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Evidence of predation pressure on sensitive species by raccoons based on parasitological studies

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ABSTRACT

To demonstrate predation and potential impacts of raccoons on various species, a total of 108 raccoons from aquatic-associated nature reserves and natural areas in three federal states of Germany, Hesse (n = 36), Saxony-Anhalt (n = 36) and Brandenburg (n = 36), were investigated from a dietary ecological perspective in the present study. Fecal analyses and stomach content examinations were conducted for this purpose. Additionally, as a supplementary method for analyzing the dietary spectrum of raccoons, the parasite fauna was considered, as metazoan parasites, in particular, can serve as indicators for the species and origin of food organisms. While stomach content analyses allow for a detailed recording of trophic relationships solely at the time of sampling, parasitological examinations enable inferences about more distant interaction processes. With their different developmental stages and heteroxenous life cycles involving specific, sometimes obligate, intermediate hosts, they utilize the food web to reach their definitive host. The results of this study clearly demonstrate that spawning areas of amphibians and reptiles were predominantly utilized as food resources by raccoons in the study areas. Thus, common toad (*Bufo bufo*), common newt (*Lissotriton vulgaris*), grass frog (*Rana temporaria*), and grass snake (*Natrix natrix*) were identified as food organisms for raccoons. The detection of the parasite species *Euryhelmis squamula*, *Isthmiophora melis*, and *Physocephalus sexalatus* with partially high infestation rates also suggests that both amphibians and reptiles belong to the established dietary components of raccoons from an ecological perspective, as amphibians and reptiles are obligate intermediate hosts in the respective parasitic life cycles of the detected parasites. The study clearly demonstrates that raccoons have a significant impact on occurrence-sensitive animal species in certain areas and, as an invasive species, can exert a negative influence on native species and ecosystems.

1. Introduction

Invasive carnivorous mammals are suspected to have a significant impact on various native species such as birds, amphibians, and reptiles. In the context of scientific research on conservation-relevant, ecosystemic impacts by non-native carnivores, the invasive raccoon (*Procyon lotor*) is particularly under scrutiny in Europe (Beasley and Rhodes, 2008; Doherty et al., 2016; Mollot et al., 2017; Nehring, 2018; Demeny et al., 2019; Oe et al., 2020; Cichocki et al., 2021). However, there are also divergent studies that do not demonstrate or show a direct influence on a habitat or organisms, and that no ecosystemic impacts by raccoons are detectable (Lutz, 1995; Hohmann, 2000; Michler, 2017). This seems to depend particularly on the respective ecosystem composition and the available food resources (Stubbe and Krapp, 1993; Hohmann and Bartussek, 2018; Nehring, 2018). The strong population increase of raccoons and their ongoing spread (e.g. Cunze et al., 2023) especially in protected natural areas, increase the predation risk for occurrence-sensitive animal species. Due to the raccoon's high dispersal ability and its dietary ecology, which allows it to inhabit nearly all natural habitats, it is suspected to be responsible for the regional decline of numerous native species.

Raccoons generally exhibit an opportunistic, omnivorous, and

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seasonally varied dietary spectrum (Stubbe and Krapp, 1993; Lutz, 1996; Michler, 2017; Hohmann and Bartussek, 2018). According to Nehring (2018), there is a significant predation pressure when raccoons occur in high densities or when prey items are concentrated in space and time, as often observed in small aquatic-associated habitats. Various studies highlight the substantial alterations in species communities and ecosystems caused by invasive alien species (IAS) as one of the most significant threats to global biodiversity, generating substantial economic costs (Clavero et al., 2009; Dueñas et al., 2018, 2021; Falaschi et al., 2020; Haubrock et al., 2021; Roy et al., 2023). In most cases, food resources are utilized based on abundance or ease of accessibility.

Considering the omnivorous and seasonally dependent feeding habits of raccoons, it is thus logical to perceive raccoons as a potential threat to native biodiversity (Beasley and Rhodes, 2008; Doherty et al., 2016; Mollot et al., 2017; Nehring, 2018; Demeny et al., 2019; Oe et al., 2020; Cichocki et al., 2021). In addition to stomach content analyses, specific investigations of the metazoan parasite fauna of raccoons can provide important insights into their dietary ecology. A clear understanding of the parasite fauna is essential for analyzing the dietary spectrum of raccoons, as parasites can serve as bioindicators for the species and origin of food organisms (e.g. Kleinertz et al., 2012; Klimpel et al., 2019). While stomach content analyses allow for a detailed recording of trophic relationships solely at the time of sampling, parasitological examinations enable inferences about more distant interaction processes and thus integrate beyond short-term variability in the food web. Helminths (including Digenea, Cestoda, Nematoda) are particularly suitable for such investigations due to their different developmental stages and heteroxenous life cycles with specific, sometimes obligate intermediate hosts (Schnieder et al., 2006; Lucius et al., 2018), utilizing the food web to reach their definitive hosts.

The aim of the present study was to describe the dietary ecology and metazoan parasite fauna of raccoons from aquatic-associated nature reserves and natural areas. Detailed stomach content analyses and the assessment of parasites as bioindicators aimed to provide insights into the dietary spectrum and preferences of the examined raccoons.

2. Material and methods

The study areas consisted of geographically distant, aquatic-associated habitat types. In Northern Germany, the federal state of Brandenburg (BB) was selected, including the UNESCO Biosphere Reserve “Elbe River Landscape.” In Central Germany, the federal state of Hesse (HE) was chosen, encompassing nature reserves in the Spessart and Wetterau regions, as well as aquatic-associated habitats in Saxony-Anhalt (ST) (Fig. 1). Between March 2020 and August 2022, 108 free-ranging raccoons (*Procyon lotor*) were captured in the federal states of Hesse (N = 36), Brandenburg (N = 36), and Saxony-Anhalt (N = 36) as part of regular hunting activities by licensed hunters using legally compliant wooden box traps. Sampling was conducted in accordance with applicable legal regulations. An exemption permit for suspending the closed season was obtained for the state of Hesse, while raccoons can be hunted year-round in Brandenburg and Saxony-Anhalt. The capture locations of the animals were recorded by hunters using GPS coordinates. Captured animals were assigned a defined sample identification number. Metadata such as capture date, location, etc., were documented in an accompanying document. Samples were frozen at minus 20 °C in stable PE bags along with the accompanying sheet until further analysis.

2.1. Recording of morphometric data, stomach contents, parasitological examinations and map display

The preparation of raccoons, morphometric measurements, and preservation of metazoan parasites were conducted following the methods outlined by Peter et al. (2023). Parasitological parameters including prevalence, mean intensity, intensity, and abundance adhere to the definitions provided by Klimpel et al. (2019). Sample map was created in Esri ArcGIS (Version 10.8.1) (Fig. 1).

2.2. Food analysis

Stomach and intestinal contents were analyzed following the methods outlined by Klimpel et al. (2019). Under a binocular microscope, stomach and intestinal contents were sorted in a 200 mm Petri dish to the smallest possible taxonomic level, and individuals of each food class were counted. Food categories were dried, blotted, and weighed. Subsamples for genetic analysis were transferred to 100% ethanol. Intestinal contents were sieved using an analysis sieve (ISO 3310–1) and water, and analyzed similarly to stomach content examinations. To quantitatively assess individual food resources, Frequency of Occurrence [F%] and Weight Percentage of Prey [W%] were calculated following the methods of Klimpel et al. (2019). Plant food components were morphologically assigned; however, genetic testing was not performed in this regard.

