and

Table 1. Overview of previously published records of trematode prevalence and intensity of infection in corvids

Host species	Trematode species	Species, prevalence, intensity range (mean)
		Macko (1957) east Slovakia, 1954–1956 Davies (1958) Great Britain, 1953–1954 Stoimenov (1962) Bulgaria, 1957–1961 Rukowska (1963) Poland, 1962–1964 Baruš et al. (1972) Czechia and Slovakia, 1960–1965 Koubek and Vojtek (1973) Czechia and Slovakia, undisclosed Chernobai (1969) River Volga, Russia, 1961–1967 Todd (1964); Todd and Worley (1967) Montana, USA, 1963–1964 Ryšavý et al. (1970) Beijing, China, 1955 Mizuno (1984) Sapporo, Japan, 1982–1983 Halajian et al. (2011) Mazandaran, Iran, 2007–2008 Dipineto et al. (2013) Campania, Italy, 2011–2012 Girişgin et al. (2019) Bursa, Türkiye, 2015–2016 Yilmaz et al. (2020) Van, Türkiye, 2019 (only fecal samples) Siko and Heneberg (2021) Czechia, 1963–2020 Budkin (1974) River Volga, Russia, 1972 Chernobai (1966) Volgograd region, Russia, 1962 and 1964 Lugovoi and Kurochkin (1962) River Volga delta, 1956 Luft (1960) Lublin, Poland, 1958–1959 Borgstede et al. (2000) Netherlands, 1970–1986 Greiben et al. (2023) Poltava and Kyiv, Ukraine, 2020–2022
<i>Corvus frugilegus</i>		105 327 48 297 11 42 207 ¹ 46
	<i>Brachylecithum</i> sp.	1%, 4
	<i>Brachylecithum ugenia</i>	0.3%, 16
	<i>Brachylecithum lobatum</i>	0.9%, 1–2 (1.7) ² 1.7%, 2–25
	<i>Echinostoma coronale</i>	1.0%, 1–2 ³
	<i>Echinostoma revolutum</i>	1.3% and 0.0%
	<i>Leucochloridium actitis</i>	0.3%, 2
	<i>Lutztrema monenteron</i>	0.6%, 1
	<i>Lyperosomum longicauda</i>	3.4%, 1–12 (3.4) 2.7%, 1–7
	<i>Lyperosomum petiolatum</i>	0.3%, 1
	<i>Plagiorchis maculosus</i>	2.6% and 0.0%
	<i>Plagiorchis multiglandularis</i>	61.0% and 0.8%
	<i>Prosthogonimus cuneatus</i>	2.7%, 1–25 (6) 1.3% and 0.0%
	<i>Prosthogonimus ovatus</i>	0.3%, 1 6.7%, 1–61 (8)
	<i>Strigea sphaerula</i>	2%, 1
	<i>Tamerlania zarudnyi</i>	0.3%, 3 ⁴ 1.0%, 2–46 (13)
	<i>Tetracotyle falconis</i>	0.3%, 6–8
<i>Corvus cornix</i>		13 10 174 73 ⁵
	<i>Echinostoma coronale</i>	1.1%, 1–2
	<i>Echinostoma revolutum</i>	0.6%, 2–4 (singly)
	<i>Echinostoma travassosi</i>	2.3%, 1–16

(Continued)

Table 1. (Continued)

Host species	Trematode species	Species, prevalence, intensity range (mean)
<i>Laterotrema vexans</i>	<i>Leucochloridium macrostomum</i>	Macko (1957) east Slovakia, 1954–1956
	<i>Lyperosomum longicauda</i>	Davies (1958) Great Britain, 1953–1954
	<i>Neodiplosomum corvillum</i>	Stoimenov (1962) Bulgaria, 1957–1961
	<i>Plagiorchis brauni</i>	Rutkowska (1963) Poland, 1962–1964
	<i>Plagiorchis elegans</i>	Baruš et al. (1972) Czechia and Slovakia, 1960–1965
	<i>Plagiorchis maril</i>	Koubek and Vojtek (1973) Czechia and Slovakia, undisclosed
	<i>Plagiorchis maculosis</i>	Chernobai (1969) River Volga, Russia, 1961–1967
	<i>Prosthogonimus cuneatus</i>	Todd (1964); Todd and Worley (1967) Montana, USA, 1963–1964
	<i>Prosthogonimus ovatus</i>	Ryšavý et al. (1970) Beijing, China, 1955
	<i>Strigea sphaerula</i>	Mizuno (1984) Sapporo, Japan, 1982–1983
	<i>Tamerlania zarudnyi</i>	Halajian et al. (2011) Mazandaran, Iran, 2007–2008
	<i>Tetracyle jalocis</i>	Dipineto et al. (2013) Campania, Italy, 2011–2012
	<i>Coloas monedula</i>	<i>Leucochloridium macrostomum</i>
<i>Lyperosomum longicauda</i>		Yılmaz et al. (2020) Van, Türkiye, 2019 (only fecal samples)
<i>Plathynosomum petiolatum</i>		Sitko and Heneberg (2021) Czechia, 1963–2020
<i>Prosthogonimus oivans</i>		Budkin (1974) River Volga, Russia, 1972
<i>Tamerlania zarudnyi</i>		Chernobai (1966) Volgograd region, Russia, 1962 and 1964
		Lugovoi and Kurochkin (1962) River Volga delta, 1956
		Luft (1960) Lublin, Poland, 1958–1959
		Borgsteede et al. (2000) Netherlands, 1970–1986
		Greben et al. (2023) Poltava and Kyiv, Ukraine, 2020–2022
<i>Corvus corone</i>	<i>Trematoda</i> gen. sp.	1
<i>Corvus corone orientalis</i>		16
		10
		30%
		42
		12
		33
		218

(Continued)

Table 1. (Continued)

