Environmental controls on parasite infection dynamics in a multihost community at the wildlife-livestock interface

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Submitted in fulfilment of the requirements for the Degree of Doctor of Philosophy

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October - 2025

Abstract

Wildlife-livestock interfaces are increasing globally, mainly due to the expansion of livestock production within a shrinking footprint for wildlife. Compressed ecosystems increase interactions of livestock, wildlife and humans, as well as the pathogens and parasites they carry. These interactions are core processes contributing to the emergence and spread of many infectious diseases and advancing our understanding of the direct and indirect ways that ecological interactions and environmental conditions shape parasite infection risk is a major priority under global change. Yet in many cases, we do not even know the composition of parasites that occur in different host species of livestock and wildlife and their transmission pathways occurring at interfaces, particularly from tropical settings. Migratory wildlife have large ecological effects along their migration routes, and with them may transfer parasites into new areas, spreading infectious diseases across management or political borders. This thesis synthesizes the role of migratory herbivores, vegetation and environmental factors such as rainfall, temperature and humidity in changing gastrointestinal nematodes infection risks across the landscape at the wildlife-livestock interfaces.

While migratory hosts move parasites and pathogens (transport effects) between areas, potentially infecting other host species, they can also have large effects on the environment via trophic effects in ways that may indirectly impact risk of transmission. Currently, we have little understanding of the magnitude, direction and net effects of migratory host's transport and trophic effects in changing infection risks across ecosystems. In chapter 2, I used an experimental approach, and integrated framework that linked migration intensity and duration versus transport and trophic effects to study how migratory herbivores change pasture infection risks across the landscape. Migration intensity (the density of migrants in an area) and duration (the period that migrants remain in an area) determined the relative size and direction of transport and trophic effects on environmental parasite abundance in pasture. High migration intensity led to both strong transport and trophic effects upon environmental parasites. Grazing led to parasite consumption (hoovering effects) and changes to microclimate conditions, that resulted in a net decrease in availability of free-living stage of environmental

parasites. Longer migration duration in an area increased both transport and trophic effects due to multiple dung depositions and multiple bouts of grazing. However, the trophic effects outweighed transport effects, and the resulting environmental parasite abundance was lower under high duration conditions compared to low duration conditions. The results suggest that grazing strongly modifies the infection risk for the subsequent hosts, and that both the intensity and duration of grazing, relative to the timing of parasite emergence, determine prevailing infection risk in pasture following herbivore migration.

Trees form an additional component of structural heterogeneity in savannas that also shape herbivore distribution and abundance, but we have a poor understanding of how heterogeneity induced by trees and herbivores, or their interactions, may drive infection risks across landscapes. In chapter 3, using a combination of observational and experimental approaches, I investigated how heterogeneity of grass cover induced by the herbivores' trophic effects or by the presence and absence of tree cover, shaped infection risk of environmental parasites across the landscape. I found that shade availability from grass and tree canopy affected the abundance of environmental parasites by modifying microclimate conditions. The presence of shade from vegetation, such as from trees canopies and grasses, reduced the amount of sunlight reaching the soil surface grass layer by half or more, compared to areas without any vegetation cover. Furthermore, maximum temperature values were, on average, up to 8.5 °C higher in unshaded areas compared to shaded areas. As a result, abundance of environmental parasites was twice as high in shaded areas compared to unshaded areas. The observed microclimate effects on gastrointestinal nematode abundance also changed with aridity conditions, where overall there was an increase in environmental parasite abundance during wet conditions compared to dry conditions in all treatments, and the infection risk increased in unshaded shorter grass compared to unshaded long grass during wet conditions compared to dry conditions. My results suggest that, by changing vegetation structure, herbivore grazing reduces infection risk across the landscape by exposing free living stages of parasites to harsh weather conditions, resulting in lower abundance of environmental parasites. Trees, in contrast, by blocking sunlight radiation, increase infection risk across the landscape by lowering temperature

and increasing humidity of grasses underneath, conditions that enhance survival of free-living stages, and lead to greater parasite abundance in the environment.

Overlap between wildlife and livestock is a common phenomenon that is currently increasing worldwide, but our understanding of ways in which overlapping wildlife and livestock are beneficial to each other under different contexts is limited. In chapter 4, I examined the consequences, in terms of infection, for livestock that overlapped spatially with migratory wildlife. Specifically, I used a natural experiment to evaluate how the intensity and composition of gastrointestinal nematode (GIN) infection in ruminant livestock changed depending on exposure to migratory wildebeest. I used a before-and-after impact design to sample GIN from livestock relative to the wildebeest migration. Wildebeest migration was associated with changes of livestock infection depending on the level of exposure to wildebeest and environmental conditions of the region where livestock occur. Livestock exposed to wildebeest migration had lower infection intensity compared to livestock not exposed to wildebeest migration. Goats' infection intensity was higher in the wetter region (West) compared to drier region (East), while for cattle the infection was higher in dry region (East) compared to wetter region (West). Wildebeest migration also decreased species richness of worms in goats in areas grazed by wildebeest compared to areas not grazed by wildebeest, but post wildebeest migration also increased species richness in area exposed to wildebeest compared to pre-wildebeest migration. In contrast for sheep, there was an increase in worm species richness post wildebeest migration compared to pre wildebeest migration timepoint. The study findings suggest overlap between wildlife and livestock may be beneficial to livestock by reducing infection intensity or harmful by introducing new worms or increasing chances of rare worm species to infect livestock in different areas. Furthermore, environmental conditions, type of livestock, and livestock husbandry modified resulting infection intensity from wildlife and livestock overlap.

The synthesized knowledge about the interconnected roles of wildlife migration, vegetation structure and environmental conditions on parasite dynamics broadens our understanding of infectious disease epidemiology at the wildlife-livestock interface and contributes to pathways that promote wildlife-livestock co-existence, by quantifying impacts and benefits of wildlife and livestock co-

existence. Furthermore, the knowledge could be used to improve intensive livestock production in tropical areas by identifying the conditions under which promoting co-grazing between livestock and migratory wildlife might reduce infectious disease in livestock and how different vegetation structures shape infection risks during wet and dry conditions.

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Acknowledgement

It is a great honour for me to have seized the opportunities and experience the challenges of working out a PhD. This experience has not only shaped my academic growth but also allowed me to pursue and work toward the realization of a long-held dream. I am profoundly grateful to all the people and institution that supported me in all stages of my PhD journey as follows:

First, I am grateful to my supervision team, particularly Dr Thomas Morrison, for the trust and accepting me as a PhD student and part of Ecology and evolutionary of infectious diseases (EEID) project. I had opportunity to have insightful discussion of ideas, experimental design and statistical help from him during my PhD. Secondly, I am grateful to Dr Jennifer McIntyre for the training and guidance related to molecular bar coding, bioinformatics and parasitology. Apart from supervision team, I am also grateful to Prof Grant C. Hopcraft for the comments and inputs throughout my PhD as well as logistical support during fieldwork in Serengeti National Park – Tanzania. I am grateful to Prof Dan Hydon for offering opportunity and time to help with statistics. Furthermore, I am grateful to all EEID team members (Prof Ricardo Holdo, Prof Mike T Anderson, Prof Vanessa Ezenwa, Prof Eileen Devaney, and Dr Jason Donaldson) for the logistical support, sharing of knowledge, and experience throughout my PhD.
I am grateful to all the people that were involved and assisted my field work including, Hussein Adam, Aidan Tresphory, Baraka Jumapili, Basil Senso, Jeremia Sarakikya, Tauta Mappi, Rigobert Tarimo, Fadhili Mshana, Felix Musyangi, Joseph Masoi, Peace Sabuni, Lameck Jacob, Meritho Katei and Nobert Munuo.

Most importantly, I am profoundly grateful to my family, foremost my wife and my mother for the lovely support throughout my PhD. To my lovely wife (Highness Yohana), thank you so much for taking care of our children, Halima and Fahima, during my absence and even during the times we were together, but I was occupied with studies. Your unwavering support and love have meant everything to me. To my mother (Halima Waziri), will forever be profoundly grateful for your love, support and guidance, and thanks for taking care of my family during my absence. Lastly, I am deeply grateful to my brothers, Masatu Mtimba and

Ramadhani Nasoro, for stepping in during my absence and taking care of our mother throughout my PhD journey. Your support made this achievement possible.

Secondly, I extend my sincere gratitude to the Commonwealth Scholarship Commission for funding my PhD studies. I am also deeply thankful to the government of Tanzania, through the College of African Wildlife Management, Mweka, for granting me a four-year study leave and providing additional financial support. My study has been possible due to support from University of Glasgow as well as logistical support and research clearance by Tanzania Wildlife Research Institute (TAWIRI). Lastly, I am grateful for the financial support from Rufford small grant organization that provided fund to cover a second chapter of my thesis.

Author's Declaration

This thesis is my original work and was carried out entirely by me. Where the work of others has been used, it has been appropriately acknowledged. This thesis has not been submitted, nor will it be submitted, for any other degree or qualification at any other university. One of the thesis chapters (chapter 2) has been published as a paper, Kimaro et al., 2025.

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Definitions/Abbreviations

BLASTN - Basic Local Alignment Search Tool for nucleotide to nucleotide

BLAST - Basic Local Alignment Search Tool

BO – Bovine

CP – Capra – in chapter 4

CP – Control plot, in chapter 2

epg – eggs per grams of faecal

FTA - Whatman Flinders Technology Associates

FEC – Faecal egg counts

GIN – Gastrointestinal nematodes

GLMM - Generalized linear mixed model

HILD – High Intensity Low Duration

HISO - High Intensity Stop-over

ITS2 - Internal transcribed spacer region 2

L1, L2, L3 – Free larval stages of strongyle nematodes. L3 is the infective stage

LIHD – Low Intensity High Duration

LILD - Low Intensity Low Duration

OV – Ovine

PCR – Polymerase chain reaction

T_A - Primer annealing temperature

1.0 General introduction

1.1 Trend of wildlife-livestock interface under global change and its implication to wildlife conservation, livestock management and disease transmission

Wildlife-livestock interfaces are increasing globally, mainly due to increasing livestock production and shrinking ecosystems worldwide (Cravino et al., 2024a; Hassell et al., 2017; Li et al., 2025; Niamir-Fuller et al., 2012; Veldhuis et al., 2019). As human population increases, many natural areas are converted to human settlements and agricultural areas for crop production and livestock keeping at the cost of biodiversity (Cravino et al., 2024b; Otuoma et al., 2009). These anthropogenic activities are the main drivers of wildlife habitat fragmentation, pollution, and over utilization of natural resources leading to declining wildlife populations and increasing extinction risk of species (Barroso & Gortázar, 2024; Du Toit & Cumming, 1999; Veldhuis et al., 2019). As a result, anthropogenic activities increase interaction of pathogens, livestock, wildlife and humans, a core process at the wildlife-livestock interface that contribute to emergence of infectious diseases (Hassell et al., 2017; Jori et al., 2021; Lane et al., 2025; Meurens et al., 2021; Pal et al., 2025; Wiethoelter et al., 2015). On the other hand, wildlife can affect livestock production through predation, competition for forage and water as well as disease transmission (Kimuyu et al., 2017; Niamir-Fuller et al., 2012). These wildlife effects on livestock, particularly predation and disease outbreaks, have triggered negative perceptions of livestock keepers on wildlife and become a source of conflict between wildlife managers and people living next to protected areas (Grootenhuis & Olubayo, 1993; Kock, 2005; Matungwa et al., 2024). It is predicted that wildlife-livestock interaction and their impact on each other will be difficult to avoid (Cravino et al., 2024b; Kock, 2005), and therefore finding a balance and equilibrium for the wildlife-livestock co-existence becomes a necessary option (Stears & Shrader, 2020). To manage such challenges of increasing livestock production and problems associated with wildlife, it is important to understand the complex ecological interplay between wildlife and livestock (Cravino et al., 2024b; Magouras et al., 2020). In this chapter, I review the nature and trend of wildlife-livestock interface, underlying drivers and challenges at the wildlife-livestock interface, global trend of infectious diseases and factors related to transmission of infectious diseases at

the wildlife livestock interface, which provides a context for the thesis whose objective is to answer key questions about dissemination of gastrointestinal nematodes (GIN) parasites by the migratory host under consumer resource interaction scenarios, and resulting development and survival of parasites under different environmental conditions, that change infection risk of pasture and livestock infection burden amid wildebeest migration.

1.2 What is the wildlife -livestock interface and where does it occur?

Wildlife-livestock interfaces occur when livestock and wildlife come into contact either directly or indirectly through shared resources such as pasture and water points, or via vectors (Grootenhuis & Olubayo, 1993; Karmacharya et al., 2024; Wiethoelter et al., 2015; Zvidzai et al., 2013). Such contacts between wildlife and livestock are common in rangeland areas outside of protected areas, particularly in areas with ungulate migrations (Kock, 2005). These areas where wildlife-livestock interactions occur facilitate cross species parasite transmission (Hassell et al., 2017; Zvidzai et al., 2013), and can lead to the emergence of new infectious diseases (Lane et al., 2025). Under global change, the intensity and frequency of interactions between wildlife and livestock have increased, particularly in low- or middle-income countries that are rich in natural resources and somewhat unaltered landscapes where wildlife continue to exist (Mertz et al., 2007; Schweitzer, 1992). In such areas people often depend directly on natural resources and livestock for food, money and socio-economic wellbeing (Banda & Tanganyika, 2021; Herrero et al., 2013), hence allowing continuous or frequent contact between livestock and wildlife (Grootenhuis & Olubayo, 1993; Jori et al., 2021; Pal et al., 2025). Due to current and predicted increase in livestock production (Magouras et al., 2020; Thornton & Herrero, 2010), and increasing interest around infectious diseases (Wiethoelter et al., 2015), wildlife-livestock interfaces offer opportunities to study epidemiology of complex multi-host communities (Hassell et al., 2017; Karmacharya et al., 2024). In this thesis, I explore how migratory host species change infection risk of pasture associated with resident herbivores that might lead to multi-host diseases transmission, as well as how infection intensity of livestock changes following migration of wildlife.

1.3 Type of wildlife-livestock interfaces

Wildlife-livestock interfaces can be grouped into two major categories. First, the direct interface, where wildlife and livestock co-occur in the same habitat resulting in direct interactions between wildlife and livestock (Caron A. et al., 2013; Magouras et al., 2020; Pal et al., 2025; Yang et al., 2021). Secondly, indirect interfaces, where different livestock and wildlife occupy a single habitat at different times, or where they occupy different habitats but their interactions occur via an intermediate medium (such as water, air and soil), as well as where interactions occur via intermediary hosts or vectors such as mosquitoes, snails and tsetse flies (Caron A. et al., 2013; Magouras et al., 2020; Pal et al., 2025; Zvidzai et al., 2013). The wildlife-livestock interface can further be modified by natural and anthropogenic features (Pal et al., 2025), that in turn regulate forms and intensity of interaction between wildlife and livestock (Barroso & Gortázar, 2024). For example, rangelands that have been fenced will reduce or completely block interaction between wildlife and livestock compared to areas that have no fence (Boone & Hobbs, 2004; Karmacharya et al., 2024; Niamir-Fuller et al., 2012; van Dam et al., 2024). Secondly, development of roads, railways and settlements might cause habitat fragmentation and completely block wildlife movement between protected areas and livestock grazing areas, thus reducing intensity of interactions between wildlife and livestock (Ogutu et al., 2009a; Porokwa, 2003). They may also block livestock from natural rotational grazing system (Boone & Hobbs, 2004; Ogutu et al., 2009a; Stokes et al., 2006), and therefore may build up large densities of parasites such as GIN as they can never move on to fresh pastures. The increasing anthropogenic pressure worldwide modifies the nature of interaction between wildlife-livestock and the intensity of such interactions which can consecutively affect spread, presentation and outbreaks of infectious diseases (Lane et al., 2025). In this work, I explored livestock infection intensity from two wildlife-livestock interfaces under wildlife migration: (1) Livestock exposed to wildlife migration due to their proximity to the park and less anthropogenic pressure between park and villages, and (2) Livestock not exposed to wildlife migration due to their distant position from the park and higher anthropogenic pressure between park and villages that reduced contact between wildlife and livestock.

1.4 Drivers of wildlife-livestock interfaces

Wildlife-livestock interfaces are shaped by different forces operating at global and local scales, resulting in increased interaction between wildlife, livestock and people (Jori et al., 2021). Such forces include climate change, human population growth and global market forces that led to increased demand for meat production and consumption of illegally harvested meat (Karmacharya et al., 2024; Magouras et al., 2020; Meurens et al., 2021). Climate change that causes changes of rainfall patterns and increased drought incidence, might lead to changes in the distribution of livestock and wildlife when searching for water, food or refuge sites (Karmacharya et al., 2024). As a result, wildlife and livestock might be forced to be aggregated into few shared resources for food and water (Keesing et al., 2010; Zinsstag et al., 2018). Secondly, climate change can also change the distribution of vectors, and promote dispersal into new areas, as well as affecting parasite survival in the environment (Meurens et al., 2021; VanderWaal et al., 2014). Rapid growth of human population and increased demand of meat and crops in global market force has also led to expansion of livestock ranches and farms, mostly in rangeland area where wildlife is found (Keesing et al., 2010), and as a result the intensity and frequency of interaction between wildlife and livestock has increased (Fynn et al., 2016). While at a local level, expansion of human settlement that contributes to rapid land use change (Pal et al., 2025), which is also mostly associated with livestock keeping, taking over grazing area of wildlife resulted into increased interaction between wildlife and livestock (Du Toit & Cumming, 1999; Otuoma et al., 2009).

1.5 Human dimensions at the wildlife-livestock interface and disease transmission

Human dimensions on wildlife-livestock interface reflect multiple interests such as economy or livelihood, culture, environmental conservation and health (Karmacharya et al., 2024; Kock, 2005). When it comes to health, humans are concerned about health of people, as well as health of wildlife and livestock, coining agenda of ‘One Health’ due to interdependence and causative interaction of health between wildlife, livestock and human beings (Cunningham et al., 2017; Lane et al., 2025; Magouras et al., 2020; Zinsstag et al., 2018). For many years, it has been difficult to quantify diseases at wildlife-livestock interface (Cunningham

et al., 2017; Preston & Johnson, 2010), thus many zoonotic diseases have been un-noticed and/or tolerated by the people (Kock, 2005). Nowadays that has changed, and infectious diseases are a serious concern for wildlife conservation and livestock production (Barroso & Gortázar, 2024; Kideghesho et al., 2021; van Dam et al., 2024; VanderWaal et al., 2014), and disease transmission has become a source of conflict between wildlife managers and local community (VanderWaal et al., 2014). On one side, local community see wildlife as a reservoir of parasites that might cause disease transmission to livestock or human beings (Barroso & Gortázar, 2024; Fynn et al., 2016), while on the other side wildlife managers perceive livestock incursion into protected areas to have been a source of infectious disease to wildlife (Barroso & Gortázar, 2024). This is further complicated by both sides viewing the other as competitor for grazing (Gambiza et al., 2010; Gordon, 2018), which in the most extreme cases could reduce the health of animals and make them more vulnerable to diseases. This situation calls for a better approach that will bring all stakeholders together (Fynn et al., 2016), and involve them in decision making and management of our ecosystem (Niamir-Fuller et al., 2012). To achieve that target there is a need to develop better understanding of wildlife-livestock interaction interface and its role on emergence of infectious diseases (Kimuyu et al., 2017; Meurens et al., 2021). As a contribution toward that goal, this work focused on infection intensity of GIN in livestock and examined how interactions and spatial overlap with migratory wildlife could be beneficial or harmful to livestock health.

