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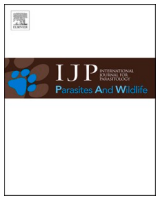

# Gastrointestinal helminth infections and ectoparasitism in wild rodents along wildlife-human interfaces in Tanzania

Venance T. Msoffe [a,b,c,*], Claus A. Thomas [d], Alfan A. Rija [a], Jahashi Nzalawahe [e], Abdul S. Katakweba [b,f], Gerald Misinzo [e,g], Ladslaus L. Mnyone [f,h]

[a] Department of Wildlife Management, College of Forestry, Wildlife and Tourism, Sokoine University of Agriculture, P.O. Box 3073, Morogoro, Tanzania
[b] African Centre of Excellence for Innovative Rodent Pest Management and Biosensor Technology Development, Sokoine University of Agriculture, P.O. Box 3110, Morogoro, Tanzania
[c] Department of Biological Sciences, Mkwawa University College of Education, University of Dar Es Salaam, P.O. Box 2513, Iringa, Tanzania
[d] Department of Microbiology and Parasitology, St. Francis University College of Health and Allied Sciences, P.O. Box 175, Ifakara, Tanzania
[e] Department of Microbiology, Parasitology and Biotechnology, College of Veterinary Medicine and Biomedical Sciences, Sokoine University of Agriculture, P.O. Box 3019, Morogoro, Tanzania
[f] Institute of Pest Management, Sokoine University of Agriculture, P.O. Box 3110, Morogoro, Tanzania
[g] OR Tambo Africa Research Chair for Viral Epidemics, SACIDS Foundation for One Health, Sokoine University of Agriculture, P.O. Box 3297, Morogoro, Tanzania
[h] Division of Science, Technology and Innovation, Ministry of Education, Science and Technology, P.O. Box 10, Dodoma, Tanzania

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ABSTRACT

*Background:* Gastrointestinal parasites pose a significant threat to human and domestic animal health across Africa. Despite numerous studies on ectoparasitism and endoparasitism in small mammals across different regions of the continent, the ecological role of rodents in transmission dynamics of gastrointestinal helminths remains poorly understood. This study aimed to identify gastrointestinal helminths in rodents and evaluate the influence of host-related factors, ectoparasite infestations, and environmental variables on helminth prevalence at wildlife-human interfaces in Tanzania.

*Methods:* Gastrointestinal helminth eggs were quantified using the modified McMaster method on samples from captured rodents. Correlations between parasitological data, host scaled mass index (SMI), and ectoparasite intensity were analyzed. Generalized linear mixed models (GLMMs) were employed to assess helminth occurrence in relation to host demographics, ectoparasite load, and environmental factors.

*Results:* The overall prevalence of gastrointestinal helminths was 53.59%. Seven distinct helminth egg types were identified, representing two major taxa: nematodes and cestodes. Among the nematodes, eggs of *Trichuris* spp., *Strongyloides* spp., *Syphacia* spp., Capillariidae and Spirurida were identified. Cestode eggs present were *Hymenolepis*-like eggs and eggs of Anoplocephalidae. Whipworms (*Trichuris* spp.) exhibited the highest prevalence (23.2%), followed by threadworms (*Strongyloides* spp.) at 22.1%. Anoplocephalid eggs showed the lowest prevalence, at 0.56%. The occurrence of gastrointestinal helminths in rodents was significantly associated with increased SMI and ectoparasite (flea and mite) infestations, while also varying across rodent species and collection sites.

*Conclusions:* This study highlights the presence of potentially zoonotic helminths, including capillariids and *Hymenolepis*-like species, in rodents at wildlife-human interfaces. Furthermore, it identifies associations between gastrointestinal helminth infections and host body condition, as well as the intensity of ectoparasite infestations. These findings underscore the importance of considering host and environmental factors in understanding helminth transmission dynamics and their potential impact on public and veterinary health.

* Corresponding author. Department of Wildlife Management, College of Forestry, Wildlife and Tourism, Sokoine University of Agriculture, P.O. Box 3073, Morogoro, Tanzania.
*E-mail address:* venance.msoffe@muce.ac.tz (V.T. Msoffe).

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## 1. Introduction

Small mammals, including rodents, play a vital role in the functioning of ecosystems at wildlife-human interfaces globally. Human activities, such as encroachment into natural habitats, lead to changes in host-parasite interactions within these ecosystems (Majewska et al., 2019; McGinnis and Kerans, 2013). These changes notably affect host population density and physiology (McGinnis and Kerans, 2013; Weil et al., 2006). In disturbed habitats, small mammals often exhibit higher population densities but lower species diversity, with increased intra- and inter-species contact. Compared to pristine habitats, animal populations in disturbed environments also experience weakened immune function due to environmental stress (Mahmud-Al-Rafat et al., 2015; Meyer-Lucht et al., 2010). Environmental changes that affect host factors can facilitate the spread, virulence, and pathogenicity of infectious agents, contributing to the emergence of previously unknown diseases (Jones et al., 2013). This indicates that any shifts in small mammal populations can disrupt ecological interactions and affect the overall balance of ecosystems (Albon et al., 2002; Frainer et al., 2018; Mouritsen and Poulin, 2002).

Various rodent species tend to inhabit areas near human settlements, where they share food resources with humans and domestic animals. Due to their close interactions with humans and domestic animals, rodents can serve as potential reservoirs or vectors for transmitting zoonotic pathogens, including helminthic infections (Berentsen et al., 2015; Khan et al., 2021; Sithay et al., 2020). They play a critical role as definitive, intermediate or amplifier hosts, facilitating the transfer of pathogens from wildlife to human communities. Through contamination of food and water sources with their feces, urine, aerosols, or hair, rodents pose a significant risk to human and animal health (Issae et al., 2023; Ribas et al., 2016). Additionally, rodents contribute to the ecology of ectoparasites, such as fleas, ticks, mites, and lice, which are vectors for many human and animal-borne diseases (Shilereyo et al., 2022). These ectoparasites also influence the health, population diversity, and ecological interactions of their hosts.

Gastrointestinal helminths are among the most prevalent endoparasites affecting vertebrates. In rodents, helminthic parasites are recognized as potential regulators of host populations and, due to their close interactions with human communities, they have a significant impact on the health of humans and domestic animals (Behnke et al., 2001; Bordes et al., 2007; Bordes and Morand, 2011; Gause et al., 2003). Mammalian gastrointestinal helminths often have complex life cycles, sometimes involving one or more organisms as intermediate, paratenic, or reservoir hosts. The primary transmission route is fecal-oral, where parasite eggs or infective larvae shed by definitive hosts are ingested by intermediate, paratenic, or reservoir hosts, and later re-established in another definitive host following ingestion of the infective larvae (Gourlay et al., 2024). Consequently, helminth transmission often involves interactions between multiple organisms across different trophic levels in the ecosystem.

The impact of rodent-borne helminths, whether through zoonotic transmission to humans or cross-species sharing with domestic animals, is species-specific and ecological context-dependent. While helminthic nematodes are primarily associated with significant socioeconomic effects in human communities, *Hymenolepis* spp. from rodents are recognized as major zoonotic cestodes (Cabada et al., 2016; Fuehrer et al., 2011; Makki et al., 2017). The severity of helminth infection can be exacerbated by polyparasitism, which may result in synergistic effects (Ezeamama et al., 2008). Although most helminth infections typically present mild clinical symptoms, severe outcomes may occur in cases of heavy infection or in immunocompromised and immunosuppressed individuals (Bentwich et al., 1999; Druilhe et al., 2005).

Recent studies have shown that human activities influence rodent population densities and ectoparasite infestations at wildlife-human interfaces in Tanzania (Laudisoit et al., 2009; Shilereyo et al., 2022). However, the link between ectoparasite infestations and endoparasite infections in rodents remains unclear. While some research has examined rodent-borne endoparasites in Tanzania (Katakweba et al., 2013; Mgode et al., 2014; Mhamphi et al., 2024), little is known about the role of wild and commensal rodents as hosts for zoonotic helminths or their transmission to humans and domestic animals. To date, only two studies have been conducted in Tanzania (Ribas et al., 2013; Thomas et al., 2023), both focusing on *Trichuris* spp. in rodents. This study aims to identify gastrointestinal helminths in rodents from Iringa and Morogoro and assess the impact of host traits and ectoparasite loads on helminth infections. The findings of this research will provide field-based data on the occurrence, prevalence, and risk factors of gastrointestinal helminths in Tanzanian rodents, which is crucial for understanding their impact on public and veterinary health. This information is vital for developing and implementing effective helminth control strategies and management programs.

## 2. Materials and methods

### 2.1. Sample collection, identification and preservation

The rodent and ectoparasite (fleas and mites) samples used in this study were obtained from a previous investigation by Msoffe et al. (in press). The rodents were trapped during a cross-sectional study conducted between April 2021 and November 2022 in the wildlife-human interfaces of Iringa and Morogoro regions in Tanzania. Six villages were purposively selected: in Iringa, the villages were Kitisi, Malizanga, and Mlenge from Idodi, Mlowa, and Mlenge wards, respectively, near Ruaha National Park; in Morogoro, the villages were Kisaki Kituoni in Kisaki ward, and Mbwade and Bonye in Bwakila Chini ward, near Nyerere National Park (see Fig. 1).

