HUNGARIAN UNIVERSITY OF AGRICULTURE AND LIFE SCIENCES

The epidemiology of *Echinococcus multilocularis* in rural areas of Transdanubia, Hungary

Sibusiso Moloi
Kaposvár
2025

The PhD School

Name:
Doctoral School of Agricultural and Food Sciences

Discipline:
Animal Sciences

Head of the Doctoral School:
Prof. Dr. Melinda Kovács
University Professor, Full Member of the Hungarian Academy of Sciences

Supervisors:
Dr. Ágnes Csivincsik, PhD
Senior Research Fellow
Hungarian University of Agriculture and Life Sciences
Department of Animal Physiology and Health

Nagy Gábor, PhD
Senior Research Fellow
Hungarian University of Agriculture and Life Sciences
Department of Animal Physiology and Health

....	....
Approval of Head of the School	Approval of the Supervisor(s)

TABLE OF CONTENTS

1. PRELIMINARIES AND OBJECTIVES

1.1. Introduction

The *Echinococcus multilocularis* (**Figure 1**) belongs to the parasite family Taeniidae. Although its very small size (maximum 4.5 mm) (Thompson and McManus, 2001), it is the causative agent of one of the most dangerous helminthozoonotic diseases in humans known as human alveolar echinococcosis (HAE) (Torgerson et al., 2010). This cestode is widely distributed across the northern hemisphere. In recent years, the parasite has shown increasing concern in Europe (Gottstein et al., 2015), including Hungary (Csulak et al., 2024), and Asia (Baumann et al., 2019). HAE is usually asymptomatic during its incubation period. It is characterised by a slow development of a malignant tumour-like lesion that can occur mainly in the liver. The untreated HAE is progressive and leads to death in 90% of cases within 10–15 years of diagnosis (Torgerson et al., 2010).

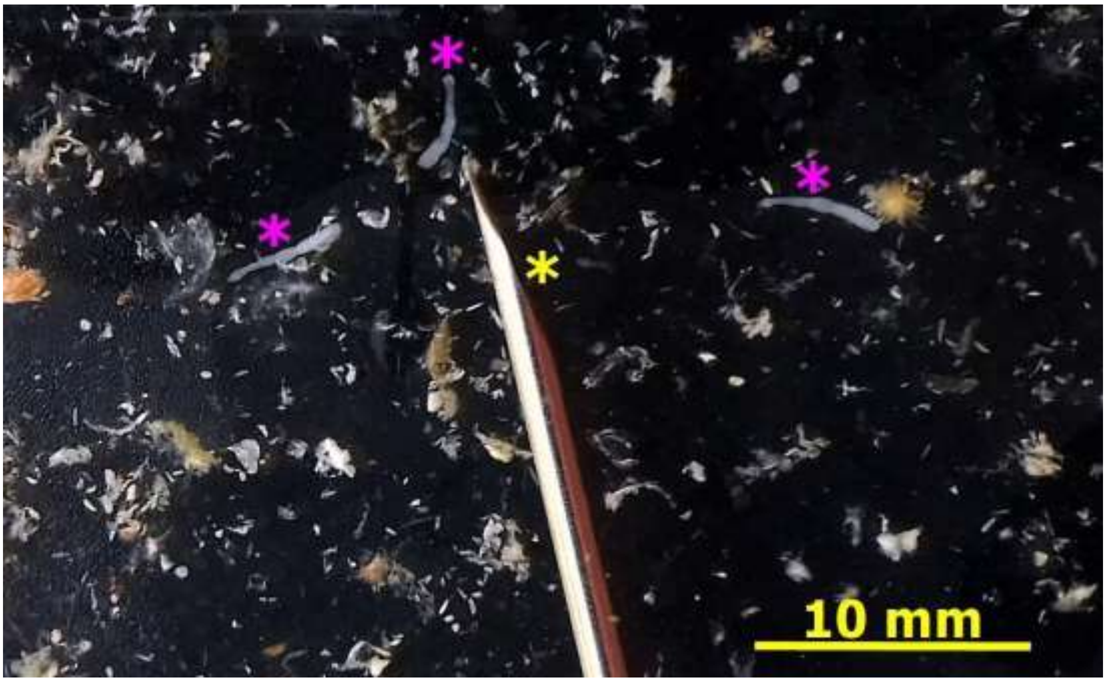

Figure 1. Habitus of *Echinococcus multilocularis*. (yellow asterisk: tip of a single-use syringe (21G 1 1⁄2) as a reference; purple asterisk: *E. multilocularis* specimen).

The first Hungarian isolation happened in 2002 from red foxes originating from the northern part of Hungary (Sréter et al., 2003), while the first HAE case was reported in 2008 (Horváth et al., 2008). A later retrospective, country-wide HAE analysis ascertained that the disease has low incidence in Hungary but a high case-fatality rate due to diagnostic delay and inappropriate treatment (Dezsényi et al., 2021).

It is assumed that the spread of *E. multilocularis* will continue in the Northern Hemisphere, which also means an increase in HAE cases. The main challenge is not restricting the spread of the parasite, which is an impossible task, but rather educating the public and health policymakers about clear and consistent communication regarding risk factors and protective measures (Davidson et al., 2012). The spatial epidemiology of *E. multilocularis* is impacted by several factors operating at different geographical scales. On a broader scale, such as the continental level, factors like the dispersion of definitive host populations and climatic indicators could help identify the boundaries of the infection's range. These factors also affect smaller spatial units (e.g. country), including local environmental characteristics of different habitats. Nonetheless, their importance may differ depending on the specific location. At the local scale, definitive host responses to changes in intermediate hosts' population densities play a crucial role in transmission dynamics. Additionally, the behaviour of carnivores - such as their defecation and marking activities - interacts with the habitat preferences of the intermediate hosts, ultimately influencing local transmission hotspots (Giraudoux et al., 2002).

Understanding the proximate drivers of a parasite distribution allows for advanced knowledge of *E. multilocularis* epidemiology, which is needed to conduct effective surveillance and prevention of humans.

