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Original paper

Environmental effects of anthropogenic waste on intestinal nematode parasites of murid rodents in Istria, Croatia

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Summary. The quantity and extent of municipal solid waste is rising as urbanization, mass consumption, and consumer lifestyles have become more prevalent worldwide. Many cities cannot effectively manage their own waste, which leads to the creation of illegal waste sites. We investigated the potential effects of illegal waste dumping on the qualitative and quantitative characteristics of rodent-parasite communities in semi-natural habitats. In particular, we studied spatial host-parasite turnover rates as a function of urbanization and the presence of illegal waste sites for four species of the family Muridae: house mouse (*Mus musculus*), wood mouse (*Apodemus sylvaticus*), striped field mouse (*A. agrarius*), and yellow-necked mouse (*A. flavicollis*). Eleven species of intestinal nematodes were found, with varying levels of prevalence, mean infection intensity and mean abundance in different habitat types. We found that the composition of parasite communities did not depend on the level of habitat degradation, although it did depend on the host community structure. Generalized Linear Model analysis showed that there was no relationship between negative anthropogenic disturbances of natural habitat and parasite abundance. However, the prevalence of *Syphacia stroma*, *S. frederici, S. obvelata*, *Heterakis spumosa* and *Rictularia proni* was significantly different between different types of habitat disturbance. These results suggest that human disturbances affect the presence and species composition of intestinal nematodes of mice at specific sites, although further and more systematic research on a larger scale is necessary.

Key words: anthropogenic influence, nematodes, parasitism, solid waste management.

INTRODUCTION

Illegal waste sites are among the most rapidly increasing threats to natural habitats associated with urbanization, and represent a significant type of human disturbance. By facilitating the spread of invasive species, disease vectors, pathogens and pollution, illegal waste dumps cause biodiversity loss, affect species interactions and harm human health (Vrijheid 2000; McKinney 2008). The rapid development of urban ecosystems generates massive amounts of waste, and landfills are the most frequent waste disposal method worldwide (Komilis et al. 1999). An increase in waste stockpiling has led to serious management problems on a planetary scale (Rodríguez et al. 2007). The expansion of urban areas into natural habitats causes significant changes in species compositions and interactions, and also impacts ecological and evolutionary processes (McKinney 2008; Aronson et al. 2014). Waste sites provide a ready source of nutrition and shelter for human-introduced rodents (Rusterholz et al. *2*012). It is well known that rodents are involved in the transmission of diseases to humans and domestic animals (Battersby and Greenwood 2004). They are a notorious reservoir for a number of pathogens and can act as either principal hosts or hosts for arthropod vectors (Desjeux 2001).

To date, the effect of uncontrolled waste dumping on the distribution of rodents and their parasites within urban and semi-natural environments has not been particularly studied. The effect of illegal waste sites on parasites and host-parasite interactions can be investigated in relation to parasite species richness and parasite prevalence. In Europe, many parasitological studies on helminth communities of small mammals have been conducted, focusing mostly on the wood mouse *Apodemus sylvaticus* (e.g. Behnke et al. 1999;

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Abu-Madi et al. 2000; Goüy de Bellocq et al. 2003; Fuentes et al. 2004; Eira et al. 2006; Milazzo et al. 2010). Other species, such as *Apodemus agrarius* and *A. flavicollis*, have attracted comparatively less attention in this regard. The prevalence of metazoan parasite fauna of *A. flavicollis* and *A. sylvaticus* from Germany was reported by Klimpel et al. (2007); while the prevalence of helminth species in *A. agrarius* from Belarus was studied by Shimalov (2002), and Hildebrand et al. (2009) reported on the nematode fauna of the striped field mouse and the yellow-necked mouse in Poland.

Evaluation of helminthiases of rodents in different zoogeographical areas is necessary due to the impact of rodent-associated diseases on human and livestock health. In addition, the study host-parasite networks in anthropogenic habitats has also been proposed in order to understand the mechanisms of urbanization disturbances (Minchella and Scott 1991). Because anthropogenic habitats mainly negatively impact species occupancy, abundance and co-occurrence, we can expect a link between spatio-temporal habitat changes and the characteristics of host and parasite communities.

The Istrian peninsula is characterized by medium-sized towns located on the coast that are oriented towards tourism, which considerably increases human concentration and waste production (Bužan et al. 2017). An additional source of waste dumping is created by small towns, villages, and small farms that are mainly dispersed in the central part of the peninsula (Gržinić 2010). A recent study published by Bužan et al. (2017) showed that commensal and non-commensal rodents are attracted by solid and decomposing organic waste discarded at illegal waste sites. The results of the same study have also shown that the seroprevalence of Lymphocytic choriomeningitis virus (LCMV) infection of rodents trapped at illegal waste sites was higher compared to LCMV infection of rodents from their natural environment.

