



Research Article

Factors affecting the dynamics of *Spirometra erinaceieuropaei* (Cestoda: Diphyllbothridae) infection in medium-sized carnivores in north-eastern Poland

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Abstract

Parasitic infections in wildlife are affected by biological, ecological and anthropogenic factors and they may have important effects on both individuals and populations. In this paper we studied spread of sparganosis – the disease caused by the diphyllbothrid tapeworm from the genus *Spirometra*, which importance is increasingly growing around the world. We analysed different factors influencing *Spirometra erinaceieuropaei* infection parameters in two carnivore hosts: raccoon dog (*Nyctereutes procyonoides*) and European badger (*Meles meles*). We found no differences in infection probability between studied hosts; however, European badger has significantly higher mean number of plerocercoid larvae than raccoon dog (35.4 and 4.2, respectively). For both host species we found significant differences in *S. erinaceieuropaei* prevalence between study sites: Białowieża Forest (BF), Knyszyn Forest (KF) and Augustów Forest (AF). Infection probability was also positively related to the proportion of wet habitats. Sparganosis prevalence decreased with time covered by the study; however, the significance of the temporal changes was confirmed only for raccoon dog. *Spirometra erinaceieuropaei* infection probability increased with the age of animals with the rate similar for both species, which suggests multiple infections. No sex difference in infection prevalence was found in both species. Our study revealed complex factors, both biological and environmental, involved in parasite transmission, spread and persistence in medium-sized carnivore hosts. Similar prevalence in studied species, may suggest similar probability of infection risk, but higher infection intensity in European badger may be related to much shorter co-evolution of this species with the parasite.

Introduction

Spread and dynamics of parasitic infections in wildlife can be strongly affected by numerous biological, ecological, and anthropogenic factors and they may have important effects on both individuals and populations (Kołodziej-Sobocińska et al., 2019; Lindenfors et al., 2007; Torres et al., 2006; Moller, 2005). Parasites may cause deleterious effects on their hosts and whole populations (Tompkins et al., 2011; Prado et al., 2009; Pedersen et al., 2007). Wild carnivorous mammals are exposed to many parasitic diseases caused by different parasite groups: nematodes (trichinellosis, toxocarosis, and dirofilariasis); tapeworms (echinococcosis, diphyllbothriasis, and flukes causing i.e. allariosis and clonorchosis), and protozoa (toxoplasmosis and babesiosis) (Kuchta et al., 2021; Duscher et al., 2017; Ionica et al., 2017; Hurníková et al., 2016; Oksanen et al., 2016; Antolova et al., 2014; Sutor et al., 2014; Poeppl et al., 2013; Thompson, 2013), many of them have zoonotic potential and cause threat to human health (Otranto and Deplazes, 2019; Bagrade et al., 2016; Laurimaa et al., 2016; Poeppl et al., 2013; Sařamatin et al., 2013).

One of the zoonotic emerging diseases of the global distribution of which the scientific and medical importance has been systematically increasing in recent years is sparganosis caused by broad tapeworms of the genus *Spirometra*. Symptoms of the disease depend on localiza-

tion of spargana (plerocercoid larvae) in the body. The most common is subcutaneous sparganosis, caused by migrating larvae in connective tissues and superficial muscles; however, cerebral, ocular, visceral, and the most dangerous, proliferative sparganosis were also noted (Kuchta et al., 2021).

The genus *Spirometra* belongs to the family Diphyllbothriidae (Lühe, 1910) and includes species that can infect many vertebrate hosts including humans. More than 1600 cases of sparganosis have been documented worldwide in humans, mostly in east and southeast Asia (Liu et al., 2015). In Europe, only one species – *Spirometra erinaceieuropaei* – has been recorded in humans, wild and domestic animals in 17 European countries (Bagrade et al., 2021; Kuchta et al., 2021; Kondzior et al., 2020). More intensive studies were conducted in Poland (e.g. Kondzior et al., 2020, 2018; Czyżewska et al., 2019; Kołodziej-Sobocińska et al., 2019, 2018, 2016, 2014) and Belarus (Anisimova, 2004; Shimalov and Shimalov, 2003a, 2002a,b, 2001a,b, 2000). *Spirometra erinaceieuropaei* has been recorded as natural definitive hosts in six carnivores, and in nearly 40 vertebrate species of amphibians, reptiles, mammals (including human) it was considered as intermediate/paratenic hosts in which plerocercoid larvae were found (Kuchta et al., 2021).

