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The hidden threat: Exploring the parasite burden and feeding habits of invasive raccoon dogs (*Nyctereutes procyonoides*) in central Europe

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ABSTRACT

Originally from Asia, the raccoon dog *Nyctereutes procyonoides* is an invasive alien species in Europe, listed since 2019 on the List of invasive alien species of Union concern. The raccoon dog is considered to have negative impact on native biodiversity, as well as a crucial role in hosting and transmitting diverse parasites and pathogens of human and veterinary importance. In the present study, stomach content analyses and parasitological examinations were performed on 73 raccoon dogs from Germany. In addition, fecal samples were analyzed. The results of the study confirm the assumption that the examined raccoon dogs were infested with a various ecto- and endoparasite fauna. A total of 9 ecto- and 11 endoparasites were detected, with 6 of the endoparasites having human pathogenic potential. *Trichodectes canis* (P = 53.42%), *Toxocara canis* (P = 50.68%) and *Uncinaria stenocephala* (P = 68.49%) were the most abundant parasite species. The stomach contents consisted of approximately one-third vegetable and two-thirds animal components, composed of various species of amphibians, fish, insects, mammals and birds. Among them were specially protected or endangered species such as the grass frog *Rana temporaria*. The study shows that the raccoon dog exerts predation pressure on native species due to its omnivorous diet and, as a carrier of various parasites, poses a potential risk of infection to wild, domestic and farm animals and humans.

1. Introduction

The raccoon dog (*Nyctereutes procyonoides*), also called tanuki, originated in Asia (Japan, southeastern Russia, western Mongolia, eastern China, Korea, northern Vietnam) (Hunter and Barrett, 2012), where it is known to have several subspecies (Wilson and Reeder, 2005). In the late 1920s, the raccoon dog was introduced into the European part of the USSR and kept for the purpose of fur farming. From there it spread to many parts of Europe until today. The fact that raccoon dogs occur outside their natural range is entirely due to anthropogenic impacts (Nowak, 1984). In Germany, the first records exist since the 1960s (Kowarik and Rabitsch, 2010) and *N. procyonoides* is considered established according to the list of invasive alien species of Union concern (Regulation (EU) No. 1143/2014) since 02.02.2019. Invasive alien species in particular are considered one of the most significant threats to biodiversity worldwide, can have social, ecological, economic, and evolutionary impacts, and can threaten human and animal health (Mooney et al., 2005; Kowarik and Rabitsch, 2010).

Assigned to the family Canidae and to the tribe Vulpini, raccoon dogs inhabit various forest types, scrublands, agricultural areas, and sometimes urban regions where they often take over old fox or badger dens (Hunter and Barrett, 2012). Similar to the raccoon, another invasive alien species, the raccoon dog is also suspected to be partly responsible for the transmission of various parasites and pathogens, which are also known to cause human pathogenic effects (e.g. Schwarz et al., 2011; Duscher et al., 2017; Kochmann et al., 2021; Pilarczyk et al., 2022), due to its further spread and the associated increased proximity to humans as well as wild, farm and domestic animals. In addition to, for example, the fox tapeworm *Echinococcus multilocularis*, rabies, and canine distemper, studies show that tanuki are also suitable reservoir hosts for SARS-CoV-2 (e.g. Chueca et al., 2021; Keller et al., 2022). Despite natural regulators such as canine distemper or rabies, which at times, such as between the years 2008–2011, led to a decline in raccoon dog populations in certain areas, population trends in the introduced range and dispersal is

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increasing (Mulder, 2012; Kochmann et al., 2021). Similarly, *N. procyonoides*, through its omnivorous diet, is thought to definitely exert predation pressure on native species, some of which are endangered or protected, thus further threatening them (Baltrūnaitė, 2002; Sutor et al., 2010; Kauhala and Kowalczyk, 2011; Dahl and Åhlén, 2019; Koshev et al., 2020).

To date, there are only sporadic studies on the raccoon dog in Europe that focus on the distribution, parasite load or diet of this invasive alien species (e.g. Shimalov and Shimalov, 2002; Bružinskaitė-Schmidhalter et al., 2012; Schuster and Shimalov, 2017). However, to better assess the current situation and understand the role of tanuki as predators and parasite carriers in the new range, it is important to continuously study more areas and collect more data. In addition, detailed stomach content analysis can be used to draw conclusions about parasitization and vice versa. This is because many parasite species use certain intermediate hosts within their life cycle that are essential for development. Thus, the presence of a certain parasite can prove that certain organisms must have been part of the diet, just as stomach contents can provide evidence that certain types of parasites may be present. The purpose of this study is to obtain information regarding the feeding ecology of raccoon dogs from defined areas in Germany and how it relates to the corresponding parasite and pathogen fauna, in order to better assess the health risk as well as the impact on native ecosystems.

2. Material & methods

2.1. Sampling

A total of 73 raccoon dogs were examined for the present study. All animals were shot between November 2018 and February 2021 in the context of legal hunting. 56 (77%) of the examined animals originated from Schleswig- Holstein, 12 (16%) from Lower Saxony, 2 (3%) each from Saxony- Anhalt and Hesse, and 1 (1%) from Saxony (Fig. 1). The raccoon dogs were stored in plastic bags at −20 °C until examination.

2.2. Analyses

The stomach contents were divided according to recognizable food fractions (insects, amphibians, fish, birds, mammals, plants, others). The individual fractions were weighed with a precision scale and stored in 70% EtOH for morphological determination and in 100% EtOH for genetic determination. For comparison of the examined animals, they were measured beforehand and different morphological parameters were collected (Table 2). For the ectoparasitological examination of the animals, the fur was first systematically divided into the subareas head, forechest, back and belly. The search of the fur was performed according to Peter et al. (2023), immediately before the beginning of the dissection. The ectoparasites were stored in a 1.5 ml Eppendorf tube for morphological determination in 70% EtOH. The internal organs trachea, lung, esophagus, stomach, heart, liver, spleen, kidneys, urine bladder and small and large intestine were examined by dissection according to Storch and Welsch (2014). Detected endoparasites were first transferred to fresh NaCl solution for cleaning, stored in 70% EtOH for subsequent morphological determination and in 100% EtOH for genetic determination. Fecal samples were collected from the rectum and stored at −20°C. Sample preparation and examination was performed using the Merthiolate-Iodine-Formaldehyde Concentration (MIFC) method according to Mehlhorn et al. (1993). To examine the raccoon dogs for *Trichinella* sp., 10 g of muscle tissue was collected from each of the tongue, diaphragm and foreleg and stored at −20 °C. Sample preparation was performed according to the protocol of Kit Trichinella AHD, manufacturer PrioCHECK (product number 7620030).

2.3. Identification of stomach contents and parasites

The plant components of the stomach contents could be visually assigned to the specific large groups. All of the found ectoparasites were determined based on external characteristics (Estrada-Peña et al., 2004; Bádr et al., 2005; Brinck-Lindroth and Smit, 2007; González-Acuña et al., 2007; Földvári et al., 2016; Sándor, 2017; Hornok et al., 2021).