Host species	Trematode species	Species, prevalence, intensity range (mean)													
	<i>Urotocus thalonetensis</i>	6%, 4													
<i>Pica pica</i>		22	71	84	342	145	7	79	8	43	169	70	62	1	
	<i>Brachylaima fuscata</i>	1.4%, 1									1.8%, 1-3 (2)				
	<i>Brachylaima sp.</i>									13.5%					
	<i>Brachylecithum fillum</i>						14%, 1								
	<i>Brachylecithum lobatum</i>										2.4%, 2-16 (6.5)				
	<i>Conspicuum acuminatum</i>	1.4%, 2													
	<i>Echinostoma revolutum</i>				0.6%, 2-4										
	<i>Echinostoma sp.</i>					2.8%				2%					
	<i>Leucochloridium macrostomum</i>				1.8%, 2-181 (27)							1.4%, 181			
	<i>Leucochloridium perturbatum</i>										0.6%, 14				
	<i>Lyperosomum alagesi</i>	4.2%, 1-4			1.8%, 1-6										
	<i>Lyperosomum longicauda</i>	4.2%, 1													
	<i>Lyperosomum petiolatum</i>										28.4%, 1-14 (3.9)			100%, 1	
	<i>Morishitium dollfusi</i>										0.6%, 2				
	<i>Plagiorchis brauni</i>				2.6%, 1-300 (44)							11.4%, 1-300 (74)			
	<i>Plagiorchis elegans</i>				2.4%, 1-2						1.2%, 1				
	<i>Plagiorchis maculosus</i>				3.6%, 1										
	<i>Prosthogonimus cuneatus</i>				5.6%, 1-25 (6)							8.6%, 1-19 (5)			
	<i>Prosthogonimus ovatus</i>				13.2%, 1-61 (8)			11.3%, 1-7			0.6%, 1	11.4%, 1-19 (6)			
	<i>Strigea sphaerula</i>				1.2%, 1	0.9%, 2-66 (29)						4.3%, 4-22 (13)			
	<i>Tamerlamia zarudnyi</i>	1.4%, 1			0.3%, 2-46 (13)										
	<i>Tetracotyle falconis</i>				0.3%, 6-8										

(Continued)

Table 1. (Continued)

Host species	Trematode species	Species, prevalence, intensity range (mean)
	<i>Uvulinus macrostomus</i>	Macko (1957) east Slovakia, 1954–1956
	<i>Trematoda</i> gen. sp.	Davies (1958) Great Britain, 1953–1954 Stoimenov (1962) Bulgaria, 1957–1961 Rutkowska (1963) Poland, 1962–1964 Baruš et al. (1972) Czechia and Slovakia, 1960–1965 Koubek and Vojtek (1973) Czechia and Slovakia, undisclosed Chernobai (1969) River Volga, Russia, 1961–1967 Todd (1964); Todd and Worley (1967) Montana, USA, 1963-1964 Ryšavý et al. (1970) Beijing, China, 1955 Mizuno (1984) Sapporo, Japan, 1982–1983 Halajian et al. (2011) Mazandaran, Iran, 2007–2008 Dipineto et al. (2013) Campania, Italy, 2011–2012 Girişgin et al. (2019) Bursa, Türkiye, 2015–2016 Yilmaz et al. (2020) Van, Türkiye, 2019 (only fecal samples) Sitko and Heneberg (2021) Czechia, 1963–2020 Budkin (1974) River Volga, Russia, 1972 Chernobai (1966) Volgograd region, Russia, 1962 and 1964 Lugovoi and Kurochkin (1962) River Volga delta, 1956 Luft (1960) Lublin, Poland, 1958–1959 Borgsteede et al. (2000) Netherlands, 1970–1986 Greben et al. (2023) Poltava and Kyiv, Ukraine, 2020-2022
		0.3%, 23
		0.6%, 2
		1.4%, 23
<i>Garrulus glandarius</i>		
	29	136
	<i>Brachylaima arcuta</i>	3%, 4 2.6%, 2-7
	<i>Brachylectium lobatum</i>	3%, 4
	<i>Lyperosomum longicauda</i>	
	<i>Lyperosomum petiolatum</i> (9)	10%, 4-18
	<i>Sirrega sphaerula</i>	1.5%, 1-3
	<i>Digenea</i> gen. sp.	
<i>Nucifraga caryocatactes</i>		
	22	
	<i>Leucochloridium macrostomum</i>	5%, 1
	<i>Plagiorchis elegans</i>	5%, 1
	<i>Sirrega sphaerula</i>	5%, 7
<i>Corvus macrorhynchos japonensis</i>		
	21	
<i>Corvus corax</i>		
	3	
<i>Corvidae</i> gen. sp.		
	473	(218+21) ⁵
	<i>Brachylaeminae</i> sp.	+
	<i>Brachylectium</i> sp.	+
	<i>Echinostoma cori</i>	+
	<i>Echinostoma revolutum</i>	+
	<i>Leucochloridium macrostomum</i>	+
	<i>Leucochloridium</i> sp.	+

(Continued)

Table 1. (Continued)

Host species	Trematode species	Species, prevalence, intensity range (mean)
		Miacko (1957) east Slovakia, 1954–1956
		Davies (1958) Great Britain, 1953–1954
		Stoimenov (1962) Bulgaria, 1957–1961
		Rutkowska (1963) Poland, 1962–1964
		Baruš et al. (1972) Czechia and Slovakia, 1960–1965
		Konhek and Vojtek (1973) Czechia and Slovakia, undisclosed
		Chemobai (1969) River Volga, Russia, 1961–1967
		Todd (1964); Todd and Worley (1967) Montana, USA, 1963–1964
		Ryšavý et al. (1970) Beijing, China, 1955
		Mizuno (1984) Sapporo, Japan, 1982–1983
		Halajian et al. (2011) Mazandaran, Iran, 2007–2008
		Dipineto et al. (2013) Campania, Italy, 2011–2012
		Girişgin et al. (2019) Bursa, Türkiye, 2015–2016
		Yilmaz et al. (2020) Van, Türkiye, 2019 (only fecal samples)
		Šitko and Heneberg (2021) Czechia, 1963–2020
		Budkin (1974) River Volga, Russia, 1972
		Chemobai (1966) Volgograd region, Russia, 1962 and 1964
		Lugovoi and Kurochkin (1962) River Volga delta, 1956
		Luft (1960) Lublin, Poland, 1958–1959
		Borgsteede et al. (2000) Netherlands, 1970–1986
		Greben et al. (2023) Poltava and Kyiv, Ukraine, 2020–2022
	<i>Prosthogonimus</i> sp.	+
	<i>Spelotrema capellae</i>	+
	<i>Strigea sphaerula</i>	+
	<i>Tamerlania zarudnyi</i>	+