The routes of sparganosis transmission in both wildlife and humans have been studied before and it was revealed that the source of infection is predominantly consumption of raw (or undercooked in case of humans) meat of amphibians, reptiles and mammals, i.e. wild boar

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(*Sus scrofa*), containing plerocercoid larvae or drinking water contaminated by copepods infected with proceroid larvae (Kuchta et al., 2021; Scholz et al., 2019). However, there is no information about factors influencing the circulation of sparganosis in wildlife.

Studying and defining specific factors influencing the distribution of diseases in the wild is difficult due to high variability of biological, environmental and anthropogenic conditions in which wild animals live. Moreover, it should be mentioned that these dependencies can change in relation to the analysed parasite, host species, sex, their overall fitness, breeding status and many others. It is also necessary to take into account climate change, including increasing temperatures, droughts, floods and other climatic disorders which has a significant impact on the spread of diseases and their appearance in new areas that were previously, for example, unfavourable (too cold, too dry etc.) for the development of a given pathogen or occurrence of their host (Kołodziej-Sobocińska, 2019; Rizzoli et al., 2019; Shaw et al., 2019; Stringer and Linklater, 2015; Fuxjager et al., 2011; Tompkins et al., 2011; Lindfors et al., 2007; Moller, 2005).

In Poland, the tapeworm from the genus *Spirometra* was first described in the 1940s for grey wolf (*Canis lupus*) and Eurasian lynx (*Lynx lynx*) from Białowieża Forest (BF). The parasite was then defined as a new species – *Spirometra janickii* (Furmaga, 1953). The rediscovery and new study done on this parasite in the second decade of the 21st century in north-eastern Poland allowed for assigning it, using genetic methods, to the species *S. erinaceieuropaei* (Kuchta et al., 2021; Kołodziej-Sobocińska et al., 2019; Kondzior et al., 2020, 2018). Our recent study on sparganosis in wildlife has revealed that in NE Poland *S. erinaceieuropaei* was present in 10 vertebrate species: 9 mammal species, including eight carnivores and wild boar, and one reptile – grass snake (*Natrix natrix*) (Kondzior et al., 2020, 2018; Kołodziej-Sobocińska et al., 2018, 2016, 2014). We also showed that frequency and level of infection may differ between selected hosts and likely depend on host diversity and habitat structure in a given area (Kondzior et al., 2020).

In this paper we aimed to analyse different factors influencing spread of sparganosis in specific wild hosts. We selected two species of mesopredators, native European badger and invasive raccoon dog, which were found to be paratenic hosts for *S. erinaceieuropaei* (Kuchta et al., 2021; Kondzior et al., 2020; Kołodziej-Sobocińska et al., 2014; Shimalov and Shimalov, 2002b). These species differ in many aspects of their ecology (e.g. diet, habitat use, lifespan) (Kowalczyk et al., 2009, 2006; Jędrzejewska and Jędrzejewski, 1998) and are common and widespread in NE Poland. Raccoon dog originate from Far East and most probably has a longer history of co-evolution with *Spirometra* tapeworms than European badger (Kołodziej-Sobocińska et al., 2019). Thus, we presumed that these two species may differ in susceptibility to the *Spirometra* tapeworms and, consequently, in infection parameters.

Materials and methods

Study area

The study was performed in north-eastern Poland (Fig. 1). The region is characterized by well-preserved forest ecosystems and greater forest cover (31 %) in comparison to majority of regions of Poland (Statistical Yearbook of Forestry, 2002). Our main sampling sites were large forested areas: Białowieża Forest (BF), Knyszyn Forest (KF), and Augustów Forest (AF). KF and AF are dominated by coniferous forests (Sokołowski, 2006). In BF over 60 % of the area is covered by deciduous and mixed forests with high species richness (Angelstam and Dönz-Breuss, 2004). Wet habitats cover over 40 % of the BF area, 20 % of AF area, and only 11 % of KF area (Sokołowski, 2006). The area is located within a zone of temperate transitional climate with marked continental influences. The study area is inhabited by well-preserved communities of mammals with locally up to 12 species of carnivores (Jędrzejewska and Jędrzejewski, 1998).

