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Efficiency of anthelmintic treatment and its effect on microparasite dynamics in wild *Mastomys natalensis*

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ABSTRACT

Co-infections between helminths and microparasites can modulate the host immune response and alter disease dynamics, with potential implications for public health. However, identifying causal relationships in natural populations is challenging due to the complexity of ecological interactions. Perturbation experiments, where a specific parasite is selectively reduced, offers a powerful framework to directly test such interactions under natural conditions. In this study, we investigated potential helminth-microparasite interactions in the multimammate mouse (*Mastomys natalensis*) in Tanzania by experimentally reducing helminth infections in both captive and wild populations. We first confirmed that two anthelmintic treatments, ivermectin and pyrantel pamoate, effectively reduced gastrointestinal nematode burdens in wild-caught individuals. We then assessed whether helminth reduction influenced the prevalence of viral and bacterial infections in free-living populations. Our results revealed no significant short-term effect of anthelmintic treatment on microparasitic infections. These findings suggest that helminth-microparasite interactions in *M. natalensis* may be subtle, context-dependent, or require longer timescales to become apparent.

1. Introduction

Co-infections are common in both humans and wildlife, often leading to complex within-host interactions that can influence host susceptibility to infection, disease severity and parasite transmission rates (Petney and Andrews, 1998; Cox, 2001; Griffiths et al., 2011; Devi et al., 2021). Among these, interactions between helminths and microparasites (viruses, bacteria and protozoa) are of particular interest due to their potential public health implications. In human populations, gastrointestinal helminth infections have been linked to increased infection rates and accelerated disease progression of HIV, malaria and tuberculosis (Brown et al., 2006; Mulu et al., 2013; Zenebe et al., 2023), suggesting that helminths may facilitate microparasite infections. Laboratory experiments in rodents support this hypothesis showing that helminth induced activation of the Th2 immune response can suppress the Th1 response, which normally provides protection against microparasites, thereby impairing the host's ability to control microparasites (Su et al., 2005; Graham et al., 2007; Pedersen and Fenton, 2007; Noland et al., 2008; Su et al., 2014).

Most of our current understanding of co-infection dynamics stems from observational field studies and controlled laboratory experiments (Lello et al., 2004; Wilson et al., 2007; Graham, 2008; Telfer et al., 2010; Salvador et al., 2011; Pol et al., 2017). While observational studies reflect real-world conditions, they are limited in their ability to disentangle causal relationships due to the confounding effects of environmental variability and host related factors (Fenton et al., 2014). In contrast, laboratory experiments offer valuable mechanistic insights but often rely on highly controlled conditions (such as the use of inbred mouse strains, standardized high infection doses and *ad libitum* feeding) that may limit their relevance to natural systems (Viney and Riley, 2017). In response to these limitations, there is a growing interest in natural perturbation experiments, which selectively reduce or eliminate

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one parasite species using antiparasitic treatment to examine the effects on co-infecting parasites (Bender et al., 1984; Ezenwa, 2016, Fenton et al. 2014). By comparing treated and untreated hosts in natural or semi-natural settings, these studies allow for causal inference while preserving ecological complexity.

Several studies have used anthelmintic treatments in wild rodent populations to experimentally reduce helminth infections and investigate their effects on co-infecting microparasites (Fenton and Pedersen, 2019). Notably, these perturbation experiments found that reducing helminths resulted in an increase in microparasite prevalence (Knowles et al., 2013; Pedersen and Antonovics, 2013; Sweeny et al., 2020), suggesting that helminth infections may suppress rather than facilitate microparasite infections. This contrasts with findings from observational and laboratory studies, which more often report facilitative effects of helminths on microparasites. These discrepancies highlight the unique value of perturbation experiments. Unlike observational studies and laboratory studies, field-based perturbation experiments allow researchers to test causal relationships directly in complex, natural environments. However, most of these experiments have been conducted in the Northern Hemisphere, and no comparable research has yet been carried out in sub-Saharan Africa, a region with a high helminth burden and emerging infectious diseases (Jones et al., 2008; Chen et al., 2024). This makes sub-Saharan Africa a critical and underexplored setting for studying the consequences of co-infections under natural ecological conditions.

To address this, we conducted a perturbation experiment in Tanzania to investigate interactions between helminths and microparasites, using the multimammate mouse (*Mastomys natalensis*) as a model system. This rodent is widespread in sub-Saharan Africa, where its population ecology has been extensively studied due to its role as an agricultural pest species and a carrier of zoonotic pathogens (Leirs et al., 2023). Previous observational studies found positive associations between helminth infections and the presence of microparasites, including Morogoro arenavirus (MORV), a non-pathogenic rodent-borne virus transmitted through direct contact (Hoffmann et al., 2021), and *Bartonella* species, a bacterium spread by bloodsucking arthropod vectors, such as fleas, lice and ticks (Gutiérrez et al., 2015; Vanden Broecke et al., 2021 & 2023). However, the causal relationship between helminth infections and microparasite dynamics, including MORV and *Bartonella* spp., remains unclear.

