Journal of Helminthology

www.cambridge.org/jhl

Research Paper

Cite this article: Heneberg P, Sitko J, Yakovleva G and Lebedeva D (2024). Severe decline in abundance of *Cyathostoma lari*, a parasite of the nasal and orbital sinuses of gulls, at their central European nesting grounds. *Journal of Helminthology*, **98**, e1, 1–12
https://doi.org/10.1017/S0022149X23000949

Received: 06 October 2023
Revised: 07 December 2023
Accepted: 08 December 2023

Keywords:
A; rable fields; common birds; earthworms; Nematoda; population dynamics

Corresponding author:
P. Heneberg;
Email: petr.heneberg@lf3.cuni.cz

Severe decline in abundance of *Cyathostoma lari*, a parasite of the nasal and orbital sinuses of gulls, at their central European nesting grounds

P. Heneberg[1], J. Sitko[2], G. Yakovleva[3] and D. Lebedeva[3]

[1]Charles University, Third Faculty of Medicine, Ruská 87, CZ - 100 00 Prague, Czechia; [2]Comenius Museum, Moravian Ornithological Station, Přerov, Czechia and [3]Institute of Biology, Karelian Research Center, Russian Academy of Sciences, Petrozavodsk, Russia

Abstract

Cyathostoma lari is a parasite of the nasal and orbital sinuses of gulls and other hosts in Europe and Canada. Here, we provide an overview of previously published data on the prevalence and infection intensity of *C. lari* in gulls. Furthermore, based on our data, we analyze the spatio-temporal trends in the prevalence and intensity of infection by *C. lari* in *Chroicocephalus ridibundus* in Czechia (central Europe; data from 1964 to 2014) and compare them with those obtained from five species of gulls in Karelia (Northwest Russia; data from 2012–2020). Based on our preliminary observations, we hypothesized that *C. lari* is subject to a decline in certain regions, but this decline is not necessarily applicable throughout its distribution range. We found that the *C. lari* population crashed in specific parts of its distribution range. The reasons are unknown, but the observed population changes correspond with the diet switch of their core host in Czechia, *C. ridibundus.* We previously observed a diet switch in Czech *C. ridibundus* from earthworms (intermediate hosts of *C. lari*) to other types of food. This diet switch affected both young and adult birds. Nevertheless, it may not necessarily affect populations in other regions, where they depend less on earthworms collected from agrocenoses affected by agrochemicals and trampling. Correspondingly, we found that these changes were limited only to regions where the gulls feed (or fed) on arable fields. In Karelia, where arable fields are scarce, gulls likely continue to feed on earthworms and still display high infection rates by *C. lari.* Therefore, *C. lari*, a parasite of the nasal and orbital sinuses of gulls, nearly disappeared from their central European nesting grounds but is still present in better-preserved parts of its distribution range.

Introduction

Cyathostoma lari Blanchard, 1849 is a parasite of the nasal and orbital sinuses of gulls and other hosts in Europe and Canada. Although it can be found in corvids and occasionally in some other passeriform, ciconiiform, accipitriform, and falconiform bird species (Burt and Eadie 1958; Pemberton 1959, 1963; Threlfall 1965b; Simpson and Harris 1992), the core hosts in central and Eastern Europe are various species of gulls (Charadriiformes: Laridae), particularly *Chroicocephalus ridibundus* (Linnaeus, 1766) and *Larus argentatus* Pontoppidan, 1763 (Table 1). In central Europe, the nesting populations of the former host species were subject to a switch in feeding strategies. Previously, before the use of heavy machinery in agriculture and before the increased use of chemical compounds in agriculture, *C. ridibundus* mainly fed on small vertebrates and invertebrates, with an admixture of grains, fruits, and other plant parts. To feed the nestlings, *C. ridibundus* preferred earthworms and invertebrate aquatic prey. Importantly, the earthworms are considered intermediate hosts of *C. lari.* However, this host species nearly completely switched to feeding on food waste from large suburban waste dumps. These anthropogenic food sources are preferred over more closely located arable fields, and nesting *C. ridibundus* often fly over long distances to use them as primary food sources. Moreover, suitable invertebrate aquatic prey is nearly unavailable to them due to the overexploitation of fishponds (Sitko and Heneberg 2020).

The presence of earthworms in the diet of *C. ridibundus* is subject to enormous regional variability. The diet availability and structure were nearly retained in less populated regions within its distribution range. For example, reports from Schleswig-Holstein in North Germany still claim the presence of 33%–75% of earthworms in the diet of *C. ridibundus* during egg incubation and 14%–63% of earthworms during the chick-rearing period (Schwemmer *et al.* 2011). The earthworms were represented mainly by *Lumbricus* spp. and, to a lesser extent, polychaetes, *Hediste* spp., *Arenicola marina*, and *Lanice conchilega* (Schwemmer *et al.* 2011).

Therefore, we compared the data obtained in the Czechia with data from Karelia, Northwest Russia (Figure 1), where only 0.4% of its area constitutes agricultural soil (Naumov *et al.* 2020). In

Table 1. Previous records of *C. lari* from gulls, including negative records from gulls examined for nematodes in known distribution range of *C. lari* (Europe, Russia, Canada). The only study that reported *C. lari* in other bird hosts was Burt and Eadie (1958); therefore, a complete list of host bird species that were positive for *C. lari* in the study by Burt and Eadie (1958) is also provided

Sampling site (country), year	Species (number of examined individuals)	Prevalence [%]; infection intensity range (mean)	Reference
Kola Bay, Barents Sea (Russia), 2015	*Larus argentatus* (n=77)	0	Kuklin and Kuklina (2021)
Lake Baikal, Baikal Siberia: Republic of Buryatia, Irkutsk Oblast, Zabaykalsky Krai (Russia), 1971–2003	*Chlidonias leucopterus* (n=7)	0	Dorzhiev *et al.* (2020)
	Chroicocephalus ridibundus (n=44)	0	
	Hydrocoloeus minutus (n=5)	0	
	Larus canus (n=199)	0	
	Larus mongolicus (n=890)	0	
Kola Bay, Barents Sea (Russia), 1991–2017	*Larus argentatus* (n=127)	0	Kuklin (2013, 2017, 2018)
	Larus marinus (n=49)	0	
	Larus heuglini (n=5)	0	
	Larus hyperboreus (n=220)	0	
	Rissa tridactyla (n=179)	0	
Strachotín (Czechia), undisclosed year	Juvenile *Chroicocephalus ridibundus* (undisclosed amount)	23.5%; 1–8 (4)	Sitko (2017/2018)
Mušov (Czechia), undisclosed year	Juvenile *Chroicocephalus ridibundus* (undisclosed amount)	0	Sitko (2017/2018)
Záhlinice (Czechia), 1963–1964	Juvenile *Chroicocephalus ridibundus* (undisclosed amount)	18.9%; 1–21 (3.8)	Sitko (2017/2018)
Záhlinice (Czechia), 1990	Juvenile *Chroicocephalus ridibundus* (undisclosed amount)	0	Sitko (2017/2018)
Northern Karelia (Russia), 2010–2012	*Larus canus* (n=3)	0	Lebedeva *et al.* (2015)
	Chroicocephalus ridibundus (n=1)	0	
Lake Kubenskoye, Northern Dvina basin (Russia), 1985–2002	*Chlidonias niger* (n=24)	0	Shabunov and Radchenko (2012)
	Chroicocephalus ridibundus (n=18 pull, n=22 adults)	0	
	Hydrocoloeus minutus (n=36)	0	
	Larus argentatus (n=38)	0	
	Larus canus (n=18 pulli, n=17 adult)	0	
Mellum Island (Germany), 2006–2008	*Chroicocephalus ridibundus* (n=3)	0	Gottschalk and Prange (2011)
	Larus argentatus and *Larus* sp. (n=24)	0	
	Larus fuscus (n=2)	0	
Galicia (Spain), 2004–2006	*Larus cachinnans* (n=324)	0	Sanmartín *et al.* (2005)
Klec and České Budějovice (Czechia), 1977–1983 and 1999	*Chroicocephalus ridibundus* (n>125)	39%; 1–11	Frantová (2002)
Lake Baikal (Russia), 1979–1994	*Larus argentatus* (n=890)	0	Nekrasov *et al.* (1999)
Beograd (Serbia), undisclosed year	*Chroicocephalus ridibundus* (n=44)	0	Lepojev *et al.* (1990)
Weser-Ems (Germany), 1980	*Chroicocephalus ridibundus* (n=82 pulli)	0	Lorch *et al.* (1982)
Czechia and South Slovakia, 1962–1976	*Chroicocephalus ridibundus* (n=1,026)	12.7%; 1–21 (8)	Baruš *et al.* (1978)
	Hydrocoloeus minutus (n=1)	0	
Agdenes (Norway), 1967–1969	*Larus canus* (n=269)	29.4%; 1–18 (2.8)	Bakke (1975); Bakke and Barus (1976a)
Agdenes (Norway), 1969	*Rissa tridactyla* (n=2)	0	Bakke and Barus (1976b)
Bautzen/Oberlausitz (Germany), 1960–1967	*Chroicocephalus ridibundus* (n=457)	1.3%; mostly <5	Creutz and Gottschalk (1969a)
Neschwitz (Germany), 1960–1967	*Chroicocephalus ridibundus* (n=29)	3.4%; 3	Creutz and Gottschalk (1969b)