The aim of this study was to assess the potential effects of illegal waste dumping on the establishment of rodent-parasite communities in semi-natural habitats. In particular, we examined differences in host and parasite community composition as a function of urbanization and the presence of illegal waste sites. Higher parasitism and infection rates (Bužan et al. 2012) of animals in illegal waste sites could be significantly associated with changes in the rodent communities. Rodents at these sites are either more exposed or more susceptible to parasites or infections, which potentially could have negative impacts on their predators and people. Monitoring parasitism and infection rates can therefore be used to measure the impact of altered rodent communities on other species that occur with them in the same geographic area.

MATERIALS AND METHODS

Study area

Fieldwork was conducted in Istria, a peninsula in the northern Adriatic shared by Italy, Slovenia and Croatia. The geological and geomorphic structure of the Istria peninsula can be divided into three different areas (Sombke and Schlegel 2007). The hilly northern and north-eastern part of the peninsula is characterized by scarce vegetation and bare karst surfaces. The south-western region is characterized by lower flysch mountainous tracts consisting mainly of impermeable marl, clay, and sandstone. Finally, the last part is the limestone terrace along the coastline covered with red soil (Krebs 1907).

One third of the Istrian peninsula is covered by forest. Pinewoods, maquis, holm oak (*Quercus ilex*) and strawberry trees (*Arbutus unedo*) prevail along the coast and on the islands. The grasslands located here are among the most species-rich habitats of Europe and maintain high small-scale densities of plant species (Kaligarič et al. 2006). They are of semi-natural origin, as they have emerged through centuries or millennia of low-intensity land use (Bohn et al. 2004; Ellenberg and Leuschner 2010). During the 20th century, the original grasslands were replaced by agrosystems, which are nowadays continuously being replaced by urban habitats. Today, the area represents a matrix of mixed urban, agricultural, and fragmented natural or semi-natural vegetation patches.

Field data collection

Sites for data collection were located at illegal waste sites designated as groups (A–C). Sherman traps of two sizes (small: 50.08 x 6.35 x 22.86 cm; large: 7.62 x 8.89 x 22.86 cm) in equal shares were used. Sardines with breadcrumbs or peanut butter were used as bait (for description of locations and trapping protocol, see Bužan et al. 2017).

The sampling sites differed significantly according to anthropogenic impact (Bužan et al. 2017) and were divided into three categories: natural habitats with low anthropogenic impact (A), habitats with medium anthropogenic impact which include small waste sites (B), and habitats with high anthropogenic impact with large waste sites and/or human settlements (C) (Fig. 1). To aid in identification, animals were weighed and total head-body length, tail, ear and hind foot lengths were measured. Blood from the axillary artery was centrifuged and sera were labeled and stored at -80 °C. Internal organs were labeled and stored at -80 °C until further use. Permits for work with animals and animal tissues were issued by the Ministry of Culture of the Republic of Croatia (No. 532-08-01-01/1-11-03) and the Veterinary Administration of the Republic of Slovenia (No. 34401-36/2012/9).

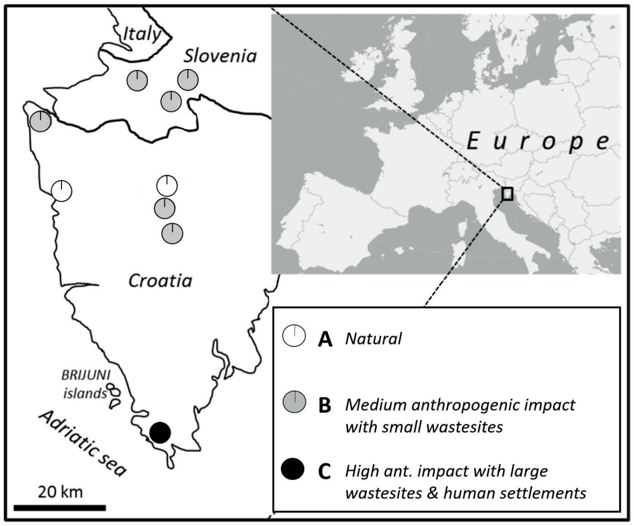

Fig. 1. Sampling sites in Istria.

Rodent identification

Identification of rodents based solely on morphological characteristics can lead to misinterpretations of species, especially for juvenile individuals (Bradley and Baker 2001). Therefore, we used amplification of fragments of the mitochondrial cytochrome b gene for species validation. The partial cytochrome b gene (500 base pairs) was amplified using universal primers and the polymerase chain reaction (PCR) (Jaarola and Searle 2002)75 specimens from 56 localities across Eurasia were examined for DNA sequence variation along the whole 1140 base pair (bp. Cycling conditions consisted of an initial stage of 95 °C, for 3 min followed by 30 cycles of denaturation (15 s at 95 °C), primer annealing (30 s at 60 °C) and extension (1 min at 72 °C). Final extension was performed at 72 °C for 10 min. 3 µl of DNA was used in PCR reactions for molecular identification of species. Sequencing reactions were done on an ABI 3130 Genetic Analyzer (Life Technologies) using BigDye Terminator Chemistry. Species were later determined using the BLAST algorithm (NCBI).