Based on these findings, we hypothesised that helminth infections modulate the host immune system by inducing a Th2 response that suppresses Th1-mediated defences, thereby facilitating microparasite infections. We predicted that experimentally reducing helminth infections with anthelmintics would alleviate this suppression and decrease the prevalence of microparasites. To test this, we first evaluated the efficacy of two anthelmintic treatments (ivermectin and pyrantel pamoate) in wild-caught *M. natalensis* in a controlled laboratory experiment. We then assessed the microparasite responses in free-living rodent populations through a short-term capture-mark-recapture field study.

2. Material and methods

2.1. Study species

Mastomys natalensis is a widely distributed rodent in sub-Saharan Africa, commonly found in agricultural fields and human dwellings (Coetzee, 1975; Chidodo et al., 2020). For over four decades populations of *M. natalensis* have been studied intensively in Morogoro, Tanzania, providing extensive insights into their population dynamics and associated parasites (Mariën et al., 2020; Leirs et al., 2023). Gastro-intestinal helminths identified in this population include *Hymenolepis* sp., *Protospirura muricola*, *Syphacia* sp., *Trichuris mastomysi*, *Gongylonema* sp., *Ptergodermatites* sp., *Raillietina* sp., *Inermicapsifer* sp. and the family Trichostrongylidae (Vanden Broecke et al., 2021). Helminth infections are highly prevalent, with approximately 78 % of individuals infected with one or more helminth species (Vanden Broecke et al., 2021). In addition to helminths, several microparasites have been detected, such as Morogoro arenavirus (MORV), *Anaplasma*, *Bartonella*, and *Hepatozoon* (Vanden Broecke et al., 2021 & 2023). MORV is an Old World arenavirus that is non-pathogenic to humans. Transmission can be vertical or horizontal via direct contact or environmental exposure to virus particles (Borremans et al., 2015; Mariën et al., 2020). Infections with MORV typically involve an acute phase of viremia followed by lifelong antibody persistence and appear to cause minimal or no pathogenic effects in *M. natalensis* (Borremans et al., 2015; Mariën et al., 2017b; Hoffmann et al., 2021). *Bartonella* spp. are facultative intracellular Gram-negative bacteria, which are primarily transmitted by fleas within wild rodent populations and include zoonotic species capable of causing human disease (such as Carrion disease, trench fever and cat-scratch disease; Gutiérrez et al., 2015). Notably, our recent work has shown that MORV-seropositive *M. natalensis* are significantly more likely to be infected with *Protospirura*, and individuals infected with *Bartonella* are more likely to harbor co-infections with other helminths, highlighting potential interactions between helminths and microparasites in this system (Vanden Broecke et al., 2021 & 2023).

2.2. Experimental setup

We first conducted a controlled laboratory experiment using wild-caught *M. natalensis* to evaluate the efficacy of two anthelmintics, ivermectin and pyrantel pamoate. This experiment took place at the Sokoine University of Agriculture in Morogoro, Tanzania, in July 2022. Rodents were trapped in nearby maize and fallow fields using Sherman LFA live traps (Sherman Live Trap Co., Tallahassee, FL). The traps were baited with a mixture of peanut butter and maize flour, set late in the afternoon and checked the following morning. Captured rodents were transported to the Institute of Pest Management (PMC) at SUA, where we recorded their sex, weight and reproductive status according to Leirs et al. (1994). Each rodent was individually housed in standard laboratory cages (28 x 11.5 × 12 cm) with wood shavings as bedding and given food and water *ad libitum*. They were randomly assigned to one of three groups: ivermectin-treated, pyrantel pamoate-treated, or control, with each group containing 20 rodents (one control died during the experiment, reducing that group to 19). Treatments were administered orally by gavage twice, with a two-week interval between doses. To minimise the risk of reinfection, cages were cleaned between treatments. Four weeks after the first treatment, the rodents were humanely euthanised with an overdose of isoflurane followed by cervical dislocation, reweighed and dissected. The entire gastrointestinal tract was preserved in absolute ethanol for parasite analysis. Eye lenses were also collected and preserved in 10 % formaldehyde. These were later extracted, cleaned and dried at 100 °C for 2 h and weighed to the nearest 0.1 mg to estimate the animal's age (Leirs et al., 1990).

Ivermectin and pyrantel pamoate were selected due to their complementary and documented efficacy against helminths in rodents. Ivermectin is widely used to treat nematode infections and also has activity against ectoparasites, such as mites and fleas, which can act as vector for microparasites (Campbell et al., 1983; Wahid et al., 1989; Pedersen and Fenton, 2015). In contrast, pyrantel pamoate specifically targets gastrointestinal nematodes and does not affect ectoparasites, making it particularly useful for investigating helminth-microparasite interactions without altering vector abundance or transmission potential, such as that of *Bartonella* spp. (Ferrari et al., 2009). We administered doses of 2 mg/kg ivermectin (Wahid et al., 1989) or 100 mg/kg pyrantel pamoate (Ferrari et al., 2009). We chose a lower dose of ivermectin to avoid potential neurotoxic effects documented in some mouse models species at higher levels (Trailovic et al., 2011; Orzechowski et al., 2012). Juveniles weighing less than 16 g or pregnant females were excluded from treatment.