2.3. Species identification

Clearly identifiable fragments of insects and amphibian species were determined based on morphological characteristics (Kerney et al., 1983; Engelmann et al., 1986; Sedlag, 1986; Chinery, 1993; Schaefer et al., 1994; HMUKLV, 2015). Literature for the identification of parasites included original descriptions and identification keys (Janicki, 1904; Neumann and Mayer, 1914; Baer, 1932; Peus, 1938; Dawes, 1968; Sprent, 1968; Páv et al., 1972; Zajícek and Páv, 1972; Priemer and Lux, 1994; Anderson, 2000; Chowdhury, 2001; Beck, 2007; Brinck-Lindroth and Smit, 2007; Anderson et al., 2009; Heneberg et al., 2016; Doanh et al., 2023). PCR amplification and sequencing followed the methods outlined by Peter et al. (2023). Primers and thermocycler settings for the PCR reactions were systematically selected based on food groups and parasitic organisms, and carried out following modified established protocols (Table 1) (Folmer et al., 1994; Tkach et al., 2003; Hebert et al., 2004; Jones et al., 2008; Pun et al., 2009; Laurimaa et al., 2016; Nugaraitė et al., 2017). The sequenced data of the genetically analyzed samples were uploaded to the NCBI Sequence Read Archive (SRA) and are available under the accession numbers given in Table 1.

3. Results

3.1. Morphometric data, ecto- and endoparasite fauna

Out of the total of 108 examined raccoons, 42 individuals were female and 66 were male. The detailed morphometric data was collected during necropsy but is not further discussed as no significant association with parasite infestation could be established. The parasite fauna of the examined raccoons consisted of 16 different ecto- and endoparasite species (Table 2). The three parasite species *Hymenolepis erinacei*, *Physocephalus sexalatus*, and *Pomphorhynchus laevis* were documented for the first time in raccoons in Europe.

Parasite fauna of Hesse (Table 2): In the study area, the key species in the group of ectoparasites were *Trichodectes octomaculatus* with a prevalence of 86.1% (with a mean intensity of mI = 40.87), the tick species *Ixodes hexagonus* with a prevalence of 41.7% (mI = 7.07), and *I. ricinus* with a prevalence of 52.8% (mI = 4.95). Additionally, the flea species *Paraceras melis* (P = 19.4%, mI = 1.29) was detected. Key species of endoparasites were the nematode species *Baylisascaris procyonis* with a prevalence of 91.7% (mI = 15.73) and the cestode species *Atriotaenia incisa* with a prevalence of 33.3% (mI = 28.5). Other endoparasitic species identified in this study for Hessen were the nematode species *Physocephalus sexalatus* (Fig. 2H) (P = 13.9%, mI = 27.6) and *Porrocaecum ensicaudatum* (P = 13.9%, mI = 7.0), the digenetic trematode *Brachylaima mesostoma* (Fig. 2C) (P = 8.3%, mI = 11.3), *Euryhelmis squamula* (P = 5.6%, mI = 44.5), as well as the acanthocephalan species

Fig. 1. Geographic origin of examined *Procyon lotor* (total N = 108 raccoons).

Table 1
Overview of used primers, methods and results of genetically species identification including literature sources.

Group	Accession number	Species	Primer name/Sequence	Thermocycling	Query Cover [%]	Per. Ident. [%]	Query Length	Sources
Amphibia	SAMN38446839	***Rana temporaria***	**LepF1** GTA AAA CGA CGG CCA GTA TTC AAC CAA TCA TAA AGA TAT TGG **LepR1** AGG AAA CAG CTA TGA CTA AAC TTC TGG ATG TCC AAA AAA TCA	60s at 94 °C, 5 x (60s at 94 °C, 120s at 45 °C 120s at 72 °C), 30 x (60s at 4 °C, 120s at 51 °C, 120s at 72 °C) 5 min at 72 °C	98	99.38	650	Hebert et al. (2004)
	SAMN38446840	***Bufo bufo***	**16SA-L** CGC CTG TTT ATC AAA AAC AT **16SB-H** CCG GTC TGA ACT CAG ATC ACG T	3 min at 95 °C, 40 x (10s at 95 °C, 45s at 60 °C), 10min at 60 °C	99	100	545	modified Pun et al. (2009)
Reptilia	SAMN38446841	***Natrix natrix***	**UKsnakecyto_F** CAA CAT CAA CTT AGC CTT CTC **UKsnakecyto_R** GTG GAA TGG GAT TTT ATC G	4 min at 96 °C, 35 x (60s at 94 °C, 60s at 50 °C,120s at 72 °C), 3min at 72 °C	99	99.77	443	Jones et al. (2008)
Pisces	SAMN38446842	***Oncorhynchus mykiss***	**16SA-L** CGC CTG TTT ATC AAA AAC AT **16SB-H** CCG GTC TGA ACT CAG ATC ACG T	3 min at 95 °C, 40 x (10s at 95 °C, 45s at 60 °C), 10min at 60 °C	98	100	567	modified Pun et al. (2009)
Aves	SAMN38446843	***Gallus gallus***	**BirdF1** TTC TCC AAC CAC AAA GAC ATT GGC AC **BirdR1** ACG TGG GAG ATA ATT CCA AAT CCT G	3 min at 95 °C, 40 x (10s at 95 °C, 45s at 60 °C), 10min at 60 °C	100	95.77	449	modified Pun et al. (2009)
	SAMN38446844	***Sturnus vulgaris***	**AvianCytbF** CCC TCA GAA TGA TAT TTG TCC TCA **AvianCytbR** CCT CAG AAK GAT ATY TGN CCT CAK GG	3 min at 95 °C, 40 x (10s at 95 °C, 45s at 60 °C), 10min at 60 °C	97	98.71	477	modified Pun et al. (2009)
	SAMN38446845	***Turdus philomelos***	**BirdF1** TTC TCC AAC CAC AAA GAC ATT GGC AC **BirdR1** ACG TGG GAG ATA ATT CCA AAT CCT G	3 min at 95 °C, 40 x (10s at 95 °C, 45s at 60 °C), 10min at 60 °C	98	99.19	632	modified Pun et al. (2009)
	SAMN38446846	***Columba palumbus***	**BirdF1** TTC TCC AAC CAC AAA GAC ATT GGC AC **BirdR1** ACG TGG GAG ATA ATT CCA AAT CCT G	3 min at 95 °C, 40 x (10s at 95 °C, 45s at 60 °C), 10min at 60 °C	99	99.57	701	modified Pun et al. (2009)
	SAMN38446847	***Cyanistes caeruleus***	**BirdF1** TTC TCC AAC CAC AAA GAC ATT GGC AC **BirdR1** ACG TGG GAG ATA ATT CCA AAT CCT G	3 min at 95 °C, 40 x (10s at 95 °C, 45s at 60 °C), 10min at 60 °C	96	99.67	629	modified Pun et al. (2009)
	SAMN38446848	***Pica pica***	**BirdF1** TTC TCC AAC CAC AAA GAC ATT GGC AC **BirdR1** ACG TGG GAG ATA ATT CCA AAT CCT G	3 min at 95 °C, 40 x (10s at 95 °C, 45s at 60 °C), 10min at 60 °C	99	98.77	574	modified Pun et al. (2009)
Mammalia	SAMN38446849	***Microtus arvalis***	**16SA-L** CGC CTG TTT ATC AAA AAC AT **16SB-H** CCG GTC TGA ACT CAG ATC ACG T	3 min at 95 °C, 40 x (10s at 95 °C, 45s at 60 °C), 10min at 60 °C	99	98.84	520	modified Pun et al. (2009)
	SAMN38446850	***Oryctolagus cuniculus***	**16SA-L** CGC CTG TTT ATC AAA AAC AT **16SB-H** CCG GTC TGA ACT CAG ATC ACG T	3 min at 95 °C, 40 x (10s at 95 °C, 45s at 60 °C), 10min at 60 °C	100	99.39	490	modified Pun et al. (2009)
Gastropoda	SAMN38446851	***Arianta arbustorum***	**16SA-L** CGC CTG TTT ATC AAA AAC AT **16SB-H** CCG GTC TGA ACT CAG ATC ACG T	3 min at 95 °C, 40 x (10s at 95 °C, 45s at 60 °C), 10min at 60 °C	100	96.78	342	modified Pun et al. (2009)
	SAMN38446852	***Helix pomatia***	**LCO1490** GGT CAA CAA ATC ATA AAG ATA TTG G **HCO 2198** ACT AAA AAA CCA GTG GGA CTT CAA AT	120s at 95 °C; 35x (60s at 95 °C, 60s at 40 °C, 90s at 72 °C); 420s at 72 °C	98	94.35	556	Folmer et al. (1994)