Parasitological analysis

The sample consisted of 67 individuals of four species: striped field mouse *(Apodemus agrarius,* 10 individuals), yellow-necked mouse (*A. flavicollis,* 15 individuals), wood mouse (*A. sylvaticus,* 27 individuals) and house mouse (*Mus musculus,* 15 individuals). All of the animals were delivered to the Laboratory of Animal Ecology at the Faculty of Sciences of the University of Novi Sad, Serbia, and kept in a freezer until dissection. The intestinal tract was removed from each mouse and cut into four segments (stomach, large intestine, caecum and colon/rectum) which were placed in separate Petri dishes filled with tap water. Each part of the intestinal tract was cut longitudinally to release its contents, which were then transferred to larger 250 mL conical glasses filled with tap water. The supernatant in each glass was decanted and replaced with more water until it became clear. At this point, excess water was removed and only a small volume containing the intestinal segment and its contents was examined under a stereo microscope. All nematodes were extracted and conserved in 70% ethanol. Species identification of intestinal nematodes was based on native slides prepared in lactic acid. Individuals were measured and their morphological traits were observed under an optical microscope. Morphological and morphometric characters were used to identify the species based on keys by Ryzhikov et al. (1979) and Genov (1984).

For each nematode species and for intestinal nematodes in general, quantitative parameters of infection were calculated both for the total host sample containing all mice species, as well as for each host species individually. These quantitative parameters are defined by Bush et al. (1997) and were calculated in QPweb (Reiczigel et al. 2019) along with 95% confidence intervals. The software also calculated the dispersion index, or the variance to mean ratio, which is a suitable measure of parasite aggregation levels within their hosts (Shaw and Dobson 1995). When this ratio is larger than one, parasite distribution is aggregated.

Parasite abundance data were fitted to a Generalized Linear Model (GLM), which allows for assessment of the relationships between specific factors and a numeric response, in this case the abundance of intestinal nematodes. The factors used were host species, host sex and habitat type (A, B or C, in accordance with field data collection; see above), as well as their two-way interactions. If the relationship between a specific factor and parasite abundance proved to be non-significant, that factor was excluded in a stepwise fashion, until only statistically significant factors and/or interactions remained. GLM analysis was performed both for intestinal nematodes as a whole, and for each individual parasite species. Additionally, the prevalence of intestinal nematode infection was compared between the three habitat types using Fisher's exact test in QPweb.

RESULTS

A total of 11 species of intestinal nematode parasites were identified from the four host species: *Aspiculuris tetraptera*, *Heligmosomoides laevis*, *H. polygyrus*, *Heterakis spumosa*, *Physaloptera* sp., *Rictularia proni*, *Syphacia agraria*, *S. frederici*, *S. obvelata*, *S. stroma* and *Trichuris muris*. Yellow-necked and wood mice both carried a total of seven parasite species. House mice were hosts of six, and striped field mice of five different intestinal parasite species. The total number of nematodes found in the 67 mice was 2838, half of which (1417, or 49.9%) were from *A. flavicollis*.

Flatworms were present sporadically. There were two digenean species: one specimen of *Brachylaima* sp. in *A. agrarius* and eight specimens of *Plagiorchis elegans* in *A. sylvaticus*. Tapeworms were represented by three species: *Hymenolepis diminuta, H. fraterna* and *H. straminea*. These parasites were registered in small numbers in all analyzed species of hosts and in all three types of site.

Of the 67 mice, 63 were infected with at least one intestinal nematode parasite, resulting in a prevalence of 94.0%. The mean intensity, or average number of parasites per infected host, was 45, whereas the mean abundance was 42.4. The value of the dispersion index was 185.4, signifying a highly aggregated distribution of parasites: the majority of nematodes were found in a small percentage of host individuals. Of the eleven nematode species, *H. polygyrus* had the highest prevalence among the total host sample. However, *S. frederici* had the highest mean infection intensity, mean abundance and dispersion index. It's worth noting that dispersion index values were higher than one for all eleven species, demonstrating their varying levels of clumping within hosts (Table 1).