Following the laboratory experiment, we conducted a field-based capture-mark-recapture (CMR) study to assess the effect of helminth infections on microparasite prevalence in free-living populations. The CMR study took place from August to December 2022 in Kiroka, Morogoro, Tanzania (Coordinates: 6°49′23.0"S 37°47′57.4"E). Three 1-ha grids were established, each more than 400 m apart with natural and artificial barriers between them to minimise movements of individuals between the grids. Within each grid, 100 Sherman LFA live traps were arranged in rows of ten, spaced 5 m apart. Trapping sessions occurred every two weeks and lasted three consecutive nights. Traps were baited as described above, set at dusk, and checked the following morning. Captured rodents were processed individually; sex, body weight and reproductive status were recorded. Blood samples were collected from the retro-orbital sinus and were stored on Whatmann filter paper for microparasite screening. Newly captured individuals were marked by clipping terminal phalanges to allow individual identification over time (Leirs et al., 2023). We chose this procedure over other less invasive procedures because we needed lifelong marks that were easily identifiable during fieldwork. Moreover, using a 17-year CMR dataset of wild-caught *M. natalensis* in Tanzania, it has been shown that toe clipping has no effect on body weight, survival and movement of the individual (Borremans et al., 2014). Each rodent was randomly assigned to receive ivermectin, pyrantel pamoate or no treatment (control) following the same dosing protocol used in the laboratory experiment. Treatments were repeated upon recapture in the subsequent trapping session. After processing, all rodents were released at their exact capture location. Individuals recaptured within the same trapping session were immediately released without further handling.

A total of 381 individual *M. natalensis* were captured, of which 75 were selected for parasitological examination (22 with ivermectin, 22 with pyrantel pamoate and 31 as control). Only individuals captured at least three times across different trapping sessions were included in the study. The initial capture was designated as time zero, with subsequent captures recorded relative to this baseline in weeks. Capture frequencies per individual ranged from 3 to 10 times over an 18-week period (Supplementary Fig. S1), with the highest capture rates during the first four weeks.

2.3. Parasitological examination

Helminths were isolated from the gastrointestinal tract according to established protocols (Ribas et al., 2011; Vanden Broecke et al., 2021). Gastrointestinal contents were examined under a stereomicroscope and helminths were identified based on their morphological characteristics using a light microscope.

In addition to helminth analysis, blood samples were screened for antibodies against Morogoro virus (MORV) and *Bartonella* to explore potential interactions between microparasites and helminth presence in the study population. Morogoro virus-specific IgG antibodies (MORVab) were detected using an immunofluorescence assay (Borremans, 2014; Mariën et al., 2017a). Each slide included positive controls and all samples were independently assessed by three observers. Samples with inconclusive results were retested to ensure accuracy. For *Bartonella* detection, DNA was extracted from blood samples and analysed using real-time quantitative PCR (qPCR) targeting the 16S-23S intergenic transcribed spacer (ITS) region. Positive qPCR samples were further amplified with conventional PCR and the resulting products were Sanger sequenced in one direction (Dahmana et al., 2020; Vanden Broecke et al., 2023). Sequence data were processed in Geneious Prime v2024.0.3, where primers were removed and low-quality regions trimmed. The cleaned sequences were then aligned using Clustal-W within Geneious Prime, incorporating reference sequences from previously identified *Bartonella* isolates and known *Bartonella* species. A Neighbor-Joining tree was generated using the Tamura-Nei model and visualised with iTOL v7 for phylogenetic analysis. Sequence similarity was calculated using MEGA 11 software and *Bartonella* subgroups were defined based on a 93.9 % similarity threshold for the ITS gene, as established by La Scola et al. (2003).

2.4. Statistical analyses

To evaluate treatment efficacy, we first ran generalised linear models (GLMs) with a binomial error distribution to analyse the presence or absence of helminths, separately for nematodes and cestodes. We then applied a zero-inflated Poisson model on the most common nematode species, *Trichuris mastomysi*, to estimate both infection probability and intensity among infected individuals. Fixed effects included treatment (control, ivermectin, pyrantel pamoate), sex (female, male) and age in days (estimated following Leirs et al., 1990). Models were simplified through backward stepwise elimination, removing non-significant terms ($p > 0.05$). To assess potential treatment effects on host health, changes in body weight before and after treatment were analysed using a two-way ANOVA, with treatment and time as predictors.

We then evaluated the impact of helminth removal on Morogoro virus (MORV) infection by focusing on seroconversion as a response variable. Since IgG antibodies indicate past exposure rather than active infection, we excluded individuals who were already seropositive at first capture to isolate recent infections during the study period. A binomial GLM was used to model the probability of seroconversion (transition from seronegative to seropositive) with fixed effects of treatment, trapping grid (three levels), sex and body weight (used as proxy for age; Leirs et al., 1990). For *Bartonella* infection, generalised linear mixed models (GLMMs) with a binomial error distribution were used to model infection presence or absence. Fixed effects included treatment, time since initial capture (week 0, 2, 4), trapping grid (three-level factor), sex, body weight, and the interaction between treatment and time, to examine how anthelmintic treatment influenced *Bartonella* infection dynamics. Individual ID was included as a random effect to account for repeated measures of the same individuals over time. To maintain a balanced sample size and minimise bias from dropouts over time, statistical analyses were restricted to data collected within the first four weeks. Missing infection status values at specific time points were imputed based on the last observed status. All statistical analyses were conducted using R (v4.4.1; R Core Team, 2024) with the 'lme4' package (Bates et al., 2015).