1.6 A growing concern: Infectious disease transmission between wildlife, livestock and humans

Emerging infectious diseases such as the COVID-19 pandemic, have demonstrated how epidemic diseases can jeopardize the economy, natural resource management and the health sector worldwide (Karmacharya et al., 2024; Kideghesho et al., 2021; Meurens et al., 2021; Walsh et al., 2020). It is becoming clear that biodiversity is of considerable interest to those working in planetary health and those applying ‘One Health’ approaches to understand and control disease spread (Daszak et al., 2000; Myers, 2017). Research into understanding ecology of pathogens and dynamics of infectious diseases under climate change and increasing human activities has dramatically increased worldwide (de Thoisy et al., 2021; Karmacharya et al., 2024; Wiethoelter et al., 2015), as it is regarded

as an essential step towards prevention, mitigation, and control of infectious disease events (Altizer et al., 2011; de Thoisy et al., 2021; Harvell et al., 2009; Karmacharya et al., 2024). Wildlife-livestock interfaces are hotspots for cross species disease transmission and can serve as a focal point of understanding and control of emerging infectious diseases (Hassell et al., 2017). This study focuses on the mechanisms of cross species transmission of GIN, a helminth group that contains generalist parasites capable of infecting different wildlife and livestock species, normally resulting to huge loss in livestock production and/or increased cost of livestock production.

1.7 A concept of parasitism and infection

Parasitism denotes an interaction between two species, one of which (the parasite) lives inside or on another (the host) for its own benefit, typically causing disease or physiological damage to the host (Haelewaters et al., 2017; Kaishian et al., 2024; Rózsa & Garay, 2023). Infection occurs when the host acquires parasites directly from the environment, from other hosts, or through vectors (Pirofski & Casadevall, 2002). Host infection risk might be affected by a range of factors such as, host distribution and behavior, distribution and abundance of parasite, weather/environmental conditions, host immunity, and vector abundance (Casadevall & Pirofski, 1999; Kaishian et al., 2024; Weinstein & Lafferty, 2015). Infection risk describes the probability of a host to acquire parasites from the environment or vectors. Once infected, hosts might suffer from a range of different costs and harms from parasite infection, including loss of appetite, reduced weight, diarrhea, and change in behavior, such conditions are referred to and interpreted as diseases (Brown, 1976). In this study I will explore infection of ungulates (wildebeest, cattle, sheep and goats) by GIN parasites, that are normally acquired from contaminated pasture following deposition of dung piles from infected hosts. Infected livestock might show reduced development and growth, which in turn might lead to reduced fecundity, low milk production as well as increasing mortality (Zajac & Garza, 2020). Infected hosts might experience reduced immunity which consequently reduces ability of the animal to fight against subsequent parasite infection.

1.8 Gastrointestinal nematode life cycle

The adult gastrointestinal nematode (GIN) lives inside the stomach (abomasum or intestine) of the ruminant host and female adult nematodes produce hundreds to thousands of eggs that are later passed into the environment through dung piles, Fig.1-2. (Zajac & Garza, 2020). Inside the dung, eggs develop and hatch into larva stage (Mkandawire et al., 2022). It takes about 24 hours for eggs to hatch to larval stage one (L1) (Stromberg, 1997). Larvae feed on bacteria, then develop and molt into larval stage 2 (L2), and lastly larval stage 3 (L3) in 5 – 6 days (Stromberg, 1997; Zajac & Garza, 2020). L3 is the infectious stage that can infect a new host (Fig.1-2). The larval stage 3 can move from dung piles onto grass under suitable environmental conditions, where it waits to infect a herbivore (Fig.1-2). L3 can stay alive in the environment for up to 90 days, an adaptation supported by availability of food reserves providing energy, and cuticles that protect them from harsh environment, while waiting to be ingested by the herbivore (O'Connor et al., 2006).

When ingested by a grazing herbivore, larvae stage three takes about 17 to 21 days (for most pathogenic species) to develop to an adult stage capable of producing eggs (Zajac & Garza, 2020), and the cycle repeats itself. However, during dry conditions, developing larvae stage four (L4) might be arrested and prevented from completing development through to an adult GIN, an adaptation known as hypobiosis (Gibbs, 1986). This adaptation ensures eggs are passed out onto environment when there are favorable environmental conditions for the egg's survival and development (Gibbs, 1986; Vlaar et al., 2021). Because of the relatively long period of development and survival in the environment, infection risk to ruminant hosts is expected to be strongly shaped by ecological and climatic conditions (Stromberg, 1997). In my first two chapters, I explore how different intensity of migratory herds distribute eggs of GIN, and how microclimate conditions facilitated by vegetation affect development as well as survival of free-living stages of GIN in pasture, and consequently infection risk across landscape.

1.9 Factors affecting development and emergence of infectious parasites in the environment

Faecal-orally transmitted parasites, such as GIN, are extremely sensitive to external parameters such as weather, and the dung moisture (Chiejina et al., 1989; Miller et al., 2012; Turner & Getz, 2010). For example, while livestock or ungulate faeces act as a medium for egg development to infective larvae ('L3s') and are important reservoirs of L3s during dry weather or the winter season (Miller et al., 2012), conditions such as rainfall (moisture), temperature, and humidity have been found to be important in both development of GIN eggs to L3s, and the migration of L3s to pasture (Wang et al., 2014). Yet these faecal reservoirs are subjected to disturbances including trampling, coprophagy, decomposition and fire (Chiejina et al., 1989; Wilgen, 2009).

Another aspect of the biology of GIN is vertical migration of L3s among different grass species under different environmental factors (Amaradasa et al., 2010; Krecek et al., 1991; Silangwa & Todd, 1964). While previous studies suggest L3s vertical migrations differ with grass species, and that lower strata (0-5 cm) have higher densities of L3s than strata closer to the inflorescence (Amaradasa et al., 2010), more studies are needed to provide strong evidence of L3s preference on different grass strata and how herbivore feeding behaviour i.e. grass strata selection and grazing height could influence exposure risk to L3s. Differential vertical migration among grass species have been reported to be influenced by the grass morphology and leaf characteristics that influence the amount of moisture retained (Silangwa & Todd, 1964). Time of the day affects amount of moisture retained in grasses and is considered as a potential factor influencing L3s vertical migration. Although Krecek et al., (1991) did not find variation of L3s during the daytime in grasses, in laboratory experimental study, darkness was found to have a slight positive influence on vertical migration of L3s compared to reduced light (Silangwa & Todd, 1964). Furthermore, a study by Amaradasa et al., (2010) recommended investigating diurnal variation in vertical migration of L3s in pastures. Currently we have a little knowledge of how herbivore grazing interacts with L3s vertical migration in different grass species and/or related grass feature and its consecutive infection risk among herbivores (Tontini et al., 2019). This project investigated how temperature and humidity affect emergence of L3 in

pasture, as well as how disproportional vertical distribution of parasites on grass change infection risk between first grazing herbivore (migrant) and subsequent grazing herbivore (residents).

1.10 Wildlife migration and parasite spillover

Highly migratory animals travelling long distances across different habitats have higher exposure risk to different parasites and thus might have a unique role in introducing and exchanging parasites across the ecosystem (Altizer et al., 2011). Spillover of parasites and pathogens between hosts can cause outbreaks of infectious diseases leading to severe crisis in wildlife conservation, human and livestock health (Ranjan et al., 2025).

An alternative hypothesis suggests that migration may allow animals to escape habitats where parasites have accumulated — a concept known as 'migration escape', and differential spatial temporal use of habitats will allow extreme weather conditions and other ecological process or disturbance to reduce parasites in habitats (Altizer et al., 2011; Mijele et al., 2016). Also infected migrating animals might become weak and be eliminated during migration i.e. 'migration culling', which contributes to reducing infection level in a habitat (Altizer et al., 2011). Central to successful spill-over transmission between species depends to what extent the parasites are generalist (multi-host parasite) or specialist i.e., single host parasite (Brown et al., 2022; Walker & Morgan, 2014). Dynamics of infectious disease and the increased potential risk from increased wildlife livestock interaction creates interest and demand for further understanding multi-host parasite diversity in different ecosystems (Cleaveland, Laurenson, et al., 2001; Mijele et al., 2016; VanderWaal et al., 2014). Here in this PhD project, I have used wildebeest as a model migratory species to understand their interaction with parasites, pasture and livestock (spreading or absorbing parasites across the landscape), and investigated the subsequent impacts of such interaction on livestock health.

1.11 Wildebeest-livestock interface in Serengeti ecosystem

The Serengeti ecosystem supports over 15 wild ruminant species, only four of which migrate: wildebeest (*Connochaetes taurinus)*, zebra (*Equus quagga)*, thomson gazelle (*Eudorcas thomsonii)* and eland (*Taurotragus oryx*) (Anderson et al., 2024; Dybas, 2022; Ogutu et al., 2009b; Rentsch & Packer, 2015). Additionally, there are over 2 million cattle, sheep and goats living within 20km of the boundary of the core protected area (TAWIRI, 2016), so the potential for migrants to shape resident infection is high. Migrant wildebeest abundance is about 1.2 million adults (Dybas, 2022), making them the dominant grazing herbivores within the Serengeti ecosystem, migrating between Tanzania and Kenya searching for nutritious grasses (Hopcraft et al., 2015). During the migration wildebeest pass through villages, where they mingle with livestock in shared grazing areas and water points (Fig. 1-1), either directly or through deposited dung piles or body fluid (Serneels & Lambin, 2001). Indeed, migratory wildebeest spend roughly 25% of their time in areas that are managed in part for ruminant livestock grazing, based on more than 25 years of monitoring GPS collared wildebeest (T Morrison, *pers. comm*). Interactions between wildebeest and cattle has been considered as a model interaction for disease transmission, due to the role of cattle in introducing *Morbillivirus* causing Rinderpest in wildebeest that led to collapse of wildebeest population (McCallum & Dobson, 1992; Sunseri, 2015). Conversely, wildebeest introduced *Macavirus,* which causes Malignant Catarrhal Fever in cattle, with associated mortality rates approaching 100% (Cleaveland, Kusiluka, et al., 2001; Mlilo et al., 2015; Wambua et al., 2016). Since then, the two species have continued to shape grazing and livestock keeping practice, as many livestock keepers have adapted separation strategies by keeping cattle away from wildebeest to avoid the transmission of Malignant catarrhal fever (Talbot & Talbot, 1963). Nowadays, climate change also shapes livestock keeping within the Serengeti. Due to prolonged drought and reduction of pastures, many pastoralists opt to keep small ruminants (goats and sheep) over cattle, thus there has been increasing of density of goats and sheep within the ecosystem (TAWIRI, 2020). We use wildebeest exposure to livestock during migration in four villages around the Serengeti National Park, Tanzania, to understand the role of different wildlife-livestock interfaces in the epidemiology of infectious diseases.

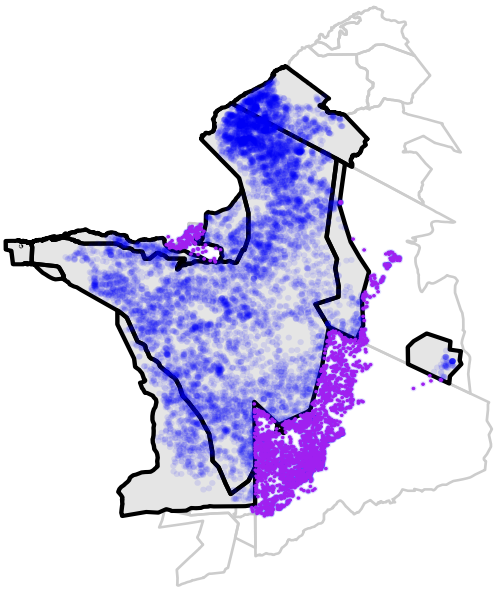

Figure 1 - 1: Wildebeest and livestock overlap in Serengeti ecosystem.
Overlap between wildebeest migration and livestock in Serengeti ecosystem, where blue colour represents GPS trajectories of collared wildebeest, while purple represents GPS trajectories of wildebeest in areas where there is a significant spatial overlap between wildebeest and livestock. Thick black line represents boundary of the core protected areas (grey shaded areas) where there are no humans' settlements, thin grey line represents boundary of the protected area that allows humans settlements.

1.12 Resident grazers of the Serengeti ecosystem

The resident grazers in Serengeti ecosystem includes all non-migratory wildlife and livestock species, ranging from resident host populations of wildebeest, zebra, eland, topi (*Damaliscus lunatus*), hartebeest (*Alcephalus buselaphus)*, waterbuck (*Kobus ellipsyprimnus)*, warthog (*Pharcocoerus africanus)* buffalo (*Syncerus caffer*), impala (*Aepyceros melampus*), grant's gazelle (*Nanger granti*), sheep, goat and cattle (TAWIRI, 2010). For the wildebeest, there are four resident sub-populations documented within the Serengeti ecosystem, located in Loliondo, Kirawira, Ngorongoro Conservation Area, and Maasai Mara. The resident populations have been found to be limited in distribution and occupy less geographic space due to their need to access local resources such as quality nutritious grasses and water (Hopcraft et al., 2015). For the resident wildlife grazers, the population of each species is as follows: wildebeest 40,000, topi 38,497 ± 12,856, zebra, eland 36,297 ± 6169, and buffalo 32,001, grant gazelle 119,707 ± 26450, hartebeest 15,908 ± 2434, impala 74,837 ± 9,106 (Hopcraft et

al., 2015; TAWIRI, 2010). For the livestock, the population of goat and sheep combined is about 980,498 ± 59,018, and cattle is 1,245,343 ± 56,560 (TAWIRI, 2016). In my PhD, I have employed both molecular and non-molecular bar-coding techniques to investigate health condition of three resident livestock species (goat, sheep and cattle) before and after wildebeest migration in villages that are exposed or not exposed to wildebeest migration.

1.13 Overall Aim:

This thesis investigated the role of wildebeest migration, livestock management practices, vegetation as well as abiotic factors (i.e., weather condition and ungulate faeces) on gastrointestinal nematode abundance in the environment and on infectious diseases dynamics in wildlife and livestock areas. We used the diverse and complex interaction of wild and domestic ungulates around Serengeti National Park in Tanzania to investigate and answer our objectives. Specifically, we aimed to achieve the following objectives:

1. **Transport vs Trophic effect of migration:** To assess the role of wildebeest movement, i.e., transport and trophic effects, on GIN (infectious L3 stage) abundance in the environment.
2. **Vegetation microclimate effect:** To assess the role of vegetation cover and shade availability (grass height and canopy cover) on microclimate conditions that affect survival of free-living stages of GIN by measuring L3 density on pasture.
3. **Wildlife-livestock overlap effects on infectious diseases**: To assess role of wildebeest migration on changes of livestock GIN infection intensity and parasite community composition in selected livestock species (goat, sheep, and cattle) in west and east region of Serengeti National Park

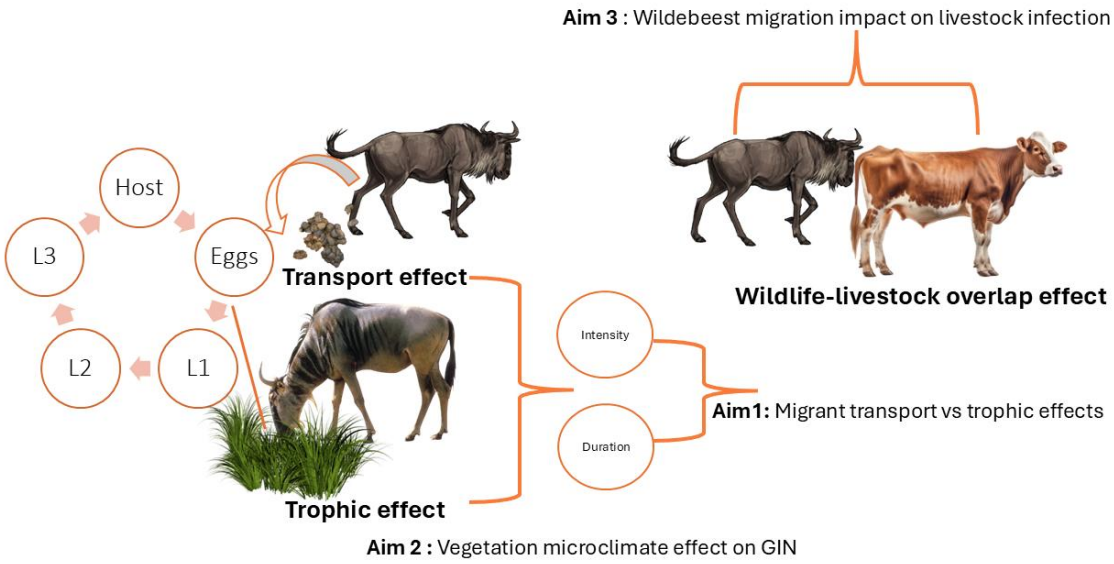

Figure 1 - 2: Interaction between GIN life cycle, hosts, and pasture.
Conceptual framework for the ecological interaction between grazing herbivores and the life cycle of the GIN, and how it might change environmental infection risk and parasite transmission for the consequent grazing herbivore. Each chapter of the thesis addresses the highlighted key ecological interactions from migrants; 1: chapter 2 - Transport vs Trophic effects - Understanding the net effects of wildebeest transport and tropic effects (via dispersal of parasites through dung deposits and grazing that might reduce parasite abundance and biomass of grass respectively) on environmental parasites abundance, 2: chapter 3 – Vegetation microclimate effect - The role of tree shade and migratory wildebeest herbivory on the architecture of the grass sward and therefore the survival of L3 in the environment, and 3: chapter 4 - Overlap between migrants and livestock - Impact of wildlife migration on livestock. Where L1 stands for larvae stage 1, L2 stands for larvae stage 2 and L3 stands for larvae 3.

This thesis consists of five chapters. This chapter has provided a general overview and introduction describing what the wildlife-livestock interfaces are, competing interests at the wildlife-livestock interface and why they are important in infectious disease epidemiology. It has further explained mechanisms that shape and drive wildlife-livestock interfaces, and how such interactions might facilitate cross species parasite transmission. It also introduced model wildlife migratory species (wildebeest) and parasites (GIN) used in this study, and how they might interact within the ecosystem with other factors and herbivores. Moreover, the chapter has also described the biology and ecology of the Trichostrongylid gastrointestinal parasites. Lastly, this chapter has also described model systems

(Serengeti ecosystem) and the interaction between migratory wildlife and resident grazing herbivores of the ecosystem.