(*Continued*)

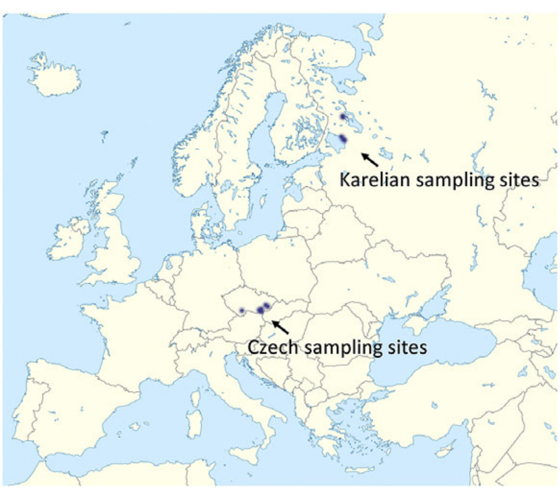
https://doi.org/10.1017/S0022149X23000949 Published online by Cambridge University Press

Table 1. (*Continued*)

Sampling site (country), year	Species (number of examined individuals)	Prevalence [%]; infection intensity range (mean)	Reference
Newfoundland (Canada), 1966–1967	*Larus argentatus* (n=410)	8.8%; 1–73 (8.4)	Threlfall (1968)
North Wales (Great Britain), 1962–1964	*Larus argentatus* (n=657)	60.1%; 1–53 (6.9)	Threlfall (1967)
Copenhagen (Denmark), 1956–1959	*Chroicocephalus ridibundus* (n=111)	0[1]	Guildal (1966)
South Moravia (Czechia), 1959	*Chroicocephalus ridibundus* (n=30)	3.3%; (9)	Zavadil (1961)
St. Andrews environment (Great Britain), the 1950s	*Chroicocephalus ridibundus* (n=30)	100%; (22)	Burt and Eadie (1958)
	Corvus frugilegus (n=26)	31%; (1.8)	
	Corvus corone (n=30)	30%; (2.1)	
	Corvus monedula (n=4)	25%; (1)	
	Tringa totanus (n=1)	100%; (1)	
	Larus argentatus (n=1)	100%; (12)	

[1]Guildal (1966) noticed that *C. lari* was present in *L. argentatus* individuals shot at the same site, but did not provide any further details.

Northwest Russia, *C. ridibundus* is common in most parts of the territory during the nesting period. Since the 1970s, this species has expanded its distribution range northward and has become more permanently established in areas where its presence was previously irregular (Noskov *et al.* 2016; Khokhlova *et al.* 2018; Khokhlova and Artemyev 2020). In contrast to *Larus canus* Linnaeus, 1758, which is also numerous in Karelia, *C. ridibundus* is a more synanthropic species mainly associated with urban areas or areas near settlements. In the second half of summer, it forms abundant flocks of hundreds to thousands of individuals where food sources are abundant. The overwhelming majority of *C. ridibundus* are nesting in the Northwest Russia winter in Western Europe and the northern Mediterranean. Only a small part of Karelian *C. ridibundus* spends the winter in southeastern and central Europe: Switzerland, Hungary, Romania, and Ukraine (Noskov *et al.* 2016).



Overview of nesting species at both sampling sites (indicated is the number of pairs of each species):

Species	Czechia	Karelia (inland)
Chroicocephalus ridibundus	50,000-100,000	Common
Ichthyaetus melanocephalus	25-50	0
Larus canus	3-10	Common
Larus argentatus	Exceptionally	Common
Larus fuscus complex	0	Nesting, decreasing
Larus marinus	0	Several pairs
Hydrocoloeus minutus	0	Common, expanding

Figure 1. Location of sampling sites in Czechia and Karelia, and the list of species nesting in the respective regions. Background map source data: http://naturalearthdata.com/.

In Karelia, we examined a broader spectrum of gulls compared to central Europe. The other examined species included *L. argentatus*, a common species in Northwest Russia (southern coast of the Barents Sea, in the White Sea and the Gulf of Finland of the Baltic Sea, and on the Onega, Ladoga, and other large inland lakes) during the breeding season (Noskov *et al.* 2016). According to Khokhlova and Artemyev (2016), the population of *L. argentatus* in Fennoscandia has been increasing since the 1970s. In Karelia, *L. argentatus* forms numerous aggregations where food is abundant, particularly at municipal waste dumps, fish works, and meat processing plants. Wintering areas of *L. argentatus* from Northwest Russia are mostly confined to waters and coastal areas of the northern and southwestern parts of the Baltic Sea. Some *L. argentatus* winter in continental reservoirs of Germany, Poland, and Sweden or settle for wintering along the whole length of the flyway. A small part of the population from the Northwest Russia regularly overwinters in small numbers on nonfreezing water bodies.

The third examined host species, *L. canus*, commonly breeds across Northwest Russia, forming numerous concentrations of hundreds to thousands of individuals near abundant food sources in the second half of summer. Birds ringed as chicks in different parts of Northwest Russia and Finland may stay within the region during September–October. Migration of *L. canus* from Northwest Russia proceeds mainly in a southwestern direction along the waters and coasts of the Baltic Sea. Birds from Onega and Ladoga Lakes and inland reservoirs of Karelia and the Leningrad Region fly through the Gulf of Finland. On the way, they often feed on city dumps, meat and fish processing plants, cattle-breeding complexes, and fur farms, stopping near them sometimes for a considerable time and even for the winter. Therefore, even in non-agricultural areas, such as Karelia, the gulls like *L. canus* are becoming common birds in cities and large settlements (Zimin and Ivanter 2002). The main wintering places of *L. canus* are located in the area of the Northern and Baltic Seas. Judging by the results of ringing, most birds spend the winter in Western Europe, from Poland to Great Britain. Single individuals reach the Mediterranean Sea. A small

Table 2. Overview of the months and years of origin of birds examined in Czechia for the presence of *C. lari*

Year	Month	Pulli	Fledged, 1st year	Adult females	Adult males
1962	06	9			
	07	4			
1963	04				1
	06	6			7
	07	19			9
1964	03				3
	04				25
	06	37		32	48
	07	9		3	6
	10			2	13
1966	10			7	5
1967	03			11	37
	04			10	43
	05			15	30
	06			14	59
	07				4
	10			4	18
1968	04			18	41
	05			18	30
	06	122		16	20
1976	04				2
1984	05			3	
	06			23	44
1985	05			2	
1988	05			8	33
1990	06	103			
1993	06			1	
2002	03			1	
2011	04			1	
2012	04				15
	05				6
	06	13			
	11			3	
2013	01			1	
2014	11		49	2	

part of *L. canus* populations winters in large ice-free reservoirs of Northwest Russia. *Lumbricus* spp. are commonly found in the diet of this host species, accounting for up to 72% of ingested animals (Kubetzki 1997).

The fourth host species, *Larus fuscus* Linnaeus, 1758, nests on islands of the Gulf of Finland, in the southwestern part of the White Sea, and islands on the Ladoga, Onega, and probably some other large lakes of Karelia. No permanent breeding settlements are known north of 66°N (Noskov *et al.* 2016). In the second half of the 20th century, a decrease in the number of this species in Fennoscandia was noted and continued until recently, probably due to its displacement by the larger, more aggressive *L. argentatus*, which predates on *L. fuscus* clutches and chicks (Khokhlova and Artemyev 2016). The migratory routes include the Black Sea and Mediterranean; the wintering grounds are in Central Africa. Preflight concentrations of *L. fuscus* can be observed near food-rich coastal areas of the Onega and Dvinsk Bays of the White Sea, the Gulf of Finland, and Lake Ladoga.