3. Results

3.1. Laboratory experiment

Seven helminths species were identified in the gastrointestinal tract of *M. natalensis* during the laboratory experiment, including five nematodes and two cestodes (Table 1). Among the nematodes, four genera were identified: *Trichuris mastomysi*, *Syphacia* sp., *Gongylonema* sp. and *Protospirura* sp. In addition, nematodes of the family Trichostrongylidae were found, although their specific genera could not be determined based on morphological identification. Cestode species included *Hymenolepis* spp. and members of the family Davaineidae. Apart from the gastrointestinal tract, cysts of the cestode *Taenia* sp. were also found in the body cavity.

Treatment with both ivermectin and pyrantel pamoate significantly reduced the overall probability of nematode infection compared to the control group (Supplementary Table S1). However, pyrantel pamoate had a stronger effect ($\beta = -3.574$, s.e. $= 0.925$, $p < 0.001$; Fig. 1A) than ivermectin ($\beta = -1.819$, s.e. $= 0.787$, $p = 0.02115$). Neither sex (male: $\beta = -0.722$, s.e. $= 0.679$, $p = 0.288$) nor age ($\beta = 0.004$, s.e. $= 0.009$, $p = 0.626$) significantly affected nematode infection status. This difference in treatment efficacy was also evident for *Trichuris mastomysi,* as zero-inflated Poisson models showed that pyrantel pamoate significantly increased the probability of being uninfected ($\beta = -2.608$ s.e. $= 1.208$, $p = 0.031$ Fig. 1B; Supplementary Table S2). Ivermectin showed a trend towards reducing worm burden, but the effect was not statistically significant ($\beta = -1.019$ s.e. $= 0.0.605$, $p = 0.092$). Among individuals that

Table 1
Prevalence, 95 % binomial confidence intervals and infection intensity ranges (minimum-maximum) for each helminth taxon found across treatment groups in *M. natalensis* during the laboratory experiment.

	Control (N = 19)			Ivermectin (N = 20)			Pyrantel pamoate (N = 20)		
	Prevalence (%)	[95 % CI]	Minimum-maximum	Prevalence (%)	[95 % CI]	Minimum-maximum	Prevalence (%)	[95 % CI]	Minimum-maximum
Cestodes	**84.2**	**[60.4–96.6]**		**90.0**	**[68.3–98.8]**		**60.0**	**[36.1–80.9]**	
Davaineidae	57.9	[33.5–79.7]	1–14	65.0	[40.8–84.6]	1–3	30.0	[11.9–54.3]	1–3
Hymenolepis sp.	36.8	[16.2–61.6]	1–129	30.0	[11.9–54.3]	1–22	25.0	[8.7–49.1]	3–200
Taenia sp.	0.0	[0.0–17.6]	–	0.0	[0.0–16.8]	–	5.0	[0.1–24.9]	1
Nematodes	**84.2**	**[60.4–96.6]**		**45.0**	**[23.1–68.5]**		**15.0**	**[3.2–37.9]**	
Trichuris mastomysi	63.2	[38.4–83.7]	1–6	40.0	[19.1–63.9]	1–5	10.0	[1.2–31.7]	1–3
Syphacia sp.	26.3	[9.1–51.2]	2–161	0.0	[0.0–16.8]	–	0.0	[0.0–16.8]	–
Gongylonema sp.	5.3	[0.1–26.0]	3	0.0	[0.0–16.8]	–	0.0	[0.0–16.8]	–
Protospirura sp.	10.5	[1.3–33.1]	12–27	0.0	[0.0–16.8]	–	5.0	[0.1–24.9]	1
Trichostrongylidae	15.8	[3.4–39.6]	1–2	5.0	[0.1–24.9]	3	0.0	[0.0–16.8]	–