Chapter 2 explores in detail important knowledge gaps in how migration intensity and duration link with migrant transport and trophic effects to change parasite infection risk in the local environment. Migration intensity is the number of migrants arriving in an area while migration duration is how long they stay in an area. Migrant transport effects involve dispersal of parasites via egg shedding in dung piles. Migrant trophic effects consider parasite consumption by herbivores and reduced grass biomass/cover by grazing herbivore. This chapter used an experimental approach to integrate migration intensity vs migration duration and connect with migrant transport and trophic effects to uncover the net effects of different sizes of migratory herds on environmental parasites across the landscapes of the ecosystem. This chapter also highlights the role of herbivores in changing microclimate conditions via grazing.

In chapter 3, I addressed a key question considering how parasites distributed through herbivore dung pile deposits, survive under different shade availability conditions as induced by vegetation cover availability. Here, I used both a field survey (observation study) and an experimental approach to investigate how shade availability from tree canopies and grass heights affected environmental parasite abundance via changing microclimate conditions (temperature and humidity) across seasons i.e., dry and wet conditions. The chapter emphasizes the role of microclimate conditions particularly from shades of trees canopies and grass height heterogeneity induced by herbivore grazing in shaping landscape infection dynamics.

chapter 4 captured a broader scale goal of the thesis, by exploring how livestock infection intensity and GIN community composition change before and after wildebeest migration. In this chapter we used a before and after impact design and the natural setting of the study system to establish an observational study that investigated changing infection intensity and worm composition of goat, sheep and cattle in wet vs dry region of the ecosystem, in area exposed vs not exposed to wildebeest migration and before and after wildebeest migration. Here we adopted PCR and sequencing techniques to characterize livestock worm

species composition, and McMaster technique to capture livestock infection intensity through faecal egg counts.

Lastly, chapter 5 comprises of conclusions and recommendations. This thesis provides information about different mechanisms of how wild ungulate migration and vegetation cover might interactively shape the epidemiology of infectious parasitic diseases. Furthermore, it also provides evidence on how wildlife migration might benefit, or harm, livestock encountered along their migration routes, and that impact of wildlife-livestock interface is context dependant.

2 Disentangling transport and trophic effects of animal movement on environmental parasite abundance

2.1 Abstract

Migratory wildlife plays an outsized role in disease transmission. Transmission risk is often assumed to be scaled with migratory host density through parasite *transport effects*, but in environmentally transmitted parasites, migratory hosts can also influence parasite availability via *trophic effects*. Trophic effects can either amplify or dampen transport effects, making the net impact of migratory hosts on resident hosts difficult to predict. We propose that the net effect is shaped by two attributes of migrant movement: intensity of use (i.e., number of migrants) and duration of use (i.e., length of stay). Using GIN as a model, we experimentally varied transport and trophic effects of a migratory grazer – wildebeest (*Connochaetes taurinus*) – by manipulating the intensity and duration of dung addition and grazing across five treatment combinations in replicated plots and measuring their effects on the density of infective third-stage GIN larvae in pasture. We found that: (1) higher dung addition increased GIN larvae density, (2) simulated grazing reduced the density of GIN, particularly in treatments with high dung addition, and (3) longer duration and lower intensities of use reduced GIN density for subsequent hosts compared to treatments with single bouts of dung addition and grazing. Our results indicate that migratory hosts directly facilitate parasite spread via transport effects, while infection risk tends to decline with increasing intensity and duration of trophic interactions. Our results highlight the underappreciated role of transport and trophic interactions in shaping parasite spread in migrant-resident systems.

2.2 Introduction

Animal migration is increasingly recognized as an important driver of parasite and pathogen transmission (Altizer et al., 2011; Daversa et al., 2017; Dickinson et al., 2024; Harvell et al., 2009). Host migration modifies parasite spread in two major ways: first, movement between areas enhances cross species transmission via "transport effects" by introducing parasites into new areas (Consortium, 2016; Fèvre et al., 2006; Poulin & de Angeli Dutra, 2021; Rodrigues et al., 2018). The capacity for migratory hosts to transport parasites often scales with the number

of infected hosts (Altizer et al., 2011; Daversa et al., 2017), because higher host densities lead to greater shedding of infectious material, which enhances parasite transmission and prevalence (Cote & Poulinb, 1995; Donaldson et al., 2024; Patterson & Ruckstuhl, 2013). For example, de Angeli Dutra et al., (2021) demonstrated how migratory birds contribute to the spread of parasites in non-migratory birds, while Morgan et al., (2007) reported the role of Saiga antelope (*Saiga tatarica*) in dispersing gastrointestinal parasites that infect livestock along their migration route. Indeed, most studies of host-parasite interactions in migratory systems focus on these transport effects (Donaldson et al., 2024). Secondly, the arrival of migrants can impose strong ecological interactions, so-called "trophic effects", that mediate the form and intensity of transport effects (Bauer & Hoye, 2014; Donaldson et al., 2024). Trophic effects can involve consumer-resource interactions that directly suppress parasites spread between two host species when one host consumes parasites (Fig.2-1), or infected hosts, and removes them from an area *i.e.*, direct trophic effects (Bauer & Hoye, 2014). Alternatively, mobile animals can indirectly modify the environment in ways that change the risk of infection for resident hosts, *i.e.*, indirect trophic effects. For example, when migratory prey arrive in an area, predators often shift from feeding on resident to migratory animals, and this dietary shift may change, either positively or negatively, exposure risk to parasites that are trophically-transmitted from prey (Donaldson et al., 2024).

Despite recognition that transport and trophic effects by migratory hosts play important roles in parasite transmission (Bauer & Hoye, 2014; Donaldson et al., 2024), there has been little attempt to quantify the relative strength and direction of these effects empirically (Daversa et al., 2017; Donaldson et al., 2024). Past work in multi-host systems has established that cross-host parasite transmission should be determined by (1) the infection status of the migrating hosts *i.e.*, whether they are carrying high or low burdens of parasites, (2) the degree of host specialisation by parasites (Streicker et al., 2013), and (3) whether there is successful contact between transported parasites and susceptible hosts (Daversa et al., 2017; de Angeli Dutra et al., 2024; Donaldson et al., 2024). An enduring challenge, however, has been to integrate variation in animal movement into this understanding of parasite spread (Altizer et al., 2011; Daversa et al., 2017). In

migratory systems, there can be orders of magnitude variation in the number and timing of migrants moving into, and out of, the home ranges of resident species. Donaldson et al., (2024) proposed that two dimensions of movement should determine the relative strength of transport and trophic effects: (4) migration intensity *i.e.*, number of animals involved in a migration event (5) migration duration *i.e.*, the time that migrating animals spend in a particular location. Higher migration intensity or longer migration duration should lead to an increase in both parasites shedding as well as the magnitude of trophic effects. For example, the arrival of large herds or the prolonged stay of migratory ungulates in an area can introduce a large number of parasites (transport effect) and alter vegetation through herbivory and trampling (trophic effects). In parasites with environmental life stages, such as GIN, these vegetation changes may concentrate or dilute the abundance of parasites (Bauer & Hoye, 2014; Donaldson et al., 2024). The magnitude of these transport and trophic interactions in jointly modifying the abundance of infectious parasites across systems is largely unknown (Donaldson et al., 2024).

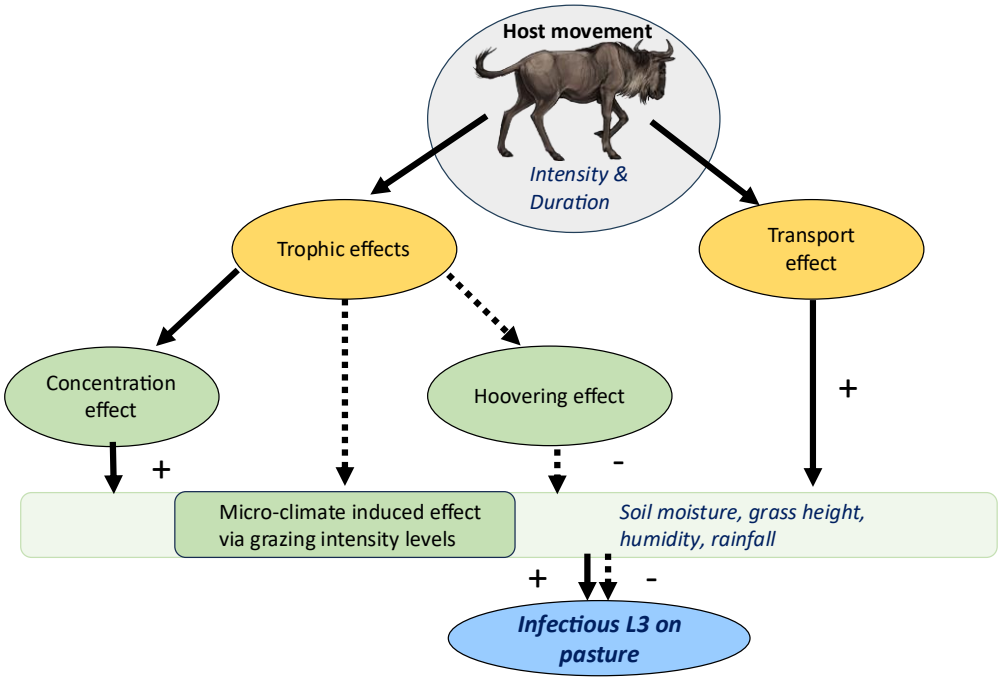

Figure 2 - 1: A conceptual framework of the direct and indirect ways that host movement, via variation intensity and duration, can modify infectious L3 abundance in the environment.

Yellow boxes represent the two main effects of host movement i.e., transport and trophic effects. Green boxes represent three potential pathways of trophic effects i.e., (1) concentration effect caused by mobile herbivores removing uninfected grass, and thereby

concentrating parasites on the remaining grass (2) hoovering effect caused by herbivores consuming L3 in infected patches of grass, (3) micro-climate effect caused by removing grass and exposing free living stage of nematodes to hotter and less humid conditions near the soil surface. All the inter-connected ecological mechanisms and events are occurring alongside variable environmental conditions (light green rectangle) and will have some effect on the microclimate conditions in which the larvae develop and reside, such as soil moisture, humidity, grass height and rainfall that determine the development and survival of early-stage nematodes, and the consequent abundance of L3s in pasture.

The trophic effects of migratory herbivores on faecal-oral transmitted parasites could be complex and depend on climatic conditions and grazing intensity (Fig. 2-1 and Fig. 2-2). Temperature and humidity change the vertical distribution and survival of parasites in pasture (Amaradasa et al., 2010; Krecek et al., 1991; Silva et al., 2008); in hotter and wetter conditions, parasites aggregate near the top of grass swards, whilst in cooler or more arid conditions, parasites aggregate near the bottom of grass swards (Rees, 1950; Silangwa & Todd, 1964; van Dijk & Morgan, 2011). Subsequent grazing by dense herds of migrants should affect the infection risk for other hosts in three possible ways (Fig. 2-1 and Fig. 2-2): (1) neutral effects occur when parasites distribute themselves uniformly throughout the grass patch, resulting in equal probabilities of a grazing herbivore encountering larvae across the grass height distribution (Fig. 2-2). (2) The 'hoovering effect', in contrast, occurs when parasites aggregate on the upper portion or leaves of grasses, and herbivores that arrive first to an area disproportionately remove parasites by grazing these uppermost parts (Fig.2-2). Finally, (3) the 'concentration effect' occurs when parasites aggregate at the bottom of the grass near the soil surface, and grazing herbivores concentrate the density of parasites by grazing the upper parts of the grass (Fig.2-2). Thus, if we assume migratory herbivores graze before the arrival of resident grazers – an assumption of our experiment (see below) – then the infection risk to migrant and resident hosts will depend on how climate has shaped the distribution of free-living parasites, and on the grazing intensity of migrants prior to the arrive of residents.

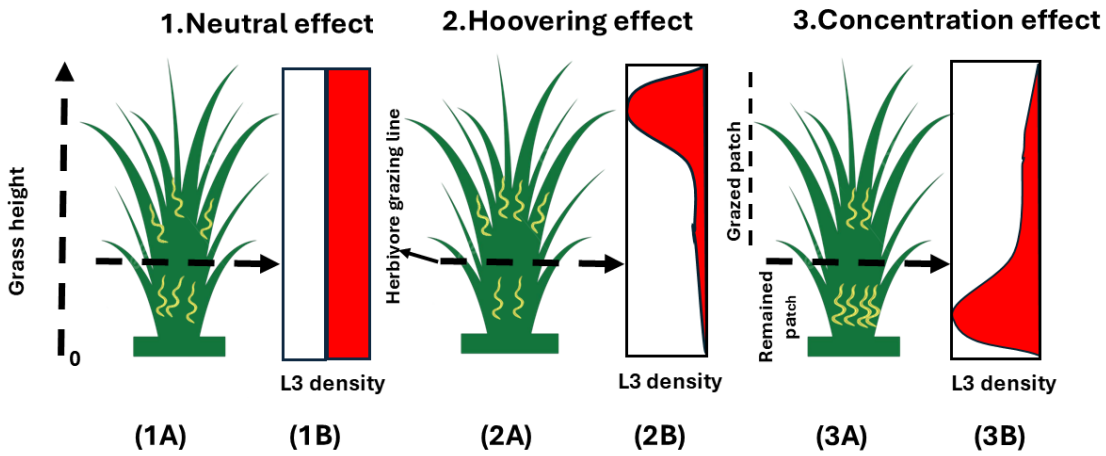

Figure 2 - 2: Conceptual framework showing the interplay between grazing and parasite distribution in grass patches.

The interplay between grazing and parasite can result in three possible trophic effects: (1A, 1B) Neutral effects, (2A, 2B) Hoovering effects and (3A, 3B) Concentration effects. Larvae distribution is depicted as yellow squiggles and red frequency distribution, while the grazing depth is depicted by the horizontal arrow. NB: L3 distribution in grass is dynamic, and could be affected by short term changes in weather, and longer term changes in grass height due to grazing and regrowth.

In this study, we aim to understand how variation in the intensity and duration of migratory hosts impact the relative strength of transport and trophic effects on the abundance of infectious-stage GIN. We hypothesize that (H1) the abundance of environmentally transmitted gastrointestinal nematode scales with the intensity of migratory transport effects; (H2) trophic effects by migrants reduce environmentally transmitted parasites and dampen transport effects; and (H3) migration duration mediates parasite infection risk for resident hosts via trophic effects. We suggest that the strength of these interdependent migrant transport and trophic effects is underlain by the prevailing climatic conditions of the area (Fig.2-1). We use the wildebeest migration in the Serengeti Ecosystem, Tanzania, as a model system to test if migration intensity and duration modify migrant transport and trophic effects on parasite abundance. The annual movement of Serengeti wildebeest involves ~1.3 million animals that exert strong local effects on vegetation (McNaughton, 1985), as they move through the system. We link transport and trophic effects with movement intensity and duration, allowing us to uncover general patterns connecting animal movement to parasite dynamics.

2.3 Materials and methods

2.3.1 Study system

The study was conducted in Serengeti National Park (hereafter, 'Serengeti'), Tanzania, which contains a diverse and abundant ungulate herbivore community. The Serengeti experiences a sub-tropical climate with annual average rainfall ranging between 500 and 1,100 mm (Williams et al., 1998). The ecosystem is home to 1.3 million wildebeest that migrate in response to forage availability and rainfall across the ecosystem (Talbot & Talbot, 1963). Because of their movement and high local densities, wildebeest strongly shape vegetation function and structure, fire intensity and occurrence, seed dispersal and nutrient cycling across the ecosystem (McNaughton, 1985; Sinclair et al., 2007), thus altering the conditions in which the community of non-migratory (i.e., resident) large herbivores occur.

To explore the effects of migration of large herbivores, such as wildebeest, on parasite infection risk of resident herbivores, we focus on gastrointestinal nematodes (GIN), one of the most common endoparasite groups of vertebrates for which transmission is tightly coupled to vegetation dynamics (Coulson et al., 2018). Adult gastrointestinal nematode infects herbivores and produces hundreds to thousands of eggs that are shed into the environment through deposition in dung piles (Miller et al., 2012; Talbot & Talbot, 1963). Deposited eggs hatch and develop from first stage larvae (L1) to third stage larvae (L3), at which point they migrate onto the leaf and stem margins of vegetation and become infectious to subsequent herbivores. While many ruminant gastrointestinal nematodes appear to be host generalists, there is some host specificity (Stephens et al., 2017). Once ingested, larval parasites complete their development into adult stages inside the host. The development time from eggs to L3 stage varies by parasite species, and generally increases with temperature and humidity, but peak emergence of infectious L3 generally occurs 10-14 days after defecation (O'Connor et al., 2006). Given this environmental stage to their development, and the fact that they move vertically on vegetation, GIN should be highly susceptible to both transport and trophic effects.

2.3.2 Experimental design

To assess the relative impacts of migratory transport and trophic effects on parasite abundance in pasture, we set up experimental plots at the Serengeti Wildlife Research Centre in central Serengeti. Five blocks with five plots per block (25 plots total) were established, and each of the 5 plots in each block were assigned one of five different dung addition and grazing treatments meant to simulate different migration intensities and durations (see below). Each experimental plot was surrounded by a chicken-wire fence to prevent natural grazing, dung addition or any other interference by vertebrate herbivores to experimental treatments. Plots were located ≥10 m from each other and were 3 x 3 meters in size (Appendix A:S1). Treatments and L3 sampling occurred in the central 2 x 2 m area to minimize boundary effects (Amaradasa et al., 2010). The experiment lasted for 28 days, and was replicated in each block, staggering the start by one day for each block. The overall experiment began on May 26th and all sampling was completed by June 22nd of 2022. Five days before the experiment began, sward height in all plots was clipped to a uniform maximum grass height of 32 cm to reduce plot-level environmental variation in starting conditions (Silva et al., 2008). We also verified that there was little or no background contamination of L3 in experimental plots prior to treatment effects by searching for L3 during the first experimental clipping (Day 6 – see below).

The five treatments were as follows: 1) High Intensity / Low Duration (HILD), which simulated high grazing intensity by migrants for a short period of time (9 dung piles added, grass clipped to 10 cm height on Day 6); 2) Low Intensity / Low Duration (LILD), which simulated low intensity grazing by migrants for a short period of time (3 dung piles added, grass clipped to 16 cm height on Day 6); 3) Low Intensity / High Duration (LIHD), which simulated low grazing intensity for a long period of time (3 dung piles added on each of Day 6 and Day 19, grass clipped to 16 cm and 8 cm height on Day 6 and Day 14 respectively); 4) High Intensity / Low Duration Stopover (HISO), which simulated high use but no grazing for a short period of time (9 dung piles added on Day 6 and no clipping); and 5) Control Plot (CP), with acted as a control with no dung addition or clipping (Fig. 2-3 and Table 2-1). The low-duration treatments (LILD, HILD) were designed to simulate migratory hosts staying for shorter periods than the parasite development period

(10-14 days after defecation), whereas the high-duration treatment (LIHD) simulated migratory hosts remaining in an area across the peak parasite emergence period. The stopover treatment (HISO) was intended to capture the effects of migratory hosts moving through an area where no feeding occurs, for example to rest, ruminate or drink. This combination of treatments reflects biologically plausible wildebeest movement scenarios, based on our understanding of the interaction between wildebeest and resources within the Serengeti (Donaldson et al., 2024). A large group of wildebeest, represented in the experiment by a high intensity grazing treatment, can only occupy a habitat for short period of time as they quickly deplete resources and must move on (Hopcraft et al., 2014). Indeed, observations from long-term camera traps in the Serengeti suggest that even small herds of wildebeest only remain for short periods in particular locations: the median duration of occupancy in front of cameras is <1 day (Donaldson et al., 2024). Thus, simulated grazing and dung addition treatments in our experiment were applied in single, instantaneous bouts, which we view as realistic. The exception was the high duration scenario (LIHD) which included multiple bouts separated by 14 days. Applying continuous grazing and dung addition treatments for any of the scenarios would have been logistically infeasible, and we were concerned that continuous application of treatments would add variability to the main treatment effects due to changing weather conditions that affect parasite emergence and survival. Thus, we assumed grazing and dung addition treatments occurred instantaneously.