The fifth host species, *Hydrocoloeus minutus* (Pallas, 1776), is distributed throughout Karelia. The rapid expansion of the range and increase in numbers of *H. minutus* in northwest Russia began in the 1960s. Since the 1970s, nesting of this species has been known in many places in Karelia, including the western coast of the White Sea. This species is thought to winter in Western Europe and the Mediterranean; ringed birds from Northwest Russia confirmed the wintering in western France and Italy.

The intermediate hosts of the study nematode species, *C. lari*, are earthworms (*Eisenia fetida* and *Eiseniella tetraedra*, but the true spectrum of permissive earthworms remains to be elucidated) and dung beetles (*Aphodius fossor*) (Threlfall 1965a, 1965b; Gottschalk and Prange 2011). The alternative direct cycle was also suggested to take place in gull colonies and takes 21 days to complete (Threlfall 1965b). The adults parasitize the nasal and orbital cavities of birds, typically gulls, although rare reports from the cloaca, duodenum, jejunum, and trachea exist (Bakke and Barus 1976a; Threlfall 1967, 1968).

In the present study, we address the spatiotemporal trends in the prevalence and intensity of infection by *C. lari* over half a century. Based on our preliminary observations and available literature data (Table 1), we hypothesized that *C. lari* is subject to a decline in certain regions, but this decline is not necessarily applicable throughout its distribution range. We previously observed a diet switch in Czech *C. ridibundus* from earthworms to other types of diets (J. Sitko, pers. obs.). This diet switch affected young and adult birds but may not necessarily affect populations in other regions where *C. ridibundus* are less dependent on earthworms collected from agrocenoses affected by agrochemicals and trampling. Therefore, we compared *C. lari* prevalence and intensity of infection in two populations of gulls in Czechia (data from 1964 to 2014) and Karelia, Russia (data from 2012–2020). We also provide the first DNA sequences of the study species.

Materials and methods

From 1963 to 2014, we examined 322 pulli, 49 fledged first-year birds (born in the calendar year when they were examined), 195 adult females, and 492 adult males of *C. ridibundus* (in records from Czechia, we considered as adults any birds that were born in any calendar year preceding the year in which the records were obtained). All these birds originated from various sampling sites in Czechia (South Bohemia: Lomnice nad Lužnicí 49.11°N, 14.74°E; South Moravia: Strachotín 48.91°N, 16.64°E; Pohořelice – Nová Ves 48.94°N, 16.52°E; Sedlec 48.78°N, 16.71°E; Mušov 48.89°N, 16.59°E; Zlín Region: Hulín – Záhlinice 49.28°N, 17.48°E; Chropyně 49.36°N, 17.38°E); an overview of sampling days is provided in Table 2. We obtained the dead birds before they were prepared for the Comenius Museum collection (Přerov, Czechia). They consisted primarily of wounded, hunted, or injured individuals. Some were sacrificed in rescue stations due to untreatable

Table 3. Species, sex, and age of birds examined in Karelia, Russia, in 2012–2020

Species	Pulli	Fledged, 1st year	2nd year	>2nd year	Total
Chroicocephalus ridibundus	0	2	2	5	9
Hydrocoloeus minutus	0	2	0	26	28
Larus argentatus	0	5	1	4	10
Larus canus	2	7	9	28	46
Larus fuscus	0	1	0	0	1

wounds, whereas others were obtained directly for helminthological studies (Sitko 1968). The birds from the 1960s were mainly hunted in nesting colonies, which caused a skewed sex ratio, as the males attacked the hunters, whereas the females kept away from their reach. The birds from the 2010s (Chropyně sampling site) were hunted at a site where a massive flock of poultry was fed. Concerning birds provided by the rescue stations, these included only individuals not treated with antihelminthic agents before being sacrificed. Governmental and local authorities authorized our long-term research; the Ministry of the Environment of the Czechia issued our most recent permit on August 3, 2009, under No. 11171/ENV/09-747/620/09-ZS 25. Raw data are provided in Table S1.

For comparison, we examined 94 gulls of five species obtained from the shores of Lake Pertozero (62.17°N, 33.98°E) and Lake Ladoga (60.90°N, 31.35°E) in Karelia (Northwest Russia). The material originated from the spring and autumn in 2012–2020. Part of the birds were shot by hunters in the licensed hunting seasons (permits No. 00006-2013, 00007-2014, and 00009-2015 by the Republic of Karelia, Russian Federation). Some of the bird specimens were found dead in the fishnets of local people and the nets covering tanks in fish farms. The species, sex, and age of the examined birds are provided in Table 3. Raw data are provided in Table S2.

We performed full-body necropsies, fixed the nematodes in 70% ethanol, stained them with borax carmine, transferred them through an alcohol series to xylene, and mounted them in Canadian balsam. We recorded the abundance of *C. lari* in each examined host individual. We stored representative specimens in the Comenius Museum collections (Přerov, Czechia). Some host–parasite records were previously described (Lebedeva *et al.* 2015; Sitko 2017/2018; Sitko and Heneberg 2020). Data on food fragments in the intestinal tract of the birds were used for the interpretation of results. We calculated the mean relative prevalence and mean intensity of infection and tested the data using Fisher exact test or χ^2 test when all the tested groups were at n≥5, and calculated Spearman correlation coefficient. We performed all the calculations in SigmaPlot 12.0, PAST 2.14, and Quantitative Parasitology 1.0.15. Data are shown as the mean ± SD unless stated otherwise.

For the molecular phylogenetic analyses, we analyzed four *C. lari* individuals (three from *L. canus* and one from *C. ridibundus*, all from Ladoga Lake coast). We isolated DNA from ethanol-fixed specimens using the DNA-Extran kit (Synthol, Moscow, Russia). We amplified one mitochondrial (COX1) and two nuclear (partial 28S rDNA and ITS) loci. We amplified 28S rDNA with primers D2A (5'-ACAAGTACCGTGAGGGAAAGTTG-3') and D3B (5'- TCG GAAGGAACCAGCTACTA-3'), ITS locus with primers TW81 (5'- GTTTCCGTAGGTGAACCTGC-3') and AB28 (5'-ATAT GCTTAAGTTCAGCGGGT-3'), and mtDNA COX1 locus with primers LCO1490 (5'-GGTCAACAAATCATAAAGATATT GG-3') and HC02198 (5'-TAAACTTCAGGGTGACCAAAAAA TCA-3'). We carried out the PCR reaction in 20 μl of reaction mixture containing ready 5× ScreenMix (Evrogen, Moscow, Russia), 1.5 pmol of 5' and 3' primers, and 2 μl of DNA. We used annealing temperatures of 40°C (COX1) and 55°C (28S rDNA and ITS) according to Folmer *et al.* (1994) and Joyce *et al.* (1994). We purified the PCR products Cleanup Standard Extraction Kit (Evrogen, Moscow, Russia) following the manufacturer's instructions and then sequenced them with ABI PRISM 3100-Avant (Applied Biosystems Inc., Foster City, CA). Consensus sequences (696 bp for COX1, 781 bp for 28S rDNA, and 961 bp length for ITS) were assembled in MEGA10 and deposited in NCBI GenBank under accession numbers OR887539-OR887540 for COX1, OR886244 for 28S rDNA, and OR886240-OR886243 for ITS. We used the Basic Local Alignment Search Tool (BLASTn) to search for previously sequenced Syngamidae representatives. We further aligned and analyzed them in MEGA10 and trimmed them to the shortest lengths. We identified the best-fitting models (T92+G for ITS and 28S rDNA, and TN93+G for COX1) and applied these models to analyze the phylogenetic relationships using maximum likelihood analysis. We used FigTree v 1.4 to visualize the resulting trees.

Results

Czechia – *prevalence of* C. lari *in* C. ridibundus

In Czechia, infection by *C. lari* was common in all age cohorts but with seasonal differences in abundance. The overall prevalence in nonfledged pulli was 11.2%, and the infection intensity range (mean) was 1–21 (2.9). In first-year birds, the prevalence was only 1.9% (only one of 53 examined birds had a single C. *lari* individual). The first-year birds originated mainly from November 2014 (49), and only four were from October 1964. Therefore, data were lacking from earlier decades and earlier parts of the year. The *C. lari* prevalence was 16.9% in adult females, and the infection intensity was 1–9 (2.3). The *C. lari* prevalence was 12.0% in adult males, and the infection intensity was 1–12 (2.7).

At an infection intensity of 10 or more *C. lari* individuals per host, the nematodes parasitized not only the nasal cavities but also the larynx and respiratory tract. The birds had difficulty breathing and were emaciated. The young birds were sitting at or near the nests, were unable to move, were breathing heavily, and would probably die within a few days.