A combination of Sherman® live traps (standard medium-size: 7.6 × 8.9 × 23 cm), wire-cage traps, and Havahart traps were used to capture live small mammals from different habitats, categorized as bushland, farmland, and peridomestic areas at the selected sites. Details about the study locations, site selection, and trapping procedures have been previously described by Msoffe et al. (in press).

The sampling of captured small mammals was conducted in accordance with the guidelines provided by the American Society of Mammalogists for the use of wild mammals in research (Sikes, 2016). The captured rodents were immobilized and euthanized using diethyl ether. The ectoparasites were removed gently from the captured rodents using a stiff brush and collected in a clean aluminum basin, then preserved separately in Eppendorf tubes with 70% ethanol considering their groups (fleas or mites) and animal removed from. During necropsy, the entire gastrointestinal tract, from stomach to rectum, was collected and preserved in 70% alcohol. These samples were then transferred to the Parasitology Laboratory at the Department of Microbiology, Parasitology, and Biotechnology, College of Veterinary Sciences and Biomedical Studies, Sokoine University of Agriculture, where they were stored at −20 °C until further processing (Schotte et al., 2023).

In the field, rodents were identified by species, sex, and age based on physical characteristics and morphometric measurements. Sex was determined using three key morphological traits: urogenital distance, presence of nipples, and testicular development. Additional data such as body mass and body length were recorded for further analysis. Species identification was supported by published taxonomic keys (Kingdon, 2015; Wilson and Reeder, 2007), and age class (juvenile or adult) was determined by considering a combination of body size, weight, pelage condition, reproductive status, as well as tooth wear and eruption patterns (Henschel et al., 1982; Hulejová Sládkovičová et al., 2019; Kuprina and Smorkatcheva, 2019; Lalis et al., 2006; Olenev, 2009).

Ectoparasites (fleas and mites) were identified morphologically using microscopy, with molecular techniques applied for confirmation of flea samples, as outlined in a previous study by Msoffe et al. (in press). Briefly, preliminary observations were made using a stereo microscope after gently washing the few specimens of fleas and mites in 1 ×

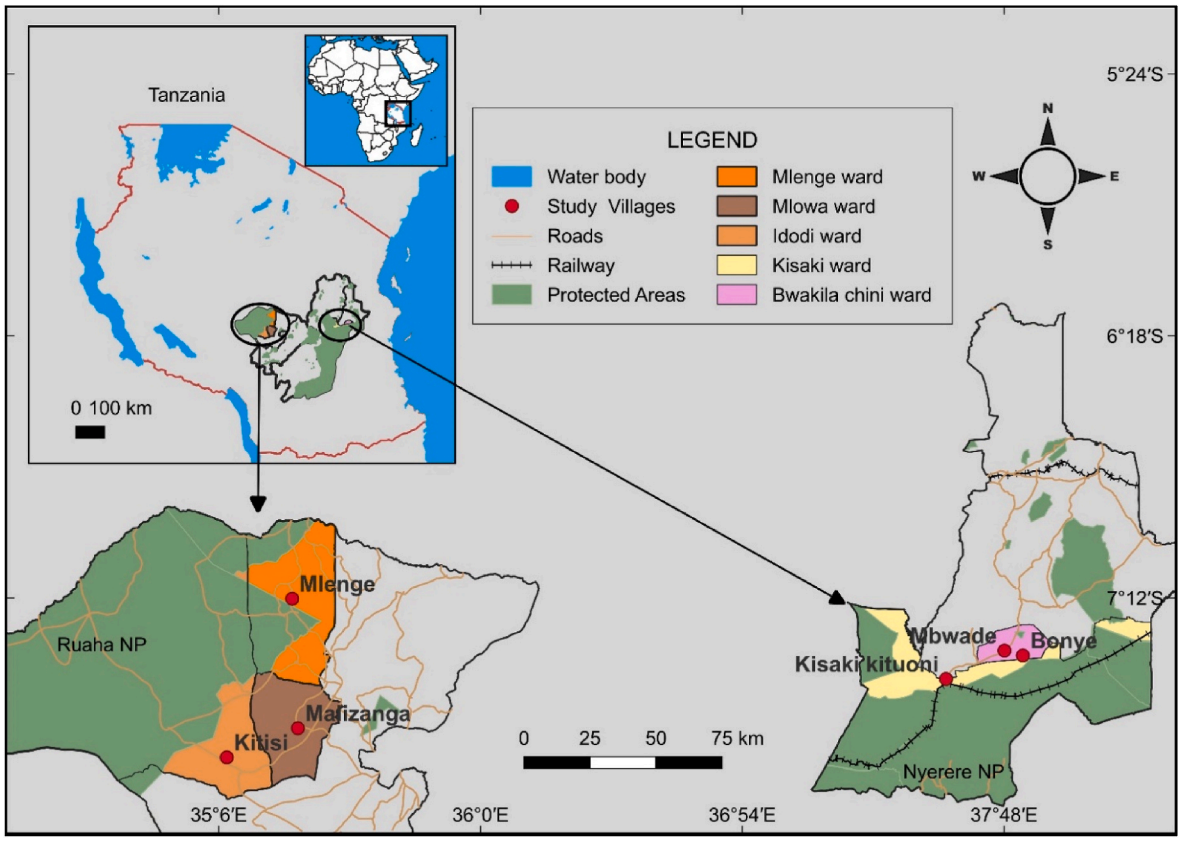


**Fig. 1.** The map of Iringa and Morogoro districts in Tanzania demonstrates wards and villages where small mammals field-sample collections were conducted.

phosphate-buffered saline (PBS), temporarily mounting them in glycerol, and placing them on slides with coverslips under 4 × and 10 × magnification. To enhance the visibility of structures, specimens were boiled in 10% KOH solution—fleas for 10 min and mites for 24 h. They were then neutralized in 10% acetic acid for 30 min. Afterwards, the specimens were dehydrated in a graded ethanol series (70%, 80%, and 100%) for 1 h each and transferred to clove oil overnight to remove any remaining water, dissolve lipids and waxes and to clear specimens. Finally, clear flea and mite specimens were mounted on slides using Dibutyl phthalate polystyrene–xylene (DPX), following the method by Campbell et al. (2018).

### 2.2. Assessing rodents body condition

Scaled body Mass Index (SMI) was calculated to establish the approximate body condition of individual captured rodents. It is an adjusted measure of body mass that accounts for body size or structural scaling differences (Peig and Green, 2009). The index was calculated by the general formula:

$$[SMI = M_i \times (L_0/L_i)^{bSMA}];$$

where by $M_i$ was the individual rodent body mass measurement (in g), $L_i$ was the individual body length (in mm), $L_0$ was the arithmetic mean of body length (in mm) for each rodent species (*Aethomys* spp. = 116, *A. niloticus* = 112, *Grammomys* spp. = 101, *M. natalensis* = 110, *R. rattus* = 114, and *T. vicinus* = 119) and ***bSMA*** is the gradient estimate of a standardized major axis (SMA) regression of the mass-length relationship (Peig and Green, 2009). Thereafter, SMI was categorized as low (SMI <40), medium (40–60) and high (>60) (Carrera-Játiva et al., 2023).

### 2.3. Microscopic examination of helminth egg types

A parasitological examination was conducted at the Parasitology Laboratory of the Department of Microbiology, Parasitology, and Biotechnology at Sokoine University of Agriculture. Helminth infections in rodent samples were assessed both qualitatively and quantitatively using the modified McMaster method (Ballweber, 2006). The gastrointestinal tract, from the pyloric sphincter to the rectum, was separated from fat tissue and placed in a Petri dish. The intestine was opened longitudinally. Its contents were rinsed over the tea strainer using up to 50 mL of normal saline and collected in a beaker. After settling for 15–20 min, the supernatant (normal saline) was removed. Approximately 3 mL of sediment from the intestinal contents was mixed with 42 mL of a saturated sodium chloride (NaCl) solution (specific gravity ~1.2) as a flotation agent in a 50 mL test tube. Faecal samples were thoroughly mixed with the flotation solution and immediately filled into two chambers of a McMaster slide and examined microscopically.

Helminth egg types were identified to the lowest taxonomic level possible using a light microscope with a digital camera at 10x and 40x magnification. Representative eggs were digitally measured (length and width in μm), and photographs were taken for record-keeping. Identification of egg types was based on reliable published taxonomic keys for helminths and protozoa (Thienpont et al., 2003; Zajac and Conboy, 2012). Finally, the total number of eggs observed for each taxon group in both chambers of the McMaster slide was multiplied by a factor of 50 to calculate eggs per gram of feces (EPG) (Ballweber, 2006).