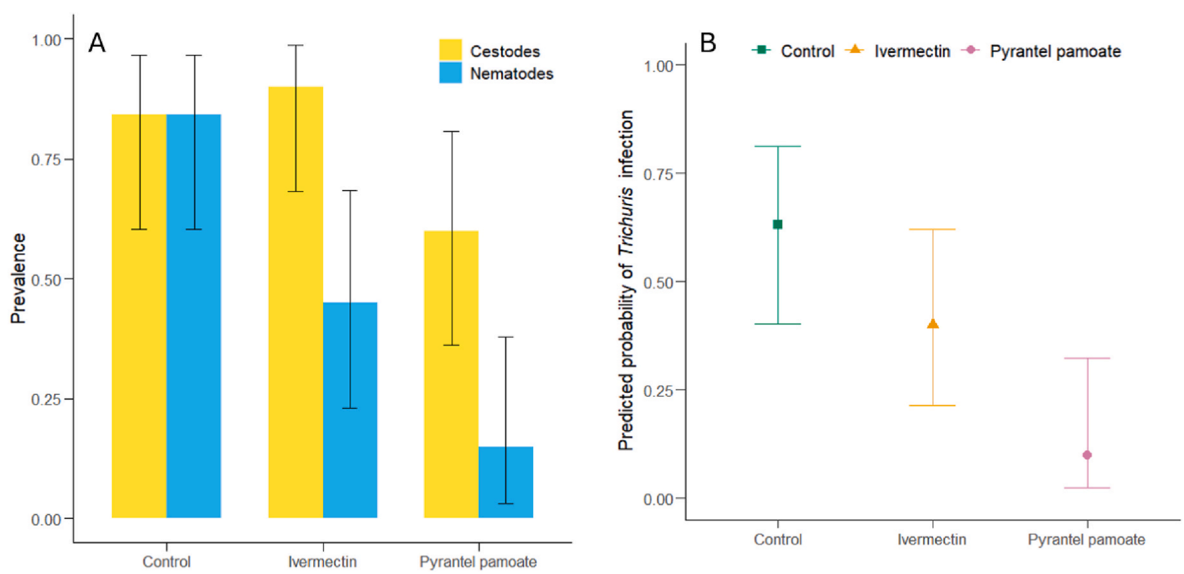

Fig. 1. **(A)** Prevalence of nematodes and cestodes, and **(B)** predicted probability of *Trichuris mastomysi* infection in *Mastomys natalensis* across treatment groups (control, ivermectin and pyrantel pamoate), with 95 % confidence intervals.

remained infected, males had significantly lower worm burdens than females (male: $\beta = -0.968$, s.e. $= 0.426$, $p = 0.023$). However, this difference appears to result from the unequal gender distribution within infected individuals, as nearly all infected animals were female. Cestode infection was not significantly affected by treatment (pyrantel pamoate: $\beta = -1.399$, s.e. $= 0.807$, $p = 0.083$; ivermectin: $\beta = 0.601$, s.e. $= 0.990$, $p = 0.543$), sex (male: $\beta = -0.795$, s.e. $= 0.703$, $p = 0.258$) or age ($\beta = 0.001$, s.e. $= 0.008$, $p = 0.899$; Supplementary Table S3). While pyrantel pamoate showed a trend toward reducing cestode infection, the effect did not reach statistical significance. Finally, there were no significant changes in body weight between the beginning and end of the experiment in the different treatment groups ($F = 0.495$, $df = 2$, $p = 0.610$), suggesting no adverse effects of the treatments on host condition.

3.2. Capture-mark-recapture study

3.2.1. Morogoro virus infection dynamics

During the study, 35 of 75 individuals (47 %) tested positive for MORV antibodies (Supplementary Fig. S2). Compared with the control group, the likelihood of seroconversion was slightly lower in the pyrantel pamoate group ($\beta = -0.875$, s.e. $= 0.914$, $p = 0.338$; Fig. 2A), although this effect was not statistically significant. Similarly, ivermectin treatment had no significant effect on seroconversion ($\beta = -0.100$, s.e. $= 0.781$, $p = 0.898$). Neither sex (male: $\beta = 0.013$, s.e. $= 0.695$, $p = 0.985$) nor body weight ($\beta = 0.044$, s.e. $= 0.041$, $p = 0.275$) affected the likelihood of seroconversion. There was also no significant effect of trapping grid on seroconversion probability ($p > 0.158$).

3.2.2. Bartonella species diversity

Out of the 294 samples screened (each representing a biological specimen collected from an individual at a specific time point), 135 (45.9 %) tested positive for *Bartonella* based on sequence analysis. We excluded 17 sequences from the phylogenetic analysis due to low quality and were classified as 'Unspecified'. The remaining sequences clustered into four distinct genogroups and seven subgroups based on sequence identity (Fig. 3; see Supplementary Fig. S3 for full tree). Genogroups A and B clustered with *Bartonella* sequences previously identified in *Arvicanthis niloticus* from Uganda (GenBank accession no. JX428757 & JX428753; Billeter et al., 2014). Notably, genogroup A was almost exclusively found in one of the trapping grids (KIR5). Genogroup C showed some similarity to *B. tribocorum* (>85 % identity, >50 % query coverage) but did not cluster closely with any previously identified *Bartonella* isolates. Genogroup D, which accounted for the majority of sequences (72.6 %), showed similarity to *B. elizabethae* (>85 identity,