2.3.3 Dung addition treatments (transport effects)

We chose 3 (LILD), 3+3 (LIHD) and 9 (HILD, HISO) piles of dung per 2x2 m-sq to represent a range of naturally occurring dung densities of wildebeest, which we calibrated from pilot data of dung densities collected from areas previously occupied by herds of wildebeest in the field (range 0-10 piles per 2x2 m-sq). Within this range, experimental treatment levels were selected to ensure we could recover sufficient numbers of larvae on pasture to detect differences between treatments, if they occurred, and so that levels were multiples of one another; thus, we set the low intensity level at 3 piles per 2x2 m-sq and the high intensity level at 9 piles, representing an extreme, but plausible, end of the distribution of possible dung densities in the wild. We also measured the weight of fresh dung

piles and used the mean wet weight (~350 g) as the standard weight for all dung piles in experimental plots.

To collect experimental dung, for each block on Day 0 we collected 50 freshly defecated dung piles from migratory wildebeest. We quantified the density of strongyle nematodes (eggs per gram of feces or "epg") in each sample by using a modification of the McMaster method, *i.e.*, 50 epg sensitivity (Ezenwa, 2003). Uninfected dung piles were discarded and the remaining infected dung piles (~30 out of 50, Appendix A:S2) were thoroughly mixed together by hand to homogenize the GIN egg density (Silva et al., 2008). We re-formed new dung piles weighing 350 g from the homogenized mix, cultured them for five days in a darkened room at room temperature, watering them after two days to keep eggs and larvae from desiccating (Donaldson et al., 2023). On Day 6, dung piles were introduced in plots HISO, HILD, LIHD and LILD, and repeated on Day 19 for LIHD (Fig. 2-3). We used a random number generator to identify random x-y locations within the inner 2x2m area of plots to place the dung piles. Upon placement in the plots, a small amount of water was used to rinse the container and poured onto grass within the plot.

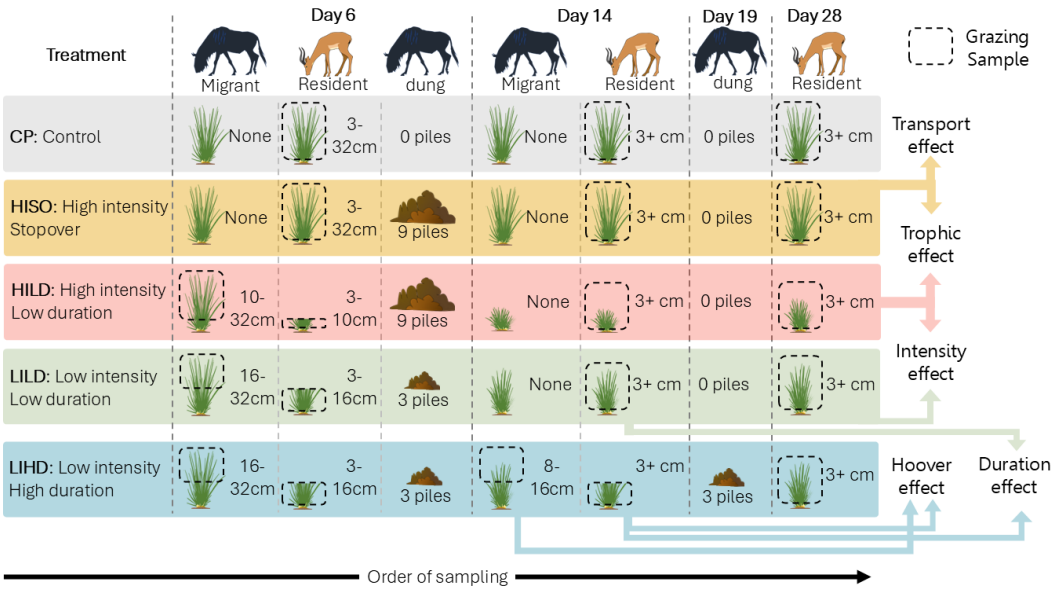

Figure 2 - 3: Experimental layout of the impacts of migration intensity and duration versus migration transport and trophic effects on L3 abundance.
Experimental design of the simulated grazing and dung addition and their impacts on the abundance of 3rd stage larvae (L3) of ruminant gastrointestinal nematodes in pasture. The experiment allowed testing of five separate effects through comparisons of different treatments, as indicated on the righthand side of the figure. The grass icons represent

pasture shared by migrants and residents. NB: All grasses were clipped to a starting height of 32 cm on Day 0. Grass associated with migrant grazing was applied, and the sample collected, from across the entire plot, whereas the grass associated with resident grazing was clipped at random from across the plot.

2.3.4 Grass clipping treatments (trophic effects)

To establish relevant trophic effects through grazing, we used previous reports from Serengeti, where herds of wildebeest grazing have been reported to remove between 56% and 76% of standing grass biomass (McNaughton, 1976, 1985). We simulated ecologically meaningful grazing intensities for this experiment by clipping grass to either 50% or 75% of original standing biomass to mimic low and high grazing intensity treatments, respectively. We clipped all pasture samples and placed them in 0.75 L bags until bags were approximately full, each bag forming a comparable sample from which we could count L3 abundances. We collected pasture samples by random systematic clipping: first, we clipped the closest grass tuft within 15 cm of one side of each dung pile, followed by random clipping from different points in the plot until each bag was full in each sampling phase. Clipping occurred on Days 6, 14 and 28 in all plots (Fig.2-3 and Table 2-1). L3 counts from these pasture samples formed the main treatment responses in our experiment (H1, H2) and represented the degree of transmission risk to “resident” hosts.

In addition to the main treatment effects, we were interested in comparing the infection risks of pasture associated with residents and migrants who were exposed to or not exposed to the trophic effects of migrants at different duration (H3). We used Day 14 pasture samples from Low Intensity High Duration and Low Intensity Low Duration treatments to compare infection risks of pasture associated with residents that were, or were not, exposed to migrant grazing. In the Low Intensity High Duration scenario, we assumed that migrant and resident grazing occurred sequentially, with migrants grazing first followed by residents. Thus, we clipped the top portion of grass to form a “migrant” sample (Arsenault & Owen-Smith, 2002; McNaughton, 1976), then clipped the bottom part of the grass to form a “resident exposed” sample (Gwynne & Bell, 1968). In contrast, the Day 14 pasture sample from the Low Intensity Low Duration scenario was not exposed to migrants and formed a second resident sample (i.e. ‘Resident-only”). Thus, we

compared L3 densities in grasses associated with grazing by migrants, residents-exposed and residents-only to test the hypothesis (H3) that migratory duration underlies the relative exposure risk between migrants and residents (Fig 2-3 and Table 2-1).

To establish baseline data of L3 abundance present prior to experimental dung addition, we collected pasture samples from each plot on Day 6. All pasture samples were collected between 05:30 and 10:00 am, as previous studies reported that L3s were most active and abundant during morning hours when temperature was low, and humidity was high

1 **Table 2 - 1: Summary of treatments in the experiment of trophic vs. transport effects.**

Treatment	Day 0	Day 6		Day 14	Day 19	Day 28
	Collect Dung	**Clip grass**	**Add dung** (#piles)	**Clip grass**	**Add dung** (piles)	**Clip grass**
CP: Control		Wildebeest grazing: No clipping (grass height 32 cm) Resident grazing: sample grass between 3 - 32 cm from the soil surface	0	Resident grazing: sample grass at 3 cm from the soil surface	0	Resident grazing: sample grass at 3 cm from the soil surface
HILD: High intensity low duration		Wildebeest grazing: 75% grass clipped (grass height 10 cm) Resident grazing: sample grass at 3 cm from the soil surface	9	Resident grazing: sample grass at 3 cm from the soil surface	0	Resident grazing: sample grass at 3 cm from the soil surface

HISO: High intensity stopover	**Collect dung & begin incubation**	Wildebeest grazing: No clipping (grass height 32 cm) Resident grazing: sample grass at 3 cm from the soil surface	9	Resident grazing: sample grass at 3 cm from the soil surface	0	Resident grazing: sample grass at 3 cm from the soil surface
LILD: Low intensity low duration		Wildebeest grazing: 50% grass clipped (to 16 cm) Resident grazing: sample grass at 3 cm from the soil surface	3	Resident grazing: sample grass at 3 cm from the soil surface	0	Resident grazing: sample grass at 3 cm from the soil surface
LIHD: Low intensity high duration		Wildebeest grazing: 50% grass clipped (grass height 16 cm) Resident grazing: sample grass at 3 cm from the soil surface	3	Wildebeest grazing: 50% grass clipped (grass height 8 cm) Resident grazing: sample grass 3 cm from the soil surface	3	Resident grazing: sample grass at 3 cm from the soil surface

2.3.5 L3 pasture recovery and identification

We soaked harvested pasture samples in 10 L of water with laundry detergent, and left until the next morning, when nematodes were isolated from pasture and concentrated using established protocols by (Hansen & Perry, 1994). To help with the identification process, we stained L3s for 1 h with Lugols iodine, then counterstained with sodium thiosulphate. During examinations and counting under 40 x magnification, we used both morphology and staining patterns to distinguish free living nematodes from ruminant-type parasitic nematodes. To establish standardized measures of parasite densities, each pasture sample was air dried and weighed, and densities converted to L3 per kg of dry grass.

2.3.6 Environmental variable measurement

To capture and separate effect of micro-climate conditions from the treatments, we monitored soil moisture and temperature in each cage using sensors. A soil moisture sensor was placed 10 cm below the soil surface at the northeast corner of each cage. Furthermore, hourly measures of relative humidity, solar radiation, volumetric water content, and temperature were recorded from automated weather stations located close (<100 m) to the experimental plots.

2.3.7 Statistical analysis

To measure the GIN transport effects under different host intensity scenarios across time (H1), we fit a generalized linear mixed model (GLMM) assuming a negative binomial distribution with L3 counts as a function of Treatments, with Block as a random intercept. We fit separate models for Day 14 (n =25) and for Day 28 (n = 25). Separating days allowed us to independently consider short (14 days) and long (28 days) duration effects. The effect of "Day" was also confounded with changes in weather across the experiment (Appendix A:S3). To account for variation in pasture biomass on L3 counts, we used an offset term for the dry grass biomass weight of each sample (Hinde et al., 2024). We used QQ plot simulated residuals to visually assess model fit by plotting observed against expected values, and found the distribution was appropriate for our data set. We investigated pairwise treatment differences by using a Tukey contrast tests from the fitted model of the first hypothesis above, in the "*mcp*" package. This allowed us to

assess the role of grazing under different host intensity and duration scenarios on GIN parasite abundance (H2).

Lastly, we assessed the impacts of migratory duration on infection risk to migrant and resident hosts (H3) using a similar GLMM approach as described above, and compared L3 counts across three sample types: (1) migrants, (2) resident exposed to simulated migrant grazing, and (3) resident hosts not exposed to simulated migrant grazing.

All analyses were implemented using R-studio version 2022.12.0+253 and R version 4.2.1 (R Core Team 2021).

2.3.8 Data accessibility

All the data supporting this manuscript are available to the public through https://doi.org/10.5525/gla.researchdata.2033, and the code for the analysis can be accessed via GitHub at https://tinyurl.com/mutth6tc.

2.4 Results

2.4.1 High movement intensity increases transport and trophic effects of wildebeest on L3 abundance

We found evidence of both strong transport and trophic effects of migrant herbivores on parasite abundance in pasture. There were extremely low background levels of L3s prior to treatments on Day 6, and no differences between treatments at that time. Across all treatments, we recovered more L3 kg^{-1} of dry grass on Day 14 than on Day 28 (Fig. 2-4). Dung addition treatments had higher L3 values than the control, and high intensity treatment L3 values were higher than the low intensity treatment L3 values (Fig. 2-4, Table 2-2, Appendix A:S5). On Days 14 and 28, High Intensity/Low Duration Stopover (HISO) had significantly higher L3 kg^{-1} of dry grass than all other treatments, followed by High Intensity/Low Duration (HILD), Low Intensity/Low Duration (LILD) and lastly Low Intensity/High Duration-LIHD (Fig. 2-4 and Table 2-3). *Post-hoc* tests showed that on Day 14, there was a significant difference between all treatments (Table 2-3). On Day 28, there was a significant difference between all treatments, except between Low Intensity/High Duration (LIHD) and Low Intensity/Low Duration (LILD), and

between High Intensity/Low Duration (HILD) and Low Intensity/Low Duration-LILD (Table 2-3).

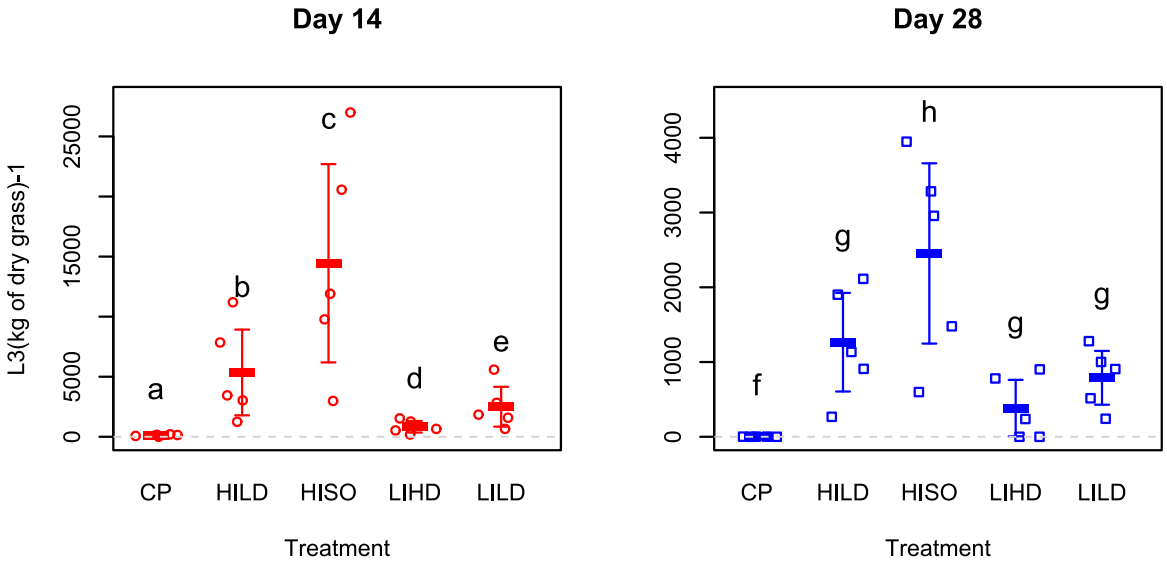

Figure 2 - 4: L3 density per treatment on Day 14 and Day 28.
Observed parasite densities (L3 per kilogram of dry grass biomass) across experimental treatments (CP: Control plot, HILD: High Intensity Low Duration, HISO: High Intensity Stop-over, LIHD: Low Intensity High Duration and LILD: Low Intensity Low Duration) on Day 14 and 28. Bars indicate mean ± 95% confidence intervals within treatments. Different letters show significant differences among the treatments (Table 2-3).

We also found that high simulated grazing in high dung addition plots (HILD) significantly reduced L3 density in pasture (by three-fold and two-fold) compared to high dung addition plots without grazing (HISO) on Day 14 and 28, respectively (Table 2-3, Appendix A:S4). The Low Intensity / High Duration treatment (LIHD) had two-fold lower L3 density in pasture compared to Low intensity / Low duration treatment (LILD) on Day 28, despite double the total number of dung additions in LIHD compared to LILD (Table 2-3, Appendix A:S6).

2.4.2 High migrant duration in an area may reduce infection risk to residents

Pasture samples were split into a top portion of the pasture, representing grass and parasites consumed by migrants, and a bottom portion of the pasture,

representing grass and parasites consumed by residents. We found that in high duration treatments (*i.e.*, simulating pasture associated with residents exposed to longer period of stay by the migrants in the area, pasture associated with resident herbivores were exposed to significantly fewer L3 (kg of dry grass)$^{-1}$ than pasture associated with migrants (*i.e.* Resident exposed versus Migrant; coefficient = 1.17, SE = 0.28, z-value = 4.15, p<0.01; Table 2-2, Fig. 2-5), suggesting a hoovering effect from migrants (Fig. 2-2). In low duration treatments, pasture associated with residents only had significantly higher densities of parasites than pasture associated with residents that had first been grazed by migrants on Day 14 (*i.e.*, Resident only versus Resident exposed samples; coefficient = -1.10, SE = 0.28, z-value = -3.96, p<0.01; Table 2-2, Fig. 2-5). We found no difference in L3 density between grasses associated with migrant and resident only (coefficient = 0.07, SE = 0.26, z-value = 0.26, p =0.96; Table 2-2, Fig. 2-5).

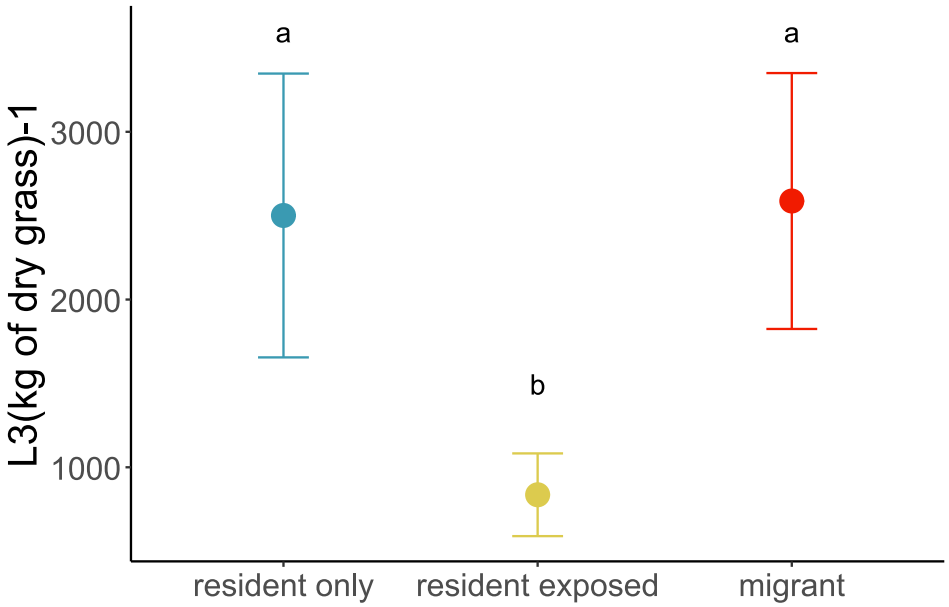

Figure 2 - 5: L3 density in pasture associated with migrant and residents' herbivores

Mean density (± standard error) of L3 (kg of dry grass)$^{-1}$ across 3 types of pasture samples collected 14 days after experimental dung addition. Resident-only samples (blue) represent parasite conditions when resident hosts graze in an area without any grazing by migratory hosts (c.f. Figure 2-3, Low intensity low duration

treatment on Day 14). Resident exposed samples (yellow) represent parasite conditions when resident hosts graze in an area after migratory hosts have grazed (c.f. Figure 2-3, Low intensity high duration treatment on Day 14). Migrant samples (red) represent parasite conditions when migrants have grazed in the upper portion of grasses prior to resident grazing (c.f. Figure 2-3, Low intensity high duration treatment on Day 14). Different letters show significant differences among the treatments from post-hoc Tukey tests.