Czechia - pulli

In nonfledged pulli, which originated from June or July, the collection date was significantly negatively correlated with the abundance of *C. lari* in the respective host individual (Spearman rho=-0.333; *p*<0.001; n=322). All pulli that were positive for *C. lari* were obtained in the 1960s. In 1962–1968, the prevalence reached 17.5%, whereas in 1990 and 2012, there were no *C. lari* found in the examined pulli (Table 4) despite 103 gulls being examined in 1990 and another 13 gulls being examined in 2012 (Table 2). The difference in prevalence in 1962–1968 and 1990–2012 was statistically significant (Fisher exact test p<0.001; Figure 2). In the 1960s, we examined the gulls at multiple sampling sites and in multiple years. The prevalence varied among the sites and years examined.

https://doi.org/10.1017/S0022149X23000949 Published online by Cambridge University Press

Table 4. Infection of gulls in Czechia in 1962–2014 by *Cyathostoma lari.* Data are shown as prevalence [%]; intensity of infection range (mean). Only data from months with six or more examined individuals in the respective category are shown. August through April are shown in italics, indicating the months in which the infections were less likely; moreover, in July, the infection intensity remained high in pulli only

Year	Month	Pulli	Fledged, 1st year	Adult females	Adult males
1962	06	31%; 1–2 (1.8)			
1963	06	0%; -			0%; -
	07	20%; 1–21 (4.5)			0%; -
1964	*04*				*20%; 1–8 (3.2)*
	06	3%; 1–1 (1)		31%; 1–4 (2.1)	15%; 1–3 (1.4)
	07	22%; 2–8 (6)			0%; -
	10				*0%; -*
1966	*10*			*0%; -*	
1967	*03*			*0%; -*	*5%; 1–2 (1.5)*
	04			*0%; -*	*5%; 1–1 (1.0)*
	05			33%; 1–4 (2.4)	27%; 1–6 (2.3)
	06			21%; 2–2 (2.0)	31%; 1–12 (3.5)
	10				*0%; -*
1968	04			17%; 1–4 (2.7)	5%; 1–10 (4:3)
	05			28%; 1–9 (3.2)	20%; 1–8 (3.8)
	06	26%; 1–9 (2.4)		31%; 1–3 (2.0)	20%; 1–3 (1.5)
1984	06			0%; -	0%; -
1988	05			25%; 1–1 (1)	3%; 1–1 (1)
1990	06	0%; -			
2012	*04*				*0%; -*
	05				17% (1–1) 1
	06	0%; -			
2014	*11*		*2%; 1–1 (1)*		

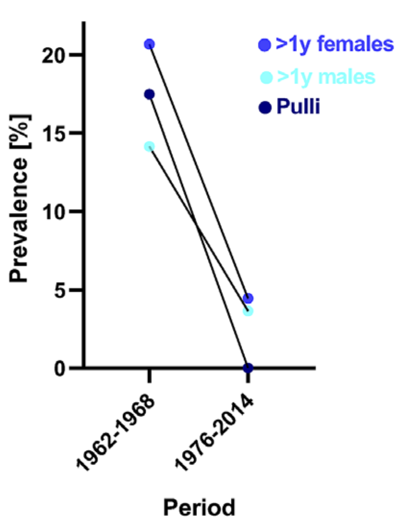


Figure 2. Changes in prevalence of *C. lari* in Czechia in 1962–1968 and 1976–2014. The data are shown separately for pulli, >1y females, and >1y males.

At the Hulín – Záhlinice sampling site, the prevalence was initially 31% (n=13) in 1962, increased to 53% (n=15) in 1963, and decreased to 18% (n=11) in 1964. These fluctuations were statistically significant (χ^2 test p=0.035 for 1962 vs. 1963, and χ^2 test p=0.024 for 1963 vs. 1964). Additionally, the variability between sites was enormous, with the Lomnice nad Lužnicí sampling site being the most parasitized (year 1968: prevalence 50%, n=42), followed by the Hulín – Záhlinice (see the data mentioned above) and Strachotín (1963: prevalence 0%, n=10; 1964: prevalence 3%, n=35) sampling sites, and *C. lari* was completely absent at the Sedlec sampling site (1968: prevalence 0%, n=40) (Table 4).

Czechia – adult females

In adult females, the prevalence fluctuated across the examined years (Spearman rho=-0.101; p=0.16; n=195). The prevalence varied enormously among the sites and years examined. In June 1964, we examined three sampling sites, Hulín – Záhlinice, Strachotín, and Pohořelice – Nová Ves. All were positive for *C. lari*, with a prevalence of 14% (n=7), 33% (n=9), and 32% (n=19), respectively. The infection intensity was also the highest at the Strachotín sampling site, reaching 3–4 (3.3) *C. lari* per host individual. We also examined large numbers of female *C. ridibundus* from two of these three sites in several later years. We did not detect any major changes at the Pohořelice – Nová Ves sampling site, as the *C. lari* prevalence was 43% (n=7) in April 1968 and 31% (n=16) in June of the same year. We further examined female gulls from the Hulín – Záhlinice sampling site later in the 1980s, namely in 05–06/1984, 05/1985, 05/1988, 06/1993, 03/2002, 04/2011, 11/2012, 01/2013, and 11/2014. *Cyathostoma lari* was absent there except on 05/1988, when two of the eight examined female *C. ridibundus* were infected, both with a single nematode (Table 4). The difference in prevalence in 1962–1968 and 1984–2014 was statistically significant (Fisher exact test p=0.03; Figure 2).

We detected seasonal dynamics in *C. lari* prevalence, but we have such data for only a single sampling site, Lomnice nad Lužnicí. At this sampling site, we examined female *C. ridibundus* on 10/1966, 03, 04, 05, 06, 10/1967, and 04 and 05/1968. *Cyathostoma lari* was absent in female *C. ridibundus* at this site from October to April (both in 1966–1967 and 1967–1968) and was present only in females examined in late spring, with 33% prevalence (n=15) on 05/1967, 21% prevalence (n=14) on 06/1967, and 28% prevalence on 05/1968 (n=18) (Table 4). The infection intensities were also the highest in May (Figure 3).

Czechia – adult males

In adult males, the prevalence also fluctuated across the examined years (Spearman rho=-0.037; p=0.42; n=499). In June 1964, we examined three sampling sites, Hulín – Záhlinice, Strachotín, and Pohořelice – Nová Ves. All were positive for *C. lari*, with a prevalence of 6% (n=15), 11% (n=18), and 19% (n=21), respectively, which was less than the prevalence in females examined at the same sampling sites and in the same period. Additionally, the infection intensity was lower, ranging between 1 and 3 *C. lari* per host individual at all sites, with mean values of 2.0, 1.0, and 1.5, respectively. In contrast to the 1960s, when all sites with large numbers of examined adult male *C. ridibundus* were positive for *C. lari* during the late summer, this species was rarely recorded in the follow-up periods. In the 1980s, *C. lari* was absent in 44 adult *C. ridibundus* males examined at the Hulín – Záhlinice sampling site. Only one host individual was infected among the 33 adult

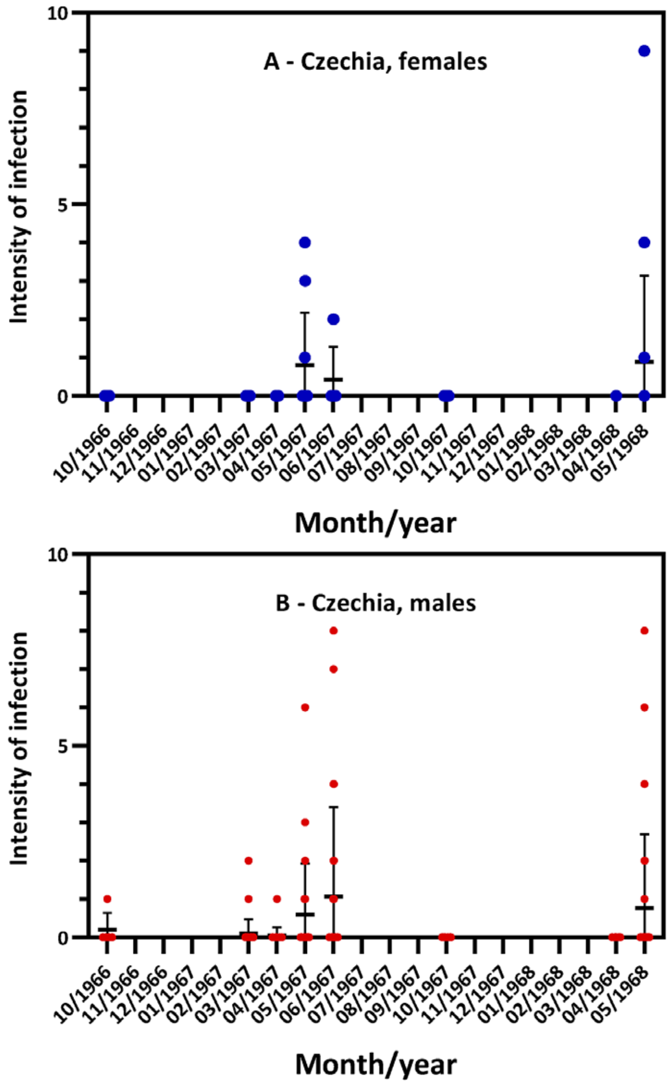


Figure 3. Seasonal dynamics of *C. lari* infection in females (a) and males (b) of *C. ridibundus* examined in the Lomnice nad Lužnicí (Czechia) sampling site from 10/1966 until 05/1968. The infection intensity data are shown for each examined host individual.

male *C. ridibundus* examined at the same site in 1988. In 2012, one host individual was positive for *C. lari* among the six adult male *C. ridibundus* examined at the Chropyně sampling site (Table 4). The difference in prevalence in 1962–1968 and 1976–2014 was statistically significant (Fisher exact test p=0.006; Figure 2).