(*continued on next page*)

Table 1 (*continued*)

Group	Accession number	Species	Primer name/Sequence	Thermocycling	Query Cover [%]	Per. Ident. [%]	Query Length	Sources
	SAMN38446853	***Monachoides incarnatus***	**LepF1** GTA AAA CGA CGG CCA GTA TTC AAC CAA TCA TAA AGA TAT TGG **LepR1** AGG AAA CAG CTA TGA CTA AAC TTC TGG ATG TCC AAA AAA TCA	60s at 94 °C, 5 x (60s at 94 °C, 120s at 45 °C, 120s at 72 °C), 30 x (60s at 4 °C, 120s at 51 °C, 120s at 72 °C), 5 min at 72 °C	95	99.51	645	Hebert et al. (2004)
	SAMN38446854	***Planorbarius corneus***	**16SA-L** CGC CTG TTT ATC AAA AAC AT **16SB-H** CCG GTC TGA ACT CAG ATC ACG T	3 min at 95 °C, 40 x (10s at 95 °C, 45s at 60 °C), 10min at 60 °C	77	97.37	541	modified Pun et al. (2009)
Insecta	SAMN38446855	***Eristalis pertinax***	**16SA-L** CGC CTG TTT ATC AAA AAC AT **16SB-H** CCG GTC TGA ACT CAG ATC ACG T	3 min at 95 °C, 40 x (10s at 95 °C, 45s at 60 °C), 10min at 60 °C	98	99.59	492	modified Pun et al. (2009)
	SAMN38446856	***Melolontha melolontha***	**C1-J-2441** CCA ACAGGA ATT AAA ATT TTT AGATGA TTA GC **TL2-N-3014** TCCAAT GCA CTA GCC AGA ATC TGC CAT ATT A	3 min at 95 °C, 40 x (10s at 95 °C, 45s at 60 °C), 10min at 60 °C	96	100	579	modified Pun et al. (2009)
	SAMN38446857	***Ocypus olens***	**C1-J-2441** CCA ACAGGA ATT AAA ATT TTT AGATGA TTA GC **TL2-N-3014** TCCAAT GCA CTA GCC AGA ATC TGC CAT ATT A	3 min at 95 °C, 40 x (10s at 95 °C, 45s at 60 °C), 10min at 60 °C	98	97.86	568	modified Pun et al. (2009)
	SAMN38446858	***Phosphuga atrata***	**C1-J-2441** CCA ACAGGA ATT AAA ATT TTT AGATGA TTA GC **TL2-N-3014** TCC AAT GCA CTA GCC AGA ATC TGC CAT ATT A	3 min at 95 °C, 40 x (10s at 95 °C, 45s at 60 °C), 10min at 60 °C	98	99.47	574	modified Pun et al. (2009)
Cestoda	SAMN38446859	***Hymenolepididae* spp**	**ZX-1** ACC CGC TGA ATT TAA GCA TAT **1500R** GCT ATC CTG AGG GAA ACT TCG	3 min at 96 °C; 38 x (40 s at 94 °C, 40 s at 43 °C, 1 min 17 s at 72 °C) 10 min at 72 °C.	100	99.05	1156	Binkiene et al. (2019)
Digenea	SAMN38446860	***Euryhelmis squamula***	**WormA** GCG AAT GGC TCA TTA AAT CAG **WormB** CTT GTT ACG ACT TTT ACT TCC	180s at 94 °C; 40x (30s at 94 °C, 30s at 56 °C, 120s at 72 °C); 420s at 72 °C	99	98.52	1137	Nugaraitė et al. (2017)
	SAMN38446861	***Isthmiophora melis***	**Brachylaima1F** AAG CAT ATC ACT AAG CGG **Brachylaima1R** GCT ATC CTG AGG GAA ACT TCG	98 °C for 10 s, 40x (50 °C for 20 s, 68 °C for 90 s, 60s at 72 °C)	100	99.64	1125	Tkach et al. (2003)
Acanthocephala	SAMN38446862	***Pomphorhynchus laevis***	**LCO1490** GGT CAA CAA ATC ATA AAG ATA TTG G **HCO 2198** ACT AAA AAA CCA GTG GGA CTT CAA AT	120s at 95 °C; 35x (60s at 95 °C, 60s at 40 °C, 90s at 72 °C); 420s at 72 °C	99	99.49	589	Folmer et al. (1994)

Polymorphus minutus (Fig. 2E and F) (P = 8.3%, mI = 96.67) and *Pomphorhynchus laevis* (P = 2.8%, mI = 112.0).

Parasite fauna of Saxony-Anhalt (Table 2): In the study area, within the group of ectoparasites, *Trichodectes octomaculatus* was detected with a prevalence of 63.9% (mI = 27.65), the tick species *Ixodes ricinus* with a prevalence of 41.7% (mI = 3.0), and *Dermacentor reticulatus* (P = 19.4%, mI = 6.43). Additionally, the flea species *Paraceras melis* was determined with a prevalence of 11.1% (mI = 1.0). Key species of endoparasites were the cestode species *Atriotaenia incisa* with a prevalence of 22.2% (mI = 24.88), the nematode species *Baylisascaris procyonis* (P = 88.9%, mI = 27.81), and the digenetic trematode species *Isthmiophora melis* (Fig. 2A and B) with a prevalence of 19.4% (mI = 83.57). The nematode species *Porrocaecum ensicaudatum* (P = 16.7%, mI = 8.0), and the acanthocephalan species *Polymorphus minutus* (P = 8.3%, mI = 7.67) and *Echinorhynchus truttae* (Fig. 2D) (P = 11.1%, mI = 2.25) were also identified.