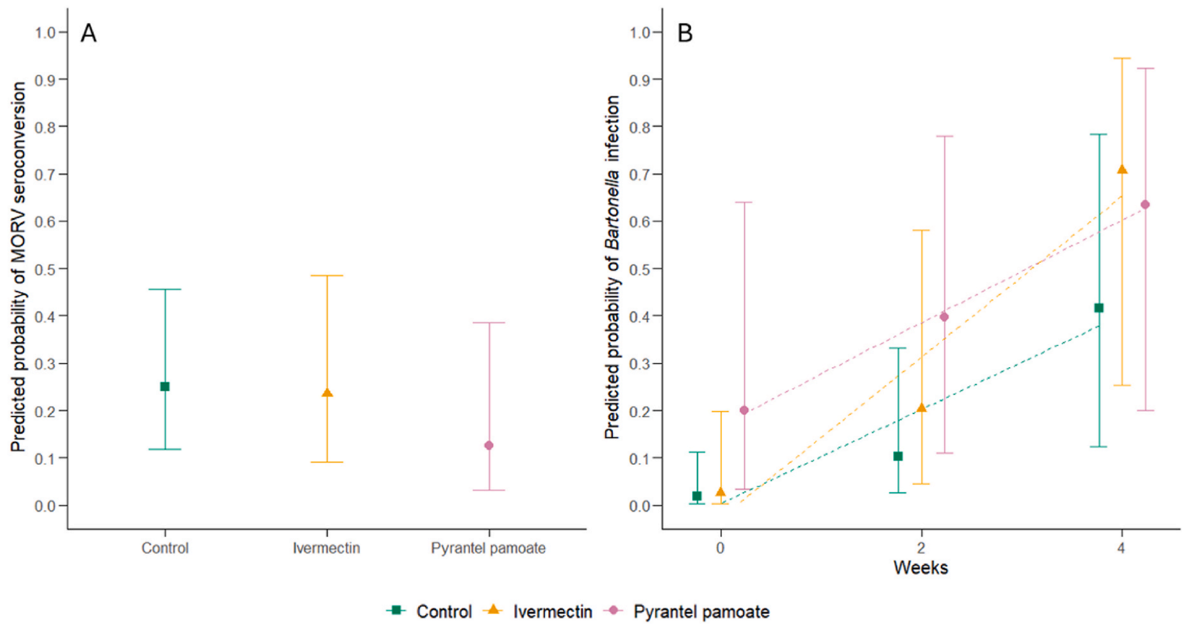

Fig. 2. **(A)** Predicted probability of Morogoro virus (MORV) seroconversion by treatment group and **(B)** *Bartonella* infection over time (weeks) for each treatment group (control, ivermectin and pyrantel pamoate) in a wild *Mastomys natalensis* population. Error bars represent 95 % confidence intervals and dashed lines indicate linear trends.

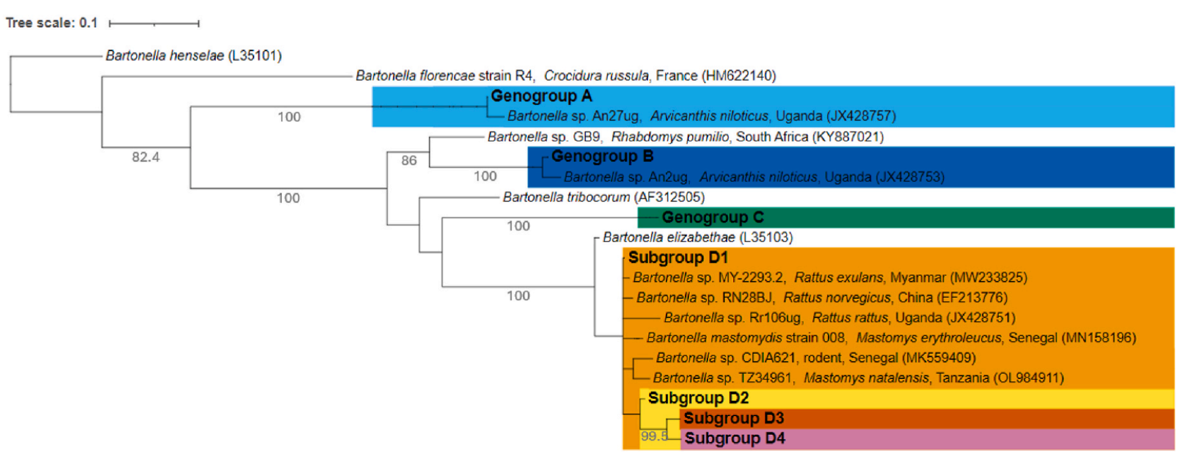

Fig. 3. Phylogenetic relationship of *Bartonella* sequences identified in this study. A Neighbor-Joining tree was constructed using the Tamura-Nei model based on ITS gene sequences, with reference sequences from previously identified *Bartonella* isolates in rodents and recognized *Bartonella* species. Bootstrap support values above 70 % are shown (1000 replicates). Subgroups were defined based on a 93.9 % similarity cut-off (La Scola et al., 2003). The scale bar represents 0.1 nucleotide substitutions per site. The representative sequences of each genogroup have been submitted to GenBank under the following accession numbers: Genogroup A – PV788829, B – PV788832, C – PV788831, D1 – PV788828, D2 – PV788830, D3 – PV788833, and D4 – PV788834.

>90 % coverage) and shares high identity with sequences previously identified from *Mastomys natalensis* in Tanzania (GenBank accession no. OL984911), *Mastomys erythroleucus* in Senegal (GenBank accession no. MN158196) and other rodents from Uganda, Myanmar and China (Billeter et al., 2014; Dahmana et al., 2020). Subgroup D1 was the most prevalent across all groups (Supplementary Table S5).

3.2.3. *Bartonella infection dynamics*

Throughout the study, 49 out of 75 individuals (65.3 %) tested positive for *Bartonella* at least once, with 42 of these testing positive on multiple occasions (Fig. 4). Infections with the same subgroup lasted up to eight weeks and some individuals carried different subgroups over time. The probability of *Bartonella* infection increased significantly over time ($\beta = 1.039$, s.e. $= 0.309$, $p < 0.001$; Fig. 2B). However, treatment with either ivermectin or pyrantel pamoate did not significantly influence this pattern (pyrantel pamoate x time: $\beta = -0.502$, s.e. $= 0.384$, $p = 0.191$; ivermectin x time: $\beta = 0.337$, s.e. $= 0.409$, $p = 0.410$). Sex also had no significant effect on infection probability (male: $\beta = -0.139$, s.e. $= 0.787$, $p = 0.860$; Supplementary Table S6). In contrast, body weight and trapping grid were significant predictors of infection: heavier individuals were more likely to be infected ($\beta = 0.225$, s.e. $= 0.063$, $p = 0.003$) and individuals from one trapping grid (KIR4) had a significantly lower probability of infection compared to those from another (KIR3) ($\beta = -4.205$, s.e. $= 1.419$, $p = 0.003$).