Table 2 - 2: Results of factorial ANOVA for three models of 3rd stage larvae abundance (L3 counts) on pasture from experimental plots in Serengeti, Tanzania.

Models 1-2 tested for differences in L3 counts on Day 14 and Day 28, respectively, among five experimental treatments (CP: Control plot, HILD: High Intensity Low Duration, HISO: High Intensity Stop-over, LIHD: Low Intensity High Duration and LILD: Low Intensity Low Duration). Model 3 tested for the difference in L3 counts from simulated grazing of resident and migrant hosts. Data were fitted with generalized linear mixed models (GLMM) using a negative binomial distribution, with an offset term for the dry weight of grass per sample.

Variable	Chi sq value	DF	P-value
MODEL 1: DAY 14			
TREATMENTS	249.26	4	2.2e-16 ***
MODEL 2: DAY 28			
TREATMENTS	79.837	4	2.2e-16 ***
Migrant vs resident grazing model			
TREATMENTS	21.08	2	2.644e-05 ***

Table 2 - 3: Post hoc Tukey analysis of differences between treatments on L3 abundance on Day 14 and Day 28 (*c.f.* Figure 2-1).

Treatments	Z – ratio Day 14	P-value Day 14	Z – ratio Day 28	P-value Day 28
HILD -CP	9.24	<0.001 ***	5.86	<0.001 ***
HISO -CP	11.78	<0.001 ***	7.76	<0.001 ***
LIHD -CP	4.52	<0.001 ***	2.77	0.043 *
LILD -CP	7.29	<0.001 ***	4.72	<0.001 ***
HISO -HILD	4.98	<0.001 ***	2.71	0.04974 *
LIHD -HILD	-7.62	<0.001 ***	-3.64	0.002 **
LILD - HILD	-3.57	0.003 **	-1.56	0.515
LIHD- HISO	-12.02	<0.001 ***	-5.99	<0.001 ***
LILD- HISO	-8.47	<0.001 ***	-4.26	<0.001 ***
LILD- LIHD	4.35	<0.001 ***	-2.22	0.165

2.5 Discussion

Due to their high local densities, migratory herbivores can have large impacts on the structure of vegetation through herbivory, raising the possibility of important, but relatively unexplored feedback between the intensity of visitation (number of animals that visit an area), and the duration of time spent defecating and grazing in each area. Our results here provide an integrated perspective linking transport

and trophic effects with movement intensity and duration of wildebeest migration. This study experimentally examined the relative effects of these transport effects via variation in deposition of infected dung, and trophic effects via variation in grazing, on the abundance of infectious environmentally transmitted parasites.

Our study shows clear transport effects by migrants through dung deposition, the strength of which depends on migration intensity. We found that high dung addition in High Intensity Low Duration (HILD) plots significantly increased L3 density in pasture compared to low dung addition in Low Intensity High Duration (LIHD) and Low Intensity Low Duration (LILD) plots. Similarly, all simulated dung addition plots (High Intensity/Low Duration Stopover-HISO, High Intensity Low Duration-HILD, Low Intensity High Duration-LIHD and Low Intensity Low Duration-LILD) had significantly higher pasture larvae densities than control plots-CP, suggesting that pasture infection risk in areas visited by migratory hosts depends on the density of infected dung piles deposited in an area (parasite shedding). These transport effects of migratory species have been well-described in Serengeti, and elsewhere, for a range of parasites and pathogens. For example, Serengeti wildebeest (*Connochaetes taurinus)* also introduce *Macavirus* into areas grazed by cattle that become exposed and contract Malignant Catarrhal Fever (MCF) when they graze in the same pasture as wildebeest (Plowright, 1963), a process that is dependent on density of wildebeest (Cleaveland et al., 2001). Similarly, in Kazakhstan, saiga antelope (*Saiga tatarica*) have been reported to transport both *Marshallagia* and *Haemonchus* nematodes between habitats along their migration routes and subsequently infect sheep in those areas (Morgan et al., 2007). Furthermore, migratory passerine birds are important carriers of ticks (*Ixodes scapularis*) to new habitats, and the number of dispersing infected birds increases the probability of establishing ticks' population in new areas (Schneider et al., 2015).

We also found strong trophic effects on parasite abundance, particularly across single High intensity (HILD), or repeated low intensity, grazing treatments (LIHD). These simulated grazing treatments reduced GIN L3 density significantly in our experimental plots based on the strength of trophic effects, as follows. First, our results based on simulations of migrant and resident hosts grazing in Low Intensity

High Duration (LIHD) plots suggested that there is a “hoovering effect” caused by a direct trophic effect of the migratory hosts, which significantly removed parasites in pasture for subsequent (resident) herbivores to ingest (Fig. 2-5). In the same way, using field grazing experiments, previous studies have reported a large reduction of L3s in pasture (i.e., ≥ 80% reduction of L3) when pasture is first grazed by cattle, followed by sheep (Moss et al., 1998; Rocha et al., 2008). Our results suggest that this hoovering effect is due to L3s being disproportionately distributed in the top sections of the sward, presumably as an adaptation to increase ingestion by initial grazers (Fig. 2-2). Yet an experimental study by Apio et al., (2006) found higher pasture contamination to be associated with lower feeding levels (pasture clipped below 20 cm) compared to higher feeding levels (pasture clipped above 20 cm). These contradictory findings on parasite pasture load between low and upper part of pasture from previous studies (Boom & Sheath, 2008; Moss & Vlassoff, 1993; Niezen et al., 1998; Silva et al., 2008) might be due to different choice of vertical strata used, duration between dung deposition and harvesting of pasture, environmental condition in a pasture at sampling period as the L3 are able to move up and down based on prevailing environmental conditions. Further work to explore where specifically L3s occur within grasses (e.g. leaf tips, stem margins, etc) would be useful for understanding differential infection risk by herbivore species that vary in selectivity in plant parts (Gwynne & Bell, 1968). Our experiment assumes that residents follow wildebeest in the order of grazing. While mixed species herds are common, dense herds of wildebeest largely displace other herbivores, except Plains zebra (*Equus quagga*) with whom they do not share gastrointestinal nematode parasites (Stephens et al., 2017), and some herbivores (e.g. Thomson gazelle, *Eudorcas thomsonii*) follow wildebeest by several weeks in order of grazing (Anderson et al., 2024).

Second, our results also suggest that there are indirect trophic effects via induced micro-climate change in short grass due to grazing. Specifically, plots with single high intensity grazing simulation and single high faecal addition (HILD) had shorter grass height (10cm) than in plots with high intensity faecal addition without grazing (HISO, 32 cm). Because dung was added in High Intensity Low Duration (HILD) after clipping grasses, the reduced L3s in High Intensity Low Duration (HILD) plots may

be due to the higher sunlight radiation, temperature, and lower humidity, compared to high intensity stop-over (HISO) plots. Though there is insufficient data in the current study to clearly understand the role of microclimate on L3s abundance in pasture, data from a second experiment provide strong evidence that these effects can be strong, at least in tropical savannas such as Serengeti (Kimaro et al., unpublished data). The role of micro-habitat conditions on pasture larvae abundance has been previously reported by other researchers. Wang et al., (2018) conducted a study in southwest France, and reported that long grass (10-25 cm) under artificial shade prevented dung desiccation and thus helped to maintain faecal moisture content, consequentially increasing larvae migration onto pasture compared to short grass (<1 cm height) under sunshine. Similar results were observed in humid subtropic areas by Gasparina et al., (2021), who found more L3s in 'high sward height grass' (~ 20 cm high) compared to 'low sward height' (~ 10 cm high) and argued that high sward height provided more favorable microclimate to L3s compared with low sward height.

We also observed that the strength of transport and trophic effects depends on migration intensity and duration. Longer duration of migrants in an area, as simulated in Low Intensity / High Duration (LIHD) plots, led to higher parasite density than in Low Intensity / Low Duration (LILD) plots due to repeated deposits of infected dung. However, as hosts continue occupying and grazing in areas for longer periods, they consume parasites that they have self-deposited. Thus, while longer duration scenarios of migration lead to higher deposits of infected dung, migrants may not necessarily cause higher pasture larvae infection risk to resident hosts due to the potential to hoover at least some of the infectious larvae. Furthermore, in our study the Low Intensity / High Duration (LIHD) plots had double the number of grazing events which likely altered microclimatic conditions. This repeated clipping removed 100% of the original standing grass biomass by the end of the study. Thus, Low Intensity / High Duration (LIHD) plots had highest cumulative grazing intensity than any other remaining treatment plots and consequently had the shortest grass height (8 cm high) of any other remaining treatment plots. Thus, in addition to hoovering effect, gastrointestinal nematode eggs and larvae in Low Intensity / High Duration (LIHD) plots were exposed to the harshest conditions i.e. higher temperature and sunlight within grass patches

leading to the lowest recovery of L3s, except the control plots. Another study by Dickinson et al., (2024), investigated how host movements (Ibex and Sheep) and climate change (temperature and rainfall) affect development of eggs in dung and consecutively L3 abundance in pasture across altitude, and found that host movements (transport effects due to density effect of host) outweighs climate change impact on prediction of abundance of L3 along elevation gradient. Therefore, we conclude, though higher migration intensity and duration scales linearly with both transport and trophic effects (Altizer et al., 2011; Daversa et al., 2017; Dickinson et al., 2024; Poulin & de Angeli Dutra, 2021) leading to a net positive effects on parasite dissemination in areas where dung piles are deposited, the pasture infection risk to other hosts in those area will depend on the strength of the trophic effects of the migrants (Fig. 2-1).

Finally, we found that migrant trophic effects should always reduce levels of pasture contamination either through direct trophic effect or indirect trophic effect. However, the vulnerability and infection risk between migrants and the subsequent host from these trophic effects could be complicated and depends on the timing and intensity of migrant grazing as well as the vertical parasite distribution in pasture. Earlier we suggested three outcomes from migrant trophic effects – neutral effect, hoovering effect and concentration effect (Fig.2-2), each outcome describing a possible interplay between intensity of grazing and vertical parasite distribution within grass patch and the resulting pasture infection risk between migrants and the subsequent host. In this study, we found evidence of the hoovering effect (Fig. 2-5), where simulated migrant grazing significantly consumed high parasites abundance from the top of the grass, and left less parasite abundance in pasture for the residents as predicted in our introduction (Fig. 2-2). This evidence demonstrates the importance of incorporating trophic effects (Fig. 2-3 & Fig. 2-4) and the need for understanding vertical parasite distribution in pasture to uncover infection risk resulting from herbivore movements. We also found higher abundance of L3 on Day 14 than Day 28 suggesting the role of environmental conditions (Appendix A:S3) on pasture larvae availability. While other mechanisms such as natural development time of nematode and their removal by the herbivores could explain the difference of density between days (Day 14 and Day 28), even multiple bouts of grazing and dung addition (i.e., in the low intensity high duration scenario, LIHD) resulted in

fewer L3 on Day 28 (when there was less humidity, Appendix A:S3) compared to single bouts of grazing and dung addition (i.e., low intensity low duration scenario, LILD). Thus, our results suggest that the interaction of H1, H2 and H3 with environmental variables play an important role in describing infection risk on pasture associated with migrants and residents in our ecosystems.

Our experimental design required several important assumptions that may have shaped the outcomes of the treatment scenarios. (1) Our treatment levels of simulated grazing and dung addition were chosen to reflect how migratory wildebeest interact with their landscapes in the Serengeti. In many migratory systems, we would expect that the intensity of visits would be lower, and that the duration of visits would be shorter, because densities of migratory herds in those systems rarely reach those of the Serengeti. However, many ruminant livestock systems are intensively grazed in fenced enclosures, so we expect that interactions between trophic and transport effects may play out in similar ways, though grazing and dung addition would be more continuous than in our simulated migratory system. (2) To ensure sufficient detection of larvae in pasture, we cultured dung piles for five days in the laboratory prior to introducing them to the plots. This prevented us from assessing the impact of trophic effects on early larval development in the dung (3) We assumed grazing by migratory herbivores would result in a uniform, maximum height of grass across plots and that migrants would only consume the upper portions of the sward. Apart from intensively grazed settings which have more uniformly short grass heights, grazing often results in highly variable pasture height, and medium sized ruminants such as wildebeest tend to preferentially consume grass leaves over stems of species and at various heights. Greater heterogeneity in grass height over small spatial scales is expected to lead to more variability in microclimatic conditions and L3 densities. We currently lack information on the extent to which L3 distributions vary across plant parts, and even whether they might vary across different plant species with different aboveground architectures and degree of palatability to vertebrate herbivores. (4) Further, our experiment assumed a sequential order to grazing, with migrants moving through an area first, followed by residents. In reality, the timing of grazing will vary, with implications for parasite exposure risk. Grazing succession, where initial grazing by one group of herbivores stimulates plant regrowth in ways that attracts later herbivores, has been

observed in some Serengeti herbivores on a similar timescale as parasite emergence (16-30 days; (Anderson et al., 2024). Whether successional grazing facilitates parasite transmission is unclear but seems plausible. (5) Our experiment assumed resident herbivores grazed near deposited dung piles, whereas in reality, some herbivores avoid grazing near dung (Hart, 1994; Sarabian et al., 2018). This avoidance should reduce the exposure risk of ingesting L3 compared to the conditions in our experiment.

Nevertheless, our results quantitively show that: (1) migratory hosts, by depositing dung in new areas, can influence local parasite abundance, and that the strength of this effect depends on migration intensity and duration; (2) through grazing, migratory hosts mediate their transport effect of parasites and hence reduce pasture contamination in the environment; (3) if migratory hosts stay for a longer period in an area than the developmental period of parasites, grazing in those areas will result in ingestion of parasites that they had self-deposited as well as desiccation of deposited eggs and/or larvae from exposure to harsher environmental conditions from short grass due to heavy migrant grazing, thus longer migration duration lead to multiple additions of infected dung piles which may not necessary cause higher infection risk to resident animals.

This study integrated transport and trophic effects with intensity and duration of animal movement to understand the role of migration on parasite abundance. Through this framework, we have managed to disentangle transport from trophic effects of animal movement, as well as understand the role of movement intensity and duration on parasites dissemination. We have quantified and provided evidence of how ecological factors such as grazing mediate the migrant transport effect, as well as how it affects development and abundance of parasites. These findings contribute to the understanding of the ecological mechanisms of parasite dissemination at dung-grass interface under different migratory host movement scenarios. Furthermore, our study contributes to understanding the role of consumer resource interaction of the migratory host on parasite dissemination and consequent infection risk to the resident animals.

3. Savanna trees and herbivory drive parasite hotspots via microclimate effects in an African Ecosystem

3.1 Abstract

Understanding how and why parasites vary across space and time is a fundamental task in predicting parasite exposure risk for a given location. However, up to now, we have little understanding of how the microclimate induced by savanna vegetation leads to changes in the local infection risk of parasites. In this study we have employed an observational field survey and a controlled experiment to understand how shade induced by vegetation cover from trees and grasses impacts gastrointestinal nematodes (GIN) in pasture during wet and dry conditions. We found our shade treatments induced by tree canopy and grazing treatments had an impact on L3 densities in pasture, and the microclimate conditions (temperature and humidity), across seasons (i.e., wet or dry conditions). From our observation study, we found higher L3 densities under tree canopy compared to outside tree canopy. We found no evidence of an impact of humidity and temperature on L3 density in pasture at the time of sampling, once accounting for the main effect of tree canopy. Similarly in our experimental study, we found higher L3 density in shaded areas (artificial tree shade) compared to unshaded areas. We also found higher L3 density in areas with high grass height compared to areas with short grass height. We found shaded areas had lower daily mean temperature and maximum temperature than unshaded areas during dry and wet conditions. Shaded areas had higher daily mean humidity and minimum humidity than unshaded areas, however overall pattern of daily mean humidity increased across treatment under wet conditions. For daily minimum humidity, we found shaded shorter grass had higher humidity than shaded tall grass during both dry and wet condition. Our results show that shade from tree canopy and grasses change temperature and humidity in ways that promote environmental stages of parasites. Thus, our study suggests trees, and herbivore grazing, interact across seasons in ways that modify the development, survival and availability of environmental parasites, helping to generate heterogeneity in infection risk across space and time in savannas.

Chapter 3

3.2 Introduction

Understanding how and why parasites vary across space and time is a fundamental task in predicting parasite exposure risk for a given location (Colombo et al., 2023; Krasnov et al., 2020; Rosendale et al., 2016; Titcomb et al., 2021). In parasites with environmental life stages, microclimate conditions can have a large effect on parasite survival (Okech et al., 2004), development time (Belle, 1959; Modabbernia et al., 2024), and infectivity (Pullan et al., 2012). For example, snow cover in arctic locations can insulate the soil surface, which helps maintain relatively higher soil surface moisture (relative humidity) and enhances tick survival (Diyes et al., 2024). Conversely, relatively low air temperatures and high wind velocities in snowy areas helps reduce flying insect (black fly and mosquito) abundances and activity (Anderson & Nilssen, 1998; Keiper & Berger, 1982). In mammalian burrows, ectoparasites such as fleas and mites accumulate over time because of low environmental variability (Butler & Ropert, 1996; Colombo et al., 2023). Aquatic amphibians inhabiting ponds in deforested agricultural areas have higher parasite abundances and richness than those living in ponds within forested areas due to higher water temperature from increased solar radiation (McKenzie, 2007). However, up to now, we have little understanding of how the microclimate induced by vegetation and/or interaction between herbivores and vegetation in savannas leads to changes in parasites development and survival and, hence, local infection risk across the landscape.

Microclimate conditions often change through time at a given location, and this has been shown to alter infection risk. For example, snow cover can restrict the dispersal of *Toxoplasma gondii* oocytes, but as snow melts, the oocytes are transported to water bodies and infect aquatic organisms (Simon et al., 2013). Heterogeneity in microclimates across landscapes and across time can interact with host and parasite life histories in ways that create localized, ephemeral transmission hotspots that drive infection risk (Titcomb et al., 2021). It is therefore important to understand where and why these hotspots occur in order to understand parasite transmission and local disease dynamics (Cecilia et al., 2018; Morgan, 2003; Pullan et al., 2012).