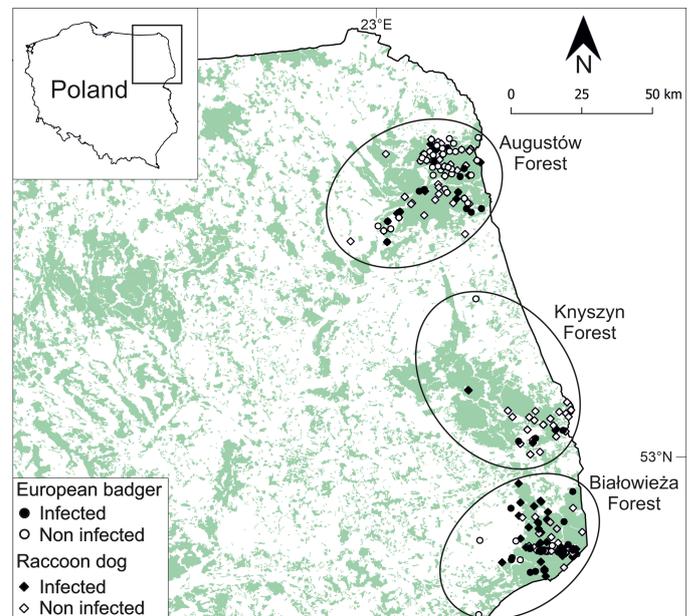


Figure 1 – The distribution of study sites and samples in the study area. Black symbols indicate European badger and raccoon dog individuals infected with *Spirometra erinaceieuropaei*, while white symbols denote non-infected individuals.

Carcasses collection

A total of 412 carcasses of raccoon dog and European badger were collected between 2013 and 2021 in BF, KF, and AF (see details in Table 1). Carcasses originated from road kills or legal culling from predator control for gallinaceous bird, i.e. the black grouse (*Lyrurus tetrix* Linnaeus, 1758) and the western capercaillie (*Tetrao urogallus* Linnaeus, 1758) conservation projects. No animals were killed specifically for this study. The collected carcasses were kept frozen at -80°C for a minimum of one week to minimize the risk of *Echinococcus multilocularis* infection (Hildreth et al., 2004). Then, the animals were necropsied, weighed, measured and sexed. Spargana were isolated from subcutaneous tissue, counted, and preserved in 99 % ethanol for molecular identification according to Kondzior et al. (2020). Prevalence was calculated as proportion of infected individuals in total number collected carcasses of a given species. The mean infection intensity in each host species was calculated as the average number of spargana per one infected individual of a particular species.

Table 1 – Number of raccoon dog and European badger carcasses collected in 2013–2021. *the sex of three raccoon dogs from BF was not determined.

Locality	Raccoon dog			European badger		
	N	Infected	Non-infected	N	Infected	Non-infected
Białowieża Forest	100*	42	55	24	13	11
Knyszyn Forest	73	36	37	4	2	2
Augustów Forest	124	62	62	87	42	45
Total	297	140	154	115	57	58

Host age analysis

The age determination of raccoon dogs and European badgers was assessed in two steps: 1) X-rays of the lower left canine to separate juveniles (<1-year), and adult individuals – the width of the pulp cavity and the tooth were measured on the X-ray plates to estimate the pulp/tooth widths ratios (P/T ratios) (Van den Broeck et al., 2022; Kauhala and Helle, 1990). Because the dentine grows inwards, gradually filling the pulp cavity, the cavity becomes smaller with age. The P/T ratios can be used to distinguish between juveniles and adults. It was assumed that all individuals with P/T ratios above 50 % are recognised as juveniles. (Knowlton and Whittemore, 2001; Kauhala and Helle, 1990)

cementum aging of animals recognised as adults based on P/T ratios. Teeth of those specimens were analysed in Matson's Laboratory (USA) – the lab specialised in animal cementum annuli aging – where age was assessed by grinding the teeth and counting the layers of annual increments of tooth cement (<https://matsonslab.com/the-science/cementum-aging/>). The age of the animals was determined taking into account estimated dates of birth: for a European badger – March 1st, for a raccoon dog – April 25th (Kowalczyk et al., 2009, unpubl. data).