### 2.4. Data analysis

Parasitological descriptors, including prevalence, mean intensity, mean abundance and range, were calculated, interpreted and presented as quantitative parameters according to Bush et al. (1997). We calculated mean helminth richness (MHR) as the average number of different

helminth taxa found within a particular host or population. We employed Kruskal wallis test to compare the median difference in SMI across rodent species and habitats, and ranked two-way ANOVA was used to test the effect of species and habitats in SMI variation (Holbert, 2022). Pearson's or Spearman's rank correlation were used to test for strength and direction of association between SMI and ectoparasite intensity (McClenaghan, 2024), and point-biserial correlation of Pearson's product-moment to measure the strength and direction of association between SMI or ectoparasites intensity (continuous) and presence/absence (dichotomous) of particular helminth groups (Kornbrot, 2014). We used Pearson's chi-squared test of independence to compare differences to evaluate the association between the prevalence of helminth infection across rodent demographics (sex, age, species) and environmental factors (habitats and agroecological zone).

The probability of gastrointestinal parasite infection in rodents for the most frequent helminth group egg types (>5% total prevalence) were examined in relation to rodent intrinsic factors (sex, age, ectoparasites-intensity status, species, SMI) and environmental factors (habitats), by using Generalized linear mixed models (GLMMs) (Bates et al., 2015). The response variables consisted of the presence/absence (binomial) of the overall and most prevalent helminth groups (with total prevalence >5%; *vis*. *Strongyloides* spp., *Trichuris* spp., hymenolepidids and spirurids). The fixed effects for the model included rodent sex (male, female), rodent age (juvenile, adult), rodent SMI categories (low, medium, high), flea intensity and mite intensity. Rodent species and habitat sites of collection were included as random factors for the model to justify variation due to changes in host behaviour and immune physiology, and variation due to changes in environmental conditions, respectively.

An initial unconditional model was obtained by screening each fixed effect without considering random variables, whereby variables potentially associated by outcomes ($p < 0.05$) were suitable to be included for the next step. Here only SMI categories, flea intensity and mite intensity pass the inclusion criteria. On the second step, conditional models were created using forward variable selection method, which included potential interactions of variables. Akaike Information Criteria (AICs) were compared to assess the best-fit model, while evaluating the biological significance of the final included variables. The statistical significance level of the models and tests was set at P-value <0.05. Only statistically significant associations are reported in the results. The "lme4" and "glmmTMB" packages were used for all calculations to fit the models. The Odds Ratio (OR) was calculated by raising the estimates of variables to the exponent using "broom.mixed" package. All statistical analyses and model fitting were performed using R statistical software using specified R packages implemented in version 4.3.1 (R Core Team, 2021).

## 3. Results

### 3.1. Captured rodent community and body conditions

A total of 362 intestinal tract samples from captured rodents were used to assess helminthic infection in this study. Two hundred and fifty-two samples belonged to *Mastomys natalensis*, 36 *Aethomys* spp., 28 *Tatera vicinus*, 20 *Arvicanthis niloticus*, 14 *Rattus rattus* and 12 *Grammomys* spp. Among the sampled specimens 43% (n = 156) were female and 57% (n = 206) male, and 302 among samples were adults while 60 were juveniles. In general, scaled body mass index (SMI) ranged from 26.7 to 86.7. Table 1 below demonstrates the demographic distribution of captured rodents corresponding to agroecological zone, habitat sites of collection and rodent species.

Analysis of body condition of captured rodents categorized 241 individuals as low SMI, 74 as medium SMI, and 47 as high SMI. No clear pattern was revealed on the variation of SMI of particular species per habitat. However, the general trend for most of rodent species showed mean SMI tend to be large in bush habitats compared to farmland and peridomestic habitats except for *Aethomys* spp. (Fig. 2). However, the difference was not statistically significant (Kruskal wallis test, $H = 2.3558$, $p = 0.3079$). Both rodent species and habitat where rodents were captured had statistically significant effects on the ranked mean SMI (ranked two-way ANOVA: Species: $F_{5,356} = 49.7$, $p = 1.02e\text{-}38$, Habitat: $F_{2,359} = 4.27$, $p = 0.0148$), but the interaction of these two factors had no statistically significant association with mean SMI (ANOVA: Species*Habitat: $F_{7,354} = 0.267$, $p = 0.966$).

**Table 1**
Demographic characteristics distribution of captured rodents corresponding to agroecological zones, habitats and species. N = total number of rodents examined; $_{M}$SMI ± SE = Mean scaled body mass index ± Standard error.

| Agroecological zones | Habitat sites | Rodent species | N | Male | Female | Adult | Juvenile | $_{M}$SMI ± SE |
|---|---|---|---|---|---|---|---|---|
| Iringa | Bush | *Aethomys* spp. | 1 | 1 | – | – | 1 | 61.3 |
| | | *Arvicanthis niloticus* | 4 | 2 | 2 | 2 | 2 | 64.5 ± 9.8 |
| | | *Mastomys natalensis* | 24 | 14 | 10 | 22 | 2 | 36.7 ± 3.3 |
| | | *Tatera vicinus* | 1 | 0 | 1 | 1 | – | 76.1 |
| | Farm | *Aethomys* spp. | 15 | 10 | 5 | 14 | 1 | 63.0 ± 3.5 |
| | | *Arvicanthis niloticus* | 9 | 4 | 5 | 6 | 3 | 53.6 ± 4.4 |
| | | *Grammomys* spp. | 6 | 4 | 2 | 4 | 2 | 26.7 ± 2.4 |
| | | *Mastomys natalensis* | 62 | 29 | 33 | 53 | 9 | 31.4 ± 1.4 |
| | | *Tatera vicinus* | 13 | 5 | 8 | 9 | 4 | 58.7 ± 5.9 |
| | Peridomestic | *Aethomys* spp. | 13 | 8 | 5 | 8 | 5 | 59.3 ± 3.9 |
| | | *Arvicanthis niloticus* | 6 | 4 | 2 | 5 | 1 | 53.8 ± 4.6 |
| | | *Grammomys* spp. | 3 | 2 | 1 | 3 | – | 28.4 ± 3.3 |
| | | *Mastomys natalensis* | 55 | 38 | 17 | 41 | 14 | 30.5 ± 1.4 |
| | | *Rattus rattus* | 9 | 6 | 3 | 8 | 1 | 35.8 ± 2.1 |
| | | *Tatera vicinus* | 6 | 2 | 4 | 5 | 1 | 50.4 ± 5.5 |
| Morogoro | Bush | *Aethomys* spp. | 1 | 1 | – | – | 1 | 44.7 |
| | | *Mastomys natalensis* | 8 | 5 | 3 | 7 | 1 | 35.1 ± 4.3 |
| | Farm | *Aethomys* spp. | 5 | 2 | 3 | 5 | – | 65.9 ± 2.0 |
| | | *Arvicanthis niloticus* | 1 | 0 | 1 | 1 | – | 49.2 |
| | | *Grammomys* spp. | 3 | 2 | 1 | 3 | – | 29.8 ± 2.2 |
| | | *Mastomys natalensis* | 77 | 47 | 30 | 70 | 7 | 33.7 ± 1.6 |
| | | *Tatera vicinus* | 5 | 3 | 2 | 4 | 1 | 70.9 ± 7.7 |
| | Peridomestic | *Aethomys* spp. | 1 | 1 | – | 1 | – | 86.7 |
| | | *Mastomys natalensis* | 26 | 12 | 14 | 23 | 3 | 30.9 ± 1.4 |
| | | *Rattus rattus* | 5 | 2 | 3 | 5 | 5 | 30.0 ± 3.1 |
| | | *Tatera vicinus* | 3 | 2 | 1 | 2 | 1 | 49.4 ± 12.6 |

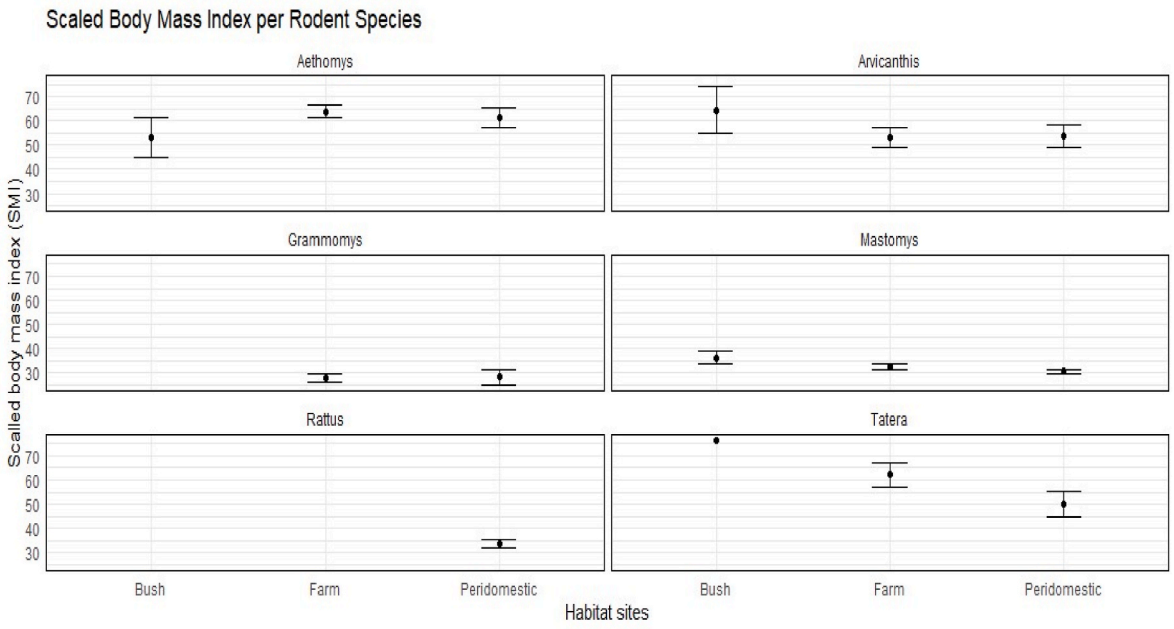


**Fig. 2.** Distribution of Scaled body mass index (SMI) categories according to rodent species across habitat sites of collection. Aethomys = *Aethomys* spp., Arvicanthis = *Arvicanthis niloticus*, Grammomys = *Grammomys* spp., Mastomys = *Mastomys natalensis*, Rattus = *Rattus rattus*, Tatera = *Tatera vicinus*.