Parasite fauna of Brandenburg (Table 2): In the study area, within the group of ectoparasites, *Trichodectes octomaculatus* was detected with a prevalence of 44.4% (mI = 15.75), the tick species *Ixodes ricinus* with a prevalence of 27.8% (mI = 3.3), and *Dermacentor reticulatus* (P = 2.8%, mI = 1.0). No flea species were detected. Key species of endoparasites were the cestode species *Atriotaenia incisa* with a prevalence of 41.7% (mI = 112.2) and the digenetic trematode species *Isthmiophora melis* with a prevalence of 30.6% (mI = 96.82). Additionally, the nematode species *Porrocaecum ensicaudatum* (P = 27.8%, mI = 6.3), *Baylisascaris procyonis* (P = 19.4%, mI = 10.57), the digenetic trematode species *Brachylaima mesostoma* (P = 8.3%, mI = 3.67), and the cestode species *Hymenolepis erinacei* (Fig. 2G) (P = 2.8%, mI = 2.0) were identified.

Table 2
Parasitological data of *Procyon lotor* (total N = 108 raccoons, N = number of infected host animals, P = prevalence of infection, I = intensity of infection, mI = mean intensity of infection, A - abundance over all examined animals.

				Hesse					Saxony-Anhalt					Brandenburg				
				N	P (%)	I	mI	A	N	P (%)	I	mI	A	N	P (%)	I	mI	A
Hesse	Ectoparasites	Insecta	*Paraceras melis*	7	19.4	1–2	1.29	0.25	4	11.1	1	1.00	0.11	–				
			Trichodectes octomaculatus	31	86.1	1–223	40.87	35.19	23	63.9	1–185	27.65	17.67	16	44.4	1–80	15.75	7.00
		Arachnida	*Ixodes ricinus*	19	52.8	1–5	4.95	2.61	15	41.7	1–5	3.00	1.25	10	27.8	1–8	3.30	0.92
			Ixodes hexagonus	15	41.7	1–20	7.07	2.94	–					–				
			Dermacentor reticulatus	–					7	19.4	1–27	6.43	1.25	1	2.8	1	1.00	0.03
	Endoparasites	Digenea	*Isthmiophora melis*[a]	–					7	19.4	2–383	83.57	16.25	11	30.6	1–566	96.82	29.58
			Brachylaima mesostoma	3	8.3	2–26	11.33	0.94	–					3	8.3	2–6	3.67	0.31
			Euryhelmis squamula	2	5.6	11–78	44.50	2.47	–					–				
		Cestoda	*Hymenolepis erinacei*[a]	–					–					1	2.8	2	2.00	0.06
			Atriotaenia incisa	12	33.3	1–92	28.50	9.50	8	22.2	2–92	24.88	5.53	15	41.7	1–576	112.20	46.75
		Nematoda	*Baylisascaris procyonis*	33	91.7	1–128	15.73	14.42	32	88.9	1–174	27.81	24.72	7	19.4	1–51	10.57	2.06
			Porrocaecum ensicauadatum	5	13.9	4–5	7.00	0.97	6	16.7	1–26	8.00	1.33	10	27.8	1–31	6.30	1.75
			Physocephalus sexalatus[a]	5	13.9	2–88	27.60	3.83	–					–				
		Acanthocephala	*Polymorphus minutus*	3	8.3	3–269	96.67	8.06	3	8.3	4–11	7.67	0.64	–				
			Pomphorhynchus laevis[a]	1	2.8	112	112.00	3.11	–					–				
			Echinorhynchus truttae	–					4	11.1	1–2	2.25	0.25	–				

N (raccoons per state):36.
[a] New for Raccoons in Europe.

The identified parasite species *I. melis* (BB, ST), *H. erinacei* (BB), *P. sexalatus* (HE), and *P. laevis* (HE) were documented for the first time in Europe for raccoons in this study.

3.2. Stomach contents

Morphological and genetic stomach content analyses revealed a diverse food composition in the study areas with a significant predation on amphibians and reptiles (Table 1).

Stomach contents Hessen (Fig. 3, Table 3): In the study area, the amphibian species grass frog (*Rana temporaria*), common toad (*Bufo bufo*), and the reptile species grass snake (*Natrix natrix*) were genetically and morphologically identified. Rainbow trout (*Oncorhynchus mykiss*) was determined as a fish species, and the bird species common starling (*Sturnus vulgaris*), common magpie (*Pica pica*), song thrush (*Turdus philomelos*), Eurasian blue tit (*Cyanistes caeruleus*), and chicken (*Gallus gallus*) were unequivocally determined. Genetic identification of insects was conducted for cockchafer (*Melolontha melolontha*), carrion beetle (*Phosphuga atrata*) and for mammals for European rabbit (*Oryctolagus cuniculus*). Gastropoda species Roman snail (*Helix pomatia*) and *Monachoides incarnatus* were identified. Morphologically, the yellow-bellied toad (*Bombina variegata*) and common newt (*Lissotriton vulgaris*) were determined for amphibians. Carabid beetles of the genus *Carabus*, dung beetles of the genus *Geotrupes*, and gastropods of the genera *Cepaea* and *Lymnaea* were identified among insects. Fragments of a thoracic bone from the family Astacidae were determined as well as specimens of *Gammarus* spp.

Stomach contents Saxony-Anhalt (Fig. 3, Table 3): Genetic evidence was obtained for the bird species common wood pigeon (*Columba palumbus*) and the insect species carrion beetle (*Phosphuga atrata*) and devil's coach-horse beetle (*Ocypus olens*) in the study area. Carabid beetles of the genus *Carabus*, dung beetles of the genus *Geotrupes*, and gastropods of the genera *Cepaea* and *Lymnaea* were identified. Mussel species of the genus *Dreissena* were morphologically determined.

Stomach contents Brandenburg (Fig. 3, Table 3): Genetic evidence for amphibian species grass frog (*Rana temporaria*) and common toad (*Bufo bufo*), bird species common starling (*Sturnus vulgaris*), and mammal species common vole (*Microtus arvalis*) was obtained in the study area. The insect species tapered drone fly (*Eristalis pertinax*) and the gastropod species copse snail (*Arianta arbustorum*) and great ramshorn (*Planorbarius corneus*) were genetically identified. Morphologically, the great diving beetle (*Dytiscus marginalis*), gastropod species of the genera *Cepaea* and *Lymnaea*, and carabid beetles of the genus *Carabus* and dung beetles of the genus *Geotrupes* were also identified as components of the diet. Fragments of a thoracic bone from the family Astacidae were also determined.

The measured and calculated values of the food components are listed in Table 3.