Statistical analysis

We tested differences in the prevalence and infection intensity of *Spirometra erinaceieuropaei* plerocercoids between species with a binomial generalized linear model (GLM1) and a negative binomial generalized linear model (GLM2), respectively. Dependent variable in GLM1 was presence/absence of *S. erinaceieuropaei* plerocercoids in checked individuals, whilst in GLM2 it was the number of *S. erinaceieuropaei* plerocercoids per host. In both models, we set species as an explanatory categorical variable and we also accounted for individual age because European badgers were remarkably older at the time of death than raccoon dogs (median age = 0.8 year (range 0-6.5) for raccoon dog and 2.3 year (range 0-9.4) for European badger).

To model which factors affect the prevalence of *S. erinaceieuropaei* for both studies species and the infection intensity we fitted binomial generalized linear models (raccoon dog: GLM3, European badger: GLM4) and negative binomial generalized linear models (raccoon dog: GLM5, European badger: GLM6) for count data which dealt with overdispersion in considered models (Zuur et al., 2009). In GLM3 and GLM4 we set presence/absence of *S. erinaceieuropaei* plerocercoids in checked individuals as dependent variable, while in GLM5 and GLM6 it was the number of *S. erinaceieuropaei* plerocercoids per host. We used the same set of explanatory variables in each model (GLM3-GLM6): study site, percentage of wet habitats, age and sex. Percentage of wet habitats was calculated for the area limited by 2 km wide buffer around the locations where samples were collected. The area of buffer (ca. 12.6 km²) corresponded to the mean size of European badger territories in the study area (Kowalczyk and Zalewski, 2011; Kowalczyk et al., 2003). Wet habitats were indexed based on map of wetlands in Poland (Piórkowski et al., 2007). All statistical analyses were done in R (R Core Team, 2022).

Results

The prevalence of *Spirometra erinaceieuropaei* infection was 36.0% for raccoon dog and 45.2% for European badger and did not differ between the species (GLM1: estimate = 0.37 ± 0.28, $P = 0.18$; Fig. 2A). For infected animals, European badger has significantly higher infection intensity – median = 35.4 (range 1-276) spargana per host than raccoon dogs – median = 4.2 (range 1-23) spargana per host (GLM2: estimate = 1.80 ± 0.26, $P < 0.001$; Fig. 2B).

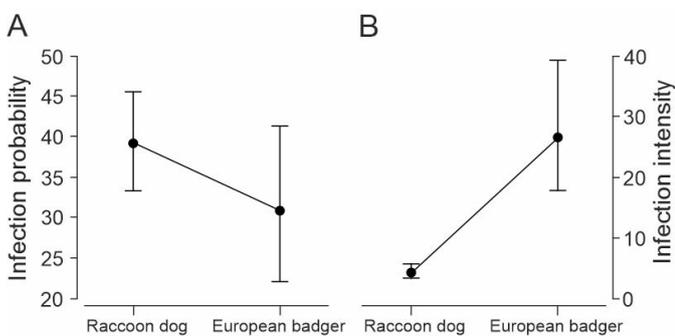


Figure 2 – Predicted probability (A) and intensity (B) of *Spirometra erinaceieuropaei* infection depending on species studied (results of GLM2 and GLM3). Infection intensity expresses the number of *Spirometra erinaceieuropaei* plerocercoids per carcass.