### 3.2. Ectoparasitism and body condition of captured rodents

Two common groups of ectoparasites—mites (Acari: Laelapidae) and fleas (Insecta: Siphonaptera)—were collected from rodents captured in Iringa and Morogoro. Results showed that 63.5% (n = 230) of the rodents were infested with spiny rat mites (*Laelaps* spp.), and 40.3% (n = 146) were infested with fleas from three species (*Xenopsylla* spp., *Ctenocephalides felis*, and *Echidnophaga gallinacea*), previously reported by Msoffe et al. (in press). The overall ectoparasite load per rodent did not show a clear infestation pattern between fleas and mites across species (Fig. 3). However, there was a significant correlation between flea infestation intensity and SMI (S = 5287, rho = 0.3313, p = 1.008e-10), but no significant correlation between mite infestation intensity and SMI (S = 7350, rho = 0.0703, p = 0.1818). The negative binomial model confirmed that flea infestation intensity was significantly influenced by SMI, with flea intensity increasing as SMI increased [OR = 1.0237 (95% CI: 1.0134–1.0348), p = 7.77e-07].

However, there was a statistically significant difference in the prevalence of infestation across rodent species for both fleas and mites ($X^2$ = 11.926, p = 0.03582 and $X^2$ = 35.647, p = 1.117e-06) respectively. Table 2 demonstrates parasitological parameters of flea and mite infestations on rodent species across captured habitats.

### 3.3. Gastrointestinal parasitism and host condition of captured rodents

One hundred and ninety-four (53.59%) of captured rodents were detected to have at least one helminth egg types of different groups. The parasite egg types included nematodes (*Trichuris* spp. eggs, *Strongyloides* spp. eggs, Capillariidae eggs, spirurid eggs, and *Syphacia* spp. eggs) and cestodes (*Hymenolepis*-like eggs and Anoplocephalidae eggs) (Fig. 4). The overall prevalence of helminth infections revealed that, there were no statistically significant differences in helminth infections (p > 0.05) between sex, habitats, agroecological zones, and seasons. However, considering age the adult rodents had a higher prevalence of helminth

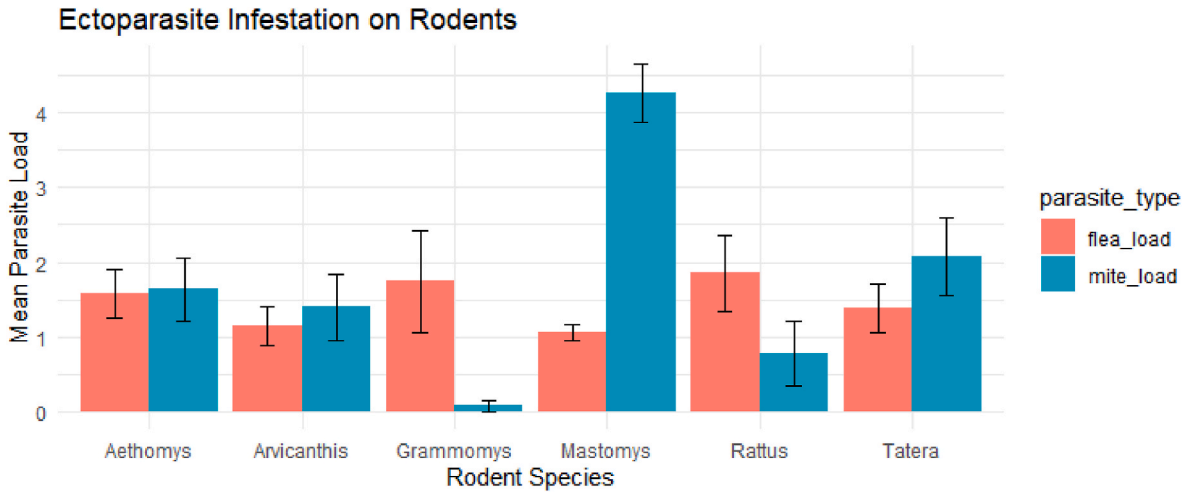


**Fig. 3.** Distribution of ectoparasite intensity of infestation according to species of rodents captured. Aethomys = *Aethomys* spp., Arvicanthis = *Arvicanthis niloticus*, Grammomys = *Grammomys* spp., Mastomys = *Mastomys natalensis*, Rattus = *Rattus rattus*, Tatera = *Tatera vicinus*.

**Table 2**
Rodents ectoparasitic infestation parameters, across habitats of collection and species of 362 rodents captured. N = total number of rodents examined; prev. = prevalence; 95% CI = 95% confidence intervals; MI ± SE = mean intensity ± standard error; MA ± SE = mean abundance ± standard error.

| Ectoparasite | Habitat sites | Rodent species | N | Infested | Prev. (95% CI) | MI ± SE | Range | MA ± SE |
|---|---|---|---|---|---|---|---|---|
| **FLEAS** | Bush | *Aethomys* spp. | 2 | 0 | 0 | 0 | 0 | 0 |
| | | *Arvicanthis niloticus* | 4 | 0 | 0 | 0 | 0 | 0 |
| | | *Mastomys natalensis* | 32 | 12 | 37.5(21.1–56.31) | 2.23 ± 0.38 | 1–5 | 0.91 ± 0.25 |
| | | *Tatera vicinus* | 1 | 0 | 0 | 0 | 0 | 0 |
| | Farm | *Aethomys* spp. | 20 | 12 | 60(36.05–80.88) | 2.75 ± 0.48 | 1–7 | 1.65 ± 0.42 |
| | | *Arvicanthis niloticus* | 10 | 6 | 60(26.24–87.84) | 2.17 ± 0.17 | 2–3 | 1.3 ± 0.37 |
| | | *Grammomys* spp. | 9 | 5 | 55.56(21.2–86.3) | 2.6 ± 0.81 | 1–5 | 1.44 ± 0.63 |
| | | *Mastomys natalensis* | 139 | 41 | 29.5(22.07–37.82) | 2.57 ± 0.22 | 1–6 | 0.81 ± 0.12 |
| | | *Tatera vicinus* | 18 | 11 | 61.11(35.75–82.7) | 2.91 ± 0.49 | 1–6 | 1.78 ± 0.45 |
| | Peridomestic | *Aethomys* spp. | 14 | 7 | 50(23.04–76.96) | 3.43 ± 0.65 | 1–6 | 1.71(0.57) |
| | | *Arvicanthis niloticus* | 6 | 4 | 66.67(22.28–95.67) | 1.75 ± 0.25 | 1–2 | 1.17 ± 0.4 |
| | | *Grammomys* spp. | 3 | 2 | 66.67(9.43–99.16) | 4 ± 3 | 1–7 | 2.67 ± 2.19 |
| | | *Mastomys natalensis* | 81 | 34 | 41.98(31.09–53.46) | 3.47 ± 0.26 | 1–7 | 1.54 ± 0.22 |
| | | *Rattus rattus* | 14 | 8 | 57.14(28.86–82.34) | 3.25 ± 0.45 | 1–5 | 1.86 ± 0.51 |
| | | *Tatera vicinus* | 9 | 4 | 44.44(13.7–78.8) | 1.75 ± 0.48 | 1–3 | 0.78 ± 0.36 |
| **MITES** | Bush | *Aethomys* spp. | 2 | 1 | 50(1.26–98.74) | 1 | 1–1 | 0.5 ± 0.5 |
| | | *Arvicanthis niloticus* | 4 | 3 | 75(19.41–99.37) | 3.33 ± 1.2 | 1–5 | 2.5 ± 1.19 |
| | | *Mastomys natalensis* | 32 | 23 | 71.88(53.25–86.25) | 5.78 ± 1.32 | 1–29 | 4.16 ± 1.05 |
| | | *Tatera vicinus* | 1 | 0 | 0 | 0 | 0 | 0 |
| | Farm | *Aethomys* spp. | 20 | 9 | 45(23.06–68.47) | 4.33 ± 1.05 | 1–9 | 1.95 ± 0.67 |
| | | *Arvicanthis niloticus* | 10 | 4 | 40(12.16–73.76) | 3.5 ± 1.19 | 2–7 | 1.4 ± 0.72 |
| | | *Grammomys* spp. | 9 | 1 | 11.11(0.28–48.25) | 1 | 1–1 | 0.11 ± 0.11 |
| | | *Mastomys natalensis* | 139 | 99 | 71.22(62.94–78.58) | 5.73 ± 0.56 | 1–31 | 4.08 ± 0.46 |
| | | *Tatera vicinus* | 18 | 7 | 38.89(17.3–64.25) | 4 ± 0.98 | 1–8 | 1.56 ± 0.6 |
| | Peridomestic | *Aethomys* spp. | 14 | 9 | 64.29(35.14–87.24) | 2.11 ± 0.65 | 1–6 | 1.36 ± 0.5 |
| | | *Arvicanthis niloticus* | 6 | 2 | 33.33(4.33–77.72) | 2 | 2–2 | 0.67 ± 0.42 |
| | | *Grammomys* spp. | 3 | 0 | 0 | 0 | 0 | 0 |
| | | *Mastomys natalensis* | 81 | 60 | 74.07(63.14–83.18) | 6.23 ± 1.06 | 1–48 | 4.62 ± 0.84 |
| | | *Rattus rattus* | 14 | 5 | 35.71(12.76–64.86) | 2.2 ± 0.97 | 1–6 | 0.79 ± 0.43 |
| | | *Tatera vicinus* | 9 | 6 | 66.67(29.93–92.51) | 4.17 ± 1.14 | 2–9 | 2.78 ± 1.01 |