At least one individual of each species of endoparasites of each examined raccoon dog as well as all of the animal stomach contents were examined genetically. For this purpose, DNA was extracted according to the protocol of the DNeasy Blood & Tissue Kit, manufacturer Qiagen (Cat. No. 69506) and the DNeasy *mericon* Food Kit, manufacturer Qiagen (Cat. No. 69514). PCR was performed with a volume of 25 μl (12.5 μl Taq PCR Master Mix, 1 μl each of the primers forward and reverse as well as $MgCl_2$, 7 μl H_2O ddest and 2.5 μl of the DNA from the extraction). The primers to be used were systematically selected by major group (for parasites by digeneas, cestodes, nematodes and for stomach contents by insects, amphibians, fish, birds, mammals) from existing literature as well as the thermocycling settings of the primers (Folmer et al., 1994; Gasser et al., 1996; Hebert et al., 2004; Vences et al., 2005; Hajibabaei et al., 2006; Holterman et al., 2006; Molaei et al., 2006; Ivanova et al., 2007; Prosser et al., 2013; Laurimaa et al., 2016; Nugaraitė et al., 2017). Agarose gel electrophoresis was performed to verify PCR. Subsequently, samples were purified after NucleoSpin Gel and PCR Clean-up (Macherey-Nagel, Düren, Germany) and sent to Microsynth Seqlab GmbH (Göttingen, Germany) for sequencing. Resulting sequences were then blasted into the GenBank NCBI sequence database and compared based on query length, query coverage, and percent identity. For each parasite species the result with the highest match was then uploaded to the NCBI database and assigned accession numbers SAMN37093833-SAMN37093858 (BioProject PRJNA1007609) (Table 1). The remaining endoparasitic specimens that could not be identified by genetic analysis were determined morphologically (Morgan and Schiller, 1950; Verster, 1969; Hildebrand et al., 2015; Saari et al., 2019).

2.4. Calculations stomach contents and parasite infection

Stomach content and parasite burden calculations were performed according to Klimpel et al. (2019). To evaluate stomach content, the Index of Relative Importance (IRI) was determined, which is composed of Frequency of Occurrence [F%], Weight Percentage of Prey [W%], and Numerical Percentage of Prey [N%]. The food component with the highest IRI is considered most significant. For parasite infection, prevalence P [%], intensity I, mean intensity mI, and mean abundance mA were calculated.

3. Results

3.1. Morphological data

Of the 73 examined raccoon dogs, 37 were male and 36 were female. The lightest animal weighed 3.65 kg, the heaviest animal 9.41 kg. The mean total body weight of the males was 7.23 kg, and that of the females was 7.37 kg. The largest animal had a total body length of 85.00 cm, the smallest 68.00 cm, with a mean body length of 76.46 cm (male) and 77.19 cm (female) (Table 2).

3.2. Stomach content analysis

Stomach contents were detected in a total of 51 of the stomachs examined. The components were previously classified into the major groups amphibians, fish, insects, mammals, birds, fruit, corn, cereals, vegetable other and mucus, shown in Table 3 and Fig. 2.

The stomach contents studied consisted of approximately 2/3 animal components and approximately 1/3 plant components. Of the identified animal components, mammals and birds were the most abundant; of the plants, cereals, apple, and corn were the most abundant. Two amphibian species were identified, of which *Rana temporaria* was determined to

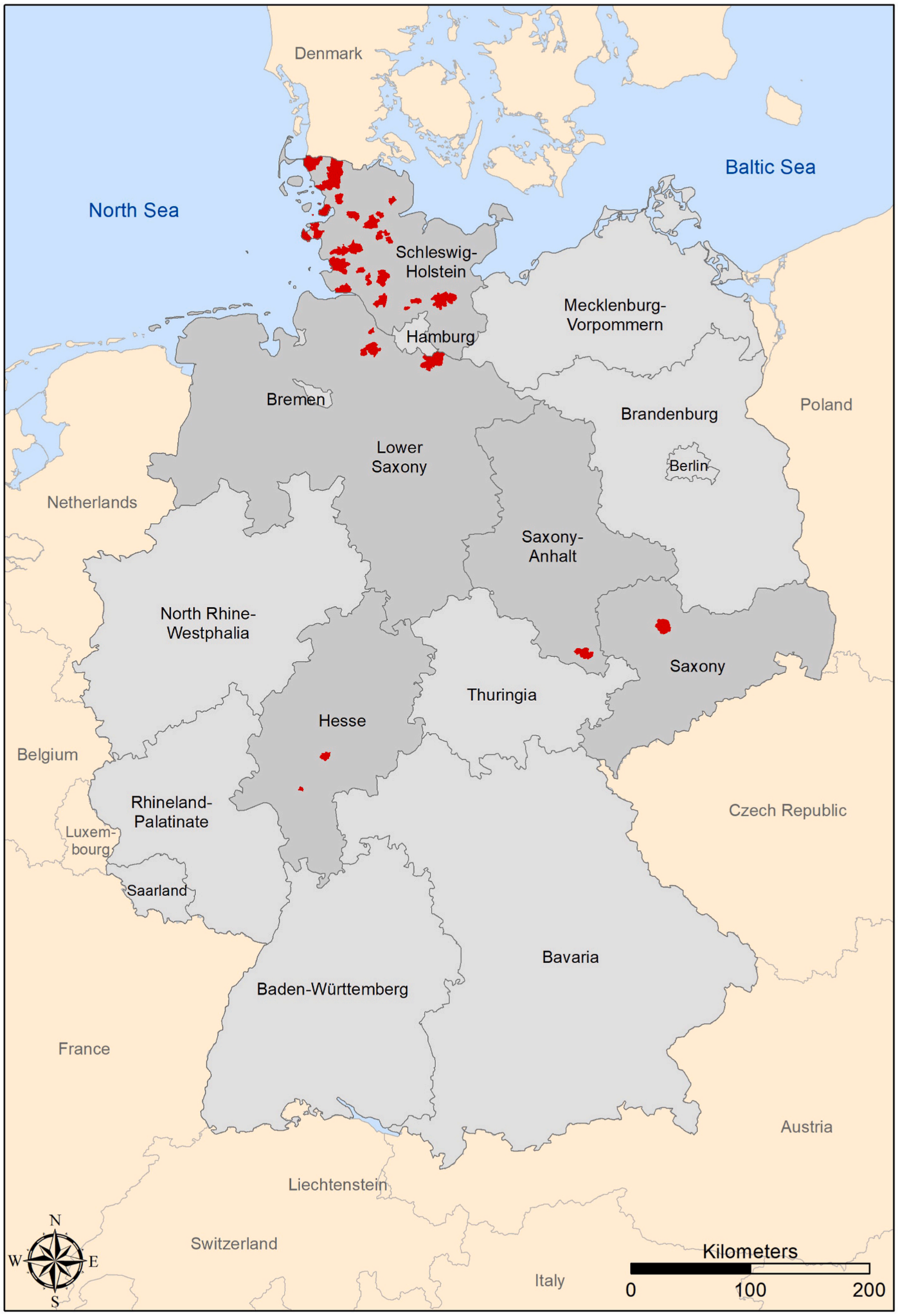

Fig. 1. Origin of the examined raccoon dogs in the different federal states of Germany, red areas show the sampling sites (N = 73). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

have the highest value with an IRI of 34.02. *Platichthys flesus* (IRI = 2.26) was the only fish species identified to species level, while of insects *Cantharis fusca* (Fig. 2D) was identified with an IRI of 21.39 and two other species. Mammals were the most represented group in the stomach contents of the raccoon dog, both in terms of number of species and volume, so seven species could be genetically identified. Other stomach contents could be assigned to mammals (IRI = 1132.46), but could not be further determined to species level. Lastly, four bird species identified to species level could be assigned to animal stomach contents, as well as additional bird samples that could not be further identified (IRI = 470.86). Grasses and cereals (IRI = 924.91) (Fig. 2E) were the most abundant plant components of the stomach contents. In addition, apple, blackthorn, cherry and maize could be identified visually well in the stomach of several raccoon dogs (Table 3).