For both host species we found remarkable differences in *S. erinaceieuropaei* prevalence between study sites. There was significantly higher infection probability of raccoon dogs and European badgers in

BF than in AF (GLM3: $P < 0.001$ and GLM4: $P = 0.03$, respectively) and higher infection probability of raccoon dogs in BF than in KF (GLM5: $P = 0.007$; Table 2, Fig. 3A). In both host species infection probability was positively related to the proportion of wet habitats (GLM3: raccoon dog: $P = 0.007$; GLM4: European badger: $P = 0.03$). With wet habitats increasing from 0 to 60%, probability of *S. erinaceieuropaei* infection in European badger increased from 24 to 66.4%, while in raccoon dog from 18.3 to 49.7% (Fig. 3A). Infection probability decreased with time covered by the study; however, the significance of the temporal changes was confirmed only for raccoon dog (GLM3: $P < 0.001$; Fig. 3A). Infection probability in raccoon dogs dropped from 76.9% in 2013 to 1.6% in 2021. *Spirometra erinaceieuropaei* infection probability increased with the age of animals with the similar rate for both species (slope: raccoon dog - 0.0017; European badger - 0.0016). The infection probability for raccoon dog increased from 27.2% in 1-year-olds to 89.8% in 6-year-olds while for European badger it changed from 17.7% in 1-year-olds to 79.5% in 6-year-olds (Fig. 3A). In both species we did not find significant differences in infection probability between sexes.

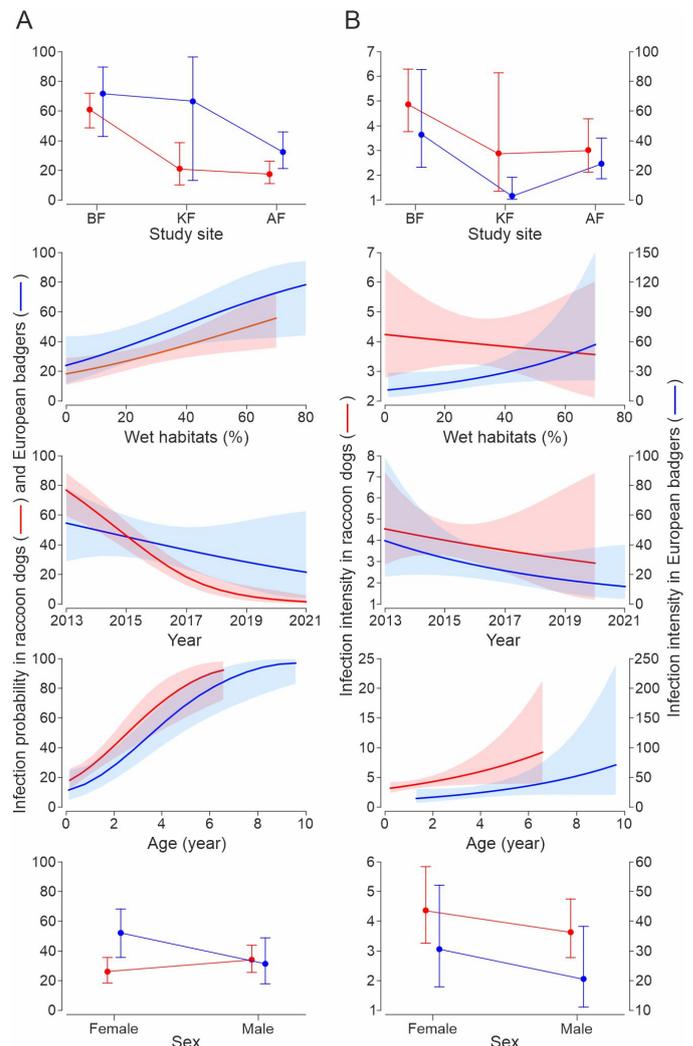


Figure 3 – The relationships between the probability (A) and intensity (B) of *Spirometra erinaceieuropaei* infection in raccoon dog and European badger and study site, percentage of wet habitats, year, individual age and sex. Results of binomial and negative binomial generalized linear models (GLM3-GLM6). Infection intensity expresses the number of *Spirometra erinaceieuropaei* plerocercoids per carcass. BF – Białowieża Forest, KF – Knyszyn Forest, AF – Augustów Forest.