infections than juveniles and the difference was statistically significant ($X^2$ = 22.281, p = 2.356e-06). The trend tends to be the same for prevalence and mean helminth richness (MHR) (*vis*. Higher in males than females, higher in adults than juveniles, higher in Iringa than in Morogoro and higher in rainy season than in dry season) except for habitats, which showed high MHR in peridomestic followed by farmland and high prevalence in bushland followed by farmland (refer to Table 3 below). In addition, the analysis revealed that, *R. rattus* had slightly higher MHR, 0.929 followed by *Grammomys* spp., 0.917 and lower in *M. natalensis*, 0.683. However, the results showed no clear pattern of species-specific variation in prevalence, mean intensity and abundance of gastrointestinal parasites infections (refer to Table 4).

Generally, for nematodes: *Trichuris* spp. had the highest prevalence of gastrointestinal parasites, 23.2% (95% CI: 18.95–27.9) followed by *Strongyloides* spp. 22.1% (95% CI: 17.93–26.73) with lower prevalence in capillariids and *Syphacia* spp., both with prevalence of 2.76% (95% CI: 1.33–5.02). However, spirurids had the highest overall mean intensity (MI) among gastrointestinal parasites, 1239.6 (range: 50–8450) eggs/gram, followed by capillariids 1010 (range: 100–4250) eggs/gram and lowest in *Syphacia* spp., 185 (range: 100–450) egg/gram. For cestodes: *Hymenolepis*-like had higher overall prevalence of gastrointestinal parasite infection, 10.5% (95% CI: 7.54–14.12) and mean intensity, 1119.7 (range: 50–3900) eggs/gram compared to anoplocephalids. Parasitological parameters of gastrointestinal helminth distribution according to demographic characteristics of rodents (species, sex and age) and geographical factors (seasons, habitats and agroecological zones) are reported in Supplementary Tables S1 and S2.

There was a statistically significant correlation between flea intensity of infestation with *Strongyloides* spp., *Trichuris* spp. And *Hymenolepis*-like species infection in rodents (r = 0.38, p = 1.367e-07; r = 0.26, p = 0.0003; and r = 0.18, p = 0.04027) respectively. Mite intensity of infestation was shown statistically significant correlated with only *Strongyloides* spp. infection in rodents (r = 0.18, p = 0.0052). On the other hand, SMI was statistically significant correlated with *Strongyloides* spp., and *Trichuris* spp. infection among captured rodents (r = 0.16, p = 0.0018; r = 0.28, p = 9.558e-05) respectively.

### 3.4. Host and ectoparasite infestation predictors associated with gastrointestinal infections in rodents

Unconditional models assessing the probability of helminth infection revealed significant associations between overall helminth presence, *Strongyloides* spp., *Trichuris* spp., and *Hymenolepis*-like species with scaled mass index (SMI), flea intensity, and mite intensity in rodent infestations ($p < 0.05$). When conditional models were fitted using glmmTMB, incorporating the variables from the unconditional models, the results indicated that higher SMI was significantly associated with the overall presence of helminths, *Strongyloides* spp., and *Trichuris* spp. ($p < 0.05$) compared to lower SMI, which was used as the basal level reference variable. Additionally, increased flea intensity was significantly associated with the presence of overall helminths, *Strongyloides* spp., *Trichuris* spp., and *Hymenolepis*-like species. ($p < 0.05$). Lastly, higher mite intensity was significantly linked to the presence of overall helminths and *Strongyloides* spp. infections in rodents ($p < 0.05$). In all model fittings, rodent species and habitat sites were included as random effects in the GLMMs. A summary of the GLMM results for the best-fitting models is presented in Table 5 below.

## 4. Discussion

Human encroachment into wildlife habitats increases interactions between humans, wild animals, domestic animals, and disease vectors, raising the risk of zoonotic transmission and cross-species sharing of pathogens. Small mammals, due to their abundance, closeness to human environments, and ability to carry zoonotic pathogens, play a key role in pathogen transmission at wildlife-human interfaces. Understanding gastrointestinal parasite infections in these mammals sheds light on host-parasite ecology and the role of host species in parasite transmission. We compared host demographic characteristics and geographical factors with parasitological parameters (diversity,

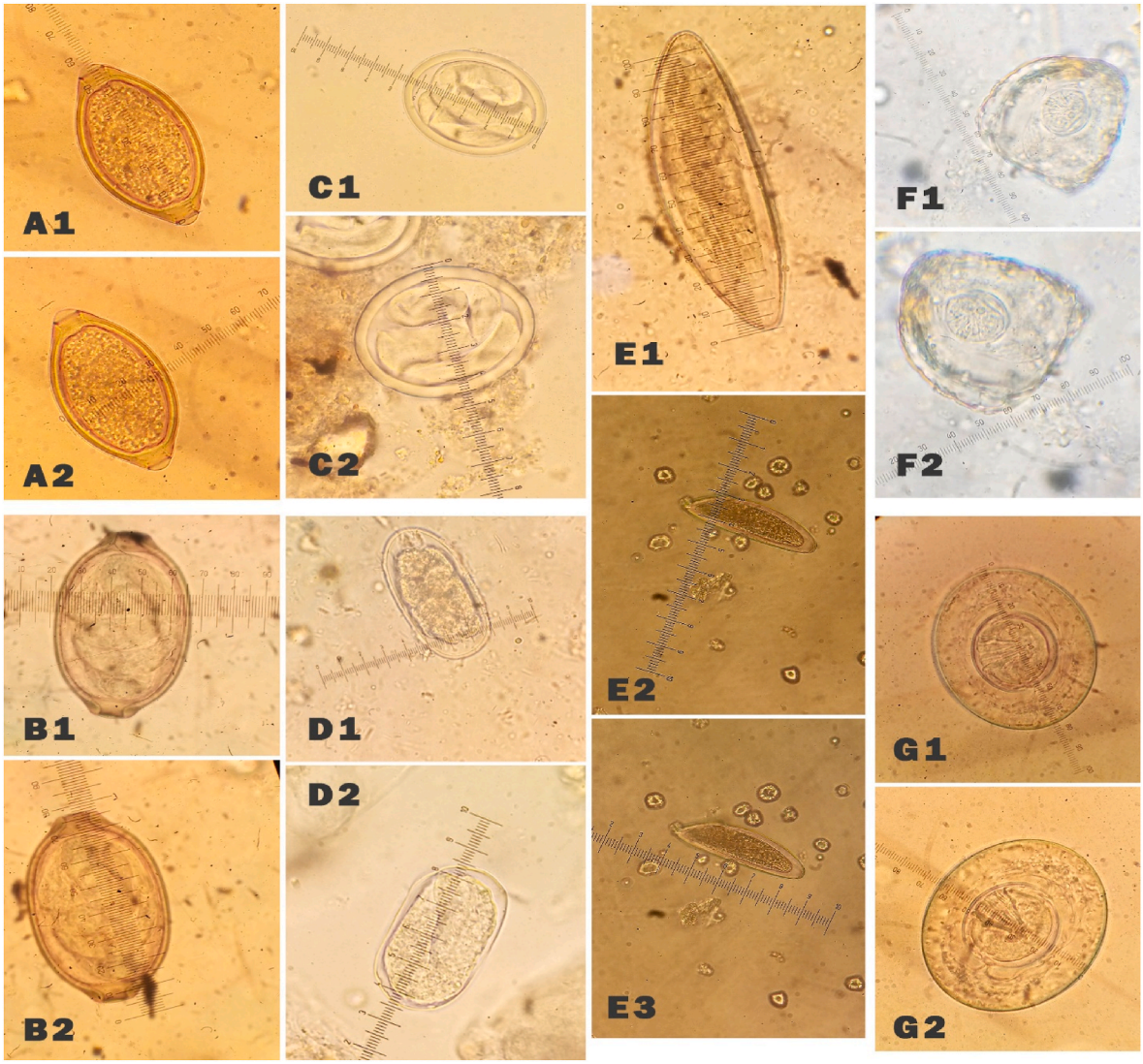


**Fig. 4.** Gastrointestinal helminth egg morphotypes with their morphometric measurements (length and width in μm) detected from rodents: A1 & A2 = *Trichuris* spp. egg type (100x), B1 & B2 = Capillariidae egg type (100x), C1 & C2 = Spirurid egg type (100x), D1 & D2 = *Strongyloides* spp. egg type (100x), E1 = *Syphacia* spp. egg type (100x), E2 & E3 = *Syphacia* spp. egg type (40x), F1 & F2 = Anoplocephalidae egg type (100x), and G1 & G2 = *Hymenolepis*-like egg type (100x).