1.2. Objectives

This thesis aimed to investigate the epidemiological characteristics of *E. multilocularis* in the southwestern part of Hungary to reveal the factors which are responsible for the maintenance of the parasite population in its sylvatic reservoir. For this reason, the populations of red fox (*Vulpes vulpes*) and golden jackal (*Canis aureus*) in Somogy and Baranya counties were studied.

The specific aims were as follows:

1. To determine which environmental factors contribute to the presence of *E. multilocularis* in a microhabitat,
2. To explore the egg production performance of *E. multilocularis* in both hosts and determine the effects of the host species and the crowding on it,
3. To investigate the diversity of the parasitic infracommunities in the two most abundant European wild canine carnivore hosts in different human-influenced conditions,
4. To describe how the infracommunity crowding affects the *E. multilocularis* occurrence.

2. MATERIALS AND METHODS

This research evaluated the occurrence and epidemiology of *E. multilocularis* in definitive host populations in southern Hungary. For this reason, we collected and dissected red fox and golden jackal carcasses to obtain parasite specimens from their small intestines. To achieve our goals, we conducted three studies.

In Study 1, the author characterised the definitive hosts' small intestinal helminthic community, including *E. multilocularis*. In Study 2, we investigated the egg-producing performance of worms isolated from fox and jackal species, examining the effects of density and species characteristics. In Study 3, the density of the tapeworm was determined in fox and jackal populations in Somogy and Baranya Counties. Additionally, we collected data on other factors that may influence the spread of the worm. The impact of the individual factors was analysed using methods used in spatial epidemiology, which made it possible to separate global and local effects in the same predictive model.

2.1. Study areas

From 2018 to 2022, a total of 293 legally hunted red foxes and 262 golden jackals were collected from the Transdanubian region of Hungary, specifically in Baranya County and Somogy County. The samples were sourced from four distinct and well-separated locations: Drava Plain (DP), Zselic (ZS), Outer Somogy (OS), and Inner Somogy (IS) (**Figure 2**).

The jackal density in this area varied between 0.05 and 0.28 groups per km², with an average group size of 4 to 5 individuals. Based on bioacoustic and scat analyses, the estimated density of golden jackals was approximately 0.2 to 1.12 individuals per km² (Lanszki et al. 2018). Hunting statistics for golden jackals indicated that in Baranya and Somogy County, the number of harvested jackals was significantly higher than the national average (National Game Management Database (http://www.ova.info.hu/vgstat.html, accessed 22/10/2023).

In the region, three distinct climate zones merge, shaping the overall climatic pattern. The northeastern area (OS) experiences a continental climate, while the southern region (DP) is characterised by a Mediterranean climate. Additionally, the western part of the area (IS) shows influences from the Atlantic climate zone. According to the European geobotanical classification, the sampling sites are categorised as submontane oak-hornbeam woodlands and thermophilous oak woodlands, which include open steppe oak woodlands and riparian vegetation (Salamon-Albert et al., 2011).

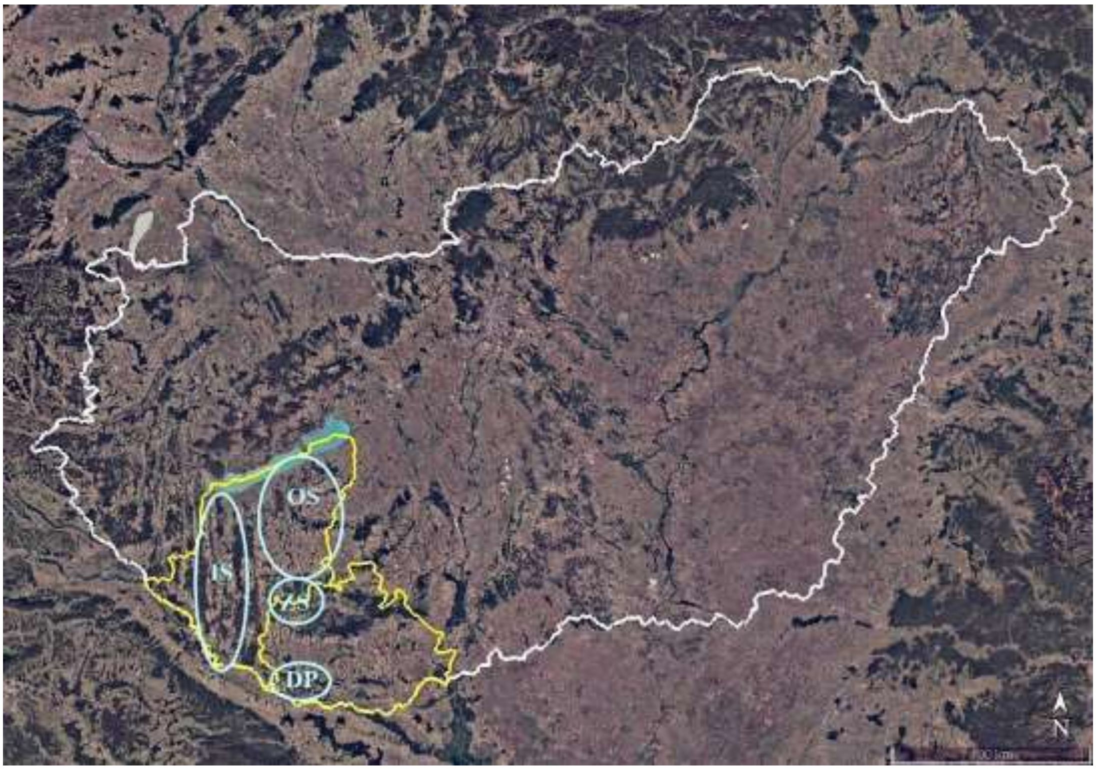

Figure 2. Localisation of Somogy and Baranya Counties (Note: white line-country border, yellow line-county border, DP-sampling area in Drava Plain, IS-sampling area in Inner Somogy, OS-sampling area in Outer Somogy, ZS-sampling area in Zselic) (source: Author's own)

The Drava Plain is situated on the floodplain of the lower section of the Drava River. The area is characterised by significant coverage of constant water flows, such as rivers, creeks, ditches, and oxbows. Agriculture is the primary land use, accounting for approximately 75% of the area (including arable land, meadows, and wood pastures). The average elevation of the sandy-soiled surface ranges from 96 to 110 meters above sea level (a.s.l.). The long-term mean annual temperature is 10.8 °C, while the mean annual precipitation is around 750 mm (Lóczy et al., 2019).