¹ Prevalence from two colonies reported separately

² *B. lobatum* and *L. petiolatum* were found in adult birds only, whereas *L. monenteron* was found in juveniles only. The restriction of *B. lobatum* and *L. petiolatum* to adult hosts was likely caused by infection events occurring only in winter quarters, as all the *B. lobatum*- and *L. petiolatum*-positive nesting birds were found in April but not in the later months.

³ In this study, the infection intensity was provided for the respective trematode species from all the host species combined.

⁴ *T. zarudnyi* and *P. ovatus* were detected in winter only, i.e., in birds nesting in Russia.

⁵ The examined birds included 54 birds examined by Dubinin and Dubinina (1940) and Dubinina and Kulakova (1960).

⁶ Numbers of examined host species were provided but the species found were provided only for all hosts combined.

the Berger-Parker dominance index to describe the species richness and diversity of the analyzed datasets. In the Gini-Simpson index, a value of one indicates complete domination of a single taxon, and zero indicates equal representation of all taxa. We used two evenness measures: equitability, in which the Shannon index is divided by a logarithm of the number of taxa, and Buzas and Gibson's evenness, in which the Shannon index is divided by the species number. Fisher's alpha is a parametric diversity measure assuming that the abundance of a particular taxon follows the log series distribution. The Berger-Parker index is calculated as the number of cases in the dominant taxon relative to the total number of cases (Harper 1999). To avoid bias caused by differences in prevalence and infection intensities in juveniles and adults and to avoid possible sex-related bias, we evaluated the adult females, adult males, and 1Y birds for each species separately. We employed one-way PERMANOVA to identify differences among adult male, female, and 1Y bird hosts. All *C. corax* host individuals were treated as a single group due to the lack of trematodes in 1Y *C. corax* and low diversity of trematodes in this host species. We further used nonmetric multidimensional scaling (NMDS) to analyze the effects of explanatory variables (age, sex, and host species). We performed all calculations in SigmaPlot 12.0 (Systat Software, San Jose, California), EstimateS 9.1.0 (<https://www.robertkcolwell.org/pages/1407-estimates>), and PAST 2.14 (<https://www.nhm.uio.no/english/research/resources/past/>). Data are shown as the mean±SE unless stated otherwise.

Results

Helminth component communities of central European corvids

We collected a total of 944 specimens belonging to 16 species of trematodes. The trematode load differed among the host species by nearly one order of magnitude (Table 2). We analyzed host species-specific component communities in *C. frugilegus* (185 specimens, 4 trematode species), *C. cornix* (314 specimens, 6 trematode species), *C. corax* (36 specimens, 1 trematode species), *C. monedula* (52 specimens, 2 trematode species), *P. pica* (239 specimens, 8 trematode species), and *G. glandarius* (118 specimens, 6 trematode species) (Table 3; Figure 1). Although *P. pica* was represented by the second highest number of examined hosts, the dataset of obtained trematodes contained several singletons and doubletons (Table 3). The Chao-1 estimates of trematode species richness in the analyzed component communities were 4.0 (95% CI [4.0, 5.4]) species in *C. frugilegus*, 5.0 (95% CI [5.0, 6.0]) species in *C. cornix*, 1.0 (95% CI [1.0, 1.0]) species in *C. corax*, 2.0 (95% CI [2.0, 2.0]) species in *C. monedula*, 7.0 (95% CI [7.4, 8.1]) species in *P. pica*, and 5.0 (95% CI [5.0, 5.2]) species in *G. glandarius*.

Species composition and diversity differed among the analyzed species. The Shannon diversity *t*-test revealed significant differences in all pairwise comparisons that involved *G. glandarius* or *C. corax*. The trematodes of *P. pica* differed from all other component communities except for that of *C. frugilegus*. The component communities of other host species were more similar, and

Table 2. Diversity indices and outcomes of the Shannon diversity *t*-test

Variable	Host species					
	<i>Corvus frugilegus</i> (n=206)	<i>Corvus cornix</i> (n=39)	<i>Corvus corax</i> (n=17)	<i>Coloeus monedula</i> (n=44)	<i>Pica pica</i> (n=169)	<i>Garrulus glandarius</i> (n=120)
Number of trematode species	4	6	1	2	8	6
Number of trematode specimens	185	314	36	52	239	118
Trematode load (mean±SE)	0.90±0.60	8.00±4.22	2.12±2.05	1.18±0.41	1.41±0.27	0.98±0.21
Gini-Simpson's dominance	0.610	0.707	1.0	0.560	0.622	0.246
Evenness	0.504	0.307	1.0	0.941	0.289	0.802
Equitability	0.506	0.340	0.0	0.912	0.403	0.877
Fisher's alpha	0.72	1.05	0.19	0.41	1.60	1.34
Berger-Parker	0.76	0.83	1.0	0.67	0.78	0.39
Shannon diversity <i>t</i> -test (<i>t</i> ; <i>d</i> _i ; <i>p</i>)						
<i>Corvus frugilegus</i>		-1.690; 434; 0.09	-11.336; 185; <0.001	0.903; 202; 0.37	1.329; 420; 0.18	-10.066; 292; <0.001
<i>Corvus cornix</i>			-10.136; 311; <0.001	-0.926; 209; 0.36	2.855; 453; 0.005	-12.347; 317; <0.001
<i>Corvus corax</i>				-12.726; 52; <0.001	10.726; 239; <0.001	-26.148; 118; <0.001
<i>Coloeus monedula</i>					2.210; 268; 0.028	-12.075; 163; <0.001
<i>Pica pica</i>						-7.494; 354; <0.001