All ten striped field mice (*A. agrarius*) were infected with intestinal nematodes, with a mean intensity and mean abundance of 41.2. Of the five nematode species found in this host, *H. spumosa* had the highest prevalence, but *S. agraria* had the highest mean intensity and mean abundance of infection, with more individuals present in fewer hosts. Consequently, *S. agraria* had the highest level of aggregation within hosts, with a dispersion index value of 172 (Table 2).

Infection prevalence of yellow-necked mice (*A. flavicollis*) was also 100%, with each mouse carrying 94.5 individual nematodes on average. This heavy load was mostly caused by the very high presence of *S. frederici* (1183 individuals, 83.5% of all nematodes recorded in this host), which had the highest mean intensity and mean abundance values. *Heligmosomoides polygyrus* had the highest prevalence. All values of the dispersion index were greater than one, except for the nematode *T. muris*. The variance to mean ratio for this species was exactly one, indicating a random distribution among the hosts (Table 3).

In the wood mouse (*A. sylvaticus*), intestinal nematodes were found in 26 out of 27 mice (96.3%), resulting in similar values of mean infection intensity (22.5) and mean parasite abundance (21.7). *Heligmosomoides polygyrus* was the most

Table 1. Quantitative infection parameters of individual intestinal nematode species and intestinal nematodes overall for all 67 mice sampled across three different habitat types in Istria, Croatia.

	I	n	d	P%	MI	MA
Aspiculuris tetraptera	5	37	9.1	7.5 (3.0-16.3)	7.4 (3.0-9.8)	0.6 (0.1-1.3)
Heligmosomoides laevis	1	5	5.0	1.5 (0.1-8.0)	5.0	0.1 (0.0-0.2)
Heligmosomoides polygyrus	40	355	60.1	59.7 (47.4-71.0)	8.9 (5.0-23.0)	5.3 (2.8-15.6)
Heterakis spumosa	7	163	37.3	10.4 (5.0-20.0)	23.3 (14.1-47.1)	2.4 (0.9-6.3)
Physaloptera sp.	2	6	3.3	3.0 (0.5-10.2)	3.0 (2.0-3.0)	0.1 (0.0-0.3)
Rictularia proni	13	38	6.9	19.4 (11.3-30.5)	2.9 (1.7-7.0)	0.6 (0.3-1.5)
Syphacia agraria	5	242	178.1	7.5 (3.0-16.3)	48.4 (5.4-166.0)	3.6 (0.3-18.5)
Syphacia frederici	18	1662	272.7	26.9 (17.2-38.8)	92.3 (46.0-187)	24.8 (10.4-57.2)
Syphacia obvelata	6	296	128.9	9.0 (4.0-18.5)	49.3 (14.5-133.0)	4.4 (1.0-15.3)
Syphacia stroma	6	29	12.4	9.0 (4.0-18.5)	4.8 (1.3-12.5)	0.4 (0.1-1.6)
Trichuris muris	3	5	2.2	4.5 (1.2-12.5)	1.7 (1.0-2.3)	0.1 (0.01-0.2)
Intestinal nematodes	63	2838	185.4	94.0 (85.3-97.9)	45.0 (28.8-76.9)	42.4 (26.0-70.8)

I – number of infected hosts; n – number of individual nematodes; d – dispersion index; P% – prevalence; MI – mean infection intensity; MA – mean abundance; 95% confidence intervals in parentheses, where applicable.

Table 2. Quantitative infection parameters of individual intestinal nematode species and intestinal nematodes overall for all 10 striped field mice (*Apodemus agrarius*) sampled across three different habitat types in Istria, Croatia.

	I	n	d	P%	MI	MA
Heligmosomoides polygyrus	3	7	2.2	30.0 (8.7-61.9)	2.3 (1.0-3.0)	0.7 (0.1-1.5)
Heterakis spumosa	6	147	30.0	60.0 (29.1-85.0)	24.5 (13.5-51.0)	14.7 (6.3-33.9)
Physaloptera sp.	2	6	3.0	20.0 (3.7-55.4)	3.0 (2.0-3.0)	0.6 (0.0-1.6)
Rictularia proni	5	10	1.3	50.0 (22.3-77.8)	2.0 (1.2-2.4)	1.0 (0.3-1.6)
Syphacia agraria	5	242	172.0	50.0 (22.3-77.8)	48.4 (6.2-165.8)	24.2 (2.5-105.0)
Intestinal nematodes	10	412	121.2	100.0 (70.9-100.0)	41.2 (14.9-113.0)	41.2 (14.7-113.0)

I – number of infected hosts; n – number of individual nematodes; d – dispersion index; P% – prevalence; MI – mean infection intensity; MA – mean abundance; 95% confidence intervals in parentheses, where applicable.

Table 3. Quantitative infection parameters of individual intestinal nematode species and intestinal nematodes overall for all 15 yellow-necked mice (*Apodemus flavicollis*) sampled across three different habitat types in Istria, Croatia.