The Zselic Hills represent the most forested landscape in South Transdanubia. The two dominant land cover types are forests and agricultural areas, comprising about 60% and 37% of the landscape, respectively. The agricultural fields—such as grasslands, pastures, arable land, and old orchards—create a mosaic landscape structure, primarily on the site's periphery. The most common forest types include swamp woodlands, pedunculate oak-hornbeam woodlands, and sessile oak-hornbeam woodlands. Additionally, steep valleys feature submontane mesophilic beech forests.

Inner Somogy displays diverse landscape characteristics, with a balanced proportion of forests and agricultural areas (arable lands, grasslands, and wood pastures) of approximately 40% and 50%, respectively. Various woodland types exist in the area, including riverine swamps in the western part and predominantly oak-elm-ash forests in the eastern part. Additionally, an extensive network of fishponds and constant water flows, such as creeks and ditches, characterise the remaining sections. The mean elevation is 173 meters a.s.l. The climate is similar to that of the Drava Plain, with a mean annual temperature of 10.7 °C and mean annual precipitation ranging from 715 to 725 mm (Salamon-Albert et al., 2010).

Outer Somogy is connected to Lake Balaton to the north with the smallest proportion of woodlands (approximately 30%) among the regions studied. The dominant land cover types are arable lands, pastures, orchards, and human settlements located along the shore of Lake Balaton. The valleys are typically home to constant watercourses, swamps, and marshes. This site features the greatest range of elevation, from 94 to 316 meters a.s.l. (with a mean of 183 meters). Outer Somogy is the driest site, with a mean annual precipitation of 640 mm and a mean annual temperature of 10.8 °C (Salamon-Albert et al., 2010).

2.2. Parasitological methods

To determine the intensity of infection in Study 1 and Study 3, we employed the Sedimentation and Counting Technique as outlined by Eckert et al. (2001) The investigation of intestines was carried out considering safety precautions, such as separate laboratory processing, protective clothing, and deep-freezing of intestines at -80 oC for five days (Eckert et al., 2011). The whole sediment was examined in Petri dishes under a stereomicroscope at magnification 40×.

In Study 2, the parasitological sampling was conducted using a multistage cluster sampling method. In this approach, the primary units consisted of two clusters: worm specimens originating from foxes and jackals. The secondary units were the infrapopulations of *E. multilocularis* found within individual host animals, while the tertiary units referred to the individual parasites within these infrapopulations (Thrusfield and Brown, 2018). To determine crowding, we counted all parasites present in the intestinal content. If the total exceeded 100, we counted a subsample and used this to estimate the size of the infrapopulation (Halász et al., 2021). We selected four specimens from each intestinal sample using unaided eyes to prevent any unintentional bias in the selection of the worm individuals. In the absence of optical assistance, choosing four specimens ensured that at least one intact worm could typically be isolated from most of the intestinal contents examined. The relatively low number of specimens from a specific infrapopulation was intentional, aiming to minimise the influence of host individuals on host species variations.

Egg counting and maturity determination were carried out after a morphometric evaluation of the worms. Only whole specimens identified as *E. multilocularis* were included in the analysis. If the number of eggs inside the worm's body was insufficient for accurate counting, we gently pressed a coverslip to open the last segment and counted the released eggs outside the helminth's body (**Figure 3**) (Jones et al., 1960; Alvarez Rojas et al., 2018).

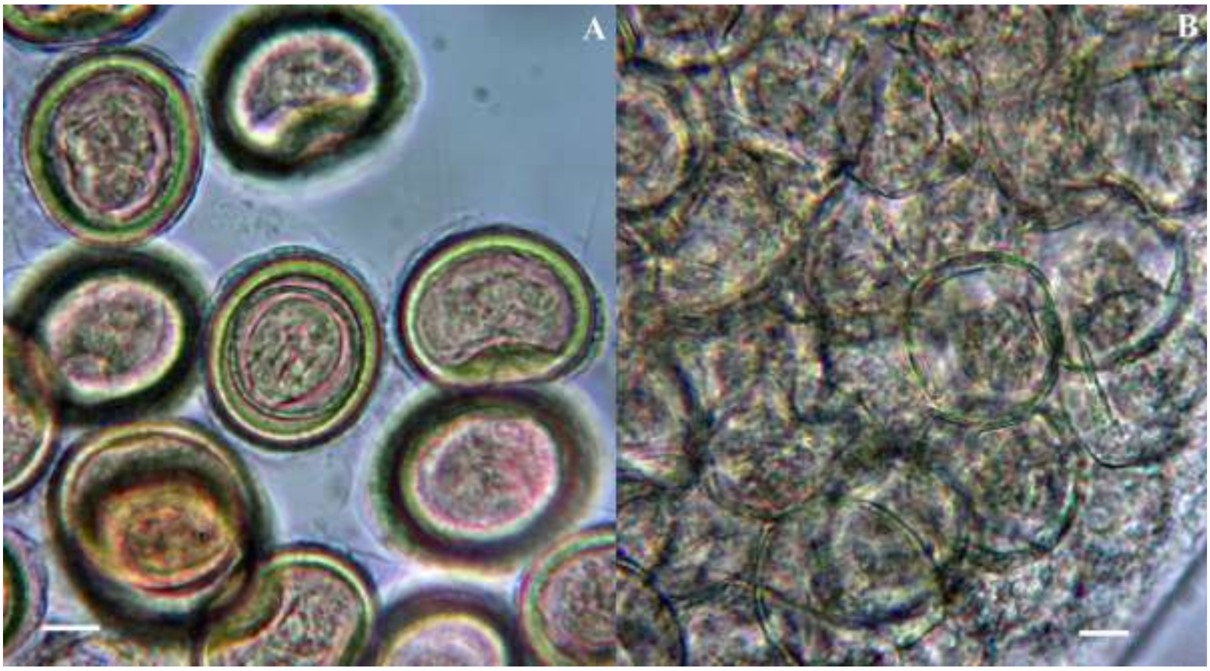

Figure 3. Mature, thick-shelled eggs (A) and immature, thin-shelled eggs (B) from fertile *E. multilocularis* (scale bar: 10 µm) (source: Author's own)