3.3. *Parasite occurrence*

By combing the coat and examining the internal organs of the raccoon dogs, 18 parasite species could be determined, 9 of which were ectoparasitic and 9 endoparasitic species (Table 4). A total of 4 tick species were identified, as well as some individuals that were assigned to the genus *Ixodes* but could not be further determined (*Ixodes* spp.). Based on morphological characteristics, the species *Ixodes canisuga* (P = 35.62%), *Ixodes hexagonus* (P = 28.77%), *Ixodes ricinus* (P = 36.99%), *Ixodes* spp. (P = 36.99%) and *Dermacentor reticulatus* (P = 2.74%) were identified. The only species of Phthiraptera and the most abundant ectoparasitic species in this study was identified as the canine chewing louse *Trichodectes canis* (P = 53.42%) (Fig. 3B). Other ectoparasites were the flea species *Archaeopsylla erinacei* (P = 15.07%), *Chaetopsylla*

Table 1
Results of genetic analysis of endoparasites and stomach contents. The sequences are uploaded to Genbank NCBI under the corresponding accession number.

	Accession number	Species	Query length	Query Cover [%]	Percent Identity [%]	Accession number of reference sequence	Primer name (forward/ reverse)	Primer sequence	Primer source
Digenea	SAMN37093833	*Alaria alata*	1235	96	98.50	AY222091.1	Worm A/ Worm B	5′-GCGAATGGCTGATTAAATGAG-3'/ 5′-CTTGTTACGACTTTTACTTCC-3′	Nugaraité et al. (2017)
	SAMN37093834	*Isthmiophora melis*	1137	99	99.29	AY222131.1			
Cestoda	SAMN37093835	*Echinococcus multilocularis*	437	99	99.54	MT461411.1	CesCox1F/ CesCox2R	5'–TGATCCGTTAGGTGGTGGTGA-3'/ 5'–GACCCTAACGACATAACATAATGAAAATG-3′	Laurimaa et al. (2016)
	SAMN37093836	*Mesocestoides litteratus*	425	97	100.00	MN514033.1			
	SAMN37093837	*Taenia* sp.	341	99	100.00	OM996999.1			
Nematoda	SAMN37093838	*Capillaria aerophila*	293	98	99.65	KF479371.1	NemF1/ NemR1	5′-TGTAAAACGACGGCCAGTCRACWGTWAATCAYAARAATATTGG-3'/ 5′-CAGGAAACAGCTATGACTAAACTTCWGGRTGACCAAAAAATCA-3′	Prosser et al. (2013)
	SAMN37093839	*Porrocaecum depressum*	940	99	99.79	U94379.1	988F/ 1912R	5′-CTCAAAGATTAAGCCATGC-3'/ 5′-TTTACGGTCAGAACTAGGG-3′	Holtermann et al. (2006)
	SAMN37093840	*Toxocara canis*	938	99	99.89	JN256976.1			
	SAMN37093841	*Uncinaria stenocephala*	796	99	98.61	MT345056.1	NC5/ NC2	5′-GTAGGTGAACCTGCGGAAGGATCATT-3'/ 5′-TTAGTTTCTTTTCCTCCGCT-3′	Gasser et al. (1996)
Amphibia	SAMN37093842	*Bufo bufo*	540	99	98.88	MN122891.1	16SA-L/ 16SB-H	5′-CGCCTGTTTATCAAAAACAT-3'/ 5′-CCGGTCTGAACTCAGATCACGT-3′	Vences et al. (2005)
	SAMN37093843	*Rana temporaria*	657	98	99.84	MW452182.1	LCO1490/ HCO2198	5′-GGTCAACAAATCATAAAGATATTGG-3'/ 5′-TAAACTTCAGGGTGACCAAAAAATCA-3′	Folmer et al. (1994)
Pices	SAMN37093844	*Platichthys flesus*	640	99	99.84	MH032491.1	FishF1/ FishR1	5′-TGTAAAACGACGGCCAGTCGACTAATCATAAAGATATCGGCAC-3'/ 5′-CAGGAAACAGCTATGACACTTCAGGGTGACCGAAGAATCAGAA-3′	
Insecta	SAMN37093845	*Calliphora vicina*	640	99	99.84	KJ394609.1	LCO1490/ HCO2198	5′-GGTCAACAAATCATAAAGATATTGG-3'/ 5′-TAAACTTCAGGGTGACCAAAAAATCA-3′	Folmer et al. (1994)
	SAMN37093846	*Cantharis fusca*	643	97	100.00	KJ963372.1	LepF/ LepR	5′-ATTCAACCAATCATAAAGATATTGG-3'/ 5′-TAAACTTCTGGATGTCCAAAAAATCA-3′	Hajibabaei et al. (2006)
	SAMN37093847	*Noctua pronuba*	650	99	100.00	KJ388684.1	LepF1	5′-ATTCAACCAATCATAAAGATATTGG-3'/ 5′-TAAACTTCTGGATGTCCAAAAAATCA-3′	Hajibabaei et al. (2006)
Mammalia	SAMN37093848	*Apodemus flavicollis*	411	100	99.03	MN122902.1	LCO1490/ HCO2198	5′-GGTCAACAAATCATAAAGATATTGG-3'/ 5′-TAAACTTCAGGGTGACCAAAAAATCA-3′	Folmer et al. (1994)
	SAMN37093849	*Apodemus sylvaticus*	631	99	98.73	NC_049122.1			
	SAMN37093850	*Capreolus capreolus*	606	98	99.50	OQ706768.1			
	SAMN37093851	*Dama dama*	655	99	99.85	KF509958.1			
	SAMN37093852	*Microtus arvalis*	632	99	99.21	NC_038176.1			
	SAMN37093853	*Myodes glareolus*	280	100	99.29	MZ661165.1			
	SAMN37093854	*Sus scrofa*	636	99	99.21	MF183225.1			
Aves	SAMN37093855	*Anas platyrhynchos*	690	98	99.85	MG654805.1	BirdF1/ BirdR1	5′-TTCTCCAACCACAAAGACATTGGCAC-3'/ 5′-ACGTGGGAGATAATTCCAAATCCTG-3′	Hebert et al. (2004)
	SAMN37093856	*Anser anser*	443	100	99.32	MN122908.1	AvianCytbF/ AvianCytbR	5′-GAC TGT GAC AAA ATC CCN TTC CA-3'/ 5′-GGT CTT CAT CTY HGG YTT ACA AGA C-3′	Molaei et al. (2006)
	SAMN37093857	*Branta canadensis*	490	99	98.36	NC_007011.1			
	SAMN37093858	*Turdus philomelos*	658	100	99.24	MK262454.1	LCO1490/ HCO2198	5′-GGTCAACAAATCATAAAGATATTGG-3'/ 5′-TAAACTTCAGGGTGACCAAAAAATCA-3′	Folmer et al. (1994)

Table 2
Recorded morphometric data of examined raccoon dogs. Minimum, Maximum and Mean value are given for M = Male (M = 37), F = Female (N = 36) and all animals M + F (N = 73).

Male (M)/ Female (F)	Value	Total weight [kg]	Carcass weight [kg]	Standard length [cm]	Tail length [cm]	Total length [cm]	Hind foot length [cm]	Ear length [cm]	Zygomatic width [cm]	Condylobasal length [cm]	Liver weight [g]	Stomach weight full [g]	Stomach weight empty [g]
M	Min	3.65	2.65	51.00	15.50	68.00	10.72	3.20	6.21	10.79	132.30	52.44	43.88
	Max	9.41	7.89	63.00	25.50	82.50	15.80	6.10	7.90	12.98	354.99	433.65	106.42
	Mean	7.23	5.95	56.19	20.27	76.46	11.57	4.74	7.10	12.20	214.09	139.15	68.77
F	Min	5.41	4.45	50.00	18.50	69.50	10.80	3.80	6.60	11.58	89.78	58.79	42.67
	Max	9.36	7.83	63.50	24.50	85.00	12.46	5.77	7.54	12.75	293.42	245.18	90.22
	Mean	7.37	6.13	55.90	21.29	77.19	11.52	4.54	7.05	12.26	192.81	105.98	68.07
M + F	Min	3.65	2.65	50.00	15.50	68.00	10.72	3.20	6.21	10.79	89.78	52.44	42.67
	Max	9.41	7.89	63.50	25.50	85.00	15.80	6.10	7.90	12.98	354.99	433.65	106.42
	Mean	7.31	6.05	56.08	20.72	76.80	11.55	4.68	7.08	12.23	201.40	122.24	68.16

Table 3
Calculations for the Index of Relative Importance (IRI) for the different food components, samples that could not be identified to species level are summarized in the respective class.