there were no significant differences when comparing those of *C. frugilegus* with *C. cornix* or *C. monedula* or those of *C. cornix* with *C. monedula* (Table 2). The species of the component communities of *C. frugilegus* and *P. pica* (Sørensen similarity index 0.545; Table 4) and *C. monedula* and *G. glandarius* (Sørensen similarity index=0.571) overlapped most in terms of the number of species, while the similarity among all other species combinations was much lower. Abundance data also suggested the highest similarity between component communities of *C. monedula* and *G. glandarius* (Bray-Curtis similarity index=0.550; Table 4). In addition, the Bray-Curtis index identified high similarity between component communities of *C. frugilegus* and *C. cornix* (Bray-Curtis similarity index=0.613). All other abundance-based comparisons showed lower values. Despite sound Sørensen similarity indices, the Bray-Curtis similarity indices were low for comparisons involving *P. pica*, suggesting that although there was species overlap between the component communities of *P. pica* and other analyzed host species, the abundance of shared species was relatively low (Table 4). In absolute numbers, most component communities shared only one trematode species; the exceptions were component communities of *C. frugilegus* and *P. pica* (three species), *C. cornix* and *P. pica* (two species), and *C. monedula* and *G. glandarius* (two species) (Table 4).

Alpha diversity, quantified using Fisher's alpha, was low in all analysed host species. The highest alpha diversity was associated with *P. pica* (1.60) and *G. glandarius* (1.34), while the lowest alpha diversity was found for *C. corax* (0.19) and *C. monedula* (0.41).

Gini-Simpson's dominance values were generally high; the lowest Gini-Simpson's dominance value was found for *G. glandarius* (0.246), and it exceeded 0.5 for all five other host species. Evenness differed among the analysed species, with a low value obtained for *P. pica* (0.29). In contrast, the *C. corax*, *C. monedula*, and *G. glandarius* component communities were associated with high evenness (1.00, 0.94, and 0.80, respectively). Equitability ranged between 0.00 (*C. corax*) and 0.912 (*C. monedula*). The Berger-Parker index ranged between 0.39 (*G. glandarius*) and 1.00 (*C. corax*) (Table 2).

From the species-specific point of view, in all three *Corvus* spp., the most abundant trematode species was *Brachylecithum lobatum*. This species was also present in *P. pica* but was only the second most abundant trematode in *P. pica* after *Lyperosomum petiolatum*. *Brachylecithum lobatum* was lacking in representatives of the other corvid genera, *Coloeus* and *Garrulus*. In *P. pica* and *G. glandarius*, the most abundant species was *L. petiolatum*. It was also present in *C. monedula* and *C. frugilegus* (in both host species as the second most abundant trematode). The most abundant trematode in *C. monedula* was *Tamerlania zarudnyi*, which was also present in *G. glandarius* (Table 3). Other trematode species were represented chiefly by rare or incidental findings, except *Urogonimus macrostomus* (present abundantly in *C. cornix* and *G. glandarius*, with rare records in *P. pica* and absent in *C. frugilegus*, *C. corax*, and *C. monedula*). Findings of another species that was previously thought to be characteristic of corvids, *Lyperosomum longicauda*, were recently subjected to integrative morphological and molecular

Table 3. Host-specific component communities of trematodes found in the present study

Trematode species	Host species, number of specimens found					
	<i>Corvus frugilegus</i> (n=206)	<i>Corvus cornix</i> (n=39)	<i>Corvus corax</i> (n=17)	<i>Coloeus monedula</i> (n=44)	<i>Pica pica</i> (n=169)	<i>Garrulus glandarius</i> (n=120)
<i>Brachylaima arcuata</i> (Dujardin, 1845)	0	0	0	0	0	16
<i>Brachylaima fuscata</i> (Rudolphi, 1819)	0	0	0	0	6	0
<i>Brachylecithum lobatum</i> (Railliet, 1900)	140	261	36	0	26	0
<i>Echinostoma revolutum</i> (Fröhlich, 1802)	0	2	0	0	0	0
<i>Leucochloridium perturbatum</i> Pojmanska, 1969	0	0	0	0	14	0
<i>Lyperosomum longicauda</i> (Rudolphi, 1809)	9	0	0	0	0	0
<i>Lyperosomum petiolatum</i> (Railliet, 1900)	35	0	0	17	186	46
<i>Metorchis xanthosomus</i> (Creplin, 1846)	0	3	0	0	0	0
<i>Morishitium dollfusi</i> (Timon-David, 1950)	0	0	0	0	2	0
<i>Plagiorchis asperus</i> Stossich, 1904	0	3	0	0	0	0
<i>Plagiorchis elegans</i> (Rudolphi, 1802)	0	6	0	0	2	0
<i>Prosthogonimus cuneatus</i> (Rudolphi, 1809)	0	0	0	0	0	5
<i>Prosthogonimus ovatus</i> (Rudolphi, 1803)	1	0	0	0	1	0
<i>Strigea sphaerula</i> (Rudolphi, 1803)	0	0	0	0	0	14
<i>Tamerlania zarudnyi</i> (Skrjabin, 1924)	0	0	0	35	0	27
<i>Urogonimus macrostomus</i> (Rudolphi, 1802)	0	39	0	0	2	10