2.3. Molecular identification

To determine the species of the collected worms, we utilised a slightly modified method originally described for taeniids by Trachsel et al. (2007). The primer sequences employed were TGCTGATTTGTTAAAGTTAGTGATC (Cest1), CATAAATCAATGGAAACAACAACAAG (Cest2), and GTTTTTGTGTGTTACATTAATAAGGGTG (Cest4) to specifically detect *E. multilocularis* specimens. PCR reactions were conducted in a total volume of 10 µl, which included 4.52 µl of 2× PCRBIO Taq Mix, 3.72 µl of distilled water, 0.8 µl of a 2 µM primer mix, and 0.96 µl of template DNA. The cycling profile for the PCR consisted of an initial denaturation at 94 °C for 4 minutes, followed by 35 cycles of denaturation at 94 °C for 30 seconds, annealing at 58 °C for 90 seconds, and extension at 72 °C for 10 seconds. A final extension was performed at 72 °C for 4 minutes. The resulting amplicons were resolved using a 2% agarose gel stained with SYBR™ Green Nucleic Acid Gel Stain and visualised under UV light. The species identification was based on a 395 bp fragment, which corresponds to *E. multilocularis*.

2.4. Statistical methods

In Study 1, we employed two spatial analytic methods to investigate the factors influencing the prevalence of *E. multilocularis* in foxes and jackals. By analysing the locations of infected and non-infected animals, we utilised scan statistics to identify areas with high and low rates of parasite infection. For this purpose, we used SaTScan™ software with a purely spatial Bernoulli model (Kulldorff, 2019).

Additionally, we conducted an ordinary least squares (OLS) regression analysis along with two local models: geographically weighted regression (GWR) and multiscale geographically weighted regression (MGWR) (Fotheringham et al., 2017; Matthews and Yang, 2012). The OLS model identified and explained the global, non-spatial relationships between the dependent variable (prevalence in hosts) and independent variables (land cover categories and climatic factors). On the other hand, the GWR and MGWR revealed the local effects of the explanatory variables. For model evaluation, we used multiple criteria, including adjusted R^2, corrected Akaike information criterion, residual sum of squares, and Moran's I of residuals. During the analysis, we used GeoDa (version 1.22) (Anselin et al., 2006) and MGWR (version 2.2) (Oshan et al., 2019) software.

In Study 2, we characterise the effect of the two hosts on the parasites. We grouped the collected worms into two clusters based on their host origin: golden jackal and red fox. We then recorded several features of individual parasites, including the presence of eggs in the uterus, the egg count in the uterus, the maturity of the eggs found, and the crowding condition of the infrapopulation in fox and jackal originated worms. From these raw characteristics, we calculated several parameters for both host species: the proportion of fertile worms, the mean number of eggs per fertile worm, the proportion of worms with mature eggs, the mean number of mature eggs per worm, and the crowding conditions of worms containing mature eggs. We applied the online version of Quantitative Parasitology (Qpweb) software (https://www2.univet.hu/qpweb/qp10/index.php) for our calculations (Reiczigel et al., 2019).

Additionally, we examined the relationship between crowding—defined as the number of worms in a host—and egg count. This relationship was analysed using a generalised linear model (GLM) approach with a Tweedie log function. For these statistical calculations, we employed SPSS software (version 25) and applied bootstrapping with 5,000 iterations for each analysis.

In Study 3, we determined the following indices for our study: species richness (the number of helminth taxa found in any individual host), overall prevalence (the percentage of hosts infected with at least one helminth taxon), the prevalence of a particular parasite taxon (the percentage of infected hosts of that specific taxon), and mean abundance (the total number of parasites found in any host, regardless of whether they are infected) (Bush et al., 1997; Reiczigel et al., 2019). To determine the impact of human presence, we sorted the specimens into two groups based on their distance from human settlements. The mean distance from the closest human settlement was calculated for both host species. In the cases of foxes and jackals, the mean distances were 1142.5 and 1256.8 m, respectively. Based on these values, we sorted the specimens into "nearby" and "farther" groups, and for a deeper analysis, the specimens were divided into "nearby foxes" (F1), "nearby jackals" (J1), "farther foxes" (F2) and "farther jackals" (J2) groups.

For comparison of prevalences and mean abundances between groups, such as different distances and species groups, we used Quantitative Parasitology (QP web) software online application (Reiczigel et al., 2019). To compare species richness between the above-mentioned groups, we used PAST (PAleontologic STatistical software package, version 5.0; https://www.nhm.uio.no/english/research/resources/past/) (Hammer and Harper, 2024).

We also compared infracommunity crowding values between the hosts, specifically *E. multilocularis*-infected and non-infected foxes and jackals. For the calculations, we used the QPweb online application (Reiczigel et al., 2019), along with SPSS (version 29.0.2.0) and PAST (version 5.0) statistical software (Hammer and Harper, 2024).

3. RESULTS

In study 1, the comparison of the two different hosts (fox & jackal) ascertained that they are very similar (the prevalence and intensity of the infection are statistically identical); therefore, we used all 391 hosts' data as one dataset to characterise the UTM quadrates.

Table 1. Findings of parasitological investigation in Study 1.

	total	fox	jackal	P-value
sample size	391	197	194	-
infected	71	30	41	-
prevalence (%)	18.2	15.2	21.1	0.15
mean intensity	874	867	894	0.95

The SaTScan analysis revealed that the epicentre of the studied endemic was at the Croatian-Hungarian border by the River Drava (**Figure 4**). However, two further highly infected areas could be revealed, one in the middle of the study area (Zselic Hills microregion) and another in the north (Outer Somogy microregion).