In hot and dry savannas, availability of moisture and amount of humidity are the main limiting factors for the development of nematode eggs to infectious larvae stage and their survival (Donaldson et al., 2023; Nielsen et al., 2007; Turner & Getz, 2010). Normally in these areas there is enough sunlight and temperature throughout the year for eggs development to L3, but during the hot period of the day and dry season of the year, high levels of solar radiation and temperature may lead to desiccation of nematode eggs and/or death of larvae (Dijk et al., 2009). However, the large structural differences in savanna ecosystems between open grasslands and scattered tall canopy trees lead to substantial variation in microclimate conditions across relatively small spatial scales (Belsky et al., 1993; Breshears et al., 1998; Isichei & Muoghalu, 1992). Tree canopies provide shade to communities living underneath trees by intercepting sunlight, simultaneously reducing the amount of sunlight reaching the herbaceous layer (Belsky et al., 1993), thus creating cooler and more stable microclimate conditions compared to open grassland (Ludwig et al., 2004; Randle et al., 2018; Roman-Ponce et al., 1977). These cooler and more stable conditions could act as refugia for parasites that are unable to cope with the more exposed conditions of open grasslands, potentially making trees a key driver of disease transmission in savanna ecosystems. The fact that woody cover is expanding in many savanna ecosystems (Kimaro et al., 2019; Kimaro & Treydte, 2021; Stevens et al., 2017; Venter et al., 2018), increases the urgency to examine the potential mechanisms by which tree cover modifies infection risks (Loss et al., 2022).

Grazing generates further heterogeneity in microclimatic conditions in the herbaceous layer (Montenegro-Díaz et al., 2022; Vaieretti et al., 2018; Yates et al., 2000), mainly through changing vegetation cover and structure (Schieltz & Rubenstein, 2016). Reduced vegetative cover and height alter microclimate conditions of the grazed grassland patch (Nash et al., 2004; Tsukada, 2011), exposing free living stages of parasites to stronger sunlight, which in-turn might reduce their development and survival (Phillips et al., 2014; Salazar et al., 2016; Santos et al., 2012; Suhardono et al., 2006; Vital-García et al., 2024). Sunlight can cause eggs to desiccate due to higher temperature or death of parasite eggs and larvae via ultra-violet radiation (Dijk et al., 2009; Salazar et al., 2016). The role of vegetation in filtering these weather elements (i.e., sunlight, relative humidity, and temperature) and defining microclimate conditions of environmental stage of

parasites have been found to be important in landscape epidemiology (Bonnell et al., 2016; O'Connor et al., 2008; Penczykowski et al., 2017). Through previous research, we know interactions between vegetation and herbivores can lead to animal vectored nutrient distribution (Riesch et al., 2025) that is shaped by herbivore activities, behaviour, and difference of structure between open grassland and trees areas (Treydte et al., 2009, 2010). However, the effects of tree cover on herbivores and the reciprocal impacts on the microclimate available to parasites are not well understood.

This study uses combined field surveys and experimental manipulations to explore the effect of microclimate, as modified by shade and grazing, on infectious gastrointestinal larvae. Specifically, we test how shade from tree canopies and tall grasses modify microclimate conditions during dry and wet conditions, potentially causing differences in densities of environmental parasite between areas under tree canopies versus outside tree canopies. We predict that (1) shaded areas under tree canopies will have higher density of environmental parasites compared to unshaded areas outside the tree canopy; (2) Areas with long grass cover will have higher density of environmental parasites compared to areas with short grass; and (3) Shaded areas under tree canopy or tall grass areas will have lower temperatures and higher humidity than unshaded areas or short grass areas due to vegetation cover that blocks direct sunlight.

3.3 Materials and methods

3.3.1 Study area

The study was conducted in central Serengeti National Park, Tanzania at the Serengeti Wildlife Research Centre. The area is dominated by fire-adapted C4 grasses, such as *Sporobolus spp, Themeda triandra*, *Panicum spp, Pennisetum spp, and Eragrostis spp* (Williams et al., 2016), and sparsely distributed trees, particularly *Vachellia robusta* and *Vachellia tortillis* (Mduma et al., 2007; Ruess & Halter, 1990; Rugemalila et al., 2020). The latter (*V. tortillis*) is known to have positive effects on ungulates by supporting nutritious grasses and shade beneath the canopies compared to open grassland areas (Treydte et al., 2010). Dominant wildlife species present include wildebeest (*Connochaetes taurinus*), plains zebra (*Equus quagga*), thompson's gazelle (*Eudorcas thomsonii*), impala (*Aepyceros*

melampus), topi (*Damaliscus lunatus*) and African savanna elephants (*Loxodonta africana)* (Bukombe et al., 2019; Hopcraft et al., 2015; Ruess & Halter, 1990). The monthly maximum temperature ranges from 25 °C to 28 °C (Huang et al., 2021; Kilungu et al., 2017; Mduma et al., 2007). The greater Serengeti ecosystem has two wet seasons: the short rains (November to December) and the long rains (March to May), with average annual rainfall ranging from 500 to 1200 mm (Anderson et al., 2007; Mahony et al., 2021).

3.3.2 Observational field survey

To study landscape-scale infection risks of environmental parasites, we assessed variation in the abundance of infectious third stage GIN larvae under, and outside of tree canopies. We collected pasture samples from a total of thirty sites (n = 30); in each site we collected two paired samples representing two treatments: (1) Canopy – pasture clipped from below canopy of mature (>3m height) *V. tortillis* and (2) Non-canopy – pasture clipped between 0-2 m from below the outer canopy edge of the same *V. tortillis* tree. This canopy periphery zone was expected to have roughly similar levels of herbivore grazing and herbivore dung as under the tree canopy (Ludwig et al., 2008; Treydte et al., 2010), but was exposed to a higher intensity of sunlight (Islam et al., 2023; Ludwig et al., 2004). For each treatment at each site, we clipped 45 random locations to 3 cm above the soil surface to fill a 25 x 17 cm sample bag. To assess whether herbivore use and dung inputs were similar under the canopies versus outside, we quantified the density of dung in each area by counting all identifiable old and fresh dung piles in each treatment area, i.e. under the canopy and within 2m of the tree canopy peripheral. For each treatment area, grass height measurements were taken in the four cardinal directions from five randomly selected locations. To measure the effects of the tree canopy on microclimatic variables, we first used Kestrel 3000 Pocket Weather Meter (Kestrel Instruments, USA) to record temperature and humidity, and an AccuPAR PAR/LAI Ceptometer (METER Group, Inc. USA) lightbar to record Photosynthetically Active Radiation (i.e. sunlight) at breast height between the canopy and the grass layer. Three temperature, humidity and sunlight measurements were taken at 2 m from the tree trunk (directly under the canopy) and another three 2 m away from peripheral of the tree canopy. All pasture samples were returned to the laboratory where we recorded wet grass

mass before L3s were recovered using the methods described below. Grass was then dried to a constant weight and the dry grass biomass recorded.

3.3.3 Shade and herbivory experiment

We experimentally manipulated microclimate by providing artificial tree shade and varying grass height to capture microclimatic differences in order to assess their impact on the abundance of environmental parasites. We set up five experimental blocks at the Serengeti Wildlife Research Centre. The experiment was replicated across each of the five blocks, with set-up occurring on sequential days. At each of the five blocks, we manipulated two main variables: (1) grass height (low and high grass height) and (2) shade cover availability (shading and no shading) to tease apart how micro-climate might affect pasture larvae densities in dry and wet conditions. The variables manipulation results into a fully factorial experimental design with 4 treatment plots (20 plots total): (1) Shaded Low Grass Height (SHALOH), (2) Unshaded Low Grass Height (UNSHALOH), (3) Shaded High Grass Height (SHAHIH), and (4) Unshaded High Grass Height (UNSHAHIH). Each plot was surrounded by chicken wire fences to prevent the destruction of experimental plots and interference by vertebrate herbivores. The 3 m x 3 m plots were set up ≥10 m from each other (Fig.3-1) and we limited our plots manipulation (treatment and sampling) to the central (2 x 2 m) area to minimize boundary effects. Temperature and relative humidity sensors (Arduino and Decagon, respectively) were installed at the center of each plot, positioned 10 cm above the soil surface., with recordings taken every 30 minutes at the plot level (n = 20 sensors) throughout the duration of the experiment.

We manipulated shade by using green shade netting (2 x 2 m each) that resulted in shade values of 39%, to mimic natural shade values of 35.3% from tree canopy (Appendix B:S3). To seed L3 in treatment plots, we collected 50 fresh dung piles from wildebeest each day to set-up the five replicate blocks. Next, we quantified dung faecal egg counts following 1:50 McMaster egg counting method and selected those with the highest faecal egg counts before thoroughly homogenising them. We then reformed new individual dung piles with a mass of 350 g (i.e. the mean mass of all field samples) and cultured them for five days before introducing them into plots. We previously showed that placing nine dung piles resulted in density of 14,444 ± 8,253 L3 emergence onto pasture (Kimaro et al., 2025), and we

therefore added nine wildebeest dung piles to each plot with each pile location determined by generating a random set of X and Y coordinates which corresponded to centimetres along the 2 m southern (X) and western (Y) sides of the sampling area of each plot. We previously found that areas that have not been exposed to wildebeest grazing have grass height ~30 cm (Kimaro et al., 2025) and we therefore clipped tall grass plots to 30 cm. Short grass plots were clipped to 5 cm, aligning with 47 measured values on heavily grazed areas in the natural environment (mean = 5.5 cm, SE = 0.38). All clipped grass was removed from the cage.

We started pasture sampling on October 17th and concluded on November 13th, 2023. Prior to applying treatments, we verified that there was little background contamination in our experimental plot by quantifying L3 in the pasture. We have previously found that in relatively wet conditions, L3 emergence in our system peaked on day 14, but continued past 28 days (Donaldson et al., 2023; Kimaro et al., 2025). To capture treatment effects, we collected pasture samples on days 14 and 28 following dung addition. Due to rainfall that started roughly halfway through this period, it allowed our experiment to include both dry conditions (Day 14) and wet conditions (Day 28), with mean rainfall of 6.3 ± 0.06 mm in days 0-14, and 44.7 ± 0.44 mm in days 14-28 (see Appendix B:S1 and B:S2). These incidental rainfall differences gave us extra insight into how treatment effects vary in different moisture conditions from a single experiment. Pasture clipping and L3 recovery from pasture followed our previous methods (Donaldson et al., 2023; Kimaro et al., 2025). We clipped pasture samples to fill 1 litre sample bag. On each sampling phase (Day 0, Day 14, or Day 28), we started with clipping grass from one side of each dung pile (i.e., grass found within 15cm from one side of dung pile), then followed by random grass clipping from different points in the plot until each bag was full. We clipped all our pasture samples between 05:30 and 10:00 am to limit variation in L3 presence on the pasture resulting from daily fluctuations.

3.3.4 Pasture larval counts

Once harvested, pasture samples were soaked in 10 L of water with laundry detergent, and left overnight, followed by isolation of nematodes from pasture and then concentrated using established protocols by Hansen & Perry, (1994). To distinguish and count ruminant parasitic nematodes from free living nematodes, we stained L3s for 1 h with Lugols iodine, then counterstained with sodium thiosulphate, and used the morphology to distinguish them at 40x magnification. We dried and weighed the grass samples to standardize L3 densities.

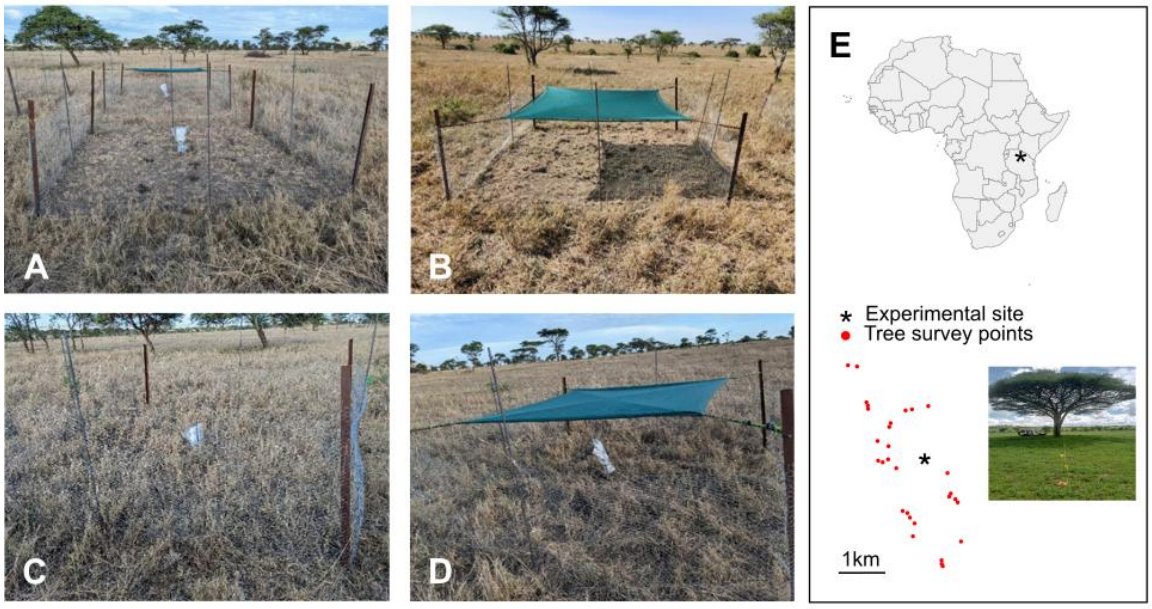

Figure 3 - 1: Tree canopy survey and experimental shade treatment layout in Serengeti National Park.

Experimental shade and grass height across the four treatments: (A) Unshaded Low Grass Height treatment, (B) Shaded Low Grass Height treatment, (C) Unshaded High Grass Height treatment, and (D) Shaded High Grass Height treatment in a 3 x 3 m cage. (E) Spatial distribution of tree survey points (heavy red points) of *V. tortilis* trees (*see* inserted image on the right-hand side) where canopy and non-canopy pasture samples were collected as part of the observational survey at the Serengeti Wildlife Research Centre, Tanzania (heavy black star).

3.3.5 Statistical analysis

3.3.5.1 Observational study

To measure the impact of tree canopy cover on free-living stages (L3s) of parasitic gastrointestinal nematodes (GIN) in our field observational study, we fit a generalized linear mixed effects model assuming a negative binomial distribution, with L3 counts as a function of the interaction between canopy cover (Canopy vs. Non-canopy) and dung density. In our most complex model, we also included humidity, temperature, sunlight, and grass height as linear fixed effects, and tree ID as a random intercept. To account for variation in the grass biomass sampled for L3, we used dry grass biomass as an offset term for each sample (Warton et al., 2015). We then used Likelihood Ratio Tests (LRTs) to compare our complex model with simpler nested models without effects of (1) sunlight and (2) grass height, (3) dung density, (4) canopy, and (5) an interaction between dung density and canopy. We purposely included the main effects of temperature and humidity in all models because of well-established relationships of L3s with these variables (Amaradasa et al., 2010; Silva et al., 2008). We based statistical significance of variables on the comparative tests (Haydon and Shaw, 2026). Dung density and tree canopy exhibited collinearity as indicated by relatively high Variance Inflation Factors. However, we found that the inclusion of dung density as an interaction with tree canopy improved our model performance based on LRTs. Thus, we opted to retain both variables and their interaction in the final model, under the justification that all effects explained variation in L3s (Haydon and Shaw, 2026). The negative binomial distribution provided a good fit to the data and met critical assumptions of dispersion (two-sided p = 0.5) and zero inflation (two-sided p = 0.4). Model performance was assessed using the “DHARMA” package (Harting, 2026).

3.3.5.2 Experimental study

To establish microclimate impacts from tree canopy covers and grass height on environmental parasites in our experimental pasture plots (testing hypotheses **H1** & **H2**), we fit a generalized linear mixed models (GLMM) using a Poisson distribution. We fit two separate models, one model for Day 14 (n= 20) and another for Day 28 (n = 20). Separating the days in modelling experimental data set

allowed us to independently consider 'season' effects i.e., dry (Day 14) and wet (Day 28). We used L3 counts as the response variable and modeled it as a function of shade treatment (shade vs. no-shade), grass treatment (low grass vs. high grass height), and average morning temperature and humidity on the day of sampling, with Block included as a random effect. To get the average morning temperature and humidity on the day of sampling for testing experimental treatment effects on environmental parasites, we included all hourly temperature and humidity on the day of sampling before 11:00 am, because all pasture samples were collected between 0530 and 10:00 am. Then we summarized hourly filtered data (< 11:00 am) to mean daily values of temperature and relative humidity and used that in analysis of experimental treatment effect on environmental parasites for two reasons: (1) Variation in morning temperature and humidity may have influenced L3 detection from pasture; we accounted for this by including these variables in our models, (2) We also found that average morning temperature and humidity improved model performance compared to mean values over 24 hours, or minimum and/or maximum daily values. We accounted for the impacts of variation of pasture biomass on L3 counts by using an offset term for dry grass biomass of each sample weight (Hinde et al., 2024; Smith, 2024; Warton et al., 2015). Our model check was done visually through QQ plots by plotting observed against expected values. To check for the significance of our variables in the model against the null hypothesis we used a likelihood-ratio test with Wald statistic. To test for pairwise differences among treatments, we used Tukey contrast tests from the fitted models using the "mcp" package (Bretz et al., 2016).

3.3.5.3 Experimental effects on microclimate

To evaluate the effects of the experimental shade and grazing treatments on the longer-term microclimate conditions within plots (testing **H3**), we developed models for Day 14 (dry conditions) and Day 28 (wet conditions) for four microclimate variables: (1) average and (2) maximum daily temperatures, and (3) average and (4) minimum daily humidity. Each variable used hourly measurements that were averaged over the two experimental periods (days 0–14 and 14–28) and modelled as a function of shade treatment, with block as a random intercept, using a general linear mixed effects model with a Gaussian distribution.
We used R studio version 2022.12 + 253 and R version 4.2.1 to complete all the analysis described above (R Core Team 2021).

3.4 Results

3.4.1 Observational survey: Impact of shade from tree canopy on environmental parasites

In our observational study, we found significant effects of canopy (X^2 = 19.317, df = 6, p < 0.001), dung density (X^2 = 10.204, df = 6, p = 0.006) and the interaction between canopy and dung density (X^2 = 6.754, df = 7, p = 0.009) on L3s. We found no effect of sunlight (X^2 = 2.223, df = 9, p = 0.136) nor grass height (X^2 = 0.016, df = 8, p = 0.900). Our top model following model selection included an interaction between treatment (canopy and non-canopy cover) and dung density, with humidity and temperature as linear fixed effects, and tree ID as a random intercept. The top model results showed higher densities of L3s under tree canopies (mean = 115.53 L3 Kg^{-1} of dry grass; SE = 23.12) than in non-canopy areas (mean = 55.47 L3 Kg^{-1} of dry grass; SE = 13.65; Table 3-1, Figure 3-2). Additionally, we found the main effect of dung density on L3s to be positive (Table 3-1), and a strong negative interaction between non-canopy areas and dung density, which indicated that the effect of dung on L3s was stronger under canopy than outside of canopy (Table 3-1). After accounting for the main effects of tree canopy, dung density and their interaction, coefficients associated with humidity and temperature at the time of sampling had no effect on environment parasites (Table 3-1). In a separate analysis, we found that non-canopy areas had higher density of dung piles than in canopy areas (Appendix B:S5, Coefficient = 1.195, SE = 0.141, Z = 8.452 , p < 0.001).