The trends in prevalence and infection intensity by *C. lari* in male *C. ridibundus* from Hulín – Záhlinice in the 1960s differed from those described above in female *C. ridibundus* from the same sampling site and sampling periods. We found that the males were infected year-round, although the prevalence differed seasonally. In October 1966, *C. lari* was present, but the number of examined hosts was low (prevalence 20%, n=5). The nematodes were also present during the rest of the season, but only in low numbers. In March and April 1967, the prevalence reached 5% (n=37 and n=43, respectively). In May 1967, the prevalence increased to 27% (n=30) and remained high in June 1967 (31%, n=59). In October 1967, *C. lari* was again absent in the examined male gulls (n=18) and remained absent at the beginning of the next nesting season in April 1968 (n=25). In May 1968, *C. lari* appeared again, at 20% prevalence (n=30) (Figure 3). At another sampling site, Pohořelice – Nová Ves, the examined adult female *C. ridibundus* were also negative for *C. lari* when examined in October 1964 (n=13) but were positive for this nematode when examined in June of the same year (Table 4).

Karelia

The gulls from the control region provided a different view of *C. lari* prevalence. Four of the five examined gull species were infected with *C. lari*, although the numbers examined were relatively low; only *H. minutus* was free of *C. lari* infection. In *L. canus* and *C. ridibundus*, the prevalence of *C. lari* was high, over 20% (Table 5). The infection intensities were relatively low. Often, only one or a few *C. lari* individuals were present. We found the highest infection intensities in *L. canus*, as some of the examined host individuals were infected with up to 22 *C. lari* individuals (Table 5).

Regarding *L. canus*, eight >2-year-old, four two-year-old, and one fledged one-year-old individuals were infected. The two infected *C. ridibundus* were adults. The infected *L. argentatus* was a one-year-old bird. The differences in the infestation of young and old *L. canus* were statistically significant (Fisher exact test $p<0.05$).

As we performed the autopsy of gulls' gastrointestinal tracts, it allowed us to briefly comment on the food composition of examined hosts. The gastrointestinal tracts of *L. canus* contained mostly pieces of plants, insects, mollusks, and fish. Four of the 13 infected *L. canus* had earthworms in their digestive tract; two were >2-years-old, and two were 2-year-old birds. The gastrointestinal tracts of *C. ridibundus* and *L. argentatus* also contained plants, insects, and fish. Only fish were present in the gastrointestinal tract of the investigated *H. minutus* and *L. fuscus.* In addition to food components of natural origin, numerous fish food granules were found in the gut of *L. canus* and *C. ridibundus*, originating from fish farm cages. The presence of earthworms in the intestines of examined birds correlated positively with their infestation by *C. lari* (Spearman $rho = 0.43$, $p = 0.002$).

Molecular analyses

The phylogenetic analysis of newly obtained sequences of *C. lari* from its two hosts, *L. canus* and *C. ridibundus*, confirmed the classification of *C. lari* into the genus *Cyathostoma* and revealed low heterogeneity among the examined isolates (Figure 4).

Table 5. Infection of gulls in Karelia, Russia, in 2012-2020 by *Cyathostoma lari*

Bird species	Number of hosts		Prevalence [%]	Intensity of infection	
	Examined	Infected		Range	Mean
Chroicocephalus ridibundus	9	2	22	1-3	1.8
Hydrocoloeus minutus	28	0	0	–	–
Larus argentatus	10	1	10	1	1.0
Larus canus	46	13	28	1-22	6.0
Larus fuscus	1	1	100	1	1.0

https://doi.org/10.1017/S0022149X23000949 Published online by Cambridge University Press

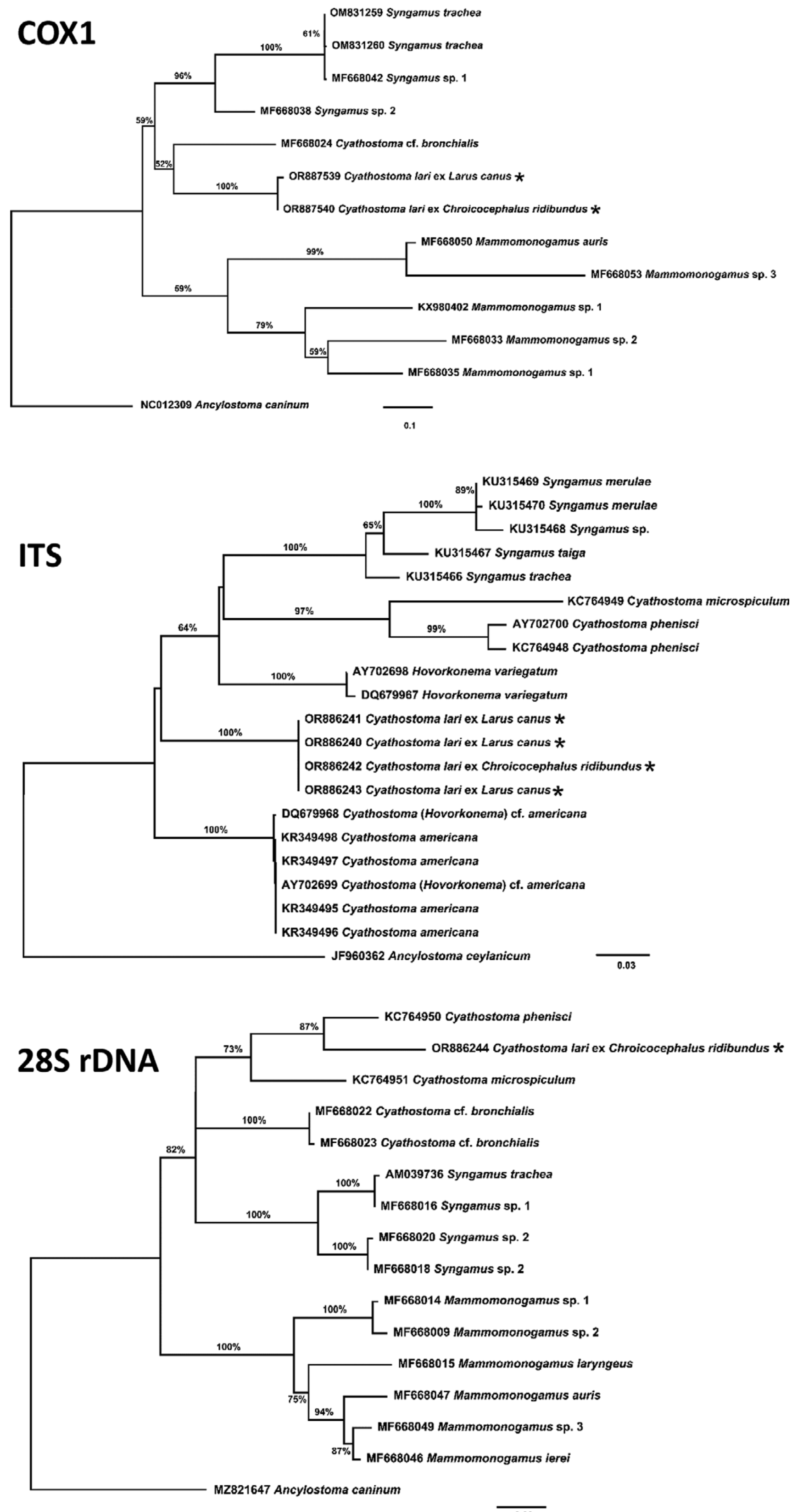


Figure 4. Maximum likelihood trees showing the phylogenetic position of *C. lari* among Syngamidae. Data are shown for COX1, ITS, and 28S rDNA loci. Newly provided sequences are labeled with asterisks.