4. Discussion

4.1. Food composition and population threat from raccoons

The decline of endangered species is multifactorial and needs to be assessed in relation to anthropogenically influenced habitat quality, occurring pathogens, and predation pressure (e.g., Díaz et al., 2019; Leclère et al., 2020; Pyšek et al., 2020). In anthropogenically shaped landscapes, targeted predation of sensitive species by non-native carnivores adds another factor, which can lead to severe consequences and local extinctions for local populations of endangered species (Ellis et al., 2007; Nehring, 2018; Oe et al., 2020). In this context, amphibians are among the most threatened vertebrate classes (Stuart et al., 2004; González-Del-Pliego et al., 2019; Akçakaya et al., 2023) and represent a particularly complex challenge for conservation due to various reasons. Conservation measures for amphibians often focus on preserving populations in remaining and often genetically isolated habitats. However,

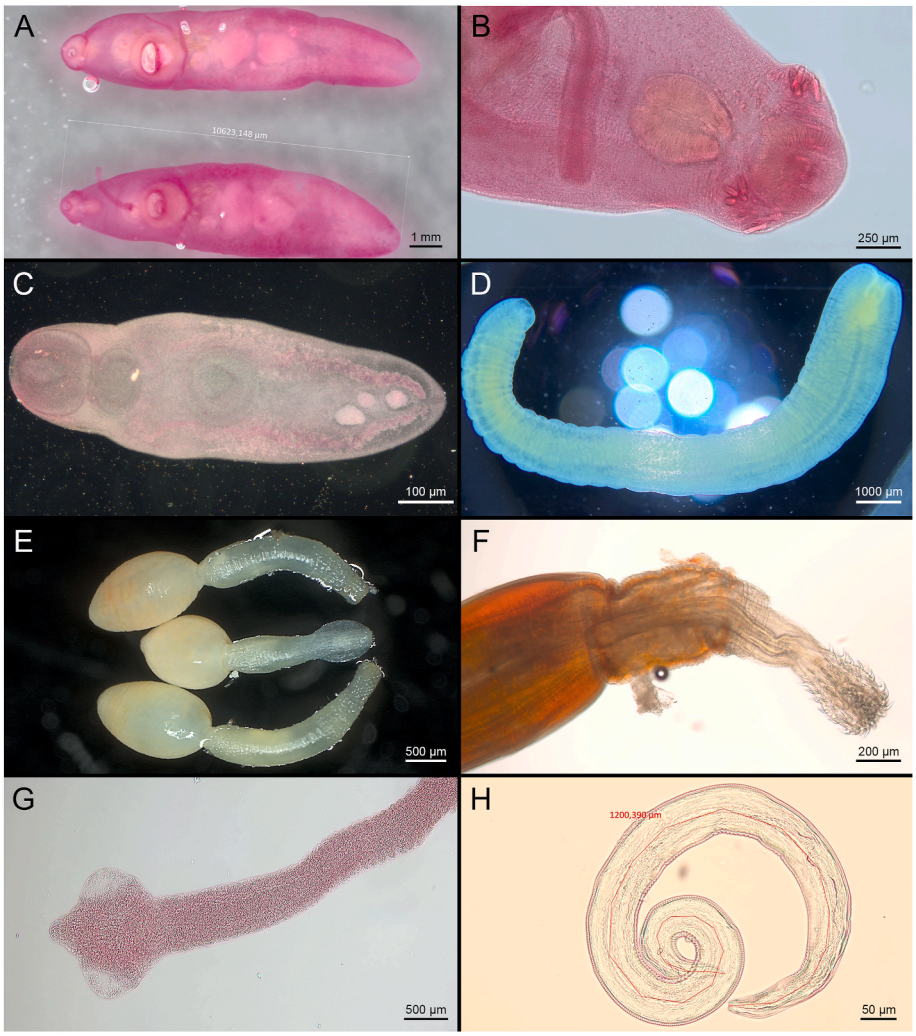

Fig. 2. Light micrographs of different endoparasite species showing the general morphology of the identified parasites in the investigated raccoons; A/B: *Isthmiophora melis;* C: *Brachylaima mesostoma;* D: *Echinorhynchus truttae;* E/F: *Polymorphus minutus;* G: *Hymenolepis erinacei*; H: *Physocephalus sexalatus*.

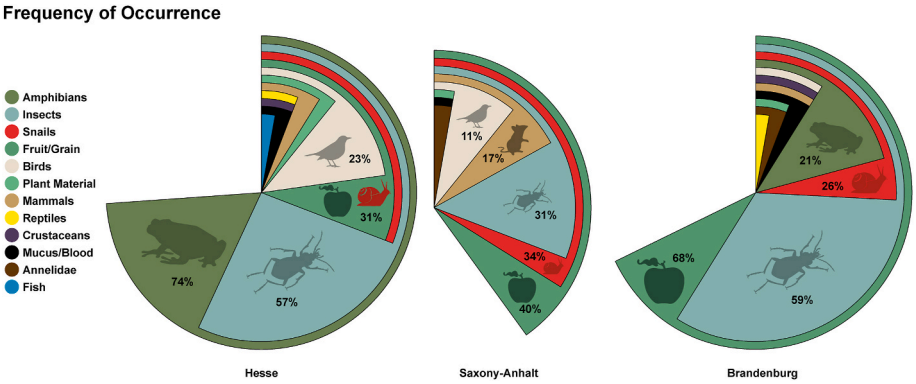

Fig. 3. Depiction of the Frequency of occurrence (F%) of prey from surveyed raccoons, Percentages mean: "Prey category found in XX% of raccoon stomachs".

the interaction of individual habitat patches, serving as stepping stones, is essential for the stabilization and long-term existence of respective metapopulations of endangered amphibian populations (e.g. Stokes et al., 2021). If these habitats are frequented by predators, changes in abundance, retardation of distribution dynamics, or niche contractions may result for prey species (Jeffries and Lawton, 1984; Sih et al., 1985). Raccoons can significantly impair the dynamics and reproductive potential at main and satellite habitats through large-scale predation, thereby existentially endangering occurring amphibian and reptile populations. The negative impacts of raccoon predation have already been demonstrated through case studies (e.g., Wüstemann, 2002; Schneeweiß and Breu, 2013; Egeter et al., 2015; Nehring, 2018; Oe et al., 2020; Cichocki et al., 2021). The exponential growth of raccoon populations and the effective exploitation of ecological niches in the study areas, combined with their dietary habits, exacerbate the pressure on occurrence-sensitive animal species (Nehring, 2018; Salgado, 2018;

Table 3
Frequency of occurrence (F%) and weight percentage of prey (W%) from surveyed *Procyon lotor* (total N = 108 racoons: N = 36 Hesse, N = 36 Saxony-Anhalt, N = 36 Brandenberug).