	I	n	d	P%	MI	MA
Aspiculuris tetraptera	1	12	12.0	6.7 (0.4-30.2)	12.0	0.8 (0.0-2.4)
Heligmosomoides polygyrus	10	178	113.6	66.7 (39.7-85.8)	17.8 (3.0-73.6)	11.9 (1.8-49.9)
Heterakis spumosa	1	16	16.0	6.7 (0.4-30.2)	16.0	1.1 (0.0-3.2)
Rictularia proni	4	5	1.1	26.7 (9.7-53.4)	1.3 (1.0-1.5)	0.3 (0.1-0.7)
Syphacia frederici	6	1183	313.7	40.0 (19.1-66.8)	197.2 (65.0-351.0)	78.9 (22.8-185.7)
Syphacia stroma	4	22	14.5	26.7 (9.7-53.4)	5.5 (1.0-13.8)	1.5 (0.1-5.3)
Trichuris muris	1	1	1.0	6.7 (0.4-30.2)	1.0	0.1 (0.0-0.2)
Intestinal nematodes	15	1417	260.1	100.0 (77.8-100.0)	94.5 (36.5-199.0)	94.5 (36.5-198.0)

I – number of infected hosts; n – number of individual nematodes; d – dispersion index; P% – prevalence; MI – mean infection intensity; MA – mean abundance; 95% confidence intervals in parentheses, where applicable.

prevalent, whereas *S. frederici* was the most aggregated species, having the highest mean intensity and mean abundance values. All seven nematode species and intestinal nematodes in general showed an aggregated distribution in wood mice (Table 4).

Intestinal nematode prevalence in the house mouse (*M. musculus*) was 80.0%. Two nematode species, *H. polygyrus* and *S. obvelata*, infected the same number of hosts, resulting in a prevalence of 40% for both. However, the latter species was far more numerous, and thus displayed higher levels of aggregation, and higher mean intensity and mean abundance values. *Syphacia stroma* was randomly distributed among house mouse hosts; all other nematode species, as well as intestinal nematodes in general, showed a clumped distribution in this host species (Table 5).

Host sample structure (Table 6), as well as the dominant species of intestinal nematode (Table 7), varied between the three types of habitat. On A sites, the host sample consisted of 21 individuals of all four species noted in this study. The yellow-necked and striped field mice were the most numerous, with 11 and 7 individuals respectively. The most abundant intestinal nematodes in these sites were, as expected, species typical of these hosts: *S. frederici* (639 worms) and *S. agraria* (212). On B sites, 22 of 27 hosts were wood mice, and the house mouse was conspicuously absent. *Syphacia frederici* was the most abundant intestinal nematode, with 948

Table 4. Quantitative infection parameters of individual intestinal nematode species and intestinal nematodes overall for all 27 wood mice (*Apodemus sylvaticus*) sampled across three different habitat types in Istria, Croatia.

	I	n	d	P%	MI	MA
Aspiculuris tetraptera	3	14	5.8	11.1 (3.1-29.2)	4.7 (1.0-6.7)	0.5 (0.04-1.5)
Heligmosomoides laevis	1	5	5.0	3.7 (0.2-18.1)	5.0	0.2 (0.0-0.6)
Heligmosomoides polygyrus	21	118	5.5	77.8 (58.5-89.9)	5.6 (4.1-8.4)	4.4 (2.9-6.7)
Rictularia proni	3	8	2.8	11.1 (3.1-29.2)	2.7 (2.0-3.3)	0.3 (0.0-0.7)
Syphacia frederici	11	431	93.3	40.7 (23.7-59.8)	39.2 (16.4-83.6)	16.0 (5.7-38.7)
Syphacia stroma	1	6	6.0	3.7 (0.2-18.1)	6.0	0.2 (0.0-0.7)
Trichuris muris	2	4	2.4	7.4 (1.3-23.7)	2.0 (1.0-2.0)	0.2 (0.0-0.5)
Intestinal nematodes	26	586	71.6	96.3 (81.8-99.8)	22.5 (12.2-47.2)	21.7 (11.6-44.6)

I – number of infected hosts; n – number of individual nematodes; d – dispersion index; P% – prevalence; MI – mean infection intensity; MA – mean abundance; 95% confidence intervals in parentheses, where applicable.

Table 5. Quantitative infection parameters of individual intestinal nematode species and intestinal nematodes overall for all 15 house mice (*Mus musculus*) sampled across three different habitat types in Istria, Croatia.