		F%	W%	N%	IRI
Amphibians	*Bufo bufo*	3.92	0.74	1.35	8.19
	Rana temporaria	3.92	7.32	1.35	34.02
Fish	Pisces	1.96	0.64	0.68	2.58
	Platichthys flesus	1.96	0.48	0.68	2.26
Insects	Insecta	21.57	4.72	7.43	262.10
	Calliphora vicina	3.92	0.31	1.35	6.52
	Cantharis fusca	3.92	4.10	1.35	21.39
	Noctua pronuba	1.96	2.00	0.68	5.25
Mammals	Mammalia	39.22	15.36	13.51	1132.46
	Apodemus flavicollis	1.96	0.76	0.68	2.82
	Apodemus sylvaticus	1.96	0.39	0.68	2.09
	Capreolus capreolus	1.96	0.02	0.68	1.36
	Dama dama	3.92	1.69	1.35	11.91
	Microtus arvalis	1.96	0.59	0.68	2.49
	Myodes glareolus	1.96	0.31	0.68	1.93
	Sus scrofa	1.96	1.43	0.68	4.14
Birds	Aves	25.49	9.69	8.78	470.86
	Anas plathyrynchos	7.84	1.35	2.70	31.78
	Anser anser	5.88	6.95	2.03	52.81
	Branta canadensis	1.96	0.72	0.68	2.74
	Turdus philomelos	3.92	1.37	1.35	10.67
Plants	Plants	31.37	4.33	10.81	475.00
	Apple	15.69	6.58	5.41	188.02
	Blackthorn	3.92	1.23	1.35	10.14
	Cherry	7.84	0.92	2.70	28.43
	Grains/ Grass	37.25	11.99	12.84	924.91
	Zea mays	11.76	9.53	4.05	159.77
Other	Mucus	39.22	4.46	13.51	705.01

globiceps (P = 31.51%) (Fig. 3A), *Ctenocephalides felis* (P = 1.37%), and *Paraceras melis* (P = 24.66%) (Table 4).

Of the 9 endoparasites, 2 species belong to the Digenea, 3 species to the Cestoda and 4 species to the Nematoda. Two species of digeneans were identified, *Isthmiophora melis* (P = 23.29%) (Fig. 3C) and *Alaria alata* (P = 39.73%). *Mesocestoides litteratus* was the most abundant cestode species with a prevalence of 13.70%. *Taenia* sp. occurred with a prevalence of 8.22% as well as *Echinococcus multilocularis* (Fig. 3D). The most common nematode species was *Uncinaria stenocephala* with a prevalence of 68.49% in all animals examined, followed by *Toxocara canis* with a prevalence of 50.68%. Furthermore, the two species *Porrocaecum depressum* (P = 15.07%) and *Capillaria aerophila* (P = 4.11%) were determined (Table 4).

3.4. Parasitological fecal examination

In total, fecal samples from 71 animals could be taken and examined from which 9 parasite species were identified. One species of Digenea, three species of Cestoda, three species of Nematoda and two species of Coccidia were identified (Table 5): *A. alata* (P = 28.17%) (Fig. 3E), *E. multilocularis* (P = 5.63%), *Mesocestoides* sp. (P = 4.23%), *Taenia* sp. (P = 8.45%), *Toxocara canis* (P = 15.49%) (Fig. 3F), *U. stenocephala* (P = 4.23%), *C. aerophila* (P = 15.49%), *Isospora* sp. (P = 4.23%), and *Monocystis* sp. (P = 14.08%).

3.5. Testing for Trichinella sp

The artificial digestion method did not identify *Trichinella* sp. in any of the 73 examined raccoon dogs.

4. Discussion

The present study is a comprehensive and detailed survey of the parasitization and feeding ecology of raccoon dogs in Germany. Especially with regard to the feeding ecology, extensive data and knowledge could be obtained. Such work is essential, as knowledge about the role as a potential reservoir host of pathogens but also as a possible predator of native species is necessary to make clear statements about the position of *N. procyonoides* in the ecosystem (Hulme, 2007; Vilà et al., 2010; Kauhala and Kowalczyk, 2011).

4.1. Morphometric data

The recorded morphological data are similar with previously known values (Hunter and Barrett, 2012). Since the raccoon dogs were captured mainly in late autumn and at the beginning of winter, the average weight was more in the upper range of known values. Raccoon dogs begin to accumulate fat reserves for winter in the fall, so the mean body weight in this study tends to be higher (Asikainen et al., 2004).

4.2. Stomach content analysis

The omnivorous diet of the raccoon dog is influenced by the food supply of the respective season. The raccoon dog's diet is very diverse in the warmer seasons, with many plant foods available, as well as birds, amphibians, small mammals, carrion and invertebrates such as the earthworm (Drygala et al., 2013). In winter the food supply is rather limited, so *N. procyonoides* feeds mainly on carrion and small mammals (Baltrūnaitė, 2002). This is also reflected in the results of this study, where the examined raccoon dogs were mostly from the winter months. Although some plant components of the stomach contents are represented to a high degree, such as cereals, maize, or apple, the number and diversity of animal food components predominate (Figs. 2 and 4). Stomach content analyses clearly identified two amphibian species, one fish species, three insect species, seven mammal species, four bird species, and five plant components. The results show how generalist the raccoon dog is in its diet. In addition, although a large component of the stomach could be assigned to one of the major groups, it could not be further determined to species level. Here, the IRI = 1132.46 was highest