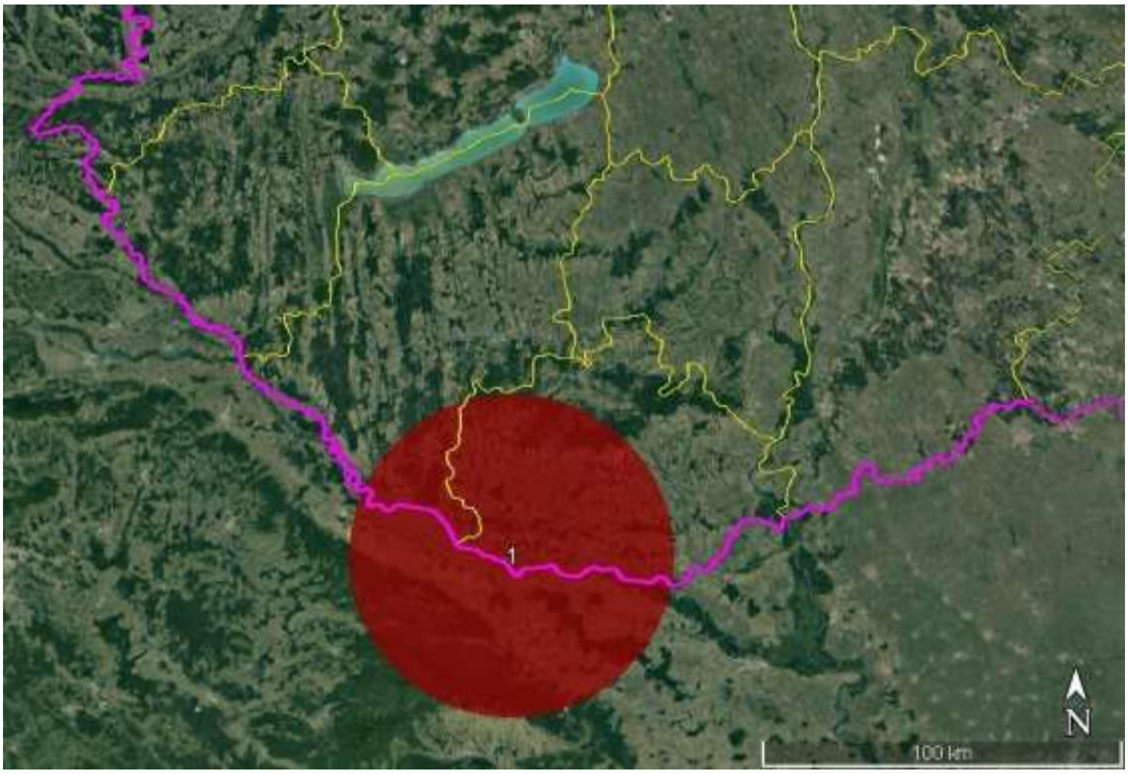

Figure 4. Location of the significant high-rated cluster (Note: red circle=the only significant cluster, purple line=country border, yellow line=county border).

The OLS model highlighted that the main factor that globally contributed to the maintenance of the Western Balkan endemic was the extension of wetlands. Wetlands are not surface waters, but those areas that are covered by water at least temporarily. E.g., wet grasslands or alder carrs belong to this type of habitat. The MGWR model revealed that mean annual precipitation and the seasonality of the precipitation are also very important factors in the maintenance of *E. multilocularis* (**Figure 5**). The amount of precipitation helps, while strong seasonality impedes the survival of eggs in the environment.

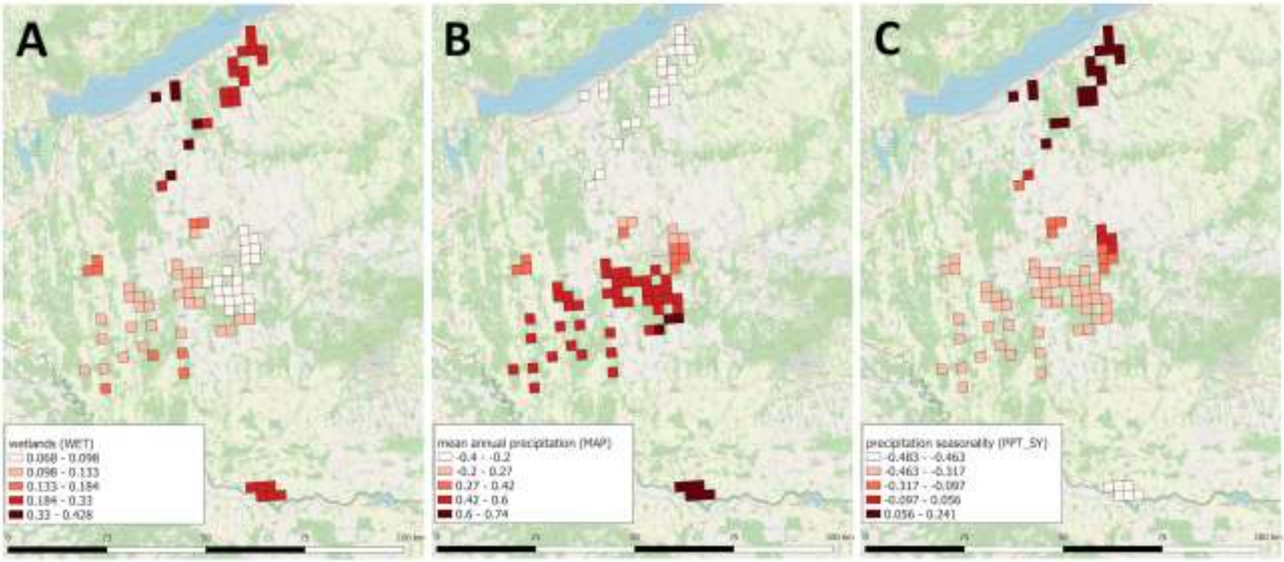

Figure 5. Spatial mapping of the significant drivers. Figure presents the spatial distribution of mean coefficients of wetlands (A), mean annual precipitation (B), seasonality of precipitation (C) variables.