The highest *S. erinaceieuropaei* infection intensity in raccoon dogs and European badgers was found for animals sampled in BF. Infection intensity of raccoon dog in BF was significantly higher than in AF (GLM5: $P = 0.03$; Fig. 3B). In European badger infection intensity in KF was significantly lower than in BF and AF (GLM6: $P = 0.002$ and $P = 0.02$, respectively; Table 2, Fig. 3B). Infection intensity sig-

Table 2 – Parameter estimates for binomial and negative binomial generalized linear models (GLM3-GLM6) describing an association between *Spirometra erinaceieuropaei* infection prevalence and intensity in raccoon dog and European badger and study site, percentage of wet habitats, year, individual age and sex. Reference levels are presented in parentheses.

Variables	Estimate	SE	z value	P value
<i>Infection prevalence</i>				
Raccoon dog				
Intercept (AF)	1346.7	269.5	5.00	<0.001
Study site				
BF (AF)	1.99	0.37	5.44	<0.001
KF (AF)	0.24	0.55	0.43	0.67
BF (KF)	1.75	0.51	3.41	0.007
Wet habitats	0.02	0.009	2.68	0.007
Year	-0.67	0.13	-5.00	<0.001
Age	0.002	0.0004	4.26	<0.001
Sex				
female (male)	0.38	0.30	1.26	0.31
European badger				
Intercept (AF)	364.5	344.5	1.06	0.29
Study site				
BF (AF)	1.65	0.70	2.36	0.02
KF (AF)	1.41	1.34	1.05	0.29
BF (KF)	0.24	1.38	0.18	0.86
Wet habitats	0.03	0.01	2.18	0.03
Year	-0.18	0.17	-1.07	0.29
Age	0.002	0.0004	4.16	<0.001
Sex				
female (male)	-0.87	0.52	-1.66	0.10
<i>Infection intensity</i>				
Raccoon dog				
Intercept (AF)	128.0	188.0	0.68	0.49
Study site				
BF (AF)	0.48	0.22	2.18	0.03
KF (AF)	-0.05	0.42	-0.10	0.92
BF (KF)	0.52	0.41	1.27	0.20
Wet habitats	-0.002	0.006	-0.40	0.69
Year	-0.06	0.09	-0.67	0.50
Age	0.0004	0.0002	2.08	0.04
Sex				
female (male)	-0.18	0.20	-0.92	0.36
European badger				
Intercept (AF)	326.4	236.3	1.38	0.17
Study site				
BF (AF)	0.59	0.45	1.30	0.19
KF (AF)	-2.17	0.90	-2.40	0.02
BF (KF)	2.75	0.88	3.14	0.002
Wet habitats	0.02	0.01	1.89	0.06
Year	-0.16	0.12	-1.37	0.17
Age	0.0005	0.0003	1.79	0.07
Sex				
female (male)	-0.39	0.42	-0.94	0.34

nificantly increased with the age of raccoon dogs (GLM5: $P = 0.04$; Fig. 3B). With an age of animals increasing from 1 to 6 years the number of *S. erinaceieuropaei* plerocercoids increased from 3.7 to 8.4 per individual. No such relationship was found in European badger.

Infection intensity in raccoon dog and European badger was not significantly related to the proportion of wet habitats, year and sex.

Discussion

Recent data on sparganosis (infection with *Spirometra* plerocercoids) and spirometrosis (infection with adult *Spirometra* tapeworms) occurrence in European wildlife came mainly from Poland, Latvia and Finland, where *S. erinaceieuropaei* was found in both paratenic and definitive hosts (mainly carnivorous mammals) (Čisovská-Bazsalovicsová et al., 2022; Bagrade et al., 2021; Kuchta et al., 2021; Kondzior et al., 2020, 2018). *Spirometra* prevalence and intensity may differ between localities and host species but the factors influencing these patterns

have been not investigated so far. It is known that there are many ecological, biological and anthropogenic factors involved in parasitism which form a complex network of interdependencies in wildlife (Kołodziej-Sobocińska, 2019; Rizzoli et al., 2019; Peacock et al., 2018; Cable et al., 2017; Stringer and Linklater, 2015; Tompkins et al., 2011). In case of *S. erinaceieuropaei* infection, we revealed that the species richness of infected carnivorous mammalian hosts from NE Poland was wider than expected (Kondzior et al., 2020).