4. Discussion

Co-infections involving helminths and microparasites may significantly influence pathogen transmission dynamics with important implications for public health. However, experimental evidence from natural populations remains limited, particularly in African ecosystems. To fill this gap, we conducted a laboratory experiment using wild-caught

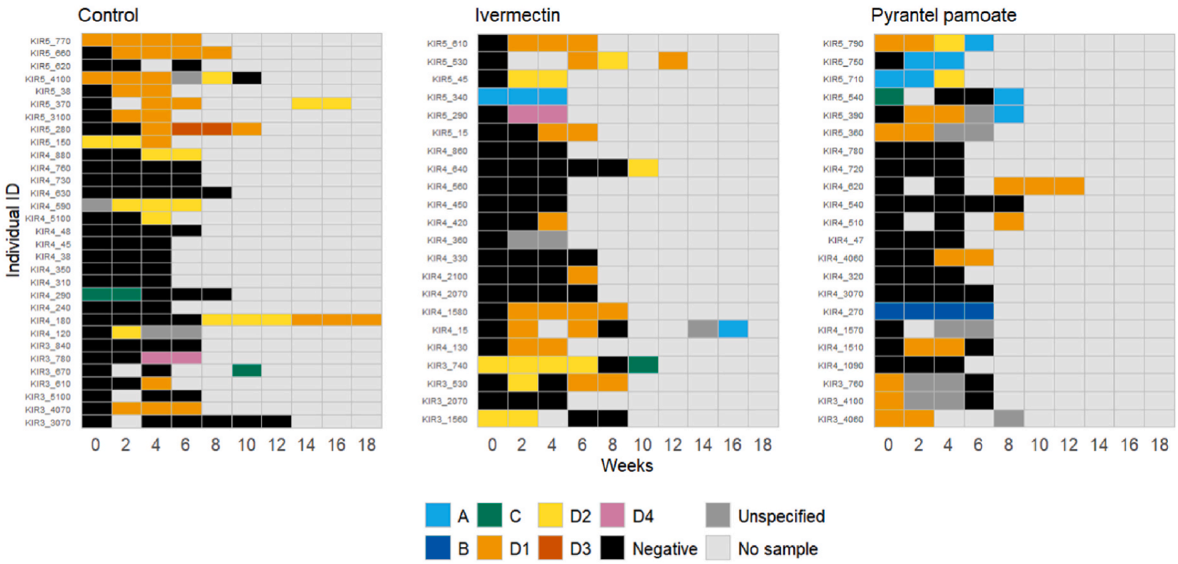

Fig. 4. Visualization of individual *Bartonella* infection patterns across 10 sampling time points for each treatment group (control, ivermectin and pyrantel pamoate) in wild *Mastomys natalensis* populations. Rasters display the infection status (positive with respective genogroup, negative or no sample) for each individual at each time point.

M. natalensis to evaluate the efficacy of two anthelmintic treatments (ivermectin and pyrantel pamoate), followed by a field-based perturbation experiment in Tanzania to investigate the effects of helminth removal on microparasite dynamics. Both treatments significantly reduced gastrointestinal nematode infections, with pyrantel pamoate proving more effective than ivermectin. While earlier observational studies in *M. natalensis* populations have reported positive associations between helminths and microparasite infections (Vanden Broecke et al., 2021 & 2023), our results showed no evidence that helminth reduction directly affects viral or bacterial infections during a short term perturbation experiment.

We identified a diverse community of gastrointestinal helminths in *M. natalensis*, including five nematodes (*Trichuris mastomysi*, *Syphacia* sp., *Gongylonema* sp., *Protospirura* sp. and Trichostrongylidae*)* and three cestodes (*Hymenolepis* spp., *Taenia* sp. and Davaineidae). Among these, *T. mastomysi* and Davaineidae were the most prevalent, with prevalence rates of 63.2 % and 57.9 %, respectively. Such helminths are commonly found in rodents across Africa (Brouat et al., 2007; Diagne et al., 2016) and the high diversity of gastrointestinal parasites observed in our study is consistent with previous reports on *M. natalensis* in Tanzania (Vanden Broecke et al., 2021). Notably, our study presents the first report of *Taenia* cysts in *M. natalensis*. While this finding is not unexpected, given that *Taenia* spp. are known to use small rodents as intermediate hosts (Thaikoed et al., 2024), it is possibly concerning due to the zoonotic potential of certain *Taenia* species. This highlights the need for further research to investigate the role of *M. natalensis* in the transmission cycle of *Taenia*.