Areas under the tree canopy had slightly higher humidity (mean = 55.48%; SE = 1.07) compared to non-canopy areas (mean = 54.63%; SE = 0.97), and sunlight radiation was lower under tree canopy (mean = 507.67; SE = 30.96 μmol $s^{-1}m^{-2}$) compared to non-canopy areas (mean = 1883.27; SE = 69.74 μmol s^{-1} m^{-2}, Appendix B:S3).

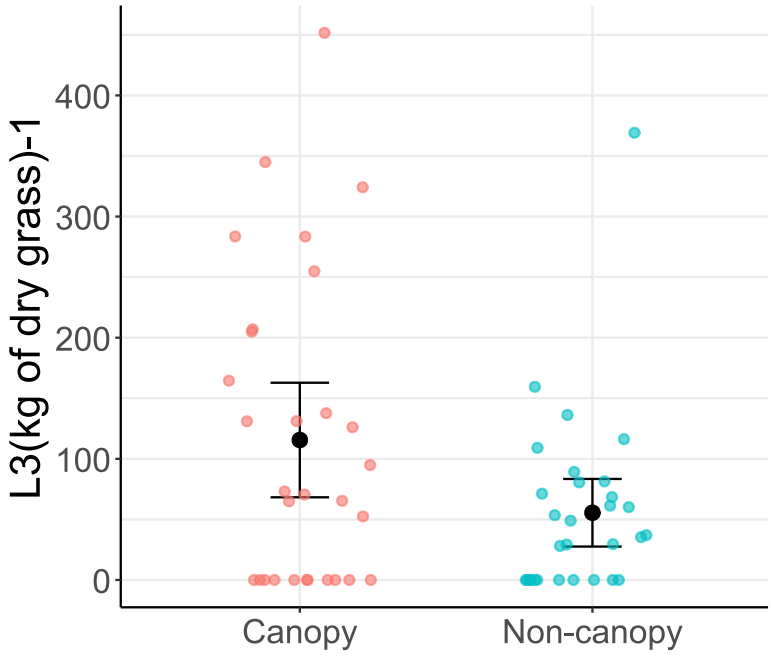

Figure 3 - 2: L3 density under tree canopy and outside tree canopy.

Observed parasite densities (L3(kg of dry grass)-1) from field survey treatments. Canopy (red colour) representing under tree canopy L3 density and non-canopy (blue colour) representing outside tree canopy L3s density. Black heavy circle and error bars represent mean ± 95% confidence intervals within treatments.

Table 3 - 1: Model results for the effects of tree canopy on L3 density

Coefficients for the top model quantifying the effects of canopy and dung density on GIN L3 counts using a generalized linear model with a negative binomial distribution and an offset term for the dry weight of the pasture sample. NB: "Canopy" was the reference level for the canopy:non-canopy variable, and dung density was measured as dung piles per square-meter.

Variable	*B*	SE	Z-VALUE	P-VALUE
INTERCEPT	1.922	8.906	0.216	0.829
NON-CANOPY	-0.571	0.418	-1.365	0.172
DUNG DENSITY	24.852	7.967	3.119	**0.002*** **
TEMPERATURE	-0.114	0.222	-0.513	0.608
HUMIDITY	-0.074	0.066	-1.117	0.264
NON-CANOPY: DUNG DENSITY	-17.851	7.122	-2.506	**0.010** **

3.4.2 Experimental study: Impact of artificial shade and grass height on environmental parasites

Similarly, our experiment found strong evidence of the impact of shade and grazing on environmental parasites. Prior to treatments (on Day 6), background levels of L3 were low (mean = 2.7 L3 Kg^{-1} of dry grass; SE = 2.7), and we found no variation of L3 counts between treatments. Following our manipulations, we found a high density of L3 in pasture, with variation among our treatments (Table 3-2). Both shade and grass height treatments had a significant impact on L3 densities (Table 3-2 & Table 3-3). We found higher L3 densities under shade treatments (mean = 457 L3 Kg^{-1} of dry grass; SE = 212 on Day 14, and mean = 940 L3 Kg^{-1} of dry grass; SE = 157 on Day 28) than in open treatments (mean = 126 L3 Kg^{-1} of dry grass; SE = 70.3 on Day 14 and mean = 434 L3 Kg^{-1} of dry grass; SE = 167 on Day 28). Similarly, during dry condition (Day 14), the Unshaded High Grass Height treatment had significantly higher L3 density (Fig.3-3 and Table 3-3) than the Unshaded Low Grass Height. Our pairwise tests (post-hoc analysis, Table 3-3) of treatments on Day 14 (dry period), showed that the Unshaded Low Grass Height (UNSHALOH) had higher L3 densities than all other treatments on day 14 (Figure

3-3 and Table 3-3), but no significant difference was found between the shaded treatments shaded treatments and Unshaded High Grass Height treatment (UNSHAHIH, Table 3-3). On Day 28 (wet period), we did not find significant difference of L3 densities from all pairwise treatments comparisons except from the followings: (1) Shaded Low Grass Height had higher L3 densities (Fig.3-3 and Table 3-3) than Unshaded High Grass Height (SHALOH -UNSHAHIH) and (2) Unshaded Low Grass Height had lower L3 densities than Shaded Low Grass Height (UNSHALOH-SHALOH). Overall, from our experiment we recovered greater L3 density during the wet period i.e., Day 28, than during dry period, i.e., Day 14 (Fig.3-3 and Appendix B:S4). Furthermore, the average morning temperature from 00:00 to 11.00 am hours had a significant effect on L3 recovery on day 14, but not on day 28, While humidity had margin effect on L3 recovery on Day 28, and no effect on Day 14.

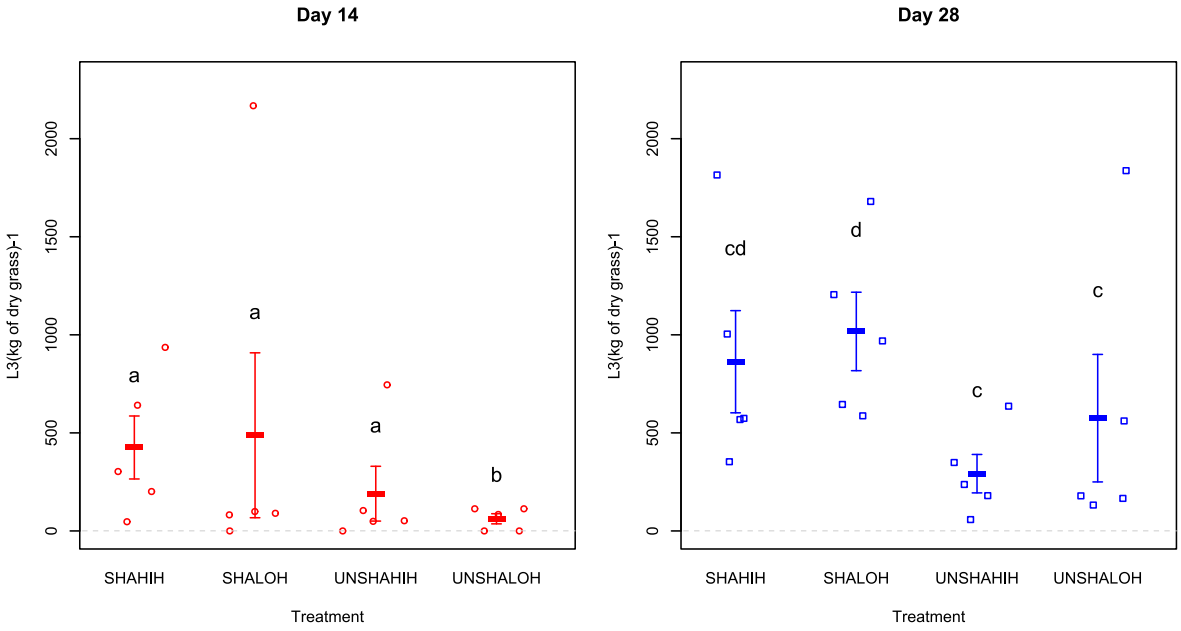

Figure 3 - 3: L3 density per shade treatment in dry (Day 14) and wet condition (Day 28).

Observed parasite densities L3 Kg^{-1} of dry grass across experiment treatments on Day 14 and Day 28. Day 14 was drier than day 28. Key to treatment acronyms: SHAHIH: Shaded High Grass Height, SHALOH: Shaded Low Grass Height, UNSHAHIH: Unshaded High Grass Height and UNSHALOH: Unshaded Low Grass Height. Mean density (± standard error) of L3 per kilogram of dry biomass) per treatment is represented by heavy bars. Different letters represent significant difference among the treatments.

Table 3 - 2: Results of factorial ANOVA for two models of 3rd stage larvae abundance (L3 counts) on pasture from experimental plots in Serengeti, Tanzania.

Models tested for differences in L3 counts on Day 14 and Day 28, respectively, among four experimental treatments: (1) Shaded Low Grass Height (SHALOH), (2) Unshaded Low Grass Height (UNSHALOH), (3) Shaded High Grass Height (SHAHIH), and (4) Unshaded High Grass Height (UNSHAHIH), as well as environmental variables i.e., morning hours temperature and humidity from 00:00 to 11.00 am hours. Data were fitted with generalized linear mixed models (GLMM) using a Poisson distribution, with an offset term for the dry weight of grass per sample.

Variable	Chi sq value	DF	P-value
MODEL 1: DAY 14			
TREATMENTS	20.288	3	**<0.001*** **
RELATIVE HUMIDITY	0.260	1	0.610
TEMPERATURE	31.424	1	**<0.001*** **
MODEL 2: DAY 28			
TREATMENTS	14.610	3	**0.002*** **
RELATIVE HUMIDITY	2.844	1	0.092
TEMPERATURE	1.769	1	0.184

Table 3 - 3: Post hoc analysis of shade treatment on L3 density

Post hoc Tukey analysis of differences between experimental treatments on L3 abundance on Day 14 and Day 28. Treatments included: (1) Shaded Low Grass Height (SHALOH), (2) Unshaded Low Grass Height (UNSHALOH), (3) Shaded High Grass Height (SHAHIH), and (4) Unshaded High Grass Height (UNSHAHIH).

Treatments	Z - Value Day 14	P-value Day 14	Z – ratio Day 28	P-value Day 28
UNSHAHIH - SHAHIH	-1.14	0.65	-1.02	0.73
SHALOH - SHAHIH	-1.82	0.25	1.60	0.36
UNSHALOH - SHAHIH	-4.67	<0.01**	-0.69	0.90
SHALOH - UNSHAHIH	-0.88	0.81	-4.58	<0.01**
UNSHALOH - UNSHAHIH	-3.80	<0.01**	0.52	0.95
UNSHALOH - SHALOH	-3.51	<0.01**	-2.81	0.02*

3.4.3 Impact of artificial shade and grass height on microclimate conditions

Artificial shade and grass height modified the surface temperature values (at 10 cm high) at plot level. On both Days 0-14 and Days 14-28, we found Unshaded Low Grass Height (UNSHALOH) had higher daily mean and maximum temperatures than any other treatments (Fig.3-4, Table 3-4), followed by Unshaded High Grass Height (UNSHAHIH), Shaded Low Grass Height (SHALOH) and Shaded High Grass Height (SHAHIH). Comparing all daily mean temperatures between plots, across days 0-14, we found that daily mean temperatures were significantly higher between Unshaded Low Grass Height (UNSHALOH) plots and shaded treatments, whether long or short grass (Table 3-4). However, there was no difference between unshaded plots whether grass was long or short. We found the same when comparing all daily mean temperatures between plots from days 14-28 (Fig. 3-4 and Table 3-4).

Moreover, between Day 0-14, we found higher daily maximum temperature in Unshaded treatments whether grass was long or short compared to shaded treatments whether grass was long or short (Fig. 3-4 and Table 3-4). We found no variation (Fig. 3-4 and Table 3-4) between: (1) shaded treatments regardless of

grass height and (2) Unshaded treatments regardless of grass height, as well as between (3) Unshaded High Grass Height (UNSHAHIH) and Shaded Low Grass Height (SHALOH).

While on Day 14-28, we found higher maximum temperature in unshaded treatments regardless of grass heights compared to shaded treatments regardless of grass height (Fig. 3-4 and Table 3-4). Notably, Unshaded High Grass Height (UNSHAHIH) had marginally higher maximum temperature than Shaded Low Grass Height (SHALOH, Fig 3-4 and Table 3-4). We found no variation (Fig. 3-4 and Table 3-4) of maximum temperature between Shaded treatments regardless of grass height, as well as between unshaded treatments regardless of grass height.

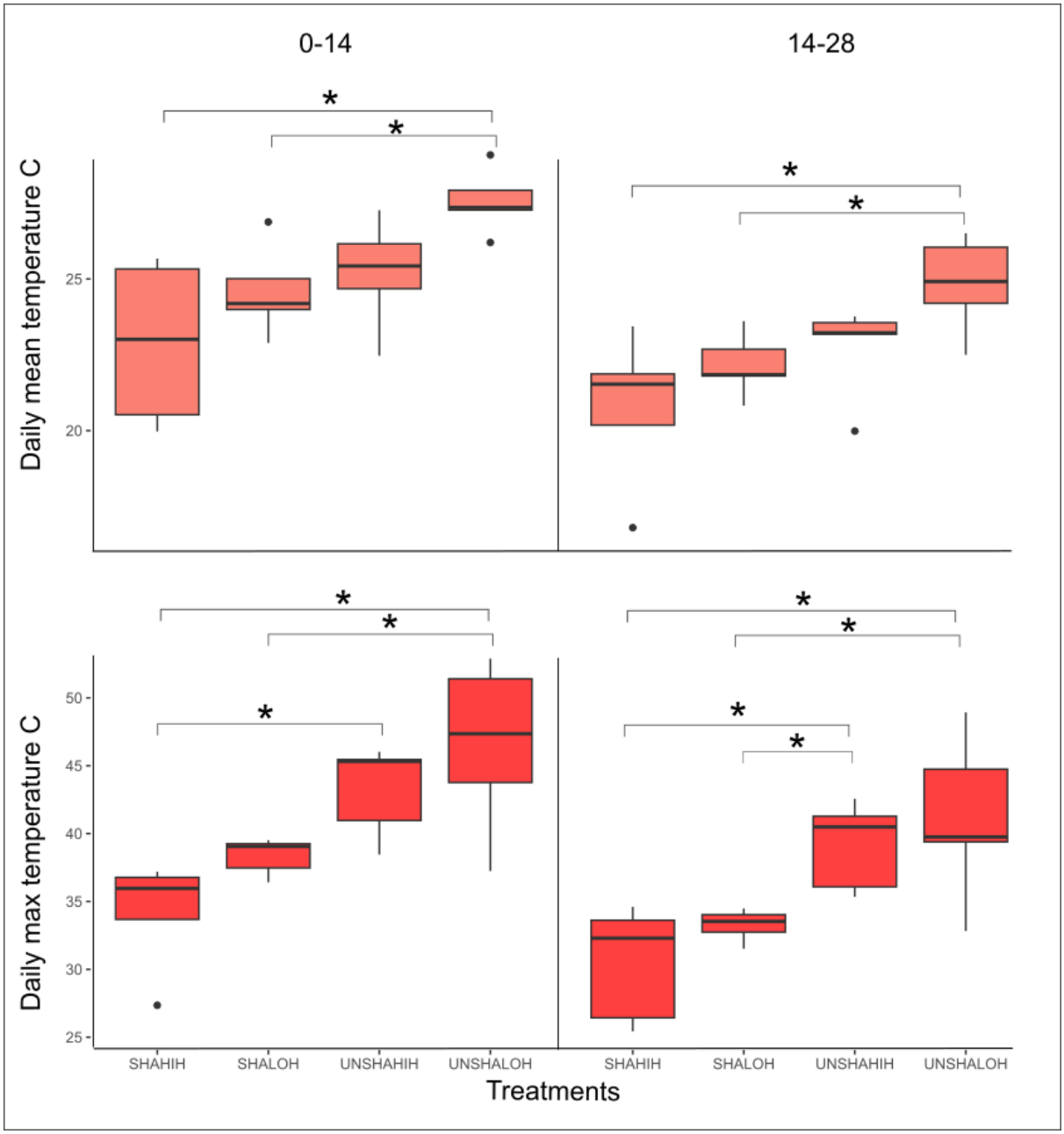

Figure 3 - 4: Effect of shade treatments on daily mean and maximum temperature

Observed range of daily mean temperature (light red) and daily maximum temperature (red) across treatments, measured at 10cm above soil surface across days 0-14 and days 14-28. Treatments were: SHAHIH: Shaded high grass height, UNSHAHIH: Unshaded high grass height, SHALOH: Shaded low grass height, and UNSHALOH: Unshaded low grass height. Heavy black line represents a median value of the recorded temperature values from each treatment. The brackets and black asterisk denote significant differences between two treatments, based on Tukey post-hoc tests.

Table 3 - 4: Post results of treatment effects on air temperature

Post hoc Tukey analysis of differences between experimental treatments on temperature on Day 14 and Day 28. Treatments included: (1) Shaded Low Grass Height (SHALOH), (2) Unshaded Low Grass Height (UNSHALOH), (3) Shaded High Grass Height (SHAHIH), and (4) Unshaded High Grass Height (UNSHAHIH).

Daily mean temperature				
Treatments	**Z - Value Day 14**	**P-value Day 14**	**Z - value Day 28**	**P-value Day 28**
SHALOH - SHAHIH	1.627	0.364	1.420	0.487
UNSHAHIH - SHAHIH	2.211	0.120	2.021	0.180
UNSHALOH - SHAHIH	4.490	**<0.001**	4.161	**<0.001**
UNSHAHIH - SHALOH	0.584	0.937	0.601	0.932
UNSHALOH - SHALOH	2.863	**0.022**	2.741	**0.031**
UNSHALOH - UNSHAHIH	2.278	0.103	2.139	0.141
Daily maximum temperature				
SHALOH - SHAHIH	1.774	0.286	1.204	0.624
UNSHAHIH - SHAHIH	3.867	**<0.001**	3.752	**<0.001**
UNSHALOH - SHAHIH	5.272	**<0.001**	4.607	**<0.001**
UNSHAHIH - SHALOH	2.093	0.155	2.548	**0.053**
UNSHALOH - SHALOH	3.498	**0.003**	3.404	**0.004**
UNSHALOH - UNSHAHIH	1.405	0.496	0.855	0.828

The relative humidity varied from 0.49 to 0.55 on Days 0-14, and from 0.66 to 0.81 on Days 14-28. We found our artificial shade and grass height also modified relative humidity (at 10 cm high) at plot level. On Day 0-14, we found higher mean daily humidity in all shaded treatments regardless of grass height compared to

unshaded treatments (Fig. 3-5 and Table 3-5), with exception between Shaded High Grass Height (SHAHIH) which had marginally higher significant humidity than Unshaded Low Grass Height (UNSHALOH). We found no variation (Fig. 3-5 and Table 3-5) between: shaded treatments and unshaded treatments regardless of grass height as well as between Unshaded Low Grass Height (UNSHALOH) and Unshaded High Grass Height (UNSHAHIH). On Day 14-28, we found Shaded High Grass Height (SHAHIH) had higher daily humidity than any other treatments, and no variation was detected among all remaining treatments, (Fig. 3-5 and Table 3-5).