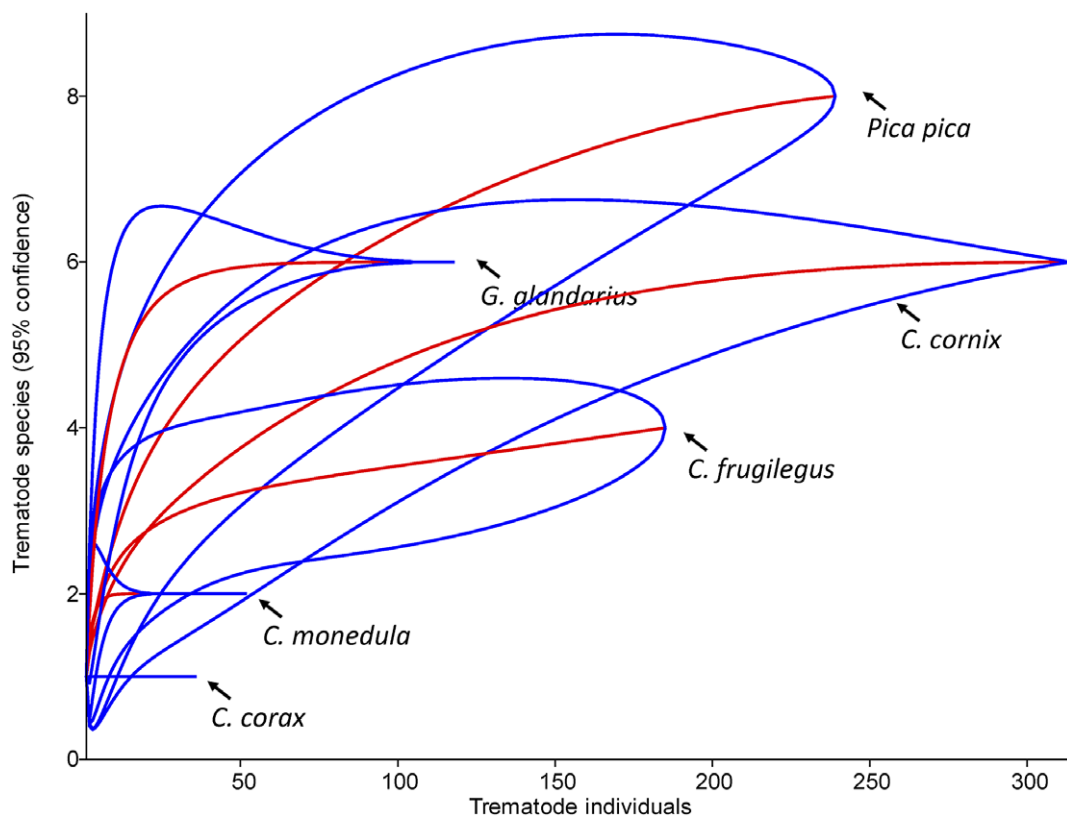


Figure 1. Rarefaction curves of the component communities of *C. frugilegus*, *C. cornix*, *C. corax*, *C. monedula*, *P. pica*, and *G. glandarius* sampled in the present study.

Table 4. Comparison of the diversities of the analysed component communities

Variable	Host species					
	<i>Corvus frugilegus</i> (n=206)	<i>Corvus cornix</i> (n=39)	<i>Corvus corax</i> (n=17)	<i>Coloeus monedula</i> (n=44)	<i>Pica pica</i> (n=169)	<i>Garrulus glandarius</i> (n=120)
Sørensen similarity index						
<i>Corvus frugilegus</i>		0.250	0.400	0.333	0.545	0.222
<i>Corvus cornix</i>			0.400	0.000	0.364	0.000
<i>Corvus corax</i>				0.000	0.250	0.000
<i>Coloeus monedula</i>					0.222	0.571
<i>Pica pica</i>						0.167
Bray-Curtis similarity index						
<i>Corvus frugilegus</i>		0.613	0.326	0.143	0.294	0.239
<i>Corvus cornix</i>			0.234	0.000	0.110	0.000
<i>Corvus corax</i>				0.000	0.190	0.000
<i>Coloeus monedula</i>					0.118	0.550
<i>Pica pica</i>						0.267
No. of helminth species found in both host species						
<i>Corvus frugilegus</i>		1	1	1	3	1
<i>Corvus cornix</i>			1	0	2	0
<i>Corvus corax</i>				0	1	0
<i>Coloeus monedula</i>					1	2
<i>Pica pica</i>						1
No. of helminth species unique for the first \second compared host species						
<i>Corvus frugilegus</i>		5	4	4	4	4
<i>Corvus cornix</i>	5		5	5	5	5
<i>Corvus corax</i>	1	1		1	1	1
<i>Coloeus monedula</i>	2	2	2		2	2
<i>Pica pica</i>	7	7	7	7		7
<i>Garrulus glandarius</i>	5	5	5	5	5	

analysis, concluding that most putative *L. longicauda* represent *L. petiolatum* (particularly the immature specimens), and *L. longicauda* is present in *C. frugilegus* but is much less common than previously thought (Heneberg and Sitko 2023).

Trematode component communities in 1Y birds were mainly simplified compared to adult bird hosts. The trematodes were completely lacking in 1Y *C. corax*, and their diversity was significantly lower in 1Y *C. cornix*, *C. monedula*, *P. pica*, and *G. glandarius*. Only adult and 1Y birds of *C. frugilegus* hosted the same number of species. The number of trematode species shared between 1Y and adult birds of the respective host species ranged between zero (*C. corax*, *G. glandarius*) and two (*C. frugilegus*, *C. monedula*, and *P. pica*). The Bray-Curtis similarity index ranged from 0.0 (*C. corax* and *G. glandarius*), to low values (0.03–0.08 in *P. pica* and *C. frugilegus*), to 0.29 in *C. cornix*, and 0.46 in *C. monedula* (Table 5).