	I	n	d	P%	MI	MA
Aspiculuris tetraptera	1	11	11.0	6.7 (0.4-30.2)	11.0	0.7 (0.0-2.2)
Heligmosomoides polygyrus	6	52	12.0	40.0 (19.1-66.8)	8.7 (3.5-14.8)	3.5 (1.1-8.0)
Rictularia proni	1	15	15.0	6.7 (0.4-30.2)	15.0	1.0 (0.0-3.0)
Syphacia frederici	1	48	48.0	6.7 (0.4-30.2)	48.0	3.2 (0.0-9.6)
Syphacia obvelata	6	296	119.6	40.0 (19.1-66.8)	49.3 (14.5-128.3)	19.7 (5.0-64.3)
Syphacia stroma	1	1	1.0	6.7 (0.4-30.2)	1.0	0.1 (0.0-0.2)
Intestinal nematodes	12	423	85.4	80.0 (53.4-94.3)	35.3 (15.4-82.3)	28.2 (11.9-67.7)

I – number of infected hosts; n – number of individual nematodes; d – dispersion index; P% – prevalence; MI – mean infection intensity; MA – mean abundance; 95% confidence intervals in parentheses, where applicable.

individuals. On C sites, which were under highest anthropogenic pressure, the house mouse was the most numerous host species (13 of 19 individual mice), with the yellow-necked mouse absent. Unsurprisingly, the house mouse specific *S. obvelata* was the most abundant intestinal nematode (285 individuals). While the most abundant nematode species differed between the three types of sites, the most prevalent – or rather, the one that infected the highest percentage of hosts – did not. At all three types of sites, *H. polygyrus* displayed the highest prevalence of infection.

GLM analysis was used to uncover whether host identity and sex, as well as habitat type, showed any type of relationship with parasite abundance. The results, however, show that the abundance of parasites was independent of these factors. The only statistically significant influences were found for host identity in *H. spumosa* ($p < 0.001$), *S. agraria* ($p = 0.017$) and *Physaloptera* sp. ($p = 0.017$). In the former two, support for 'host species:host sex' ($p < 0.001$ for *H. spumosa* and $p = 0.002$ for *S. agraria*) and 'host species:habitat type' ($p < 0.001$ for both) interactions was also found, but this

Table 6. Sample structure on all three habitat types (A, B and C) present in the study area in Istria, Croatia, with regards to the number of individuals of each host species.

	A	B	C
Apodemus agrarius	7	1	2
Apodemus flavicollis	11	4	0
Apodemus sylvaticus	1	22	4
Mus musculus	2	0	13
Total per habitat type	21	27	19

is almost certainly derived from the influence of host species. The significant influence of host identity on the abundance of these three species is unsurprising, considering that they were heavily localized: all *S. agraria* and *Physaloptera* sp., as well as 90.2% of *H. spumosa* individuals were found in striped field mice. GLM analysis found no relationship between host sex or habitat type (low, medium or high anthropogenic impact) and parasite abundance. A statistically significant difference in infection prevalence between the three types of habitats was found for *H. spumosa* (p = 0.012), *R. proni* (p = 0.044) and three *Syphacia* species: *S. frederici* (p = 0.027), *S. obvelata* (p = 0.027) and *S. stroma* (p = 0.037) (Table 8).

DISCUSSION

In the present study, we investigated the impact of urbanization and inadequate waste management on native wildlife. Most of the previous work dealing with urban ecology focused on the effects of urbanization on habitat quality and other environmental conditions (Sims et al. 2007; Grimm et al. 2008) in cities, and how species' ecological and life history traits influence their ability to colonize and survive in urban areas (Lim and Sodhi 2004; Kark et al. 2007; Croci et al. 2008; Thompson and McCarthy 2008)interest is growing in the traits of urban plants. We classified 822 UK vascular plants on the basis of their occurrence along an urban2013rural gradient in 26\u00a0710 samples of vegetation from 2508 UK 1-km grid squares, including a wide range of rural habitats and Sheffield and Birmingham, two of the UK's largest cities. Both alien and native species were classified with respect to mean proportion of urban land cover in the 1-km grid squares in which the species occurs (urbanity. The impact of solid waste disposal upon communities of small mammals at the outskirts of cities and towns has not yet been studied. Cavia et al. (2009) reported that accumulated organic waste and litter provide food and shelter for rodents. Although we agree that human impact through waste disposal almost necessarily changes local species community (Cavia et al. 2009), the influence may vary between habitats and regions.

The host community composition differed between the three habitat types, with regard to the intensity of anthropogenic influence. The richest host community was present at natural localities (A), with the yellow-necked mouse as the most abundant rodent. This mouse species is characteristic of deciduous forests that provide enough seeds and fruits for its diet (Marsh and Harris 2000; Juškaitis 2002). The striped field mouse, which prefers forest edges and damper habitats such as occasionally flooded woodland (Garms and Borm 1981; Tsvetkova et al. 2008), was the second most abundant species in natural habitats. At semi-natural (B) sites, the wood mouse was the dominant species, with the yellow-necked and striped field mouse much fewer in number. Finally, the house mouse was the most numerous host species

Table 7. Comparison of quantitative infection parameters of individual intestinal nematode species and intestinal nematodes overall between the three habitat types (A, B and C) present in the study area in Istria, Croatia.