Discussion

We found that *C. lari* is subject to prominent spatiotemporal changes in its distribution. The decline in *C. lari* abundance started earlier than that of bird trematodes (see Sitko and Heneberg 2020, 2021). Therefore, the causes of this decline appear to be different from those causing the decline of a broad spectrum of trematodes in recent years. Here, we performed an observational study and, therefore, cannot identify the causes themselves. However, there is a time coincidence of the observed decline in *C. lari* abundance with the increases in the trampling of agricultural soil and with the onset of earthworm diversity and abundance deterioration. Note that earthworms are core *C. lari* intermediate hosts and are extremely sensitive to soil trampling. Some studies (e.g., Curry *et al.* 2002) suggest that trampling can induce dramatic crashes in earthworm populations within a year or several years. Since the 1980s, *C. lari* has become a rare parasitic nematode of Czech gulls, and the situation did not improve until recently (Table 4).

The populations of *C. lari* were subject to dramatic seasonal dynamics. Infections were rare or completely absent in birds examined from August to April of the following year. Then, the prevalence increased by one or more orders of magnitude and remained high until June. In pulli, the C. *lari* prevalence remained high until July. However, in adult birds, the *C. lari* prevalence declined in July. We hypothesize that the seasonality of *C. lari* prevalence and infection intensity is related to the diet switch to earthworms used primarily to feed the nestlings. Since the 1980s, earthworms have become rare in the diet of *C. ridibundus* nestlings. They started to be fed prevalently with dipterans and carabid beetles (one- to five-day-old birds), with hymenopterans added when the young are six to ten days old, and small mammals, fish, plants, and elaterid beetles added at the age of 11–20 days. Only the young of 21–30 days of age were fed earthworms to some extent (in combination with carabid beetles) (Honza 1993). In the diet of adults, earthworms are also represented the most in the spring (particularly May) and autumn (particularly September and October) (Satchell 1958; Boháč 1968; Vernon 1972). In June, earthworms are usually replaced by elaterid, carabid, and staphylinid beetles, sometimes with ants, plants (e.g., cherries and grain), and often with small mammals captured in plowed fields (Ingram 1944; Boháč 1968; Vernon 1972). A second peak of infections may occur in autumn when arable fields are plowed, but we did not examine birds in September. The October and November birds were negative for *C. lari* or hosted it only rarely (Table 4). Importantly, Bakke (1970) hypothesized that the direct life cycle could play a role in gull nests, with reinfections occurring due to the ingestion of objects contaminated by feces and regurgitated food. The seasonality peak in May and June was also reported by other studies (which also mention July because the nesting season was somewhat delayed in the study regions, as they were located in Norway and Wales) (Threlfall 1967; Bakke 1975). We failed to identify the second infection peak following the autumn arable field plowing in the birds examined in October. Nevertheless, this peak might occur sooner or later in the season when we did not examine the birds. There were no December birds available in the 1960s through the 2000s, as *C. ridibundus* was migratory at that time, and only at the end of the indicated period did it start to spend winter in large cities or at waste dumps.

Seasonality of diet composition was also confirmed for gull species nesting in inland Russia. For example, Shabunov and Radchenko (2012) concluded that the proportional representation of prey items in a diet of *C. ridibundus*, *L. canus*, and *L. argentatus* in Vologda region (located in East European Plains region in Russia) differs significantly during the season, and these changes are associated with differences in abundance and availability of the prey organisms. In fact, the diet of *C. ridibundus* was subject to more prominent seasonal variations compared to other gull species. In early spring, *C. ridibundus* diet in Vologda region is poor and the gulls are increasingly more dependent on fish and aquatic insects. In June, *C. ridibundus* diet is dominated by insects developing both in water and on the land. In July, *C. ridibundus* increases the time spent on water bodies, which is related to the increased share of fish and terrestric animals collected in nearby habitats in their diet. In August and September, the *C. ridibundus* diet contains proportionally more earthworms and molluscs (Shabunov and Radchenko 2012). Even in inland Russia, evidence is available for a greater synanthropization of gulls, including *C. ridibundus* (Melnikov 2021), as the gulls generally tend to switch to easier feeding opportunities (Goumas *et al.* 2020).

The seasonal and age-related differences in *C. lari* prevalence and intensity of infection were also reported in several previous studies. In *L. canus* in Norway, *C. lari* infected adult and immature gulls equally, but unfledged pulli were infected to a lesser extent (Bakke 1975). In contrast, Threlfall (1967, 1968) reported higher prevalence and higher infection intensities in pulli of *L. argentatus* compared to full-grown birds based on the data from Europe (Wales) as well as North America (Newfoundland). The infections of *L. canus* in Norway had a seasonal pattern, with the prevalence of infections in May through July reaching between 35% and 45%. In contrast, the prevalence in April or September through October was low, at or below 5%. The seasonal decline in prevalence occurred earlier in the adults, in which a low prevalence was already found in August. In contrast, the prevalence in immature individuals decreased a month later, and in August, it still exceeded 35%. However, the spring onset of infection was delayed in juvenile gulls relative to adults of the same host species (Bakke 1975). Interestingly, Bakke (1970) noted that the examined pulli were mainly fed vegetables, insects, and mink fodder but not earthworms and, therefore, speculated that they became infected by ingesting objects contaminated by infective eggs and larvae from adults' feces and regurgitated food. The switch between the high and low infection rates is explained by a switch to marine feeding habitats by the study population of *L. canus* during August, while juvenile *L. canus* were occasionally spotted feeding on earthworms even during autumn (Bakke 1975). Studies from other gull species and locations also reported seasonality in *C. lari* prevalence, but the maxima did not match in time (Threlfall 1967; Guildal 1968). Threlfall (1967) agreed on an infection peak in July but detected a secondary peak in December and hypothesized that the second peak could be related to autumn agricultural activities, as plowing exposes earthworms to the gulls. Importantly, Threlfall (1965a, 1966) noted that the prevalence of *C. lari* in *L. argentatus* chicks in a heavily infested colony in Wales declined when the birds were approximately five weeks of age. Threlfall (1966) proposed that this decline is associated with a change in the bird's metabolism once it starts flying and demonstrated cellular and humoral immunity changes following *C. lari* infection. However, despite these correlations being correctly observed, available evidence allows us to hypothesize that the decline in *C. lari* prevalence results from a diet switch from earthworms to other dietary items in fledged birds. The study nematode species is short-lived; it reaches maturity 14 days after infection, and the eggs are present for approximately one week. After that, their presence in feces drops to only several percent, or the adult nematodes disappear completely (Threlfall 1965b).

https://doi.org/10.1017/S0022149X23000949 Published online by Cambridge University Press

The described trends in *C. lari* prevalence and infection intensity are valid for Czechia and likely for the nearby regions but do not apply to the whole area of distribution of *C. ridibundus* and European gulls in general. As we show in the present study by analyzing multiple species of gulls in Karelia, a Northwest Russian region with minimal areas of arable soil and thus unlikely to be affected by arable soil trampling, *C. lari* is still abundant in gulls in this region, and further studies should examine the species spectrum of permissive intermediate hosts. The two previously described permissive earthworm hosts are present in this region, but the spectrum of available meadow-bound earthworms is much broader. At least 13 earthworm species were recorded in the study region (Terhivuo 1988; Vsevolodova-Perel 1997; Ivask *et al.* 2006; Blakemore 2007).

Limitations

This study has a major limitation: the regional trends in the abundance and diversity of earthworms at the examined sites remain unknown. The highest abundance of earthworms available during *C. ridibundus* breeding in Czechia probably occurred in areas where sugar beet was cultivated. When discussing this topic with local farmers, we received feedback that in the mid-1970s, heavy tractors started to be used, and the sugar beet was transported by heavy lorries. This combination led to soil trampling and likely to a first decline in earthworm abundance at the end of the 1970s. Later, sugar beet cultivation was discontinued in the study regions due to a sharp decline in sugar refineries after economic liberalization during the 1990s (Bavorová 2003). Increased use of agrochemicals that have adverse effects on earthworms, such as various neonicotinoids and pyrethroids, has also become more common since the 1990s (Miglani and Bisht 2019). These effects led to observations concluding that *C. ridibundus* are less commonly observed behind tractors when plowing or harrowing (Sitko, pers. obs.). Although direct observations from the study region are not available, the above-described conditions generally lead to a deterioration in earthworm assemblages and declines in their abundance in arable fields (Curry *et al.* 2002; Birkás *et al.* 2004; Nieminen *et al.* 2011; Crittenden *et al.* 2015). An important limitation stems also from a limited knowledge of the contribution of earthworms to the completion of *C. lari* life cycle. Taking into account the possibility of a direct life cycle as pointed out by Bakke (1975), it is unclear, whether the direct life cycle is limited only to nesting sites within the nesting season or whether there may be conditions under which the population of these parasites would be sustainable in the absence of ingestion of earthworms that serve as intermediate hosts.