**Table 3**
Overall prevalence of helminth infection across demographic factors and environmental factors of collected rodents. MHR = mean helminths richness, N = number of infected rodents.

| Variables | Categories | N | Prevalence (%) | 95% CI_lower | 95% CI_upper | p_Value |
|---|---|---|---|---|---|---|
| Sex | Female: MHR = 0.655 | 78 | 50 | 41.9 | 58.1 | |
| | Male: MHR = 0.744 | 116 | 56.3 | 49.2 | 63.2 | 0.2775 |
| Habitat: | Bush: MHR = 0.686 | 25 | 64.1 | 47.2 | 78.8 | |
| | Farm: MHR = 0.691 | 101 | 51.5 | 44.3 | 58.7 | |
| | Peridomestic: MHR = 0.734 | 68 | 53.5 | 44.5 | 62.4 | 0.3557 |
| Age | Adult: MHR = 0.789 | 179 | 59.3 | 53.5 | 64.9 | |
| | Juvenile: MHR = 0.309 | 15 | 25 | 14.7 | 37.9 | 2.36E-06 |
| District | Iringa: MHR = 0.72 | 122 | 53.7 | 47 | 60.4 | |
| | Morogoro: MHR = 0.68 | 72 | 53.3 | 44.6 | 62 | 1 |
| Season | Dry: MHR = 0.697 | 135 | 51.3 | 45.1 | 57.5 | |
| | Rainy: MHR = 0.723 | 59 | 59.6 | 49.3 | 69.3 | 0.198 |

prevalence, mean intensity, and abundance) and examined how host body condition and ectoparasite intensity influence helminth infections across species and habitats.

The results indicated that, per species mean SMI of rodents in bushland habitats were slightly higher than in farmland and peridomestic habitats, which suggests the wellbeing of animals in relatively pristine natural habitats (bushland) compared to disturbed habitats (farmland and peridomestic)(Peig and Green, 2010). Ranked two-way ANOVA for SMI reveals that both rodent species and habitat characteristics have a significant ($p < 0.005$) strong influence on SMI. This means significant independent differences in the ranked SMI across different rodents and habitat sites exist. This suggests that factors like

**Table 4**
Parasitological parameters of gastrointestinal parasites determined through egg morphology from faecal samples of captured rodents in Iringa and Morogoro districts. MHR = mean helminth richness, Prev. (95% CI) % = prevalence with 95% confidence intervals, MI = mean intensity, Range = intensity range, MA ± SE = mean abundance ± standard error.

| Category | Prev. (95% CI) % | MI | Range | MA ± SE |
|---|---|---|---|---|
| ***Aethomys* spp.: 24/36; MHR = 0.892** | | | | |
| **Nematodes** | | | | |
| *Strongyloides* spp. | 25(12.1–42.2) | 428 | 150–1300 | 106.9 ± 42.8 |
| *Trichuris* spp. | 27.8(14.2–45.2) | 670 | 150–2000 | 186.1 ± 67.7 |
| Capillariidae | 2.78(0.0703–14.5) | 100 | 100 | 2.78 ± 2.78 |
| Spirurida | 5.56(0.68–18.7) | 2925 | 2700–3150 | 162.5 ± 113.6 |
| *Syphacia* spp. | 8.33(1.75–22.5) | 167 | 100–200 | 13.9 ± 8.12 |
| **Cestodes** | | | | |
| *Hymenolepis*-like species | 16.7(6.37–32.8) | 575 | 50–1550 | 95.8 ± 53.4 |
| ***Arvicanthis niloticus*: 14/20; MHR = 0.9** | | | | |
| **Nematodes** | | | | |
| *Strongyloides* spp. | 40(19.1–63.9) | 638 | 200–1850 | 255 ± 102.7 |
| *Trichuris* spp. | 25(8.66–49.1) | 560 | 200–1500 | 140 ± 79.2 |
| Capillariidae | 5(0.127–24.9) | 800 | 800 | 40 ± 40 |
| Spirurida | 10(1.23–31.7) | 900 | 850–950 | 90 ± 62.1 |
| **Cestodes** | | | | |
| *Hymenolepis*-like species | 10(1.23–31.7) | 1175 | 200–2150 | 117.5 ± 107 |
| ***Grammomys* spp.: 6/12; MHR = 0.917** | | | | |
| **Nematodes** | | | | |
| *Strongyloides* spp. | 33.3(9.92–65.1) | 1075 | 150–2600 | 358.3 ± 224.5 |
| *Trichuris* spp. | 8.33(0.211–38.5) | 300 | 300 | 25 ± 25 |
| Capillariidae | 8.33(0.211–38.5) | 900 | 900 | 75 ± 75 |
| *Syphacia* spp. | 8.33(0.211–38.5) | 200 | 200 | 16.7 ± 16.7 |
| **Cestodes** | | | | |
| *Hymenolepis*-like species | 25(5.49–57.2) | 417 | 50–850 | 104.2 ± 73.7 |
| Anoplocephalidae | 8.33(0.211–38.5) | 150 | 150 | 12.5 ± 12.5 |
| ***Mastomys natalensis*: 125/252; MHR = 0.681** | | | | |
| **Nematodes** | | | | |
| *Strongyloides* spp. | 18.3(13.7–23.6) | 501 | 100–1750 | 91.5 ± 16.4 |
| *Trichuris* spp. | 21.8(16.9–27.4) | 733 | 50–3000 | 159.9 ± 29.1 |
| Capillariidae | 2.38(0.879–5.11) | 1342 | 100–4250 | 31.9 ± 18.6 |
| Spirurida | 9.13(5.87–13.4) | 1183 | 50–8450 | 107.9 ± 41.5 |
| *Syphacia* spp. | 1.98(0.647–4.57) | 190 | 100–450 | 3.77 ± 2.04 |
| **Cestodes** | | | | |
| *Hymenolepis*-like species | 8.73(5.55–12.9) | 1461 | 150–3900 | 128.6 ± 32.1 |
| ***Rattus rattus*: 10/14; MHR = 0.929** | | | | |
| **Nematodes** | | | | |
| *Strongyloides* spp. | 21.4(4.66–50.8) | 1717 | 950–2850 | 367.9 ± 221.8 |
| *Trichuris* spp. | 35.7(12.8–64.9) | 820 | 250–1500 | 292.9 ± 141.4 |
| Spirurida | 7.14(0.181–33.9) | 500 | 500 | 35.7 ± 35.7 |
| *Syphacia* spp. | 7.14(0.181–33.9) | 200 | 200 | 14.3 ± 14.3 |
| **Cestodes** | | | | |
| *Hymenolepis*-like species | 14.3(1.78–42.3) | 1400 | 150–2650 | 200 ± 188.8 |
| Anoplocephalidae | 7.14(0.181–33.9) | 350 | 350 | 25 ± 25 |
| ***Tatera vicinus*: 15/28; MHR = 0.821** | | | | |
| **Nematodes** | | | | |
| *Strongyloides* spp. | 35.7(18.6–55.9) | 470 | 100–1450 | 167.9 ± 65.5 |
| *Trichuris* spp. | 28.6(13.2–48.7) | 556 | 150–1200 | 158.9 ± 64.3 |
| Capillariidae | 3.57(0.0904–18.3) | 250 | 250 | 8.93 ± 8.93 |
| Spirurida | 3.57(0.0904–18.3) | 600 | 600 | 21.4 ± 21.4 |
| **Cestodes** | | | | |
| *Hymenolepis*-like species | 10.7(2.27–28.2) | 183 | 100–250 | 19.6 ± 11.6 |

species-specific physiology and environmental conditions of the habitats are important in shaping the body condition of these rodents (Dantas et al., 2021; Layton-Matthews et al., 2021; Villar and Naya, 2018). However, the interaction of rodent species and habitat captured had no statistically significant association ($p > 0.05$) which signifies that the effect of species on SMI does not significantly differ across habitats. In other words, the relationship between species and SMI is consistent across the different habitats studied.