Food type	Frequency of Occurrence (F%)			Weight percentage of prey (W%)		
	Hesse	Saxony-Anhalt	Brandenburg	Hesse	Saxony-Anhalt	Brandenburg
Mammals	8.57	17.14	8.82	5.13	9.24	9.54
Microtus arvalis	–	–	2.94	–	–	6.83
Muroidea indet.	5.71	17.14	5.88	1.47	9.24	2.71
Oryctologus cuniculus	2.86	–	–	3.67	–	–
Birds	22.86	11.43	8.82	3.07	1.11	2.03
Aves indet.	8.57	5.71	2.94	0.68	0.60	0.62
Columba palumbus	–	5.71	–	–	0.51	–
Cyanistes caeruleus	2.86	–	–	0.46	–	–
Gallus gallus	5.71	–	–	0.34	–	–
Pica pica	2.86	–	–	0.78	–	–
Sturnus vulgaris	–	–	5.88	–	–	1.41
Turdus philomelos	2.86	–	–	0.81	–	–
Fish	2.86	–	–	1.48	–	–
Oncorhynchus mykiss	2.86	–	–	1.48	–	–
Amphibians	74.29	–	20.59	36.83	–	3.61
Bombina variegata	2.86	–	–	2.10	–	–
Bufo bufo	17.14	–	2.94	13.32	–	0.42
Lissotriton vulgaris	5.71	–	–	1.81	–	–
Rana temporaria	2.86	–	2.94	5.45	–	0.52
Rana spp	51.43	–	14.71	14.15	–	2.66
Reptiles	5.71	–	2.94	0.37	–	0.20
Natrix natrix	5.71	–	2.94	0.37	–	0.20
Gastropoda	31.42	34.29	26.47	1.94	9.94	5.48
Arianta arbustorum	–	–	2.94	–	–	0.57
Cepaea spp	11.43	25.71	17.66	0.43	4.97	2.64
Dreissena polymorpha	–	8.57	–	–	4.97	–
Helix pomatia	2.86	–	–	0.64	–	–
Lymnea spp	17.14	–	–	0.42	–	–
Monachoides incarnatus	2.86	–	–	0.45	–	–
Planorbarius corneus	–	–	5.88	–	–	2.27
Crustacea	5.71	–	8.82	0.35	–	1.53
Astacoidea indet.	2.86	–	8.82	0.33	–	1.53
Gammarus spp	2.86	–	–	0.02	–	–
Insects	57.14	31.43	58.82	4.84	4.80	5.62
Carabus spp.	28.57	22.86	47.06	2.37	3.14	3.15
Dytiscus marginalis	–	–	2.94	–	–	0.65
Eristalis pertinax	–	–	5.88	–	–	0.46
Geotrupes spp	20.00	–	–	1.47	–	–
Lepidoptera indet.	–	–	5.88	–	–	1.36
Lithobius spp	–	2.86	–	–	0.26	–
Melolontha melolontha	2.86	–	–	0.03	–	–
Ocypus olens	–	2.86	–	–	1.31	–
Phosphuga atrata	5.71	2.86	–	0.97	0.08	–
Annelidae	–	2.86	5.88	–	0.57	1.42
Fruit/Grain	31.43	40.00	67.65	25.28	73.95	63.19
Plant Matter	11.43	2.86	5.88	20.26	0.29	6.55
Mucus/Blood	5.71	2.86	8.82	0.44	0.11	0.83

Kochmann et al., 2021; Cunze et al., 2023).

The results of the present study clearly demonstrate (Table 3, Fig. 3) that raccoons effectively utilize those food resources in the study areas that are most abundant in the respective habitats at specific times, confirming previous statements regarding the preference for prevalent food resources (Stubbe and Krapp, 1993; Taulman and Williamson, 1994). The choice of habitat also seems closely linked to the availability of food resources (Fiderer et al., 2019). For example, during the sampling period in the Spessart study area in Hesse, over 400 skinned toads were counted in 1 day at a surface water area of approximately 2000 m^2. This specialized hunting behavior and the preference for specific prey confirm previous observations that raccoons can develop specialists through traditional hunting behavior, which then favor certain food resources and actively pursue them (Urban, 1970).

The results of the stomach content analysis show a preference for predominantly animal food components depending on their relative and temporal occurrence. In the Hessian study area, the Frequency of Occurrence (F%) for amphibian food sources was determined to be 74.29%, clearly indicating seasonal adaptation to available food resources. The majority of the raccoons studied in Hesse and Brandenburg came from the spring and summer months, when the amphibians spawn and are therefore most active. The fact that no amphibians were detected as food organisms in Saxony-Anhalt may be due to the fact that no or only very few amphibians are present in the study area. This may be due to habitat changes, climatic changes and the resulting less favorable living conditions (Luedtke et al., 2023). Although other animal groups such as birds, small mammals, or gastropods are represented in the diet spectrum of the examined raccoons in the three areas, amphibians were more abundant in Hesse and Brandenburg. The three study areas in Hesse, Brandenburg, and Saxony-Anhalt are characterized by their proximity to water bodies and the presence of numerous amphibians, confirming that raccoons primarily feed on the food resources

available in an area at a given time of year. Accordingly, the impacts of predation by raccoons in natural areas with extensive aquatic ecosystems are not comparable to those in areas with a lower proportion of water bodies and amphibian habitats, highlighting the necessity of local studies.

4.2. Ectoparasites and diet-related endoparasitism

In total, five ectoparasitic species were identified among the 108 examined raccoons from the three study areas. The raccoon louse *Trichodectes octomaculatus* (ST: prevalence = 63.9%, HE: prevalence = 86.1%, BB: prevalence = 44.4%) was the most commonly found ectoparasite species and was identified in all three areas. The high prevalence of this species was expected since *T. octomaculatus* is specific to raccoons and was introduced to Europe with them from their native range (Haitlinger and Łupicki, 2009). The badger flea *Paraceras melis* was detected in Saxony-Anhalt and Hesse. This flea primarily infests the European badger but can also be transmitted to other mammals (Ancillotto et al., 2014). Additionally, the tick species *Ixodes ricinus* was found in all three study areas. Other identified tick species included the hedgehog tick *I. hexagonus* (HE) and the marsh tick *Dermacentor reticulatus* (ST, BB). All ectoparasite species identified here are already known to be part of the parasite fauna of raccoons in Germany and Europe.

The effective utilization of different animal food components is reflected in the prevalence of specific endoparasites (Tables 2 and 3). Many metazoan parasite species require specific intermediate hosts for their life cycle to reach the definitive host through the food chain. The presence of such parasites in the examined host is an indication of the organisms from which the animal must have fed. Compared to stomach content and fecal analysis as short-term snapshots, the analysis of diet-related parasite infection provides additional interpretative assistance to derive recommendations for nature conservation and health-related management measures (Fig. 4).

Compared to previous studies on the metazoan parasite fauna of raccoons from Germany (Priemer and Lux, 1994; Lux and Priemer, 1995; Gey, 1998; Rentería-Solís, 2015; Michler, 2017), recent research shows that the parasite and pathogen diversity of raccoons is increasing (Keller et al., 2022; Langner et al., 2022; Peter et al., 2023). Evidence of the expanding parasite fauna of raccoons is also confirmed by studies in the European context (Karamon et al., 2014; Cybulska et al., 2018; Piróg et al., 2018; Duscher et al., 2020; Romeo et al., 2021; Lombardo et al., 2022).