The combined data suggest that the trematodes of corvids have low prevalence and limited preferences for specific corvid host

species, age, and sex. Their limited host preferences are supported by the NMDS analysis of all analysed host cases, using host species, age, and sex as explanatory variables, which did not identify any specific drivers of the analysed communities (Figure 2). Differences among component communities of adult males, adult females, and 1Y corvids were significant (one-way PERMANOVA (Bray-Curtis distance measure): permutation N=9999, total sum of squares=210.3, within-group sum of squares=193.7, $F=6.735$, $p=0.0001$). Subsequent pairwise comparisons revealed that all the variability was attributed to species-specific differences and that species-specific component communities of 1Y birds did not differ significantly from those in adult males or females of the same host species (Bonferroni-corrected $p>0.05$ each). Interestingly, all the differences between component communities of the host species were attributable to differences between component communities of adult host individuals. In contrast, there were no significant differences between species-specific component communities of 1Y birds of

Table 5. Comparison of component communities in adult and 1Y host individuals

Variable	Host species					
	<i>Corvus frugilegus</i> (n _{adults} =380; n _{1Y} =32)	<i>Corvus cornix</i> (n _{adults} =66; n _{1Y} =12)	<i>Corvus corax</i> (n _{adults} =20; n _{1Y} =14)	<i>Coloeus monedula</i> (n _{adults} =74; n _{1Y} =14)	<i>Pica pica</i> (n _{adults} =314; n _{1Y} =24)	<i>Garrulus glandarius</i> (n _{adults} =210; n _{1Y} =30)
Species observed (adults)	3	5	1	2	5	4
Species observed (1Y)	3	1	0	2	4	1
Shared species (observed)	2	1	0	2	2	0
Chao shared species (estimated)	0	0	0	0	2	0
Sørensen similarity index	0.67	0.40	0.00	1.00	0.44	0.00
Bray-Curtis similarity index	0.076	0.294	0.000	0.462	0.034	0.000
Shannon diversity t-test (t; df; p)	-1.37; 18.2; 0.19	14.8; 542.0; <0.001	N/A	-2.05; 103.5; 0.043	-5.69; 23.4; <0.001	5.52; 13.0; <0.001

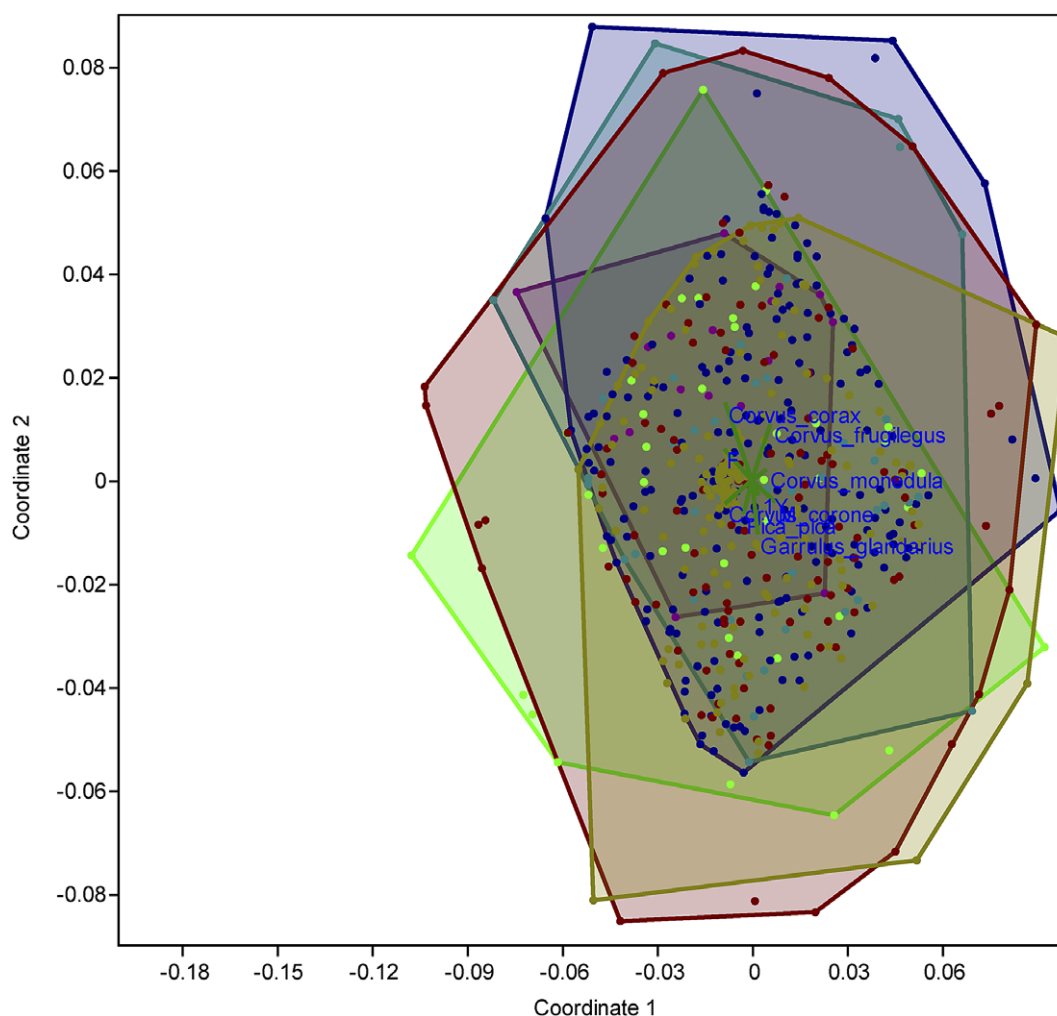


Figure 2. Nonmetric multidimensional scaling (Bray-Curtis distance measure) plots of the effects of explanatory variables (species, sex (adult M=1, adult F=0), and age (1Y=1, adult=0)) on the analysed trematode component communities in corvid birds. Colors indicate individual species, but there was complete overlap of the trematode communities from all six analysed host species. Points show host cases; convex hulls indicate host cases of the same type.

multiple corvid host species (Bonferroni-corrected $p > 0.05$ each). Some of the singletons were found in 1Y birds. These included, for example, *Prosthogonimus cuneatus* (e.g., *G. glandarius*), *Prosthogonimus ovatus* (e.g., *P. pica* and *C. frugilegus*), *Plagiorchis asperus* (e.g.,

C. cornix), and *Morishitium dollfusi* (e.g., *P. pica*) (Figure 3). These records could be attributable to an increased share of insects (intermediate hosts of *Prosthogonimus* and *Plagiorchis*) and snails (intermediate hosts of *Morishitium*) in the diet of juveniles.