Analysis of ectoparasitism revealed that, there was a significantly positive correlation between flea infestations and SMI (rho = 0.3313, $p < 0.05$) contrary to mite infestations. The fact is, small mammals with high SMI indicate better fat stores or nutritional status, hence they provide a more resource-rich environment for ectoparasites including fleas and mites, compared to those with low SMI (Sánchez et al., 2018; Van Der Mescht et al., 2013; Zduniak et al., 2023). The difference in infestation status between fleas and mites observed in this study may be due to differences in transmission dynamics between these two ectoparasites. Mites often rely on close contact transmission (e.g., between mother and offspring or during social interactions), which might not correlate directly with host size or body condition (Klimov and He, 2024; Roper et al., 2023). In other words, mite infestations might be more strongly influenced by behavioral or environmental factors, such as the small mammal's nesting habits or hygiene practices, which may not directly relate to SMI. On the other hand, fleas have a higher ability to detect chemical signals or physiological cues from well-nourished hosts, increasing their likelihood of infestation (Krasnov et al., 2002, 2003). Additionally, fleas have long hind limbs and are able to jump off the host when sensing high vibrations such as host-grooming. Heavier animal may be less agile and flexible, which in turn might limit their ability to groom effectively and remove fleas (Stanko et al., 2002). This could lead to higher flea burdens for animals with high SMI compared to those with low SMI.

More than half (53.59%) of the rodents examined under this study had gastrointestinal parasites within two main groups (nematodes: *Trichuris* spp., *Strongyloides* spp., Capillariidae, Spirurida and *Syphacia* spp., and cestodes: *Hymenolepis*-like species and Anoplocephalidae). However, the general richness of helminths infecting rodents in this study was dominated by nematodes (5 nematode groups), mostly represented by *Strongyloides* spp. And *Trichuris* spp. with high prevalence and spirurids with high mean intensity of EPG. These results are in line with studies conducted elsewhere which reported the dominance of nematode groups over other groups of helminths (Behnke et al., 2000; Grandón-Ojeda et al., 2022; Rahdar et al., 2017). The possible reason for observed pattern of nematode diversity and prevalence dominance can be due to monoxenic nature of lifecycle in most nematodes as suggested by Abu-Madi et al. (2010), upon which single host is enough to complete the life cycle of most nematode parasites.

Rodent infections caused by gastrointestinal helminths have multifaceted impacts, including direct effects on the rodents' health, which can, in turn, alter their ecological interactions with the environment and other living organisms. Furthermore, gastrointestinal parasites may play an important role in impacting humans and domestic animals health. In this study, we identified seven groups of helminth egg types in rodents, some of which include species known to substantially infect domestic animals or pose zoonotic risks. Additionally, while certain helminth species specifically infect rodents, their biological similarities to human parasites make them valuable for use in laboratory research models to study human biological systems.

Substantial prevalence (23.3%) of Trichuridae has been detected in the present study. Whipworms are common cosmopolitan nematodes and have been recorded from rodents in Tanzania before (Ribas et al., 2013; Thomas et al., 2023). Our results slightly comply with these other previous studies conducted in Tanzania. However, lower prevalence (6.7%) of *Trichuris* spp. was reported in a coprology study conducted from Chile (Carrera-Játiva et al., 2023). The variation in the detected prevalence of helminths may be attributed to differences in geographic location, host population density, or the parasite infection status at the sites where rodents were collected. *Trichuris* spp. is among the soil-transmitted helminths and always establishes host species-specific adaptation. However, *T. muris* which specifically infects rodents,

**Table 5**
Generalized linear mixed models with binomial error demonstrating the scaled mass index (SMI) categories and ectoparasite infestations as predictors for gastrointestinal helminth infection in rodents, whereby rodent species and habitat sites were kept as random factors for the models. OR = odds ratio; CI_lower = 95% lower confidence interval; CI_upper = 95% upper; SE = standard error.

| Parasite | Predictors | Parameters | | OR | 95% CI_Lower | 95% CI_Upper | SE | p-Value |
|---|---|---|---|---|---|---|---|---|
| | Fixed effect | | | | | | | |
| Overall | Intercept | | −0.7206 | 0.4864 | 0.3492 | 0.6777 | 0.1682 | 2.04E-05 |
| | SMI | Low | Reference | | | | | |
| | | Medium | 0.2076 | 1.2307 | 0.689 | 2.1983 | 0.296 | 0.483024 |
| | | High | 1.718 | 5.5732 | 2.3395 | 13.2765 | 0.4429 | 1.05E-04 |
| | Flea infestation | Flea intensity | 0.4253 | 1.53 | 1.3045 | 1.7946 | 0.0814 | 1.72157E-07 |
| | Mite infestation | Mite intensity | 0.0576 | 1.0593 | 1.0079 | 1.1133 | 0.0254 | 0.02323379 |
| *Strongyloides* spp. | Intercept | | −2.1312 | 0.1187 | 7.72E-02 | 0.1824 | 0.21928 | <2e-16 |
| | SMI | Low | Reference | | | | | |
| | | Medium | 0.0217 | 1.022 | 0.5108 | 2.0448 | 0.35387 | 0.951 |
| | | High | 1.0013 | 2.7219 | 1.3457 | 5.5053 | 0.35939 | 0.00533 |
| | Flea infestation | Flea intensity | 0.3157 | 1.3712 | 1.1881 | 1.5825 | 0.07312 | 1.58E-05 |
| | Mite infestation | Mite intensity | 0.0643 | 1.0665 | 1.0199 | 1.1152 | 0.02279 | 4.76E-03 |
| *Trichuris* spp. | Intercept | | −1.6648 | 0.1892 | 0.1314 | 0.2725 | 0.186 | <2e-16 |
| | SMI | Low | Reference | | | | | |
| | | Medium | 0.2133 | 1.2379 | 0.6568 | 2.333 | 0.32335 | 0.50928 |
| | | High | 0.875 | 2.3988 | 1.2118 | 4.7487 | 0.34842 | 0.01203 |
| | Flea infestation | Flea intensity | 0.2076 | 1.2307 | 1.0722 | 1.4126 | 0.07033 | 0.00316 |
| *Hymenolepis*-like species | Intercept | | −2.4929 | 0.0827 | 0.0448 | 0.1525 | 0.1525 | 1.55E-15 |
| | Flea infestation | Flea intensity | 0.1902 | 1.2095 | 1.013 | 1.444 | 1.444 | 0.03546227 |

shares significant biological similarities with *T. trichiura*, the species that infects humans. Consequently, *T. muris* is frequently used as a biological laboratory research model to study human trichuriosis, employing rodents as experimental models.(Klementowicz et al., 2012).

In this study, we observed a substantial prevalence (22.1%) of *Strongyloides* spp. infection in rodents. These findings are comparable to reports from various regions worldwide. For instance, Kusumarini et al. (2022) documented a prevalence of 28% in wild rodents in Indonesia, while Al-Zihiry et al. (2015) reported a prevalence of 34.2% in rodents from Malaysia. *Strongyloides* species are host-specific, with two species; *S. ratti* and *S. venezuelensis* known to infect rodents. Neither of these species has been reported to infect humans. Although *S. ratti* is not zoonotic, it shares significant biological similarities with the human threadworm (*S. stercoralis*). Consequently, *S. ratti* is widely utilized as a laboratory model for studying human biological systems, using rodents as experimental models (Viney and Kikuchi, 2017).

The prevalence of capillariids observed in this study was relatively low, with the highest occurrence recorded in *Grammomys* spp. (8.33%), followed by *Arvicanthis niloticus* (5%). To date, various genera under the family Capillariidae have been reported to infect different rodent species globally. Examples of these helminths include *Capillaria* spp., *Aonchotheca* spp., *Paracapillaria* spp., *Calodium* spp. And *Eucoleus* spp. (Behnke and Jackson, 2024; Chaisiri et al., 2012; Debenedetti et al., 2014). Several studies have reported a high prevalence of capillariid species, particularly *Capillaria hepatica*, in *Rattus* spp. For instance, Quilla and Paller (2020) reported a prevalence of 21.11% in *Rattus* spp. in the Philippines, while Rothenburger et al. (2014) documented a prevalence of 36% in *Rattus* spp. in Canada. Interestingly, no Capillariidae egg types were detected in *Rattus rattus* samples in this study. The low prevalence and absence of these helminths in *R. rattus* may reflect underestimation or misdetection due to the low sensitivity of the methods used to identify helminth eggs. To improve detection and identification of common capillariid species in rodents, microscopic examination of feacal content, urine, and tissues is recommended (Berentsen et al., 2015).

Among capillariids, *C. hepatica* is a zoonotic nematode that primarily infects the livers of rodents but can occasionally cause hepatic capillariosis and spurious infections in humans (Fuehrer et al., 2011; Kazemi Aghdam et al., 2014; Koea and Smith, 2008; Rocha et al., 2015). Humans acquire *C. hepatica* infection by ingesting embryonated eggs from contaminated soil, food, or water. However, human infection is rare and considered accidental, as humans are not natural hosts in the parasite's life cycle. Despite its rarity, unsanitary conditions, such as drinking water contaminated by infected rodents and high rodent population densities, are significant risk factors for human infection (Berentsen et al., 2015).

In this study, we observed a notable prevalence of spirurid infections, with an infection rate of 8.01%. Most spirurid species infecting rodents require an arthropod intermediate host, such as beetles, cockroaches, or crickets. Rodents become infected by ingesting these intermediate hosts, which carry the infective larvae. As reservoirs for spirurid parasites, rodents can transmit these parasites to higher trophic level hosts, such as carnivores or birds, when they consume infected rodents (Maldonado et al., 2020; Rahdar et al., 2017).