Table 2. The main results of Study 2, which evaluated the host suitability of the red fox and the golden jackal

	Red fox (N=33)	**Golden jackal (N=29)**	**P-value**
No. of worm specimens examined	111	81	-
No. of worms with eggs	96 (86.5%)	75 (91.5%)	0.36
Mean no. of eggs per worm*	87.7	76.7	0.25
No. of worms with mature eggs	91 (82.0%)	63 (76.8%)	0.02
Mean no. of mature eggs per worm**	91.3	88	0.74
Crowding conditions of worms with mature eggs	669.6	231	0.01

*Immature parasites without egg production were excluded

**Only worms with mature eggs were included in the calculation

In the number of fertile parasites (worms with eggs), the mean number of eggs per worm, and the mean number of mature eggs per worm, the two host species were similar.

However, we found two main differences between the two host species:

1. In the fox cluster, we detected more parasites that produced mature eggs.

2. Parasites with mature eggs originated from more crowded infrapopulations in the fox cluster than in the jackal cluster.

In Study 3, we ascertained that the individuals of the two host species had the same probability of living close to a human settlement (P=0.661 by Fisher's exact test). The finer distribution pattern can be seen in the diagram of **Figure 6**.

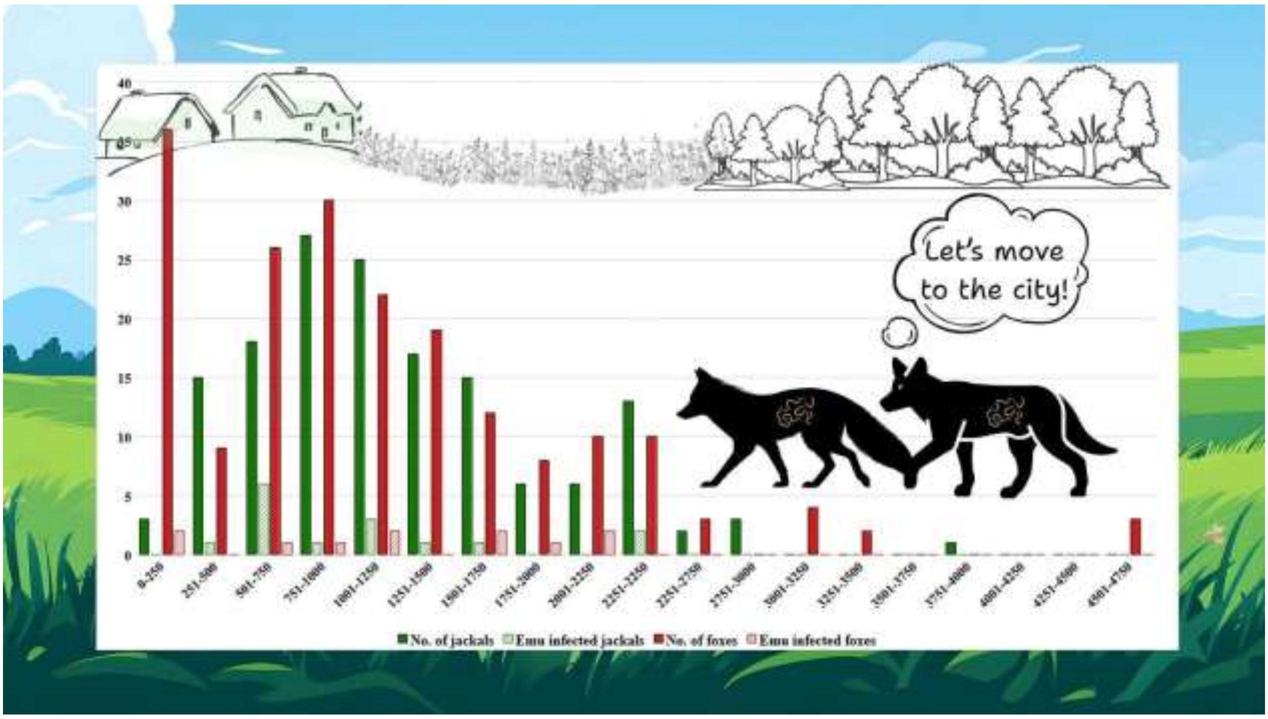

Figure 6. The distribution of red foxes (red column) and golden jackals (green column), and *E. multilocularis* infected hosts (striped columns) around human settlements

Most of the investigated specimens originated from the close surroundings of the human settlements. This phenomenon is very similar in both host species, with one difference: a large number of foxes live almost within the territories of the settlements.

The parasitological results can be summarised as follows:

- The prevalence of helminth infection was the same in the two hosts (fox=91.2%, jackal=89.4%, P=0.59).
- Hookworms were the most prevalent taxon in both hosts (over 60% of the individuals were infected with hookworms), and roundworms were the second.
- The least prevalent taxa were *Echinococcus multilocularis* and *Dipylidium caninum.*
- The parasite species richness (diversity) was also similar in the two hosts.
- Comparing nearby and farther groups, we found a more remarkable difference than between the two hosts:
    - The diversity of infracommunities was higher in nearby carnivores.

    - The infracommunity crowding index was significantly higher in nearby carnivores and nearby foxes than in the farther groups. However, in nearby jackals, the difference was not significant → The overall difference was mostly due to the foxes.
    - Ancylostomatidae (hookworms) were more abundant in nearby carnivores (almost significant difference: $P=0.058$).
    - Toxocaridae (roundworms) were more prevalent in nearby carnivores (significant difference, $P=0.02$)
- Analysing the correlation between the abundances of the two most prevalent taxa (hookworms and roundworms), we confirmed a moderate negative relationship between them (Spearman's $\rho = -0.445$, $p < 0.001$).
- Comparing the *E. multilocularis*-infected and non-infected groups, we confirmed that infected animals had a significantly stronger parasite load (infracommunity crowding) than those free from *E. multilocularis*.
- Additionally:
    - Roundworms were more characteristic of foxes.
    - Hookworms were more characteristic of jackals.
    - Both hookworms and roundworms were more prevalent and abundant (though not significantly) in the nearby host populations.