Note that this was an observational study of free-living birds. The acquisition of host birds for examination was affected by a number of factors that make the analysis of this short-lived parasite difficult. Any sample is just a snapshot appropriate to provide relevant data for only the respective week or several weeks prior the collection date. Therefore, the obtained data should not be misinterpreted as a detailed overview of seasonal changes in *C. lari* abundance but should rather be considered as an overview of the status of this species in the examined host individuals.

Conclusions

In conclusion, the *C. lari* population crashed in specific parts of its distribution range. The reasons are unknown, but the observed population changes correspond with the diet switch of their core host in central Europe, *C. ridibundus*. Due to difficulties obtaining earthworms and other invertebrates, this species changed the diet provided to the nestlings. It also changed the diet obtained in arable fields, meaning that the abundance of earthworms in the diet of *C. ridibundus* became negligible. In contrast, the share of *Microtus arvalis* in *L. ridibundus* diet increased dramatically (J. Sitko, pers. obs.). Furthermore, we found that these changes were limited only to regions where the gulls feed (or fed) on arable fields. In Karelia, where arable fields are scarce, they likely continue to feed on earthworms and still display high infection rates by *C. lari*. Therefore, *C. lari*, a parasite of gull nasal and orbital sinuses, nearly disappeared from central European nesting grounds of *C. ridibundus* but is still present in better-preserved parts of its distribution range.

Supplementary material. The supplementary material for this article can be found at http://doi.org/10.1017/S0022149X23000949.

Data availability statement. Representative specimens of the helminths analyzed in this study are available in the collections of the Comenius Museum in Přerov and in the collections of the Institute of Biology, Karelian Research Center, Russian Academy of Sciences. All data are available in the main text.

Acknowledgements. We thank the governmental and local authorities for providing the necessary permissions to conduct this long-term research. We also thank the landlords, gamekeepers, and the staff of local rescue stations for providing us with carcasses of untreatable birds. The authors are grateful to Drs. Eugeny Ieshko and Alexey Parshukov (Institute of Biology, Karelian Research Center, Russian Academy of Sciences) for help with bird sampling. We would like to thank Dr. Alexandr Artem'ev (Institute of Biology, Karelian Research Center, Russian Academy of Sciences) for identifying bird species and the ages of birds collected in Karelia.

Author contribution. JS and PH conceived the study; JS, GY, and DL collected the data; DL conducted the molecular analyses; PH analyzed the data and wrote the manuscript; and all authors revised the manuscript and agreed on its final version.

Financial support. The study was supported by the Ministry of Culture of the Czech Republic project DE07P04OMG007 and by the Russian Ministry of Science and Education state order 122032100130-3.

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

Ethical approval. Not applicable. All the host birds were obtained dead and therefore no ethics permit was required by Czech and Russian law. The research on Czech gulls was authorized by the Ministry of the Environment of the Czech Republic; the most recent permit was issued on August 3, 2009, under No. 11171/ENV/09-747/620/09-ZS 25. Part of the gulls of Russian origin were hunted by licensed hunters under licenses 00006-2013, 00007-2014, and 00009-2015 by the Republic of Karelia, Russian Federation.

References

Bakke TA (1970) Feeding habits of the common gull, *Larus canus*, in the Agdenes area, Tröndelag. *Fauna* **23**, 253–271 [in Norwegian]

Bakke TA (1975) Studies of the helminth fauna of Norway XXIX: the common gull, *Larus canus* L., as final host for *Syngamus* (*Cyathostoma*) *lari* (Blanchard, 1849) [Nematoda, Strongyloidea]. *Norwegian Journal of Zoology* **23**, 37–44.

Bakke TA and Barus V (1976a) Studies of the helminth fauna of Norway XXXVII: the common gull, *Larus canus* L., as final host for Nematoda. II. Qualitative and quantitative data on species of Acuariidae, Capillariidae, Strongyloididae, Syngamidae, and Tetrameridae; with notes on host-parasite relationship. *Norwegian Journal of Zoology* **24**, 7–31.

Bakke TA and Barus V (1976b) Studies of the helminth fauna of Norway XXXIX: nematodes from *Hydrobates pelagicus* L. and *Rissa tridactyla* L. (aves) in Norway. *Norwegian Journal of Zoology* **24**, 185–189.

Baruš V, **Sitko J, and Tenora F** (1978) *Nematoda* and *Pentastomida* parasitizing gulls (*Aves: Laridae*) in Bohemia and Moravia. *Acta Universitatis Agriculturae et Silviculturae Mendelianae Brunensis* **26**, 169–182.

Bavorová M (2003) Influence of policy measures on the competitiveness of the sugar industry in the Czech Republic. *Agricultural Economics* **49**, 266–274.

Birkás M, **Jolánkai M**, **Gyuricza C, and Percze A** (2004) Tillage effects on compaction, earthworms and other soil quality indicators in Hungary. *Soil and Tillage Research* **78**, 185–196.

Blakemore RJ (2007) *Scandinavian earthworms- a checklist of species.* Available at http://www.annelida.net/earthworm/Scandinavian.pdf (accessed on December 3, 2023).

Boháč D (1968) Potrava a hospodářský význam racka chechtavého (*Larus ridibundus* L.). CSc. Thesis. Prague: Faculty of Science, Charles University.

Burt DRR and Eadie JM (1958) *Cyathostoma lari* Blanchard, 1849 [Nematoda, Strongyloidea]: its anatomy, intraspecific variation and hosts, with a re-definition of the genus. *Zoological Journal of the Linnean Society of London* **43**, 575–586.

Creutz G and Gottschalk C (1969a) Endoparasitenbefall bei Lachmöwen in Abhängigkeit vom Alter. *Angewandte Parasitologie* **10**, 80–91.

Creutz G and Gottschalk C (1969b) Vogelberingung und Parasitologie. *Beiträge zur Vogelkunde* **14**, 187–190.

Crittenden SJ, **Huerta E**, **de Goede RGM, and Pulleman MM** (2015) Earthworm assemblages as affected by field margin strips and tillage intensity: an on-farm approach. *European Journal of Soil Biology* **66**, 49–56.

Curry P, **Byrne D, and Schmidt O** (2002) Intensive cultivation can drastically reduce earthworm populations in arable land. *European Journal of Soil Biology* **38**, 127–130.

Dorzhiev TsZ, **Badmaeva EN, and Dugarov ZhN** (2020) [Ecological and faunistic analysis of helminths in wetland birds of Baikal Siberia: 3. *Laridae].* Nature of Inner Asia **14**, 66–78. [in Russian]

Folmer O, **Black M**, **Hoeh W**, **Lutz R, and Vrijenhoek R** (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* **3**, 294–299.

Frantová D (2002) Some parasitic nematodes (Nematoda) of birds (Aves) in the Czech Republic. *Acta Societatis Zoologicae Bohemicae* **66**, 13–28.

Gottschalk C and Prange H (2011) Über Vogelparasiten auf der Insel Mellum an der niedersächsischen Nordseeküste. *Der Zoologische Garten (Neue Folge)* **80**, 29–86.

Goumas M, **Boogert NJ, and Kelley LA** (2020) Urban herring gulls use human behavioural cues to locate food. *Royal Society Open Science* **7**, 191959.

Guildal JA (1966) Some qualitative and quantitative investigations on the endoparasitic fauna of the Scandinavian population of the black-headed gull (*Larus ridibundus* L.). *Proceedings of the First International Congress of Parasitology* **1**, 517–519.

Guildal JA (1968) Investigations on the endoparasitic fauna of the Scandinavian-Baltic population of the herring gull (*Larus argentatus* Pontoppidan, 1763). A qualitative and quantitative study. *Den Kongelige Veterinær- og Landbohøjskole Ärsskrift* **1968**, 59–78.

Honza M (1993) Factors influencing the foraging patterns of the Black-headed Gull (*Larus ridibundus*) from breeding colonies. *Folia Zoologica* **42**, 243–249.

Ingram GCS (1944) Feeding habit of the black-headed gull. *British Birds* **38**, 12–13.