Our previous study on multispecies reservoir of *S. erinaceieuropaei* in carnivorous mammals community revealed that raccoon dog and European badger had the highest infection parameters among all studied hosts (Kondzior et al., 2020). This may result, among others, from consumption of infected prey or food (amphibians, reptiles and carrion) (Kondzior et al., 2018; Kołodziej-Sobocińska et al., 2016). Both species differ in their food habits, with raccoon dog being more omnivorous, with a large proportion of carrion in its diet, while European

badger being mainly earthworm specialist (Jędrzejewska and Jędrzejewski, 1998). However both species feed on amphibians, which can serve as a source of *Spirometra* infection (Badri et al., 2022; Liu et al., 2015). Also wild boar, which is one of the *Spirometra* host (Kołodziej-Sobocińska et al., 2016) and is depredated by large carnivores in NE Poland (Jędrzejewska and Jędrzejewski, 1998), may play a role in parasite spread. Its carrion is highly consumed by raccoon dogs (Jędrzejewska and Jędrzejewski, 1998).

Both host species had quite similar prevalence of *S. erinaceiropaei* infection; however, intensity was over eight times higher in European badgers. It can be related to the higher longevity of European badgers and gathering parasites in tissue in multiple infections over life. The second factor influencing this can be geographical origin of *Spirometra* tapeworms and raccoon dogs. European badger may be related to much shorter co-evolution of this species with the parasite. Genetic analysis revealed that the Polish clade of *S. erinaceiropaei* arose approximately 242 kya (kiloyears ago), while Chinese clade is much older, dated to approximately 2,693 kya (Kołodziej-Sobocińska et al., 2019). Demographic expansion of Polish clade of *S. erinaceiropaei* started approximately 12.5 kya, so at the end of the glaciation. Raccoon dog originating from Far East and introduced to Europe during the first half of the 20th century (Kauhala and Kowalczyk, 2011), may have much longer period of co-evolution with the parasite than European badger. The evidence of evolution on the sides of both the host and the parasite, with potential reciprocal co-evolution between host resistance and parasite infectivity/virulence has been proved (Webster et al., 2004). Increased host resistance promotes increased parasite infectivity, while virulence increases the selection for host resistance except where tolerance is an alternative host response. Variability in this phenomenon was demonstrated to be maintained through cost-benefit trade-offs at all stages (Webster et al., 2004). Long-term host-parasite co-evolution may lead to a relatively stable relationship tending towards commensalism or mutualism and the establishment of parasite-host balance, as it is in the evolutionary interest of the parasite that its host thrives (Rook, 2007). This phenomenon is probably observed in raccoon dog having much longer period of co-evolution with the parasite than European badger and – as a result – lower numbers of spargana.

In presented study we checked whether the proportion of wet habitats also increases the likelihood of infection with *S. erinaceiropaei*, because life cycle of this tapeworm is dependent on water and wet habitats – freshwater copepods serve as intermediate hosts in which the 1st stage larvae – procercooids develop. Also amphibians, which may play a role in *Spirometra* transmission, are more abundant in wet habitats (Pikulik et al., 2001). Indeed, in both hosts we observed higher infection prevalence for areas with larger share of wet habitats. Such association was also found in helminths infecting rodents (Pakdeenarong et al., 2014) or monkey (Chapman et al., 2010). Other reason for higher infection parameters in more wet conditions is that water sources that are foci of animal activity have great potential to promote disease transmission, because water resources can aggregate many different hosts in small areas, concentrate infectious material, and function as disease hotspots (Titcomb et al., 2021). Of all the study sites, BF has the highest proportion of wet habitats (approx. 40%) (Sokołowski, 2006) and for this study site we found both the highest proportion of infected raccoon dogs and European badgers and the highest infection intensity. In KF, European badgers had the lowest infection rate what may be explained by the low diversification of habitats and the smallest proportion of wetlands compared to other study sites (Sokołowski, 2006; Angelstam and Dönz-Breuss, 2004).