4. CONCLUSIONS AND PROPOSALS

During my series of investigations, I aimed to determine the sylvatic factors that enhance the risk of human alveolar echinococcosis in a hyperendemic region of Hungary. I could confirm that microclimatic effects, even in small spots, can provide appropriate conditions for the survival of E. multilocularis, even among less suitable macroclimatic circumstances. This finding suggests that predictions, which expect the risk-mitigating effect of a warming climate, need to be revised.

In the case of the golden jackal, I found that *E. multilocularis* develops more slowly in the small intestine of this host than in the fox. Based on a deductive approach supported by a thorough literature review, I concluded that the coexistence of the red fox and the golden jackal increases the egg contamination of the environment, thus the risk of human infection. This conclusion agrees with the HAE situation of my study area, which is a HAE hot spot in Hungary.

Analysis of human impact on the occurrence of *E. multilocularis*, I found that wild carnivores around the human settlements carry more crowded parasite infracommunities, and crowding increases the risk of *E. multilocularis's* presence in an infracommunity. Though this evidence is indirect and needs to be supported by future studies, it calls attention to the increasing risk around human settlements.

As a result of my research, I could identify a HAE risk factor which could be influenced by humans directly. This factor is the antiparasitic management of rural dogs within the hyperendemic regions. My hypothesis is supported by the study of Csulak et al. (2024), which ascertained that a lower development level of an area increases the risk of HAE. My study was carried out in one of the less developed regions of Hungary (Ragadics, 2020). The low-income communities might not provide appropriate antiparasitic defence to their dogs. In these circumstances, dogs could accumulate high numbers of parasites, thereby increasing the risk of *E. multilocularis* occurring around human settlements.

Based on this observation, a knowledge dissemination campaign is recommended to initiate within the hyperendemic regions. Besides general hygiene rules of HAE prevention, it is strongly recommended to educate the inhabitants about the necessity of antiparasitic treatment of their dogs.

For future research, I recommend the investigation of *E. multilocularis* infection of rural dogs and egg contamination of the human-dominated rural environment to assess the human health risk caused by dog ownership.

In the case of wild carnivores, it is suggested to investigate the correlation between the diet, the microbiota, the parasite community, and the occurrence of *E. multilocularis* at the individual level to ascertain the risk factors that contribute to the maintenance of the parasite by the two different host species.

5. NEW SCIENTIFIC RESULTS

1. I confirmed the South Transdanubian endemic area of *Echinococcus multilocularis* and detected an epidemiological hotspot along the River Drava at the southern border of Hungary.
2. Applying a multiscale geographically weighted regression (MGWR) model, I confirmed that the microclimatic conditions, especially humidity, can compensate for the potentially disadvantageous effects of a warm climate on *E. multilocularis* at the local geographic level.
3. In the golden jackal host, I detected a higher proportion of less developed eggs than in the red fox. By this finding, I indirectly confirmed that the ontogeny of E. multilocularis in the golden jackal is slower than in the red fox.
4. I confirmed that in more crowded populations of *E. multilocularis*, a higher proportion of parasites contains less mature eggs. By this finding, I indirectly confirmed that ongoing infection reduces the possibility of reinfection.
5. In comparison of small intestinal parasites of red foxes and golden jackals at different distances from human settlements, I confirmed that the vicinity of settlements showed a bigger impact on parasite diversity, prevalence and mean abundance of infracommunities than host species did.
6. I confirmed that *E. multilocularis*-infected infracommunities proved higher crowding than those free from the cestodes.

6. LIST OF PUBLICATIONS AND PRESENTATIONS

Peer-reviewed papers published in foreign scientific journals

Moloi, S., Tari, T., Halász, T., Gallai, B., Nagy, G., Csivincsik, Á., 2023. Global and local drivers of *Echinococcus multilocularis* infection in the western Balkan region. *Scientific Reports,* 13(1):21176. https://doi.org/10.1038/s41598-023-46632-9

Moloi, S., Halász, T., Csivincsik, Á., Nagy, G., 2024. Suitability of red fox (*Vulpes vulpes*) and golden jackal (*Canis aureus*) as hosts of *Echinococcus multilocularis* based on egg production characteristics and literature data on the intestinal ecosystems of carnivores. *Current Research in Parasitology and Vector-Borne Diseases,* 6: 100225. https://doi.org/10.1016/j.crpvbd.2024.100225

Moloi, S., Csivincsik, Á., Nagy, E., Tari, T., Halász, T., Polgár, K., Nagy, G. 2025. Human impact on the composition of small-intestine helminth Iifracommunities in canine mesocarnivores, with a special focus on *Echinococcus multilocularis*. *Parasitologia,* 5(3):30. https://doi.org/10.3390/parasitologia503003013.2

Oral Presentation

Moloi, S., Tari, T., Halász, T., Gallai, B., Nagy, G., Csivincsik, Á., 2023. Global and local drivers of *Echinococcus multilocularis* infection in the Western Balkan region. 32nd International Symposium. Animal Science Days Conference, Oberaichwald, Austria 2024.

Moloi, S., Tari, T., Csivincsik, Á., Nagy, G. Human impacts on helminth fauna diversity in wild carnivores. Tendon: 30th International Symposium Animal Science Days 2022.Conference, Zadar, Croatia 2022.