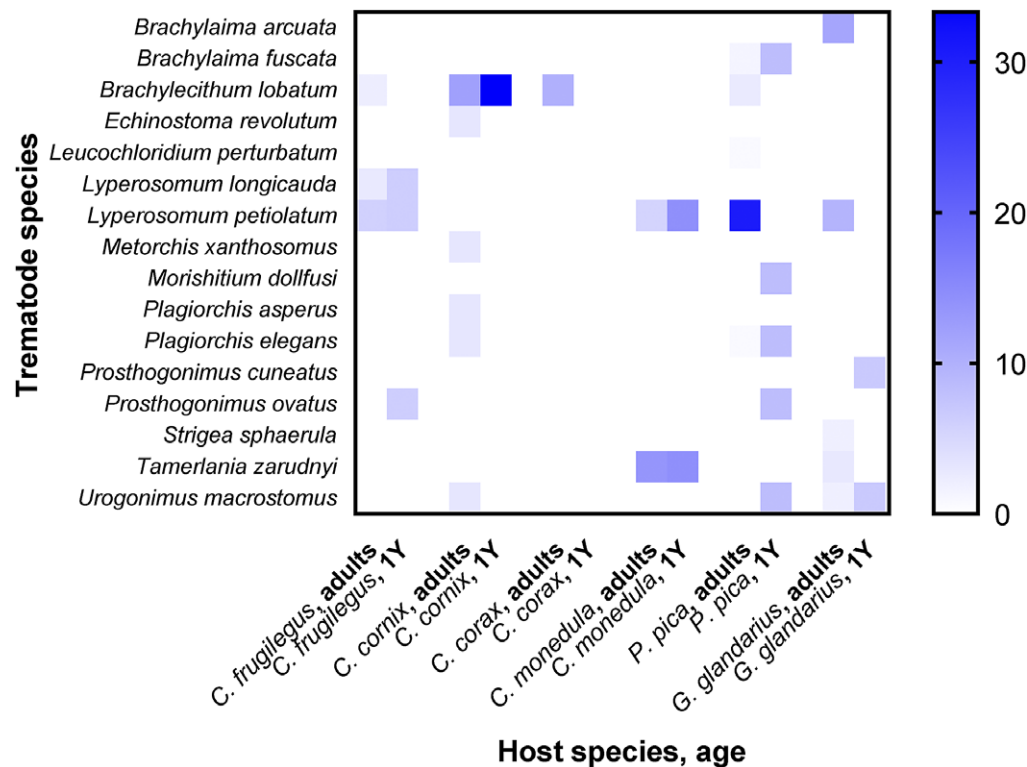


Figure 3. Heatmap comparing the prevalence [%] of the trematode species in adult and 1Y host birds. Trematode species are indicated on the left; host species and age are on the bottom. Color intensity corresponds to the prevalence in hosts of the respective age.

Discussion

We identified corvids as hosts of mutually overlapping component communities of only a few species of trematodes (*B. lobatum*, *L. petiolatum*, *L. longicauda*, *T. zarudnyi*, *U. macrostomus*), with the presence of many rare and incidental findings of other trematode species. The obtained data only partly overlapped with results of previous studies. Some of them were of limited size and thus may not be considered representative. Some originated from specific environments, like the river Volga delta, where the birds have different food opportunities compared to the examined habitats in the present study. Spatiotemporal factors may also play important roles, as different regions are associated with different intermediate hosts, and as most of the bird trematode communities have experienced simplification in recent decades due to changes in food composition of the host birds and due to adverse effects of various chemicals, such as benzimidazoles that are massively used due to their fungicidal effects in agriculture.

Previous reports identified *B. lobatum* in only two of the eight studies on *C. frugilegus* listed in Table 1. This trematode was identified at 0.9% prevalence in Czechia and Slovakia (Baruš *et al.* 1972) and at 1.7% prevalence in the Volga River region in Russia (Chernobai 1969). However, other studies of *C. frugilegus* from the same regions failed to identify *B. lobatum*. In the present study, we found *B. lobatum* at a 1.9% prevalence in *C. frugilegus*. Previous studies did not report *B. lobatum* from *C. cornix*, *C. corone*, or *C. monedula*; we reported it previously from *P. pica* (Sitko and Heneberg 2021), and Macko (1957) found it in *G. glandarius* with a 4% prevalence (Table 1). In the present study, we report it from *C. cornix* at 15% prevalence, from *C. corax* (in 1 out of 17 examined birds), and *P. pica* at 2.4% prevalence. All examined *C. monedula* and *G. glandarius* were free of *B. lobatum* (Table 3). In line with

previous findings (Baruš *et al.* 1972), we identified *B. lobatum* in adult *P. pica*, *C. corax*, and *C. frugilegus* but not in 1Y *P. pica*, *C. corax*, or *C. frugilegus*. However, we found it equally in adult and 1Y *C. cornix* (Figure 3).

Previous studies of *C. frugilegus* trematodes identified *L. petiolatum* in only one host case (Table 1; Baruš *et al.* 1972). It was absent from *C. cornix*, *C. corone*, and *C. monedula* but was present in two of 13 studies of *P. pica* trematodes (Table 1; Borgsteede *et al.* 2000; Sitko and Heneberg 2021), and Macko (1957) found it in 10% of examined *G. glandarius*. In the present study, we found *L. petiolatum* in 28% of *P. pica*, 8% of *G. glandarius*, 7% of *C. monedula*, and 6% of *C. frugilegus*. We did not find *L. petiolatum* in *C. corax* or *C. cornix* (Table 3). In contrast to previous findings (Baruš *et al.* 1972), we found that the prevalence of *L. petiolatum* was higher or equal in 1Y *C. frugilegus* and *C. monedula* compared to adult individuals of the same host species, and the intensity of infection was also higher in 1Y than in adult individuals of these two host species. However, *L. petiolatum* was absent from 1Y *P. pica* and *G. glandarius* despite being present in adult individuals of the same species (Figure 3).