		At	*Hl*	*Hp*	*Hs*	*Ph*	*Rp*	*Sa*	*Sf*	*So*	*Ss*	*Tm*	nem
A	P%	4.8	0.0	52.4	23.8	9.5	38.1	14.3	19.0	9.5	19.0	0.0	100.0
	MI	12.0	NA	16.1	26.4	3.0	1.8	70.7	159.8	5.5	5.5	NA	58.3
	d	12.0	NA	115.5	40.1	3.2	1.4	201.7	291.2	5.3	14.7	NA	186.3
B	P%	11.1	3.7	70.4	0.0	0.0	11.1	0.0	44.4	0.0	0.0	7.4	96.3
	MI	4.7	5.0	5.3	NA	NA	2.7	NA	79.0	NA	NA	1.0	41.4
	d	5.8	5.0	6.4	NA	NA	2.8	NA	278.9	NA	NA	1.0	248.8
C	P%	5.3	0.0	52.6	10.5	0.0	10.5	10.5	10.5	21.1	10.5	5.3	84.2
	MI	11.0	NA	7.8	15.5	NA	8.0	15.0	37.5	71.3	3.5	3.0	33.5
	d	11.0	NA	8.6	15.5	NA	14.0	14.2	38.5	127.9	5.2	3.0	66.4

P% – prevalence; MI – mean infection intensity; d – dispersion index; *At* – *Aspiculuris tetraptera*; *Hl* – *Heligmosomoides laevis*; *Hp* – *H. polygyrus*; *Hs* – *Heterakis spumosa*; *Ph* – *Physaloptera* sp.; *Rp* – *Rictularia proni*; *Sa* – *Syphacia agraria*; *Sf* – *S. frederici*; *So* – *S. obvelata*; *Ss* – *S. stroma*; *Tm* – *Trichuris muris*; nem – intestinal nematodes; NA – not applicable.

Table 8. Results of Fisher's exact test for comparison of prevalence between the three habitat types (A, B and C) present in the study area in Istria, Croatia.

	Fisher's exact test (p value)
Aspiculuris tetraptera	0.725
Heligmosomoides laevis	1
Heligmosomoides polygyrus	0.363
Heterakis spumosa	0.012*
Physaloptera sp.	0.172
Rictularia proni	0.044*
Syphacia agraria	0.104
Syphacia frederici	0.027*
Syphacia obvelata	0.027*
Syphacia stroma	0.037*
Trichuris muris	0.621
Intestinal nematodes	0.129

Values with an asterisk denote statistically significant differences.

at sites with pronounced human influence (C), in line with its status as a typical synanthropic species (Garms and Borm 1981). The host sample collected at these sites also contained wood and striped field mice but, as we expected, not the forest dwelling yellow-necked mouse.

All of the intestinal nematode parasites recorded in this study are typical of *Apodemus* and *Mus* species. A pattern that emerges from quantitative analyses of parasite infection is that the most numerous nematodes – the *Syphacia* pinworms – were not the most prevalent ones. The nematode that infected the highest percentage of hosts in all habitat types was *H. polygyrus*. This disparity is a consequence of differences in the life strategies of these two nematode groups, as noted by previous studies (Ondriková et al. 2010; Debenedetti et al. 2016; Čabrilo et al. 2016). *Heligmosomoides polygyrus* is a widely distributed intestinal parasite of murid rodents (Anderson 2000) and a highly frequent parasite of the wood mouse, which explains its highest prevalence at B sites where *A. sylvaticus* was well represented in the host sample. In the present study, *H. polygyrus* is listed as a parasite of *A. agrarius*, since our nematode identification procedure precedes the paper by Zaleśny *et al.* (2014), which reports on the highly cryptic species *H. neopolygyrus* infecting European striped field mice. According to Genov (1984) and Feliu et al. (1997), *A. tetraptera* parasitizes on *Apodemus*, *Mus*, *Rattus* and *Myodes* species. In the present study, it was found in all types of habitats with similar prevalence levels. *Rictularia proni* was similarly present in all three categories of sites, predominantly in *Apodemus* mice in accordance with earlier findings (Tenora 2004; Kirillova 2010; Bjelić Čabrilo et al. 2013; Čabrilo et al. 2016). *Heterakis spumosa* was absent in B sites; its prevalence and infection intensity were highest in natural habitats, where its most frequent host, *A. agrarius*, was most numerous. It was less present in yellow-necked mice, and absent in house and wood mice. This is in accordance with Genov (1984), who reported it only from striped field mice, whereas Ryzhikov et al. (1979) describe it from all three *Apodemus* species. Within the group of *Syphacia* species, *S. obvelata* is limited only to *M. musculus* (Anderson 2000), while *Syphacia agraria* is similarly specific, parasitizing only *A. agrarius* (Genov 1984). *Syphacia frederici* and *S. stroma* have a wider spectrum of host species: according to Hugot (1988), the former is found in yellow-necked and wood mice, while the latter is a parasite of *Apodemus* mice throughout the Palearctic. *Trichuris muris* is another nematode found in a wide range of rodent host species (Genov 1984; Anderson 2000).