7. REFERENCES

1. Alvarez Rojas, C. A., Mathis, A., Deplazes, P., 2018. Assessing the contamination of food and the environment with Taenia and Echinococcus eggs and their zoonotic transmission. Current Clinical Microbiology Reports 5(2):154–163). https://doi.org/10.1007/s40588-018-0091-0
2. Anselin, L., Syabri, I., Kho, Y., 2006. GeoDa: An introduction to spatial data analysis. Geographical Analysis, 38(1):5–22 (2006). https://doi.org/10.1111/j.0016-7363.2005.00671.x
3. Baumann, S., Shi, R., Liu, W., et al., 2019. Worldwide literature on epidemiology of human alveolar echinococcosis: a systematic review of research published in the twenty-first century. Infection, 47(5):703–727. https://doi.org/10.1007/s15010-019-01325-2
4. Bush, A. O., Lafferty, K. D., Lotz, J.M., et al., 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. Journal of Parasitology, 83:575-583.
5. Csulak, E., Csivincsik, Á., Sréter, T., et al., 2024. Retrospective multidisciplinary analysis of human alveolar echinococcosis in Hungary using spatial epidemiology approaches. Scientific Reports, 14(1):31435. https://doi.org/10.1038/s41598-024-83119-7
6. Davidson, R. K., Romig, T., Jenkins, E., et al., 2012. The impact of globalisation on the distribution of Echinococcus multilocularis. Trends in Parasitology, 28(6):239-47. https://doi.org/10.1016/j.pt.2012.03.004
7. Dezsényi, B., Dubóczki, Z., Strausz, T., et al., 2021. Emerging human alveolar echinococcosis in Hungary (2003–2018): a retrospective case series analysis from a multi-centre study. BMC Infectious Diseases, 21(1):168. https://doi.org/10.1186/s12879-021-05859-5
8. Eckert, J., Gemmell, M. A., Meslin, F.-X., et al., 2001. WHO/OEI Manual on echinococcosis in humans and animals: A public health problem of global concern, World Organisation for Animal Health (Office International des Epizooties) and World Health Organization, pp. 72-99.
9. Fotheringham, A. S., Yang, W., Kang, W., 2017. Multi-scale geographically weighted regression. Annals of the American Association of Geographers, 107(6):1247–65. https://doi.org/10.1080/24694452.2017.1352480
10. Giraudoux, P., Delattre, P., Takahashi, K., et al., 2002. Transmission ecology of Echinococcus multilocularis in wildlife: what can be learned from comparative studies and multiscale approaches? P. Craig, Z. Pawlowski (Eds.) Cestode Zoonoses: Echinococcosis and Cysticercosis: An Emergent and Global Problem, IOS Press, pp. 251–266.
11. Gottstein, B., Stojkovic, M., Vuitton, D. A., et al., 2015. Threat of alveolar echinococcosis to public health - a challenge for Europe. Trends in Parasitology, 31(9):407–412. https://doi.org/10.1016/j.pt.2015.06.001
12. Halász, T., Nagy, G., Nagy, I., et al., 2021. Micro-epidemiological investigation of Echinococcus multilocularis in wild hosts from an endemic area of southwestern Hungary. Parasitologia, 1(3):158–167. https://doi.org/10.3390/parasitologia1030017
13. Hammer, Ø., Harper, D. A., 2024. Paleoecology and paleobiogeography. Hammer, Ø., Harper, D.A. (Eds.), Paleontological data analysis. John Wiley & Sons Ltd., pp. 216-262.
14. Horváth, A., Patonay, A., Bánhegyi, D., et al., 2008. A humán Echinococcus multilocularis infectio első hazai esete. Orvosi Hetilap, 149(17):795–799. https://doi.org/10.1556/OH.2008.28281

15. Jones, A. W., Segarra, J. M., Wyant, K. D., 1960. Growth and hatching of taeniid eggs. Journal of Parasitology, 46:170-4.

16. Lanszki, J., Schally, G., Heltai, M., et al., 2018. Golden jackal expansion in Europe: First telemetry evidence of a natal dispersal. Mammalian Biology, 88:81–84. https://doi.org/10.1016/j.mambio.2017.11.011

17. Lóczy, D., Dezső, J., Gyenizse, P., et al., 2019. Oxbow lakes: Hydromorphyology. Lóczy, D. (Eds.) The Drava River, Springer International Publishing, pp. 177–198.

18. Matthews, S. A., Yang, T. C., 2012. Mapping the results of local statistics: Using geographically weighted regression. Demographic Research,26:151-166. https://doi.org/10.4054/DemRes.2012.26.6

19. Oshan, T. M., Li, Z., Kang, W., et al., 2019. mgwr: A Python implementation of multiscale geographically eeighted regression for investigating process spatial heterogeneity and scale. ISPRS International Journal of Geo-Information, 8(6):269. https://doi.org/10.3390/ijgi8060269

20. Ragadics, T. (2020). Social Processes Affecting Families in Rural Hungary. Family Forum, 10: 111-126. https://doi.org/10.25167/FF/2392

21. Reiczigel, J., Marozzi, M., Fábián, I., et al., 2019. Biostatistics for parasitologists - A primer to quantitative parasitology. Trends in Parasitology, 35(4):277-281. https://doi.org/10.1016/j.pt.2019.01.003

22. Salamon-Albert, É., Ortmann-Ajkai, A., Horváth, F. et al., 2010. Climatic conditions of semi-natural habitats in Belső-Somogy, Külső-Somogy and Zselic regions I. Climatic surface and climatic envelope of woodlands. Natura Somogyiensis, 17:65–76.

23. Salamon-Albert, É., Ortmann-Ajkai, A., Horváth, F., 2011. Climatic conditions and habitats in Belső-Somogy, Külső-Somogy and Zselic as vegetation-based landscape regions II. Temperature and precipitation sensitivity of woodlands. Natura Somogyiensis, 19:51–66.

24. Sréter, T., Széll, Z., Egyed, Z., et al., 2003. Echinococcus multilocularis: An emerging pathogen in Hungary and Central Eastern Europe? Emerging Infectious Diseases, 9(3):384-6. https://doi.org/10.3201/eid0903.020320

25. Thompson, R. C. A., McManus, D. P., 2001. Aetiology: parasites and life-cycles. In WHO/OIE Manual on echinococcosis in humans and animals: a public health problem of global concern. World Organization for Animal Health (OIE) ed. Eckert, J., Gemmell, M. A., Meslin, F. X., Pawlowski, Z. S., Paris.

26. Thrusfield, M., Brown. H, 2018. Surveys. Thrusfield, M., Chrisley, R. (Eds.), Veterinary Epidemiology (4th ed.), Wiley Blackwell, Hoboken, pp. 270-295.

27. Torgerson, P. R., Keller, K., Magnotta, M. et al., 2010. The global burden of alveolar echinococcosis. PLoS Neglected Tropical Diseases, 4(6):e722. https://doi.org/10.1371/journal.pntd.0000722