In the present study, the core species in the Hessian study area was the human-pathogenic nematode species *Baylisascaris procyonis* (Kazacos, 2016; French et al., 2019) with very high prevalence rates (P = 91.7%). In the study by Peter et al. (2023), a *Baylisascaris* infection of raccoons in an adjacent study area in Hesse was determined with a prevalence value of P = 95% (N = 234). This nematode species was also identified in 88.9% of the raccoons examined in the Saxony-Anhalt study area. The prevalence of *B. procyonis* in the Brandenburg study area was significantly lower at P = 19.4%. Among the over 120 possible intermediate hosts of this parasite are birds and smaller mammals (Kazacos, 2001), which are also natural food resources for raccoons (Stubbe and Krapp, 1993). Shared latrines are suspected as the main route of infection, which can also be visited by potential intermediate hosts (Page et al., 1998, 2016; Kazacos, 2001; Roussere et al., 2003). Eggs of *B. procyonis* are excreted with raccoon feces and can survive in the environment for several years (Kazacos, 2001) until they are ingested by a potential host and can continue their development. Especially in urban and agricultural areas where adaptable raccoons utilize anthropogenic food resources, they reach increasingly higher population densities. Consequently, there can be an increasing risk of infection for humans as well as domestic, livestock, and wild animals with the raccoon roundworm *B. procyonis* in these areas (French et al., 2019, 2022; Peter et al., 2023). The distribution of *B. procyonis* will further increase with the rising raccoon populations, which can also be accelerated by the presence of suitable intermediate hosts (Kazacos, 2001; Peter et al., 2023). Future studies should also consider the infection dynamics in potential intermediate hosts.

Furthermore, L3 larvae of the nematode species *P. ensicaudatum* were found in Hesse (P = 13.9%), Sachsen-Anhalt (P = 16.7%), and Brandenburg (P = 27.8%). This species mainly parasitizes the small intestine of birds (Borgsteede et al., 2003). The genus *Porrocaecum* is the only

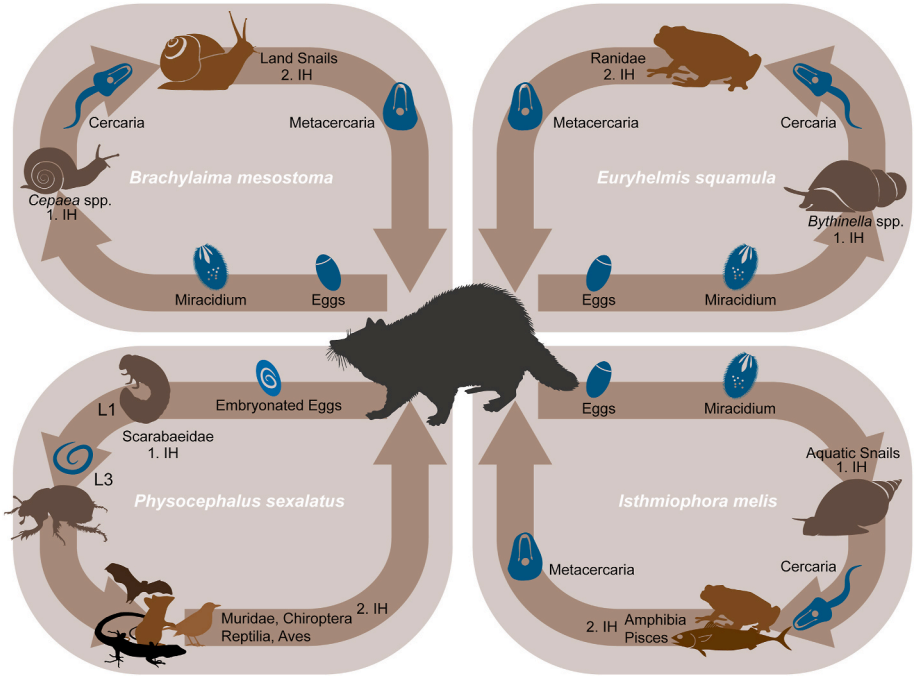

Fig. 4. Presentation of 4 parasite species not found in the original habitat of raccoons *(Brachylaima mesostoma, Euryhelmis squamula, Physocephalus sexalatus, Isthmiophora melis)*, their lifecycles and how the raccoon takes over the role as final host within the new environment. IH = Intermediate host, L = larval stage.

genus of autochthonous bird parasites within the Ascaridoidea that can be transmitted to mammals (Osche, 1959; Anderson, 2000; Borgsteede et al., 2003). According to Levin (1961) and Anderson (2000), earthworms or bird species of the genera *Sturnus* and *Turdus* can serve as intermediate hosts in the life cycle of *P. ensicaudatum*. A likely infection with *P. ensicaudatum* through intermediate hosts from the family Lumbricidae can also be inferred from Wharton's (1979) studies, which found gravid female *P. ensicaudatum* in the small intestine of *Corvus frugilegus*. However, in mammals such as raccoons, this parasite does not develop further but remains free in the intestinal lumen (Osche, 1959). This is also evident in this study, as this parasite was freely detected in the small and large intestines, and partially in the stomach of infected animals. Stomach content analyses indicate that in an infection with *P. ensicaudatum*, bird components were detected in the stomach and intestinal tract. However, the nutritional ecological calculation of avifaunistic food resources ranks the importance of birds as secondary during the investigated season in the three study areas (Table 3, Fig. 3).

Physocephalus sexalatus is a first record for raccoons in Europe and was only identified in the Hessian study area (P = 13.9%). This species uses beetles from the family Geotrupidae as intermediate hosts, and wild boars serve as definitive hosts, where infection can lead to spiruridosis (Páv et al., 1972; Chowdhury, 2001). This suggests that the infected raccoons have utilized Coleoptera as a food resource. This is confirmed, especially in one examined raccoon, where 42 individuals of *P. sexalatus* were identified in the intestinal tract and simultaneously 26 beetle individuals were detected. The absence of individuals of *P. sexalatus* in both Brandenburg and Sachsen-Anhalt is likely because the raccoon is not an established host of this parasite and had not been identified until this study.

The second most common endoparasite (Hesse P = 33.3 %, Saxony-Anhalt P = 22.2 %, Brandenburg P = 41.7 %) of raccoons in the present study was the cestode species *Atriotaenia incisa*. The species has already been detected as a small intestinal parasite in both badgers and raccoons in Germany (Priemer and Lux, 1994; Peter et al., 2023). Not much is known about the development cycle, possible intermediate hosts or triggered diseases and symptoms, but Coleoptera serve as intermediate hosts in another species of this genus (Gallati, 1959; Loos-Frank and Zeyhle, 1982; Torres et al., 2001). However, the high infestation numbers (max. Intensity 576 in Brandenburg) confirm the importance of the raccoon as host and vector of this parasite.

Cestodes from the family Hymenolepididae are characterized by a strictly stenoxenous host spectrum. The genus *Hymenolepis* is unique among Hymenolepididae because its representatives parasitize hosts from various orders such as Rodentia and Eulipotyphla (Vaucher, 1982; Binkienė et al., 2019). *Hymenolepis erinacei* is another first record for raccoons in Europe and was exclusively detected in the Brandenburg study area (P = 2.8%) in this investigation. *Hymenolepis erinacei* is considered a widely distributed parasite in European hedgehogs (Pfäffle et al., 2014; Binkienė et al., 2019). In the life cycle of *H. erinacei*, coprophagous insects such as dung beetles (Beck, 2007) and species from the families Scarabaeidae and Silphidae serve as intermediate hosts (Valkounova and Prokopič, 1980; Makarikov and Tkach, 2013; Binkienė et al., 2019). Therefore, infection can only occur through predation by raccoons on these intermediate or definitive hosts. However, explicit statements are difficult due to the low infection rates.