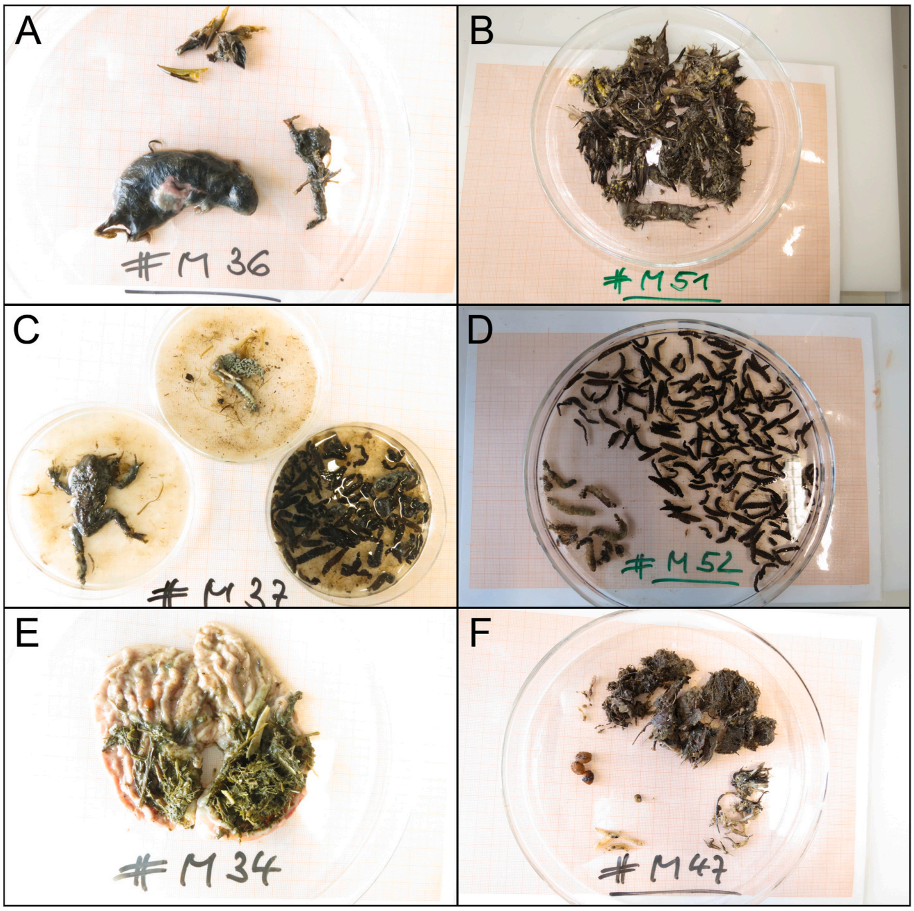

Fig. 2. Examples of different stomach contents of the examined raccoon dogs, A-F each from one stomach. A: mouse, plants, amphibian; B: grass, maize, feathers and bird foot; C: amphibian, insects; D: insects; E: opened stomach filled with grass; F: hair, plant material, feathers, bones and hair.

for the mammals not further identified. This indicates that raccoon dogs feed on what is immediately available. This also underlines the suggestion that *N. procyonoides* may be a problem for smaller, locally occurring, and potentially endangered animal populations if it feeds on this one food source over an extended period of time (Sutor et al., 2010). The fact that the amphibian and fish species were found in low numbers in the stomach contents is due to the time of year, as these species are rarely active in winter, retreating to frost-proof locations (Hurst, 2007; Glandt, 2016) and thus are not a suitable food source at this time of year. Nevertheless, two amphibian species could be detected, the common toad *Bufo bufo* and the grass frog *Rana temporaria*, which have the status "especially protected" according to the Federal Nature Conservation Act (BNatSchG) and the Federal Species Protection Ordinance (BArtSchV). *R. temporaria* is also on the early warning list of the German Red List Centre. Also rather inactive in winter are insects such as the soldier beetle *Cantharis fusca* or the large yellow underwing *Noctua pronuba*,

Table 4
Parasitological calculation on the infection with endo- and ectoparasites of the examined raccoon dogs. Prevalence [%], Mean and Maximum Intensity and Mean Abundance were calculated for M = Male (N = 37), F = Female (N = 36) and all animals M + F (N = 73).

Male (M)/ Female (F)	Value	Ectoparasites							
		Ixodes canisuga	*Ixodes hexagonus*	*Ixodes ricinus*	*Ixodes* spp.	*Dermacentor reticulatus*	*Trichodectes canis*	*Archaeopsylla erinacei*	*Chaetopsylla globiceps*
M	Prevalence [%]	40.54	35.14	51.35	40.54	0.00	59.46	16.22	29.73
	mean Intensity	23.13	5.85	4.00	9.20	0.00	37.05	2.83	7.82
	max. Intensity	137.00	52.00	16.00	49.00	0.00	313.00	12.00	39.00
	mean Abundance	9.38	2.05	2.05	3.73	0.00	22.03	0.46	2.32
F	Prevalence [%]	30.56	22.22	22.22	33.33	5.56	47.22	13.89	33.33
	mean Intensity	26.09	3.63	13.00	6.50	2.00	57.71	1.20	4.67
	max. Intensity	128.00	14.00	59.00	19.00	3.00	360.00	2.00	11.00
	mean Abundance	7.97	0.81	2.89	2.17	0.11	27.25	0.17	1.56
M + F	Prevalence [%]	35.62	28.77	36.99	36.99	2.74	53.42	15.07	31.51
	mean Intensity	24.38	5.00	6.67	8.00	2.00	46.05	2.09	6.17
	max. Intensity	137.00	52.00	59.00	49.00	3.00	360.00	12.00	39.00
	mean Abundance	8.68	1.44	2.47	2.96	0.05	24.60	0.32	1.95

whose larvae may have been dug up by the raccoon dog. Only the blowfly *Calliphora vicina*, will have been ingested here by eating carrion, since that is where the eggs of this species are laid (Reibe and Madea, 2010) and not by actively eating this species. In the case of mammals and birds, it is not possible to distinguish with certainty whether the animals were actively hunted or whether ingestion of carrion was involved. Only in the case of the wild boar *Sus scrofa*, European fallow deer *Dama dama* and roe deer *Capreolus capreolus* it can be assumed, based on the size of the animals, that they were not actively hunted but consumed as carrion by the raccoon dog. The remaining food components of the large group of mammals consist mainly of small rodents such as wood mouse and common vole. Some studies already show that birds are also part of the food spectrum. For example, Dahl and Åhlén (2019) proved the scavenging of nests of ground-nesting birds after the observed raccoon dogs had scared away the adults. However, because eggshells are usually not eaten, reliable detection later is often difficult. Three of the bird species recorded here, Mallard *Anas platyrhynchos*, Greylag Goose *Anser anser*, and Canada Goose *Branta canadensis*, breed on the ground (Langgemach and Bellebaum, 2005), making them easy prey for the raccoon dog. The song thrush *Turdus philomelos*, on the other hand, breeds in trees (Spaar and Hegelbach, 1994), so this species may have been ingested by eating carrion, which of course cannot be ruled out for the other three bird species. Further stomach contents could be assigned to the large group of birds, but could not be determined to species. Accordingly, with an IRI of 470.86, this group also represents an important dietary component, again indicating active predation rather than carrion feeding.

4.3. Ectoparasites

A total of four tick species were identified (*I. canisuga*, *I. hexagonus*, *I. ricinus*, *D. reticulatus*). Ticks are considered vectors of numerous pathogens, some of which can be human pathogenic and cause diseases such as Lyme disease or tick-borne encephalitis (TBE) (Süss and Schrader, 2004; Stanek, 2005). *Ixodes canisuga*, is widely distributed in Europe and can infest a wide range of hosts, including primarily carnivores and other mammals, but also birds (Hillyard, 1996; Sándor, 2017). Infestation of humans has not been reported to date (Estrada-Peña and Jongejan, 1999). In Germany, *I. canisuga* primarily infests foxes (Meyer-Kayser et al., 2012; Najm et al., 2014), but also dogs, minks and stone martens (Gothe et al., 1977; Christian, 2010; Waindok et al., 2021). Infestation of raccoon dogs with this tick species has not been known in Germany before. *Ixodes hexagonus* is one of the most common tick species in Europe (Camacho et al., 2003; Nijhof et al., 2007) and predominantly infests hedgehogs (Dziemian et al., 2014), but also carnivores (Claerebout et al., 2013) and has been described in tanuki from Poland and elsewhere (Wodecka et al., 2016). *Ixodes ricinus* is the most prevalent tick species in Europe that parasitizes mainly on mammals and has a very wide host range (Randolph, 2009; Medlock et al., 2013; Rizzoli et al., 2014). Matysiak et al. (2018) previously observed this tick species in the subcutaneous tissue of raccoon dogs in Poland. *Dermacentor reticulatus* can also infest a wide range of hosts, which includes humans and it shows high tolerance to a changing environment (Földvári et al., 2016; Matysiak et al., 2018). This could be the reason why *D. reticulatus* has been spreading more and more in Europe since 1990 (Rubel et al., 2016; Karbowiak, 2021). That this species also parasitizes on raccoon dogs is already known (Matysiak et al., 2018). The tick species identified here all have a very high host range, which is mainly mammals. Thus, the raccoon dog is a suitable host and can be infested while, for example, roaming through grasses and bushes in search of food.