We found also that infection prevalence decreased in subsequent years of the study (between 2013 and 2021) what coincided with strong decline of wild boar numbers due to the African Swine Fever (ASF) epidemic (Frant et al., 2022; Morelle et al., 2020). The most significant decline in probability of *S. erinaceiropaei* infection in raccoon dog was observed for years (2017-2019) when the percentage of ASF-positive wild boars reached its maximum (Frant et al., 2022). In European badger this tendency was not so clear. Unlike raccoon dog

for which the occurrence of wild boar carcass in diet in BF was up to 37.4% in autumn-winter period, wild boar carcasses in European badger diet in BF accounted for only approx. 1% of occurrence (Goszczyński et al., 2000; Jędrzejewska and Jędrzejewski, 1998).

Previous studies have demonstrated that the age of hosts modulates parasite infectivity, virulence and reproduction as well as within-host parasite competition (Izhar and Ben-Ami, 2015; Izhar et al., 2015). Although studies on wild mammals are scarce, Bellay et al. (2020) revealed that host age is a major driver of the intestinal helminth parasites occurrence and their species richness in long-finned pilot whales (*Globicephala melas*). We also observed that older animals – both raccoon dogs and European badgers were more likely to be infected with *S. erinaceiropaei* larvae than younger ones. This may reflect a lifelong parasite accumulation in older host individuals (Balbuena and Raga, 1993). We detected significantly higher number of spargana in European badger than in raccoon dog what may be due the longer lifespan of European badger – up to 10 years in our study – in comparison to 6 years for raccoon dogs; however, majority of individuals (80.5%) were less than two years old. But when we corrected for the age of animals, the difference between species was still highly significant, which indicate much higher susceptibility of European badgers as discussed above.

Hosts during their life are also more likely to get infected but there is known that adult parasites may be removed from alimentary tract of their definitive hosts by consuming medicinal plants to self-medicate (de Roode et al., 2013; Lefèvre et al., 2010; Allonby and Urquhart, 1973). The plant-eating behaviour in obligate carnivores, such as Felidae is one of the mysteries (Yoshimura et al., 2021) but for Canidae it is known that consumption of grasses is considered to work as scouring agent against intestinal parasites such as roundworms and tapeworms (Bosch et al., 2015). In our study we focused on two paratenic (not definitive) hosts in which plerocercoid larvae settle in tissue. Parasite larvae can persist for years in the tissues of these hosts, “waiting” for a given individual to be eaten by carnivore or scavenger. In this situation, zoopharmacognosy and self-medication has no effect, because they play role only in digestive tract but they do not influence larvae in the tissues. Thus, they cannot be excreted from the host body like intestinal parasites.

We did not observe differences in infection prevalence and intensity of *S. erinaceiropaei* between sexes in both studied hosts. More frequent occurrence of parasites in male hosts compared with females is known as “male-biased parasitism” and is a common phenomenon in vertebrate-parasite systems (Gear et al., 2009). It is explained – among others – by the Immunocompetence Handicap Hypothesis, which suggests an immunosuppressive effect of testosterone that increases susceptibility to infection (Folstad and Karter, 1992). However, male-biased infection is not universal (Kiffner et al., 2013; Fuxjager et al., 2011). The lack of sex-specific differences may stem from the complexity of routes of sparganosis transmission in nature.

To conclude, our study revealed a network of independencies influencing *S. erinaceiropaei* infection in two host species – the raccoon dog and the European badger, with environmental (habitat structure, carrion availability) and biological (host species and age) factors involved. It also shows that spread and dynamic of the parasite species with a complex life cycle, that include wide range of groups of organisms serving as hosts, and number of non-specific hosts differing in their susceptibility to parasite, may vary locally and temporarily in response to changing conditions and factors. Our knowledge on *Spirometra* tapeworms and the disease – sparganosis is still limited and require studies in various environmental conditions and animal communities to discover more uniform patterns responsible for the distribution of this still neglected parasitic disease. ☞

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