Adult digenetic trematodes of the species *Isthmiophora melis* were found in the Brandenburg (P = 30.6%) and Sachsen-Anhalt (P = 19.4%) study areas. The high numbers of adult individuals (max. 566 in BB) indicate the raccoon's ecological use of intermediate hosts in the life cycle of *I. melis*. In this context, the first intermediate host is the freshwater snail *Lymnaea stagnalis*, while numerous amphibians and freshwater fish serve as the second intermediate hosts. The list of definitive hosts includes more than 30 species of vertebrates, including humans (Radev et al., 2009; Hildebrand et al., 2015). The ecological investigations also suggest a possible raccoon infection through intermediate hosts of *I. melis*. In Brandenburg, the Frequency of Occurrence [F %] for amphibious food resources was determined to be 20.59%, and for gastropods, it was 26.47%. Therefore, the studies confirm that the examined raccoons utilize both gastropods and amphibians, which can serve as intermediate hosts for this trematode species, as a food resource and thus could become infected. Since raccoons can act as suitable definitive hosts for *I. melis*, as confirmed by the discovery of gravid individuals of *I. melis*, the parasites may have accumulated in the intestinal tract over a longer period, indicating a previous predation event, even though no amphibians were detected as dietary components in Saxony-Anhalt.

Brachylaima mesostoma was detected in two of the study areas with low infestation rates (HE P = 8.3%, BB P = 8.3%). Similar to *Isthmiophora melis*, the life cycle of *B. mesostoma* involves two intermediate hosts. Freshwater or land snails serve as the intermediate hosts, while amphibians, birds, mammals, and reptiles act as final hosts (Heneberg et al., 2016; Gérard et al., 2020).

Euryhelmis squamula was exclusively identified in the Hesse study area (P = 5.6%). This species also requires at least two intermediate hosts during its life cycle. Freshwater snails of the Hydrobiidae family serve as the first intermediate host, while various amphibians such as the common frog *Rana temporaria* act as the second intermediate host (e.g. Baer, 1932). It is already known that raccoons can serve as definitive hosts (Peter et al., 2023). The infestation here is also solely explained by the predation of infected intermediate hosts.

Adult Acanthocephala of the species *Pomphorhynchus laevis* (P = 2.8%) were only detected in the Hesse study area. *Polymorphus minutus* was identified in both Hesse and Saxony-Anhalt with a prevalence of P = 8.3%. Both species were found freely in the gastrointestinal tract as well as anchored in the intestinal wall. Adult *P. minutus* parasitize the intestines of various waterfowl, while *P. laevis* is a typical fish parasite. Both parasite species utilize amphipods and fish as intermediate hosts (Romanovski, 1964; Itämies et al., 1980; Gaillard et al., 2004; Kochmann et al., 2023). The presence of both parasite species in the examined raccoons suggests that they must have preyed on infected amphipods, waterfowl, or fish in the study areas, even if no direct evidence of such species was found in the stomach or intestine, except for the rainbow trout *Oncorhynchus mykiss* in Hesse (Table 3) (Itämies et al., 1980; Piróg et al., 2018). *Gammarus* spp. was detected as a food resource in raccoons infected with *P. laevis*.

Adult Acanthocephala of the species *Echinorhynchus truttae* were exclusively identified in Saxony-Anhalt (P = 11.1%). Various salmonids are known as definitive hosts for *E. truttae*, while amphipods are also used as intermediate hosts (Awachie, 1966). This suggests that the raccoons' intake and infection occurred through cystacanth-infected amphipods or predation of fish. However, no corresponding food components were detected in any of the infected raccoons at the time of examination. Nonetheless, the infection indicates a previous predation event.

Comparing the three study areas, it was shown in the present study that the same parasite fauna and food components could be identified, albeit with varying frequencies. The observed parasite fauna is similar to that of recent related studies (Biedrzycka et al., 2020; Peter et al., 2023), but shows that there are still gaps in knowledge about parasites that can be harbored by raccoons. All study areas are characterized by the presence of water bodies and amphibians. The assumption that raccoons mainly prey on these sensitive animal species, as they are sufficiently available at certain times of the year, can be supported by both stomach content and fecal examinations, as well as by the analysis of the parasite fauna. In order to protect endangered native animal species, it will be necessary in the future to identify special management measures in certain areas to minimize the impact of raccoons on native fauna and ecosystems.

4.3. Conclusions

Through the examination of raccoons from three different natural

and water-adjacent areas in Hesse, Saxony-Anhalt and Brandenburg, nutritional ecology and parasitism could be correlated. The effective utilization of various animal food components is reflected in the prevalences of the identified endoparasites. The specific metazoan parasite species require certain intermediate hosts for their life cycle to reach the definitive host through the food chain. If such parasites can be detected in the examined host, this is an indication of how the animal must have been feeding. The results of this study confirm that raccoons can indeed be responsible for the decline of various sensitive native species. For example, stomach content and fecal analyses revealed amphibian food components in 74.29% of the examined raccoons in Hesse. It also becomes clear that the presence of parasites should be used to interpret predation events in such studies, in order to explain more distant predation events. In the 108 examined raccoons from the three study areas, a total of 16 parasite species (5 ecto-, 11 endoparasite species) could be identified, of which at least three utilize amphibians as intermediate hosts, thus indicating that raccoon infection can only be explained by predation on these hosts. The detection of the parasite species *Hymenolepis erinacei*, *Physocephalus sexalatus* and *Pomphorhynchus laevis* expands the known parasite fauna of raccoons from previous studies in other regions of Central Europe and Germany. The fact that the spread of raccoons in Germany and Europe does not seem to be complete yet, partly due to their high adaptability and omnivorous diet, is confirmed in part by the new parasite findings, indicating that raccoons are increasingly integrating into new areas. On the other hand, this means that sensitive native animal species could continue to be increasingly threatened by raccoon predation in the future as they inhabit new areas, where, for example, very small, local populations of native species occur. Furthermore, it is necessary to establish management measures for raccoons in areas where rare species occur in order to ensure the overarching nature conservation objective of "conservation of endangered species".

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Declaration of competing interest

The authors declare no competing interests.

CRediT authorship contribution statement

Norbert Peter: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Validation, Writing – original draft, Funding acquisition. **Anna V. Schantz:** Conceptualization, Investigation, Validation, Writing – review & editing, Formal analysis, Methodology, Data curation. **Dorian D. Dörge:** Conceptualization, Project administration, Software, Supervision, Validation, Visualization, Writing – review & editing, Funding acquisition. **Anne Steinhoff:** Data curation, Formal analysis, Investigation, Methodology. **Sarah Cunze:** Methodology, Software, Validation, Visualization. **Ajdin Skaljic:** Investigation, Software, Validation. **Sven Klimpel:** Conceptualization, Funding acquisition, Project administration, Resources, Supervision, Validation, Writing – review & editing.

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