Trichodectes canis (Fig. 3B) was the most common ectoparasite with a prevalence of 53.42%, but it was also the only louse species detected in this study. Canine chewing lice feed on scales and wound secretions of the infested host. Since larval development takes only 3–6 weeks, spread can be very rapid. *T. canis* most commonly parasitizes on dogs (Mehlhorn and Mehlhorn, 2020) and has already been described for raccoon dogs for example in the Czech Republic and Japan (Bádr et al., 2005; Oi et al., 2015). Transmission of this parasite occurs through physical contact or use of the same burrow or den of an infested animal. The ecological niche of raccoon dogs overlaps with that of foxes and badgers and they often use the same burrows (Nowak, 1984; Baltrūnaitė, 2002; Saeki et al., 2007), so infestation with *T. canis* via, for example, infested foxes in the same burrow is conceivable.

Four species of fleas have been identified. *Archaeopsylla erinacei* is a parasite adapted to the European brown-breasted hedgehog, but it also infests other mammals such as dogs and cats (Brinck-Lindroth and Smit, 2007; Gilles et al., 2008; Hornok et al., 2014) and rarely humans (Greigert et al., 2020). It occurs in hedgehogs with high infestation rates of up to 1000 individuals per animal (Boch, 2006). *Ctenocephalides felis* primarily uses cats as hosts but can infest up to 70 other hosts, including dogs and humans (Visser et al., 2001; Brinck-Lindroth and Smit, 2007). *C. felis* can also act as an intermediate host for various nematodes and tapeworms and is equally known to cause flea allergy dermatitis (FAD) (Dryden and Rust, 1994). Since fleas are transmitted through contact with infected animals, this means that the infested raccoon dog must have been in the vicinity of cats, respectively their sleeping or resting places. However, since only one specimen of *C. felis* was identified in this study, it is more likely an accidental finding. With a prevalence of 31.51%, the fox flea *Chaetopsylla globiceps* (Fig. 3A) was the most frequently detected flea species. Foxes are the main hosts of this flea but other canines are also infected (Visser et al., 2001; Foley et al., 2017;

Ectoparasites		Endoparasites								
Ctenocephalides felis	*Paraceras melis*	*Alaria alata*	*Isthmiophora melis*	*Echinococcus multilocularis*	*Mesocestoides litteratus*	*Taenia* sp.	*Capillaria aerophila*	*Porroceacum depressum*	*Toxocara canis*	*Uncinaria stenocephala*
2.70	37.84	35.14	24.32	10.81	10.81	5.41	8.11	16.22	56.76	67.57
1.00	3.36	46.62	16.22	479.50	4.50	14.50	1.00	2.67	3.43	8.56
1.00	19.00	165.00	89.00	1509.00	13.00	28.00	1.00	9.00	8.00	41.00
0.03	1.27	16.38	3.95	51.84	0.49	0.78	0.08	0.43	1.95	5.78
0.00	11.11	44.44	22.22	5.56	16.67	11.11	0.00	13.89	44.44	69.44
0.00	1.25	14.94	9.00	969.50	75.00	9.75	0.00	1.00	5.06	8.96
0.00	2.00	51.00	48.00	1479.00	257.00	21.00	0.00	1.00	25.00	48.00
0.00	0.14	6.64	2.00	53.86	12.50	1.08	0.00	0.14	2.25	6.22
1.37	24.66	39.73	23.29	8.22	13.70	8.22	4.11	15.07	50.68	68.49
1.00	2.89	29.14	12.82	642.83	46.80	11.33	1.00	1.91	4.14	8.76
1.00	19.00	165.00	89.00	1509.00	257.00	28.00	1.00	9.00	25.00	48.00
0.01	0.71	11.58	2.99	52.84	6.41	0.93	0.04	0.29	2.10	6.00

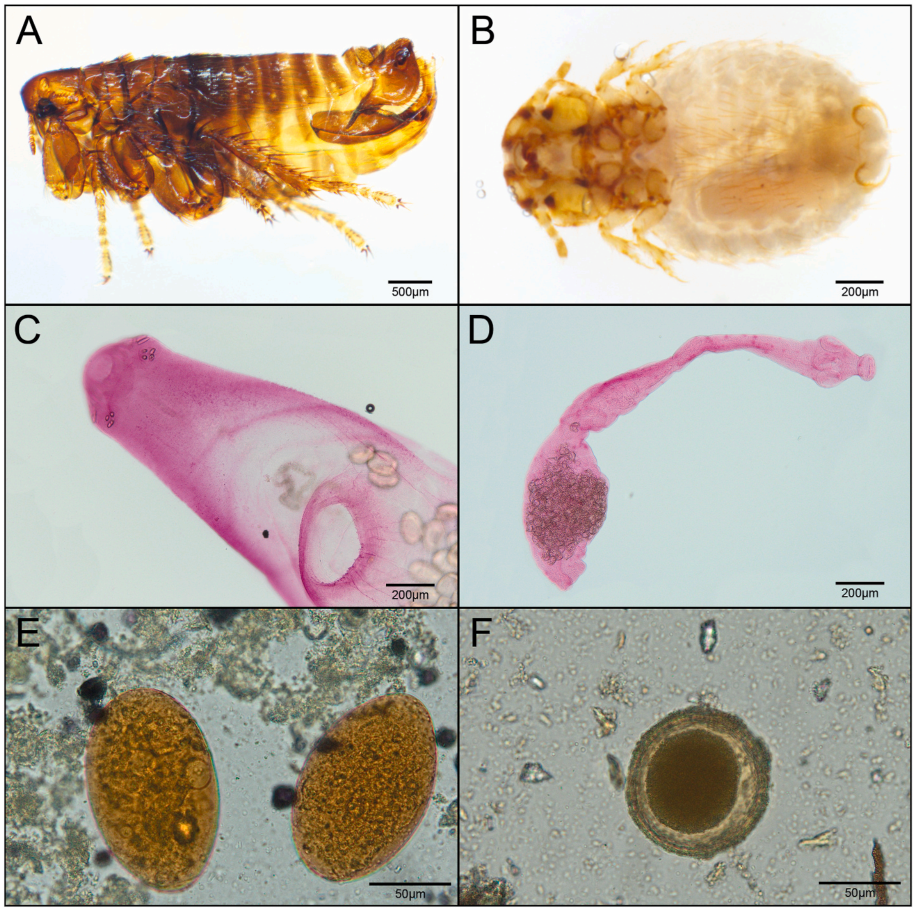

Fig. 3. Examples of ecto- and endoparasites and parasite eggs found in fecal investigation of the examined raccoon dogs, A-B ectoparasites, C-D endoparasites, E-F eggs from endoparasites found through MIFC. A: *Chaetopsylla globiceps*; B: *Trichodectes canis*; C: *Isthmiophora melis*; D: *Echinococcus multilocularis*; E: eggs from *Alaria alata*; F: Egg from *Toxocara canis*.

Table 5
Results of the Merthiolate-Iodine-Formaldehyde-Concentration (MIFC) for analyzing the fecal samples for parasitic development stages. Calculated was the Prevalence [%] for all animals (N = 71).