Several spirurids can cause patent infections in rodents, primarily in the gastrointestinal system. These infections often result in the production of eggs, which are shed into the environment, completing the parasite's life cycle within the rodent host. Examples of spirurids associated with patent infections in rodents include *Gongylonema* spp. (Gongylonematidae), *Mastophorus* spp. (Spirocercidae), *Streptopharagus* spp. (Spirocercidae), *Protospirura* spp. (Spiruridae), and *Spirura* spp. (Spiruridae) (Behnke et al., 2000; da Costa Cordeiro et al., 2018; Diouf et al., 2013; Lafferty et al., 2010; Montoliu et al., 2013). Although rodents are typically considered as paratenic hosts for *Physaloptera* spp. (Physalopteridae), some species of *Physaloptera* including *Physaloptera hispida* have been reported to establish patent infections in rodents under specific conditions (Thompson et al., 2019).

Relatively low prevalence (2.8%) was observed for *Syphacia* spp. in this study. *Syphacia* (Oxyuridae) are a genus of pinworms commonly detected in laboratory and wild rodents (Abdel-Gaber, 2016; Perec and Okulewicz, 2006; Pisanu et al., 2002). Two species have been reported to infect rodents; *Syphacia muris* and *S. obvelata* (Grandón-Ojeda et al., 2022). These helminths primarily reside in the intestines, where they can cause mild to severe infections depending on the worm burden. Although *Syphacia* spp. infections are often asymptomatic in rodents, in cases of high infections, they can lead to symptoms such as weight loss, decreased growth rates, and gastrointestinal disturbances. Detection of

*Syphacia* spp. in rodents is significant for both veterinary and research settings, as these parasites can affect the health and well-being of laboratory animals, potentially influencing experimental outcomes. In wild rodent populations, the presence of *Syphacia* spp. is of ecological importance, as it reflects the health status of the host population and the dynamics of parasite transmission within rodent communities.

*Hymenolepis*-like species were the most prevalent cestodes detected in this study, with an overall prevalence of 10.5% among the examined rodents. *Hymenolepis*-like eggs were found in notable proportions across nearly all rodent species studied, indicating the endemicity of these pathogens and the potential role of rodents in their maintenance and transmission. Genera commonly associated with *Hymenolepis*-like egg types in rodents include *Hymenolepis* spp. And *Rodentolepis* spp. (Hymenolepididae), however, species of *Raillietina* spp. (Davaineidae) with similar egg morphology, have also been reported in rodents (Macnish et al., 2003; Pakdeenarong et al., 2014; Spickett et al., 2020).

*Raillietina* spp. primarily parasitize poultry and rodents but are occasionally zoonotic, infecting humans (Sithay et al., 2020). Within *Hymenolepis*, two species, *H. nana* (the dwarf tapeworm) and *H. diminuta* (the rat tapeworm), are well-documented as infecting rodents (Khan et al., 2021; Yang et al., 2017). Both species are zoonotic and have been reported to infect humans worldwide (Cabada et al., 2016; Mijatović et al., 2024; Sirivichayakul et al., 2000; Tiwari et al., 2014). The life cycle of *Hymenolepis* spp. in rodents is indirect, with rodents serving as definitive hosts and insects, such as fleas and beetles, acting as intermediate hosts. Humans can inadvertently acquire infections by consuming food contaminated with cysticercoid-infected insects. The presence of *Hymenolepis*-like egg types in prevalent commensal rodent species such as *Rattus rattus* and *Mastomys natalensis* suggests a significant risk of zoonotic transmission in human-wildlife interface areas, particularly in Tanzania.

A relatively low prevalence (0.6%) of Anoplocephalidae-type eggs was identified in *Grammomys* spp. And *Rattus rattus*. Although these tapeworms are primarily non-zoonotic, they hold significance in wildlife due to their impact on rodent populations, particularly in disturbed or fragmented habitats (Haukisalmi, 2008; Haukisalmi et al., 2009). Various species within the Anoplocephalidae, including *Microcephaloides* spp., *Paranoplocephaloides* spp., and the African *Afrobaeria* spp., have been reported to infect rodents (Haukisalmi, 2008; Spickett et al., 2020). Anoplocephalid species typically inhabit the intestines of rodents, where they absorb nutrients and may cause varying degrees of harm to their hosts. Infections range from asymptomatic cases to severe outcomes, such as weight loss, stunted growth, or intestinal obstruction. The life cycle of these parasitic helminths involves an intermediate host, often oribatid mites, which are ingested by rodents during feeding (Denegri, 1993; Jászayová et al., 2023). Once ingested, the parasites develop into adult tapeworms within the rodent's digestive system. Although anoplocephalids do not pose a direct threat to human health, their presence in rodent populations is significant for ecological studies, as they can influence rodent population dynamics and serve as indicators of environmental health. Additionally, anoplocephalid infections in rodents are relevant in research settings, as they may impact the health and behavior of laboratory animals, potentially affecting the validity of experimental results.

Our results generally show that, presence of helminths in rodents is most likely influenced by body condition (SMI) and degree of ectoparasite infestation. Rodents with higher SMI exhibited a high risk of helminth infection compared to other body condition categories, whereas increase in ectoparasites (fleas and mites) infestation on rodents increase the risk of helminth infections. In particular, rodents with higher SMI had a 2.7 times higher risk of acquiring *Strongyloides* spp., and a 2.4 times higher risk of acquiring *Trichuris* spp. relative to those rodents with lower SMI. These observations are in line with other studies conducted elsewhere (Carrera-Játiva et al., 2023).The possible reason for this observation can be due to the fact that, high body condition implies high body mass and body sized rodents which provides big room for parasite colonization (Kołodziej-Sobocińska, 2019; Wilson et al., 2002). Rodents with high body mass and size provide wider opportunity for ectoparasite-vector attachment, have active movement and a variety of food items which increase the probability of contact with the infective stage or intermediate host of helminths (Sánchez et al., 2018; Van Der Mescht et al., 2013). In addition, higher body mass and body size is an indirect indicator of age, in which older rodents incur cost of higher accumulation of parasites compare to younger rodents (Poulin, 2011).

On the other hand, *Strongyloides* spp. were most likely to increase by 1.4 times and 1.1 times more with increase in one unit of flea and mite infestation on rodents respectively. Additionally, *Trichuris* spp. And *Hymenolepis*-like species were likely to increase by 1.2 times more with an increase in one unit of flea infestation on rodents. Ectoparasites, especially fleas, can act as vectors or intermediate hosts for certain helminths including *Hymenolepis* spp., facilitating the transmission and spread of these parasites (Abu-Madi et al., 2010). Ectoparasites have been reported to enhance the spread of helminths by weakening the host's immune system through blood feeding, increasing vulnerability to infection, or by directly transmitting infective stages of helminths through their feces (Abu-Madi et al., 2010; Khokhlova et al., 2004). Generally, this relationship suggests that ectoparasite infestations not only directly affect rodent health but also may play an essential role in amplifying the transmission of parasites, which could have broader implications for both human and veterinary health. Understanding this dynamic is crucial for managing rodent-borne helminths and controlling helminth transmission in wildlife-human interfaces.

## 5. Conclusion

We present new data on gastrointestinal helminth infections in rodents collected from wildlife-human interfaces in Tanzania. This study emphasizes the crucial role of wild rodents as reservoir hosts for potential zoonotic helminths, including capillariids and *Hymenolepis*-like species which pose risks to human and veterinary health worldwide. This study also highlights the association between ectoparasite infestations and helminth infections in wild rodents. However, further research is needed to identify the specific helminth species circulating in these areas to better understand the zoonotic potential of rodents at wildlife-human interfaces in Tanzania.

## CRediT authorship contribution statement

**Venance T. Msoffe:** Writing – original draft, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Claus A. Thomas:** Writing – review & editing, Validation, Software, Methodology, Investigation, Data curation. **Alfan A. Rija:** Writing – review & editing, Validation, Software, Methodology, Investigation, Data curation. **Jahashi Nzalawahe:** Writing – review & editing, Validation, Software, Methodology, Investigation, Data curation. **Abdul S. Katakweba:** Writing – review & editing, Validation, Software, Methodology, Investigation, Data curation. **Gerald Misinzo:** Writing – review & editing, Validation, Supervision, Resources, Methodology, Investigation, Data curation, Conceptualization. **Ladslaus L. Mnyone:** Writing – review & editing, Validation, Supervision, Resources, Methodology, Investigation, Data curation, Conceptualization.

## Ethics statement

Risk assessment for conducting this study was submitted to and approved by the Ethical Committee and Decision Board of Sokoine University of Agriculture, SUA/PFC/D/2020/0001/14, issued on December 22, 2020, and the Tanzania Wildlife Research Institute (TAWIRI) under the Tanzania Commission for Science and Technology (COSTECH), 2021-154-NA-2021-08, issued on April 13, 2021. The study followed the guidelines provided by American Society of Mammalogists

(Sikes and the Animal Care and Use Committee of the American Society of Mammalogists, 2016) on sampling and use of wild mammals in research.

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## Declaration of competing interest

The authors declare no conflicts of interest to disclose.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ijppaw.2025.101040.

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