Previous studies identified *L. longicauda* in three of the eight studies on *C. frugilegus* listed in Table 1. This trematode was identified at 3.4% prevalence in Czechia and Slovakia (Baruš *et al.* 1972), at 2.7% prevalence in the Volga River region in Russia (Chernobai 1969), and at 2.2% prevalence in a recent study from Ukraine (Greiben *et al.* 2023). Other studies of *C. frugilegus* from the same regions failed to identify *L. longicauda* and also did not report other *Lyperosomum* spp. In previous studies, *L. longicauda* was absent from *C. corone*. Nevertheless, it was identified in a large study on *C. cornix* (0.6% prevalence) in Russia (Chernobai 1969), one of six studies on *C. monedula* (3% prevalence, Great Britain

(Davies 1958)), one of 13 studies on *P. pica* (4.2% prevalence, Bulgaria (Stoimenov 1962)), and one of four studies on *G. glandarius* (2% prevalence, Poland (Luft 1960)). In the present study, we found *L. longicauda* in 4% of *C. frugilegus*, but it was absent from all other corvids (Table 3). Recently published molecular analyses have shown that it is possible to identify only well-developed adult *L. longicauda* based on morphological traits, and it is challenging to distinguish the juvenile *L. longicauda* from *L. petiolatum*; therefore, previously published data on these two species must be interpreted with caution as misidentifications are likely common (Heneberg *et al.* 2023).

Previous studies identified *T. zarudnyi* in two of the eight studies on *C. frugilegus* listed in Table 1. This trematode was identified at 0.3% prevalence in Czechia and Slovakia (Baruš *et al.* 1972) and at 1.0% prevalence in the Volga River region in Russia (Chernobai 1969). This trematode species was absent from studies on *C. corone* and *G. glandarius*. Nevertheless, it was identified in the course of the large study on *C. cornix* (0.6% prevalence) in Russia (Chernobai 1969), in two of six studies on *C. monedula* (prevalence of 3% in Great Britain (Davies 1958), and of 3% also in Russia (Chernobai 1969)), and in two of 13 studies on *P. pica* (prevalence of 1.4% in Bulgaria (Stoimenov 1962) and of 0.3% in Russia (Chernobai 1969)) (Table 1). In the present study, *T. zarudnyi* was present in both adult and 1Y *C. monedula* and adult *G. glandarius* (Figure 3).

The fifth trematode species, *U. macrostomus*, was previously reported as absent from all corvid species, and the only report consisted of our previous study on *P. pica* (Sitko and Heneberg 2021) (Table 1). In the present study, we confirmed it from adult *C. cornix*, 1Y *P. pica*, and both adult and 1Y *G. glandarius* (Figure 3).

Further research is needed to validate the differences between 1Y and adult birds and address the presence of the respective trematodes in nestlings. The nestlings are fed diets of different compositions, with a high share of insects and other soft-bodied animals. They are, therefore, more exposed to infections by trematodes hosted by insects (as shown for *Prosthogonimus* spp. and *P. asperus*). The component communities of trematodes in corvids are species-poor, but corvids serve as core hosts of several trematode species, including *L. longicauda* and *B. lobatum*). The limited prevalence of trematodes in *C. corax* in contrast to other corvid species is interesting and may be related to its specialization in carrion and vertebrate prey. Therefore, it would be interesting to compare the trematode data obtained for *C. corax* with that from regions where its diet includes a larger share of insects (Nogales 1997). However, it is also possible that the limited prevalence of trematodes in *C. corax* may be an artefact of relatively low sample size as we examined only 17 *C. corax* individuals.

Limitations

The present study relied on an opportunistic sampling design since we depended on the provision of carcasses of the examined hosts by rescue stations and hunters. A high proportion of the examined birds consisted of wounded or injured individuals. As such, the sample may not have necessarily contained representative trematodes that would be present in birds of good health. It is also highly likely that species with low prevalence escaped detection due to the limited number of examined host cases. However, none of these factors affected the ability of the present study to explore the composition of dominant species within the analysed component communities or to identify host species- and host age-specific differences in the analysed component communities.

Conclusions

We performed a large-scale analysis of the species composition and community structure of trematodes parasitizing central European corvids (*C. frugilegus*, *C. cornix*, *C. corax*, *C. monedula*, *P. pica*, and *G. glandarius*). The analysed carcasses represent one of the largest datasets analyzed thus far, as data for some corvid species (*C. corax*) are poorly available or include mostly host individuals analyzed in the 1950s through 1970s (*C. frugilegus* and *G. glandarius*). The examined samples originated from rural environments and, therefore, can serve as good comparative material for subsequent studies addressing issues associated with the synanthropization of most of the examined corvids and their increasing dependence on anthropogenic food sources or on feeding in urban habitats. Only a few trematode species use corvids as their core hosts (*L. longicauda* and *B. lobatum*), but corvids serve as permissive hosts for a broad range of trematodes as long as their intermediate hosts are included in the corvid diet.

Data availability. Representative specimens of the helminths analysed in this study are available in the collections of the Comenius Museum in Pířerov. All data are available in the main text or the supplementary materials.

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Authors' contribution. JS and PH conceived the study, JS collected the data, PH analyzed the data and wrote the manuscript, and both authors revised the manuscript and agreed on its final version.

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Competing interest. On behalf of both authors, the corresponding author states that there is no conflict of interest.

Ethical standard. Not applicable.

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