		Digenea	Cestoda			Nematoda			Coccidia	
Male (M)/ Female (F)	**Value**	***Alaria alata***	***Echinococcus multilocularis***	***Mesocestoides* sp.**	***Taenia* sp.**	***Toxocara canis***	***Uncinaria stenocephala***	***Capillaria* sp.**	***Isospora* sp.**	***Monocystis* sp.**
M	**Prevalence**	14.08	2.82	1.41	4.23	7.04	1.41	8.45	2.82	4.23
F	**[%]**	14.08	2.82	2.82	4.23	8.45	2.82	7.04	1.41	9.86
M + F		28.17	5.63	4.23	8.45	15.49	4.23	15.49	4.23	14.08

Waindok et al., 2021). Raccoon dogs are systematically assigned to foxes, use the same dens and thus represent a quite suitable host for *C. globiceps*. It can therefore easily be transferred from fox to raccoon dog and vice versa. *Paraceras melis* is a species that is typically parasitic on badgers, but has also been found in martens or dogs (Visser et al., 2001; Brinck-Lindroth and Smit, 2007). The species is also commonly found in foxes (e.g. Foley et al., 2017), which as in *C. globiceps* is due to the continuous use of the same burrows by raccoon dogs, badgers and foxes in the study area. Partly low flea infestation may be due to the fact that fleas leave their host very quickly when the host dies (Hsu and Wu, 2001). Thus, it is likely that the flea infestation of the raccoon dogs could have been much higher than detected here, since the fleas had already left the animal before it was frozen in the plastic bag for later examination. The large number of detected ectoparasite species on raccoon dogs in the present study underlines the need for intensive screening of ectoparasites. Because ectoparasites such as ticks can be vectors of a variety of disease-causing pathogens that can sometimes be dangerous to humans, it is important to continue to study the distribution and occurrence of potential reservoir hosts and their ectoparasites, including the raccoon dog. Ultimately, the results show that the raccoon dog has a similar ectoparasitic fauna as the fox or badger. On the one hand, this can be explained by the relationship, but also by the similar way of life, since often the same habitats and burrows are used (Nowak, 1984; Baltrūnaitė, 2002; Saeki et al., 2007; Kutzscher and Weber, 2015).

4.4. Endoparasites

Nine endoparasites (two digeneas, three cestodes, four nematodes) were detected during the examination of the internal organs. The fluke *Alaria alata*, occurred in almost 40% of the examined raccoon dogs. This species is distributed worldwide and parasitizes in the small intestines of carnivores. Larval development requires two intermediate hosts (1. Intermediate host snails, e. g. *Planorbis planorbis*; 2. Intermediate host amphibians, e. g. *Rana temporaria* (Wasiluk, 2013)) (Fig. 4). Infection of the final host occurs by eating the second intermediate host infected with mesocercaria or by paratenic hosts, which may represent a variety of animal species. *A. alata* is therefore also a potential risk to human health, as if undercooked meat (e. g. from wild boar) infected with *A. alata* is consumed, humans may become infected. The resulting disease is called alariasis and may have respiratory and cutaneous effects (Bialasiewicz, 2000; Möhl et al., 2009; Zajac and Conboy, 2012). In addition to the raccoon dog, foxes and raccoons are also known as final hosts in Europe (Bružinskaitė-Schmidhalter et al., 2012; Al-Sabi et al., 2013; Duscher et al., 2017; Lempp et al., 2017; Korpysa-Dzirba et al., 2021; Pilarczyk et al., 2022; Peter et al., 2023). The stomach content analyses of this study revealed that amphibians are food organisms for the raccoon dog, including the grass frog *R. temporaria*, which serves as a second intermediate host for *A. alata*. Thus, it is clear that the infection of raccoon dogs can be traced back to the feeding of these infected animals (Fig. 4). *R. temporaria* was detected in the stomach contents with an IRI of 34.13, but almost 40% of the raccoon dogs studied were infected with *A. alata*, suggesting that far more amphibians were eaten than could be detected in the stomach contents analysis in this study. *Isthmiophora melis* (Fig. 3C) is distributed in Europe, Asia and North America, with the freshwater snail *Lymnaea stagnalis* as the first intermediate host and various species of amphibians and freshwater fish as the second intermediate host (Radev et al., 2009). As the final host, a large number of vertebrates can ultimately be infected, including humans. Since amphibians are part of the raccoon dog's diet, the presence of *I. melis* in the *N. procyonoides* studied is due to predation by amphibians, which must have been infected with this parasite. An infection of raccoon dogs in Germany is already known (Schuster and Shimalov, 2017).

Of the three cestode species, *Echinococcus multilocularis* (Fig. 3D) occurred only in a few animals, but with a maximum intensity of 1509 individuals. The fox tapeworm infests foxes, as intermediate hosts serve small mammals, mostly rodents and also humans can become infected. As a highly pathogenic parasite, *E. multilocularis* can cause human echinococcosis (Craig, 2003). According to RKI (Robert Koch-Institut, 2021) there were a total of 135 cases of echinococcosis in Germany in 2020, of which only 55 suggest Germany as the country of origin of the infection. Already in a previous study by Schwarz et al. (2011) it has been shown that raccoon dogs can act as hosts for the fox tapeworm in Germany. The infection may be due to the close relationship of raccoon dogs with foxes and also to the diet. The stomach content analyses were able to detect, among other things, four rodent species as food, which are suitable intermediate hosts for the fox tapeworm in the study area (Fig. 4). The results of this study confirm the raccoon dog as a suitable final host of *E. multilocularis*. In the future, the focus should continue to be on the contamination of raccoon dogs in order to clearly show whether they play a central or rather subordinate role in the life cycle of the fox tapeworm. The life cycle of *Mesocestoides litteratus* is not yet completely known, but it can be said that the genus *Mesocestoides* parasitizes as an adult mainly in the small intestine of carnivores. In Europe, this is often the fox (Literák et al., 2006). Already Schuster and Shimalov (2017) were able to determine *Mesocestoides litteratus* from raccoon dogs. Species of *Taenia* spp. have a rostellum with hooks, but the genus is characterized by a high individual variability of the morphological criteria, which may possibly be due to the influence of the final host (Sweatman and Henshall, 1962; Verster, 1969). Thus a purely morphological determination is very difficult, since various species occur in the genus *Taenia*. However, genetic testing also proved to be difficult because the genetic values identified several species to the same extent. Certainly this tapeworm could not be determined at species level. However, it may also be explained by the fact that several *Taenia* species were co-infected in the examined raccoon dogs, but they could not be separated further. This could confirm previous results, since in Germany so far *T. krabei* in wolves, as well as *T. polyacantha* and *T. crassiceps* in foxes and raccoon dogs were described (Priemer et al., 2002; Schuster and Shimalov, 2017).

Capillaria aerophila was a rare endoparasite in this study with a prevalence of 4.11%. This nematode is widespread worldwide and parasitizes in the respiratory tract (trachea, bronchi, bronchioles) of dogs, cats and other carnivores and can also infect humans. Eggs are ingested either from the environment or by earthworms acting as optional intermediate hosts (Bowman et al., 2008; Burgess et al., 2008; Traversa et al., 2011). The parasitism of *C. aerophila* in raccoon dogs has already been reported in Denmark, Lithuania and Germany (Bružinskaitė-Schmidhalter et al., 2012; Schuster and Shimalov, 2017; Lemming et al., 2020). *Porrocaecum depressum* is a globally distributed