Both anthelmintic treatments, ivermectin and pyrantel pamoate, effectively reduced nematode prevalence with pyrantel pamoate significantly more effective, especially in reducing *T. mastomysi* infections. Ivermectin achieved only partial clearance, possibly due to the relatively low dose used to minimise side effects. Since no adverse effects on host body weight were observed post-treatment, future studies might explore higher ivermectin doses to improve efficacy (Wahid et al., 1989). Neither treatment significantly reduced the prevalence of cestodes, consistent with the known limited efficacy of both agents against this parasite group and reflecting their primary action against nematodes (Wahid et al., 1989).

Contrary to our initial hypothesis and previous observational studies, anthelmintic treatment did not affect Morogoro virus and *Bartonella* infection in the short term. We had anticipated that reducing helminth infections would alter host susceptibility and thereby influence microparasite dynamics. The lack of such effects suggests that helminth-microparasite interactions may be more context-dependent or subtle than previously assumed. Notably, heavier individuals had a higher probability of *Bartonella* infection. Given the positive correlation between body weight and age in *M. natalensis* (Leirs et al., 1990), this likely reflects cumulative exposure in older animals (Vanden Broecke et al., 2023). Age-related increases in helminth infections have similarly been reported (Vanden Broecke et al., 2021), potentially explaining prior associations between helminths and *Bartonella* infection. Additionally, heavier animals may be at greater risk due to their larger body size: they can carry more ectoparasites and have a greater surface area, increasing their exposure to vectors as they move through the environment. This relationship between body size and ectoparasite abundance has also been observed in other rodent species, such as *Oligoryzomys nigripes* (Fernandes et al. 2015). Additionally, *Bartonella* infection probability also varied spatially between grids, likely due to environmental factors, such as vegetation type and density, which can affect the presence and abundance of ectoparasites (Santos et al., 2018; Smith et al., 2023).

This spatial variation was apparent not only in infection probability but also in strain distribution, with genogroup A detected almost exclusively in one grid. Such patterns may result from differences in local vector species composition, influencing *Bartonella* strain adaptation (Chomel et al., 2009). Most *Bartonella* strains identified in this study belonged to *B. elizabethae*, a rodent-associated species known to cause human diseases, including endocarditis (Kosoy et al., 2012; Hayman et al., 2013), further underscoring that *M. natalensis* is an important reservoir for zoonotic pathogens. In addition, genogroup C may represent a new *Bartonella* species, as it did not cluster with previously identified isolates but showed some similarity *to B. tribocorum*. However, further research is needed to confirm this classification and fully characterise this group (Kosoy et al., 2018).

One limitation of our study is the absence of pre-treatment nematode burden estimates, which could have strengthened the robustness of our findings. While faecal egg counts (FECs) are often used to estimate helminth burden, they pose logistical challenges under field conditions and have limited sensitivity, especially for immature or low-intensity infections (Gassó et al., 2015; Crawley et al., 2016; Ngongeh, 2017). However, previous work in the same population reported a high prevalence of helminth infections (~78 %; Vanden Broecke et al., 2021) and individuals in our study were randomly assigned to treatment groups.

This combination of high baseline prevalence and random assignment supports the reliability of our treatment comparisons, although pre-existing variation across groups cannot be completely ruled out. To enhance accuracy in future studies, incorporating standardized FEC protocols alongside postmortem assessments could be beneficial if strong correlations with actual helminth burden or diversity are established.

In conclusion, our study underscores the importance of complementing observational research with experimental approaches to better control for confounding factors. Although conducting perturbation experiments in wild populations presents challenges, such as ensuring effective antiparasitic treatments and the difficulty of recapturing individuals, they remain essential for directly testing how helminths affect microparasite infections. While observational studies have suggested associations between these parasites, our experimental results indicate that such interactions may be more subtle, context-dependent, or operate over longer timescales than previously assumed. To understand the full complexity of co-infections in natural populations, long-term experimental efforts in varied environments are needed.

CRediT authorship contribution statement

Marre van de Ven: Writing – review & editing, Writing – original draft, Investigation, Formal analysis, Data curation, Conceptualization. **Bram Vanden Broecke:** Writing – review & editing, Formal analysis. **Alexis Ribas:** Investigation. **Herwig Leirs:** Funding acquisition. **Christopher Sabuni:** Resources. **Joachim Mariën:** Writing – review & editing, Supervision, Project administration, Methodology, Conceptualization.

Ethics statement

All experimental procedures were approved by the Ethics Committee for Animal Experimentation of the University of Antwerp (2021–04) and adhered to the EEC Council Directive 2010/63/EU. The research also adhered to the animal ethics guidelines from the Sokoine University of Agriculture's 'Code of Conduct for Research Ethics' (Revised version of 2012) and the guidelines by Sikes, R.S., the Animal, C., Use Committee of the American Society of, M. (2016).

Availability of data

The representative sequences of each genogroup have been submitted to GenBank under the following accession numbers: Genogroup A – PV788829, B – PV788832, C – PV788831, D1 – PV788828, D2 – PV788830, D3 – PV788833, and D4 – PV788834.

Declaration of generative AI in scientific writing

During the preparation of this work the authors used ChatGPT in order to improve readability. After using this tool, the authors reviewed and edited the content as needed and takes full responsibility for the content of publication.

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Declaration of interest

All authors declare that there is no conflict of interest.

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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.2025.101098.

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