A noteworthy finding was the presence of *Physaloptera* nematodes at the Istarske toplice site in Croatia (type A). Six individual worms (two adults and four juvenile stages) were found in the stomachs of two individual striped field mice. Roundworms of this genus are parasites of a number of different hosts: rodents, insectivorous mammals and carnivores (Ryzhikov et al. 1979; Genov 1984; Anderson 2000). Nematodes of this genus were reported from striped field mice in Japan (Hasegawa et al. 1993) and Mongolia (Tinnin et al. 2011). The species *Physaloptera ngoci* was recorded in the same host species in south-east Asia (Veciana *et al.* 2013). In Europe, *P. clausa* is a parasite of hedgehogs *Erinaceus roumanicus* and *E. europaeus* (Genov 1984; Jarosz et al. 2016). In Spain, *P. dispar* and *P. getula* were found in *Atelerix algirus* and *Mus spretus* respectively, with unidentified worms of the genus also present in *Rattus rattus* (Mas-Coma et al. 2000). In Serbia, the only published finding of *Physaloptera* nematodes was in *Myotis oxygnathus* and *M. myotis* bats (Horvat 2017).

Significant differences in parasite prevalence between habitat types were found for five intestinal nematode species, three of them from the genus *Syphacia*. *Syphacia obvelata* infected the highest proportion of hosts on sites with high human influence (type C). This finding is unsurprising: the species is a specific parasite of *M. musculus*, which was most abundant on said sites. *Syphacia frederici* had significantly higher prevalence on moderate sites (B), and *S. stroma* on sites with low human influence (A). Explaining these between-habitat differences in prevalence proves more difficult. It is entirely possible, for example, that *S. frederici* prevalence at B sites was highest because *S. stroma* was absent there. The two species infect the same hosts, and may compete with each other; however, they occupy different parts of the intestine. Additionally, a convincing claim that interactions, competitive or otherwise, exist between intestinal nematode species cannot be made without experimental studies or adequate null models (Poulin 2001). Significant differences in prevalence between habitat types were also noted in *H. spumosa* and *R. proni*. *Rictularia proni* is a heteroxenous nematode, with insects of the orders Orthoptera, Coleoptera and Dermaptera serving as intermediate hosts (Anderson 2000). Its higher prevalence on sites with low anthropogenic impact would suggest either a higher abundance of said insect groups, or their higher contribution to the diet of murid rodents living there. Unlike *R. proni*, *H. spumosa* infects hosts via embryonated eggs. Its higher prevalence in A sites compared to C sites may reflect better conditions for egg development in natural habitats with low anthropogenic pressure. The assumptions noted in this paragraph all serve to emphasize the need for further research on the rodent-parasite associations in these study areas.

In contrast with these findings, the abundance of intestinal nematodes showed no relationship with habitat type. Rather, it was only host identity that affected the parasite abundance distribution, but only in three species (*H. spumosa*, *Physaloptera* sp. and *S. agraria*) that were highly localized in a specific host in the current study – in this case, *A. agrarius*, which carried all *S. agraria* and *Physaloptera* sp. individuals, as well as the majority of *H. spumosa* worms. Of the 163 *H. spumosa* individuals, 147 (90.2%) were recovered from *A. agrarius*; the remaining 16 were found in a single *A. flavicollis*, which appears to serve only as an auxiliary host of the parasite (Zaleśny et al. 2010).

Taken together, the findings listed above suggest that the level of anthropogenic disturbance and waste dumping may influence the qualitative and quantitative characteristics of their intestinal nematode assemblages, primarily by affecting the composition of local rodent communities. The markedly different structure and abundance of mice species at each of the three habitat types, as well as the notable prevalence differences found for nearly half of all intestinal nematodes identified in the study, illustrate a possible connection between anthropogenic pressure and host-parasite systems. At the same time, the present study has its limitations, most apparent in the number of study sites, host sample size and host species representation. Our preliminary results, therefore, call for a more thorough and robust examination of the habitat characteristics at the studied localities, and the ways they influence rodent and intestinal nematode community composition.

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