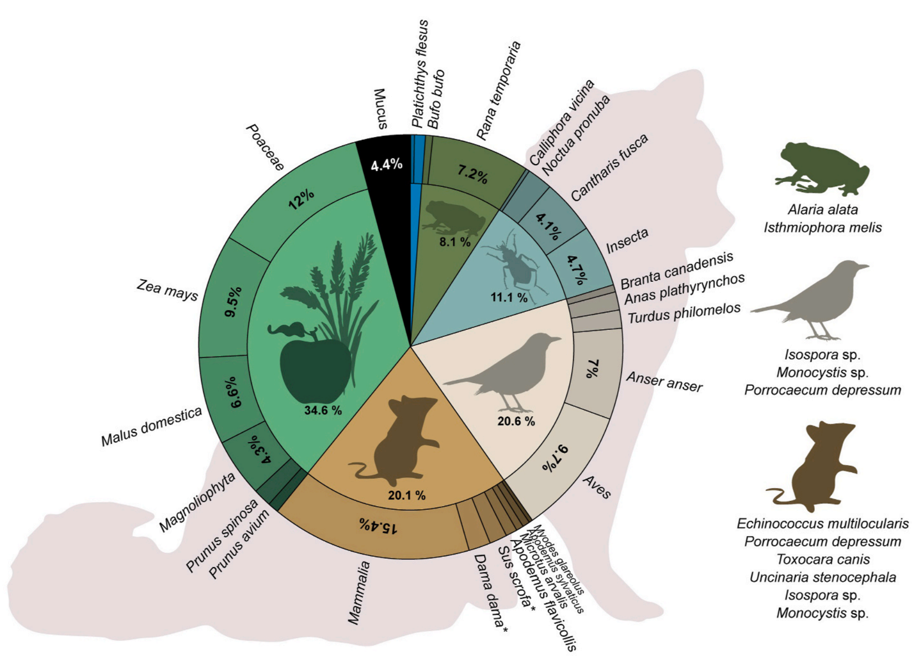

Fig. 4. Diet of the raccoon dog *Nyctereutes procyonoides* according to percentages of the individual components, components that cannot be further determined are summarized in the respective class, with * marked species are most likely to have been eaten as carrion. On the right side are listed the parasites, which are transmitted via a known intermediate host, which made up part of the food of the examined animals.

nematode species that parasitizes in the small intestines of birds of prey (Morgan and Schiller, 1950). The life cycle is terrestrial, earthworms serve as intermediate hosts, with smaller mammals serving as paratenic hosts (Fagerholm and Overstreet, 2008). Since *P. depressum* is not a typical parasite species in foxes or other canids, it can be assumed that it is a so-called intestinal passer that has been ingested via food. The presence of *C. aerophila* and *P. depressum* is therefore an indication that the infected raccoon dogs must have fed on earthworms, small mammals and/or birds, otherwise infection could not have occurred. The dog roundworm *Toxocara canis* occurred in about half of the examined raccoon dogs. This roundworm parasitizes in dogs and foxes worldwide and has a high importance for human medicine. The development of *T. canis* takes place in a single host, often puppies are infected more often than adults, transmission via the placenta as well as transmammary transmission is possible. Rodents or other small mammals can be included in the life cycle of the parasite as paratenic hosts, where the larvae penetrate the intestinal wall and migrate to the organs, where they can survive infectious for several years (Lucius et al., 2018). Humans can also be infected, which can lead to visceral or ocular larva migrans (Schnieder et al., 2011). The fact that the raccoon dog belongs to the canine species and is therefore a suitable host explains the occurrence of this parasite. The dog roundworm has also been described as a parasite in raccoon dogs in further studies from Poland, Lithuania, Denmark, Austria and Germany (Bružinskaitė-Schmidhalter et al., 2012; Al-Sabi et al., 2013; Duscher et al., 2017; Schuster and Shimalov, 2017; Waindok et al., 2021; Pilarczyk et al., 2022). *Uncinaria stenocephala* was recently identified as an endoparasite. In addition, this species was the most common nematode species with a prevalence of 68.49% and a maximum intensity of 48. This type of hookworm is common in dogs (Bowman et al., 2010). Infection occurs via free-living larvae or paratenic hosts (e. g. mice). If humans become infected, it can lead to the cutaneous larva migrans (Bowman et al., 2010; Štrkolcová et al., 2022). The infection of the studied raccoon dogs was probably caused to a large extent by eating infected mice, which could have been species such as *Microtus arvalis* which could be detected in this study.

The identified parasite species and the food spectrum in general provide indications of parasitization and vice versa which is shown in Fig. 4. As described above, the two trematode species *A. alata* and *I. melis* require two intermediate hosts in their development cycle, while both species use amphibians as their second intermediate host. Thus, the presence of these parasites in raccoon dogs is already an indication that amphibians belong to their food spectrum. The fact that two species, *B. bufo* and *R. temporaria* could be detected in the stomach contents further confirms the results. Many cestodes, such as the fox tapeworm *E. multilocularis*, usually use small mammals and rodents as intermediate hosts (Craig, 2003). These are part of the raccoon dog's diet, as shown by this study and others (e.g. Baltrūnaitė, 2002; Sutor et al., 2010), so the infection with these parasites is easily explained. The nematode species *P. depressum* is a parasitic species in the small intestines of birds. The evidence that the raccoon dog feeds on birds could explain the occurrence of this nematode in the small intestines of the raccoon dogs investigated. Since *N. procyonoides* is not one of the actual hosts, this infection can only be interpreted as an intestinal passer that was ingested via the feeding on earthworms as an intermediate host, or the feeding on birds.

4.5. Fecal examination

The fecal examination via MIFC confirmed the presence of seven endoparasite species: *A. alata* (Fig. 3E), *E. multilocularis*, *Mesocestoides* sp., *Taenia* sp., *Capillaria* sp. *T. canis* (Fig. 3D) and *U. stenocephala*. In addition, two other species (Apicomplexa) were detected by this method. *Isospora* sp. is usually found in the small intestine of dogs or cats. Infection occurs through the ingestion of sporulated oocysts or through paratenic hosts such as rodents, birds or other prey animals that are consumed by the final host. Younger animals are often infected, and infection may lead to diarrhea or weight loss (Zajac and Conboy, 2012). *Monocystis* sp. parasitizes in the seminal vesicles of the earthworm *Lumbricus terrestris*. Infection occurs via ingestion of sporozoites from the soil (Field et al., 2003; Field and Michiels, 2006). This parasite is widespread, so that almost every population of earthworms is infected with *Monocystis* sp., the further spread is via the excrements of birds that feed on earthworms (Lucius et al., 2018). This suggests that the infected raccoon dogs must have eaten either earthworms or birds. The results of the two examination methods dissection and MIFC on parasite infection of raccoon dogs show clear differences. Although the two other species, *Isospora* sp. and *Monocystis* sp. which, presumably due to their small size, could not be found by the dissection, but many more parasite species were discovered during the examination of the organs. In addition, the MIFC does not allow any statement about the infestation of ectoparasites, nor about the intensity or abundance of the infection with endoparasites, quite the opposite of dissection. For example, if we look at *U. stenocephala*, the most commonly identified endoparasite, it could only be confirmed with a prevalence of 4.23% in the fecal examination, while it could be detected with a mean intensity of 8.76 in 68.49% of the examined raccoon dogs. These results underline that, in order to obtain the best possible result, a combination of both methods should be used to detect an infection with parasites, because with only one method something can easily be overlooked or not be detected at all.

The present study confirms the hypothesis that the raccoon dog, as an invasive alien species, plays a role as a predator of native animal species and may endanger human and animal health due to the spread of parasites and other pathogens. Comprehensive, continuous data should be collected over the entire new range of *N. procyonoides* in order to better assess its impact and to develop appropriate management methods to help manage this invasive species in the best possible way.

Author's contributions

Anna V. Schantz designed and conceptualized the study, wrote the main manuscript text, executed the laboratory and statistical analysis, interpreted the data and prepared Figs. 1–4. Dorian D. Dörge executed the statistical analysis, interpreted the data and prepared Figs. 2–4. Norbert Peter designed and conceptualized the study, executed the laboratory analysis and interpreted the data. Sven Klimpel designed and conceptualized the study, interpreted the data and wrote the manuscript. All authors reviewed the manuscript and approved the final draft.

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Declaration of competing interest

The authors declare no competing interests.

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