Ivask M, **Ööpik M, and Kuu A** (2006) Abundance and diversity of earthworm communities in flooded semi-natural meadows. *Agricultural University of Iceland Publications* **9**, 90–94.

Joyce SA, **Reid A**, **Driver F, and Curran J** (1994) Application of polymerase chain reaction (PCR) methods to identification of entomopathogenic nematodes. pp. 178–187 in Burnell AM, Ehlers R-U, and Masson JP (Eds), *Cost 812 Biotechnology: Genetics of entomopathogenic nematode-bacterium complexes*. Proceedings of Symposium & Workshop, St. Patrick's College, Maynooth, Co. Kildare, Ireland. Luxembourg, European Commission, DG XII.

Khokhlova TYu and Artemyev AV (2016) Herring gull *Larus argentatus* and lesser black-backed gull *Larus fuscus* in the Kizhi skerries of Lake Onega (Transactions of Karelian Research Centre of Russian Academy of Science). *Biogeography* **8**, 57–67. [In Russian]

Khokhlova TYu and Artemyev AV (2020) Changes in the avifauna of the Kizhi skerries of Lake Onega over the past 20 years. *Russian Journal of Ornithology* **29**, 5289–5291. [in Russian]

Khokhlova TYu, **Artemyev AV, and Yakovleva MV** (2018) Long-term dynamics of the borders of bird species ranges in the North-West Russia. *Russian Journal of Ornithology* **27**, 1171–1173. [in Russian]

Kubetzki U (1997) Ernährungsökologie von Sturmmöwen (*Larus canus*) verschiedener Kolonien Norddeutschlands. *Hamburger avifaunistische Beiträge* **29**, 5–84.

Kuklin VV (2013) [The peculiarities of helminthofauna of seabirds on offshore water of the Barents Sea]. *Russian Journal of Parasitology* **25**, 16–21. [in Russian]

Kuklin VV (2017) [Glaucous gull (*Larus hyperboreus* Gunnerus, 1767) in the Barents Sea: a review of helminthfauna and the possibility of using as an indicator of parasitological situation]. *Russian Journal of Parasitology* **41**, 1–21.

Kuklin VV (2018) [Species composition and ecological features of freshwater helminthfauna of seabirds on the Barents Sea]. *Russian Journal of Parasitology* **12**, 24–40. [in Russian]

Kuklin VV and Kuklina MM (2021) Age dynamics of helminth fauna of the herring gull (*Larus argentatus*) in Kola Bay, Barents Sea. *Biology Bulletin* **48**, 1160–1169.

Lebedeva DI, **Yakovleva GA, and Ieshko EP** (2015) Parasites of gulls (*Larus canus* L. 1758 and *L. ridibundus* L. 1766) from Northern Karelia. *Transactions of the Karelian Research Centre of the Russian Academy of Sciences* **7**, 84–88.

Lepojev O, **Kulišic Z**, **Aleksic N, and Dimitrijevic S** (1990) Nematodes of gulls (*Larus ridibundus* L.) in the Belgrade area. *Acta Veterinaria* **40**, 159–162.

Lorch H-J, **Schneider R, and Loos-Frank B** (1982) Parasitologische Untersuchungen nestjunger Lachmöwen (*Larus ridibundus*) in Brutkolonien des Binnenlandes und der Küste. *Journal für Ornithologie* **123**, 29–39.

Melnikov YuI (2021) [Changes in the behavior of the black-headed gull *Larus ridibundus* Linnaeus, 1766 in the city of Irkutsk: the first stages of synanthropization]. *Baikal Zoological Journal* **29**, 73–77. [in Russian]

Miglani R and Bisht SS (2019) World of earthworms with pesticides and insecticides. *Interdisciplinary Toxicology* **12**, 71–82.

Naumov A, **Akimova V**, **Sidorova D, and Topnikov M** (2020) Agriculture and land use in the North of Russia: case study of Karelia and Yakutia. *Open Geosciences* **12**, 1497–1511.

Nekrasov AV, **Pronin NM**, **Sanzhieva SD, and Timoshenko TM** (1999) [Diversity of helminth fauna in the herring gull (*Larus argentatus*) from the Baikal Lake: Peculiarities of spatial distribution and invasion]. *Parasitologia* **33**, 426–436. [in Russian]

Nieminen M, **Ketoja E**, **Mikola J**, **Terhivuo J**, **Sirén T, and Nuutinen V** (2011) Local land use effects and regional environmental limits on earthworm communities in Finnish arable landscapes. *Ecological Applications* **21**, 3162–3177.

Noskov GA, **Rynkevich TA, and Gaginskaya AR** (2016) *Migration of bird of Northwest Russia. Nonpasserines*. Vol. **1**. St. Petersburg, ANO LA Professional. [in Russian]

Pemberton RT (1959) Life-cycle of *Cyathostoma lari*, Blanchard 1849 (Nematoda, Strongyloidea). *Nature* **184**, 1423.

Pemberton RT (1963) Helminth parasites of three species of British gulls, *Larus argentatus* Pont., *L. fuscus* L. and *L. ridibundus* L. *Journal of Helminthology* **37**, 57–88.

Sanmartín ML, **Cordeiro JA**, **Álvarez MF, and Leiro J** (2005) Helminth fauna of the yellow-legged gull *Larus cachinnans* in Galicia, north-west Spain. *Journal of Helminthology* **79**, 361–371.

Satchell JE (1958) Earthworm biology and soil fertility. *Soils and Fertilizers* **21**, 20919.

Schwemmer P, **Tischler T**, **Rehm R, and Garthe S** (2011) Habitatnutzung, Verbreitung und Nahrungswahl der Lachmöwe (*Larus ridibundus*) im küstennahen Binnenland Schleswig-Holsteins. *Corax* **21**, 355–374.

Shabunov AA and Radchenko NM (2012) *[Parasites of fish, amphibians and seagull birds in the ecosystems of large reservoirs of the Vologda region].* Vologda, Vologda State Pedagogical University. [in Russian]

Simpson VR and Harris EA (1992) *Cyathostoma lari* (Nematoda) infection in birds of prey. *Journal of Zoology (London)* **227**, 655–659.

Sitko J (1968) Trematodes of birds of the family Laridae in Czechoslovakia. *Věstník Československé společnosti zoologické* **32**, 275–292.

Sitko J (2017/2018) Some results of studies of parasitic worms of birds using the collection of Přerov Ornithological Station. *Zprávy MOS* **75/76**, 18–31. [in Czech]

Sitko J and Heneberg P (2020) Systemic collapse of a host-parasite trematode network associated with wetland birds in Europe. *Parasitology Research* **119**, 935–945.

Sitko J and Heneberg P (2021) Long-term dynamics of trematode infections in common birds that use farmlands as their feeding habitats. *Parasites & Vectors* **14**, 383.

Terhivuo J (1988) The Finnish Lumbricidae (Oligochaeta) fauna and its formation. *Annales Zoologici Fennici* **25**, 229–247.

Threlfall W (1965a) *The helminth parasites of the herring gull (Larus argentatus Pontopp.) on the Newborough Warren Nature Reserve, Anglesey*. PhD Thesis. Cardiff, University of Wales.

Threlfall W (1965b) Life-cycle of *Cyathostoma lari* Blanchard, 1849 (Nematoda, Strongyloidea). *Nature* **206**, 1167–1168.

Threlfall W (1966) Studies on the blood of herring gulls and domestic fowl with some observations on changes brought about by infection with *Cyathostoma lari* Blanchard, 1849 (Nematoda: Strongyloidea). *Bulletin of the Wildlife Disease Association* **2**, 41–51.

Threlfall W (1967) Studies on the helminth parasites of the herring gull, *Larus argentatus* Pontopp., in northern Carnarvonshire and Anglesey. *Parasitology* **57**, 431–453.

Threlfall W (1968) Studies on the helminth parasites of the American herring gull (*Larus argentatus* Pont.) in Newfoundland. *Canadian Journal of Zoology* **46**, 11–19.

Vernon JDR (1972) Feeding habitats and food of the black-headed and common gulls. *Bird Study* **19**, 173–186.

Vsevolodova-Perel TS (1997) *[Earthworms of the fauna of Russia]*. Moscow, Nauka. [in Russian]

Zavadil R (1961) Nález *Cyathostoma lari* E. Blanchard 1894 u racka chechtavého (*Larus ridibundus* Linné 1766) z Jižní Moravy. *Československá parasitologie* **8**, 415–419.

Zimin VB and Ivanter EV (2002) *Pticy. 3-e izd., ispr. i dop.* Petrozavodsk, PetrGU. [in Russian]