For daily minimum humidity, on both Days 0-14 and 14-28, we found Shaded Low Grass Height (SHALOH) had higher daily minimum humidity than remaining treatments, followed by Shaded High Grass Height (SHAHIH), Unshaded High Grass Height (UNSHAHIH) and lastly by Unshaded Low Grass Height (UNSHALOH). Post hoc test on Days 0-14 showed there was a significantly different minimum relative humidity (Fig. 3-5 and Table 3-5) between all treatments, except between Unshaded Low Grass Height (UNSHALOH) and Unshaded High Grass Height (UNSHAHIH, Fig. 3-5 and Table 3-5). While on Days 14-28, post hoc test showed significant difference of minimum relative humidity (Fig. 3-5 and Table 3-5) between all treatments, except between Unshaded Low Grass Height (UNSHALOH) and Unshaded High Grass Height (UNSHAHIH, Fig. 3-5 and Table 3-5).

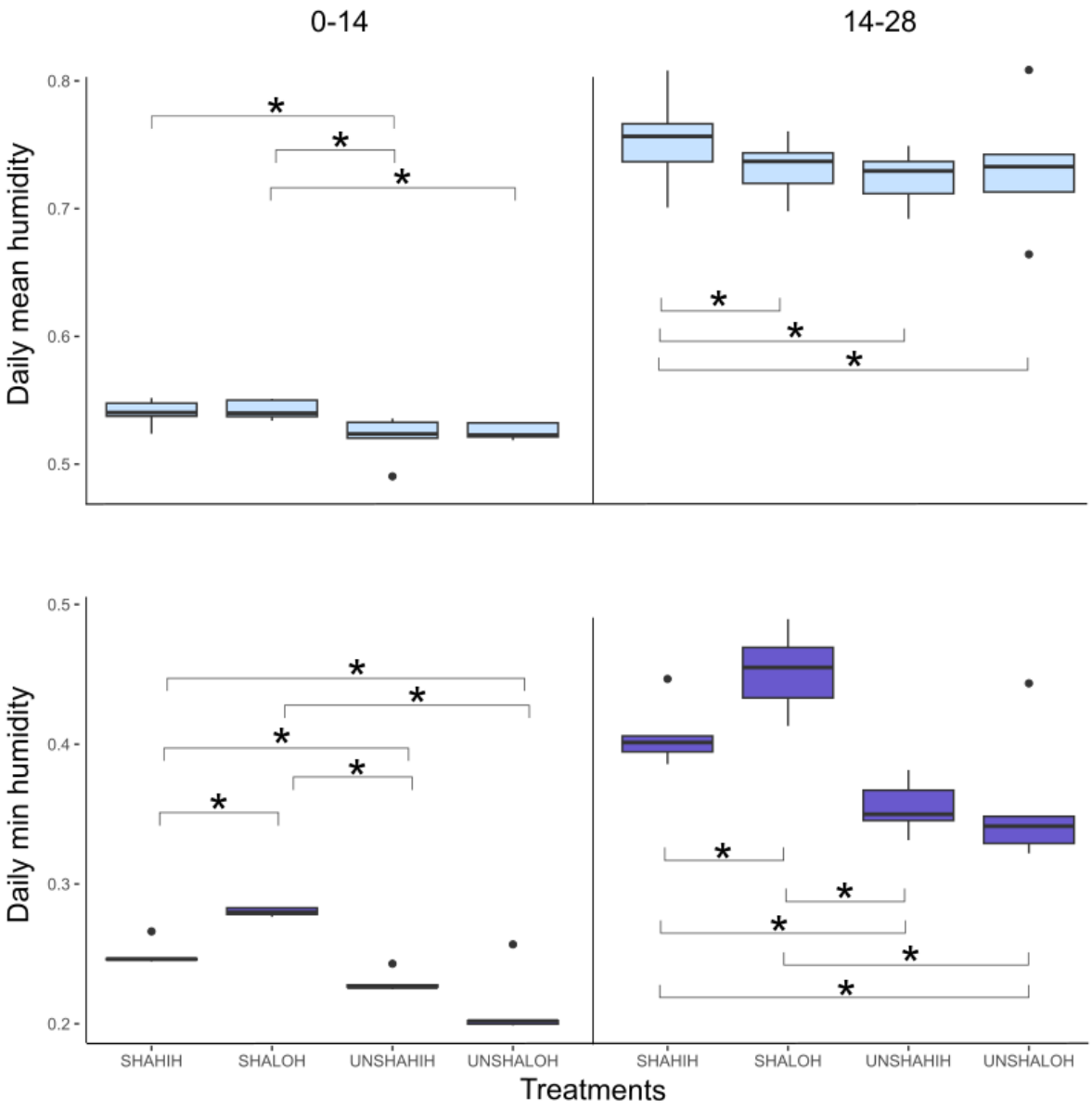

Figure 3 - 5: Effects of shade treatment on daily mean and minimum humidity Observed range of daily mean humidity (light blue) and daily minimum humidity (dark blue) across treatments (SHAHIH: Shaded High Grass Height, UNSHAHIH: Unshaded High Grass Height, SHALOH: Shaded Low Grass Height, and UNSHALOH: Unshaded Low Grass Height) measured at 10cm above soil surface in the period of Day 0 - 14 and Day 14 – 28. Heavy black line indicates a median value of the recorded relative humidity values from each treatment. The grey line and black asterisk denote significant difference between two treatments.

Table 3 - 5: Post hoc analysis of treatment effects on humidity

Post hoc Tukey analysis of differences between experimental treatments on daily mean and minimum humidity on days 0-14 and days 14-28 measured at 10cm above the soil surface. Treatments included: (1) Shaded Low Grass Height (SHALOH), (2) Unshaded Low Grass Height (UNSHALOH), (3) Shaded High Grass Height (SHAHIH), and (4) Unshaded High Grass Height (UNSHAHIH).

Daily mean humidity				
Treatments	**Z – Value Day 14**	**P-value Day 14**	**Z – value Day 28**	**P-value Day 28**
SHALOH - SHAHIH	0.372	0.982	-2.612	**0.045**
UNSHAHIH - SHAHIH	-3.268	**0.006**	-3.554	**0.002**
UNSHALOH - SHAHIH	-2.451	0.068	-2.558	**0.052**
UNSHAHIH - SHALOH	-3.640	**0.002**	-0.942	0.782
UNSHALOH - SHALOH	-2.822	**0.025**	0.054	0.999
UNSHALOH - UNSHAHIH	0.817	0.846	0.996	0.751
Daily minimum humidity				
SHALOH - SHAHIH	3.863	**<0.001**	3.962	**<0.001**
UNSHAHIH - SHAHIH	-2.594	**0.047**	-4.543	**<0.001**
UNSHALOH - SHAHIH	-4.853	**<0.001**	-4.385	**<0.001**
UNSHAHIH - SHALOH	-6.457	**<0.001**	-8.505	**<0.001**
UNSHALOH - SHALOH	-8.716	**<0.001**	-8.347	**<0.001**
UNSHALOH - UNSHAHIH	-2.259	0.108	0.157	0.999

3.5 Discussion

Trees form a significant part of vegetative structure in both agricultural and biodiversity conservation areas. Trees can impact herbivore distributions and behaviour, as well as the microclimate conditions. Whether the interaction between trees and herbivores is an important driver of environmental parasite density has remained relatively unexplored, but this interaction may have

potentially large implications for the spatial patterns of infection risk in some ecosystems where trees are heterogeneously distributed, such as many savannas. In this study we explored the effect of tree canopies and herbivore grazing on L3 density in pasture and establish a mechanism of how shade from tree canopy and variable grass heights lead to different densities of L3 in pastures. To achieve our goal, we used both observational and experimental approaches to study how L3 density varied under tree canopy (or shade) versus outside tree canopy (or unshaded areas), and across different grazing intensities.

Our observational field survey showed a positive effect of dung density on L3s in pasture, but this effect was much stronger in canopy areas than in non-canopy areas (Table 3-1). Similarly, from our experimental results, we found higher L3 parasites in shaded areas compared to unshaded areas, suggesting tree canopy shade creates better microclimate conditions for environmental parasites compared to non-canopy areas (Table 3-2). Lastly, we found our treatments had effects on microclimate conditions, where the shaded area had lower daily or maximum temperatures values and higher daily or minimum humidity values compared to unshaded areas (Tables 3-4 & 3-5). Grass height also appears to drive microclimate conditions in a manner comparable to tree canopy effects; for instance we found no difference in daily and maximum temperature values between unshaded high grass height and shaded low grass height.

Our results show tree canopy shade increased density of L3 by two to three times compared to non-canopy areas. Similar effects of trees on nematode abundance were previously reported from tropical savanna areas in a study by Coleman et al., (1991) which tested whether soil nematodes (nematode groups of bacterial- and fungal-feeders) were more abundant under tree canopies than outside tree canopies. They found that bacterivorous nematode abundance was significantly higher under tree canopy of *V. tortillis* and *Adensonia digitata* than outside the tree canopy. The observed difference in abundance of soil nematode was attributed to the ability of trees to retain soil moisture and attract animals in ways that lead to higher microbial biomass (mainly bacteria) due to leaf shedding and droppings from different animals compared to a site far from tree. This localized enrichment effect from shade complements earlier findings that emphasize the broader influence of microclimatic conditions on the persistence

and transmission of environmental parasites. For example, Wang et al., (2018) reported long grass (10-25 cm) under artificial shade helped dung to retain moisture and thus increased larvae migration onto pasture, consequently increasing L3 abundance in pasture, compared to short grass. Finally, an experimental study found lower L3 density on pasture in areas exposed to direct sunshine compared to areas with shade (Gasparina et al., 2021).

Our results also demonstrate that high grass height creates better microclimate conditions for environmental parasites compared to short grass. For instance, our experiment found the Unshaded High Grass Height treatment (UNSHAHIH) had significantly higher pasture larvae density than Unshaded Low Grass Height treatment (UNSHALOH) on Day 14 (dry condition). This finding suggests different herbivore grazing intensities on pasture resulting in different grass heights, could cause different environmental parasite densities due to shading effect from the grass. The role of heavy grazing in changing microclimate conditions has also been reported from humid montane areas of southern Ecuador, where an experimental study reported a significant difference of albedo (fraction of sunlight reflection) between areas that were heavily grazed versus ungrazed control plots (Montenegro-Díaz et al., 2022). Furthermore, high grass height (i.e., 20 cm) has been previously reported to offer better microclimate condition for L3s in pasture, leading to higher density compared to short grasses (i.e., 10 cm) (Gasparina et al., 2021).

We found that shade from the tree canopy and grasses change microclimate conditions, as measured by variation of temperature and relative humidity among our treatments. Shading and tall grass treatments decreased temperature and increased humidity, hence providing better conditions for the emergence and survival of eggs and larvae. For example, both Shaded Low Grass Height (SHALOH) and Shaded High Grass Height (SHAHIH) had lower temperature than Unshaded High Grass Height (UNSHAHIH) and Unshaded Low Grass Height (UNSHALOH). Similar findings on trees and grass microclimate effects have been found by Fernández et al., (2025), who reported lower temperature and higher humidity under tree canopies compared to nearby areas. The authors also detected distance dependent effects of tree canopy and trunk on temperature and humidity. Moreover, other studies reported tree canopies are more effective in lowering air

temperature compared to grass (Fernández et al., 2025; Shashua-Bar et al., 2011; Speak et al., 2020; Wang et al., 2016). This was also observed in our study, where we found Shaded High Grass Height (SHAHIH) had lower temperature than Unshaded High Grass Height (UNSHAHIH). Furthermore, Speak et al., (2020) reported that a combination of tree shade and grass offered the lowest levels of thermal stress. In our study we found Shaded High Grass Height (SHAHIH) had slightly lower temperature than Shaded Low Grass Height (SHALOH), although statistically it was not significant. Furthermore, we observed similar values of daily mean humidity in Shaded High Grass Height (SHAHIH) and Shaded Low Grass Height (SHALOH) on Day 14, that were relatively higher than unshaded treatments. Yet, on Day 28, Shaded High Grass Height (SHAHIH) had higher daily mean humidity compared to any other treatment; this could be due to extra blockage effects of air circulation offered by tall grass in addition to that of tree canopy under shade condition (Bhardwaj et al., 2024). Our experimental design for the tree canopy effect deployed the simulated shade treatment at 1.5 m high for logistical convenience, but adult savanna tree canopies often start around 2 m, which is the maximal browsing height for many small to medium sized vertebrate browsers (Du Toit, 1990). Thus, our experimental setup may have slightly decreased moisture and air circulation relative to natural conditions. While our effect sizes related to shade may have consequently been larger than those expected in natural settings, the observed microclimate pattern with temperature and humidity aligns with findings reported by other researchers, as discussed above and in the next paragraph below.

The capacity of trees and vegetation cover in general to modify microclimate conditions have been previously reported (Keppel et al., 2017; Taha & Rosenfeld, 1989). For example, a study by Breshears et al., (1998) reported that woody canopy modifies soil microclimate (lowering soil temperature) under tree canopies compared to inter-canopy patches. The role of lower temperature and high humidity on survival of nematodes have been previously reported by Kung et al., (1991) under laboratory conditions, where he found higher survival of infective juvenile stages of nematodes at 5 – 25 ^{o}C compared to 35 ^{o}C. While survival infective juvenile stages of nematodes decreased from higher humidity (100%) to low humidity (25%). Moreover, other studies have also reported the role of temperature and humidity on environmental parasite development, survival,

activity such as L3s migration from dung to pasture and consequently L3 pasture abundance (DeCesare et al., 2024; Heckler & Borges, 2016; Stromberg, 1997; Trzebny et al., 2024; Wang et al., 2018). Thus, overall, our results suggest that shade from tree canopies and grasses modify microclimate conditions by lowering temperature, particularly maximum temperature, and increasing humidity, providing more conducive microclimate conditions that support development, activity (L3 migration from dung to pasture) and survival of gastrointestinal nematodes. However, the observed effect of our experiment on pasture larvae between shaded area and non-shaded area should be carefully interpreted when compared to other conditions, as our study used cultured dung piles (i.e. kept moist for 5 days in the laboratory) instead of placing fresh dung piles. This approach was necessary to ensure treatment effects were detectable even under dry weather conditions but prevented us from studying the impact of shade from vegetation on early development of eggs to larvae. If anything, we would expect the effect sizes associated with experimental treatment to have been larger if using fresh dung because hot and dry microclimate conditions (i.e. those in unshaded and/or short grass) would have reduced survival of eggs and early-stage larvae compared to shaded/tall grass treatments. Hence, the observed effects in our experiment could be mainly associated with how tree and grass shade impact latter stages of egg and larvae survival, and larvae migration from dung piles onto pasture.

Furthermore, our study also suggests L3 density in pasture is mediated by season (dry or wet condition). We found relatively higher density of environmental parasite from pasture during wet conditions (Day 28) compared to dry conditions (Day 14). This was in agreement with our work in chapter 1, where we found a similar trend, although the time period was reversed; day 14 being more humid than day 28. Previous work reported a higher density of soil nematodes during the wet season compared to the dry season, which could be due to desiccation of free-living stages of nematodes (eggs and larvae) during dry season or by an increase of organic matter (that increases food availability for nematodes) in wet season (Steinberger et al., 1988).

Contrary to our expectation from the design of our observational study, we found higher dung density in non-canopy areas compared to areas under tree canopies

(Appendix B:S5), which could be attributed to different levels of use of herbivore between the two areas. This could imply that the observed difference in L3 between canopy and non-canopy areas from our observational study with higher L3 densities found under canopy might have been driven mainly by the cumulative long-time effects of microclimatic conditions under canopies that improve survival of parasite eggs or larvae, relative to non-canopy areas. In addition to their microclimate effects, savanna trees act as focal points of activity and use by various animal taxa, including birds and mammals (Dean et al., 1999; Silva et al., 2020). Shade from trees attracts large-bodied mammalian herbivores trying to escape the heat of the day (de Sousa et al., 2021; Dean et al., 1999; Giro et al., 2019; McNaughton, 1983) and these animals use trees as sites for resting and rumination (Carnevalli et al., 2019; de Sousa et al., 2021). Herbivores also rub and scratch themselves against trees to help deter or remove ectoparasites (Agudelo et al., 2013; Blaise et al., 2023; Buss, 1961; Carnevalli et al., 2019; Moncada et al., 2020). Furthermore, grasses under tree canopies have also been found to be more nutritious and stay greener longer than nearby open grasslands, providing an additional attractant to large herbivores (Dean et al., 1999; Treydte et al., 2007). Grass quality is improved because trees uplift water from deep soil layers through roots and make the water more available in the upper soil surface (Ludwig et al., 2003). Further, trees create fertilized islands of soil beneath them by (1) nitrogen fixation through roots, mainly from leguminous family such as *Acacia* and, (2) falling litter and trapped dust, as well as bird nests and faecal material from animals in the canopy that decompose, providing nutrients (Dean et al., 1999; Rhoades, 1996). Because of the relatively high use of areas beneath savanna trees by large herbivores relative to nearby open grasslands (Dean et al., 1999; Treydte et al., 2010), dung can accumulate in these areas at high density over relatively short periods of time (Carnevalli et al., 2019; McNaughton, 1983; Riesch et al., 2025; Treydte et al., 2010). Due to improved microclimate, high animal densities, and high dung input under tree canopies mean that shade-casting trees could act as important hotspots of environmental parasites transmission in savanna landscapes. In this study, we found higher dung densities in non-canopy areas compared to canopy areas, which might be explained by the fact that the non-canopy plots were located adjacent to canopy edges. We would expect lower dung densities (and reduced herbivore effects and activities) if samples were taken farther away from the canopy. Other savanna features such as water points

have previously been reported to regulate distribution of herbivores and hence aggregate dung deposits and microclimate condition of the parasite, hence increase infection risk (Titcomb et al., 2021). However other studies show trees are far more important key drivers of herbivore behaviour and distribution than water points (de Sousa et al., 2021; Deniz et al., 2020). Thus, trees could have a significant implication in transmission of faecal deposited parasites compared to water points.

Our results have larger implications for the ecosystem management of the savanna areas, where there are many of the world's ruminant livestock and a high diversity of wild ungulates (Riginos et al., 2009; Sankaran et al., 2005). Generally, in tropical areas, savanna trees have been promoted to enhance livestock production by providing relief from heat stress, and a means of contributing to mitigation of greenhouse gas emissions (Giro et al., 2019; Roman-Ponce et al., 1977). Yet savannas have also experienced a significant change of woody vegetation through woody encroachment (Archer et al., 2017; Kimaro et al., 2019), implying microclimate also change across Savanna ecosystems where woody encroachment is occurring (He et al., 2010; Thomas et al., 2018; Wang et al., 2021), consequently affect development and survival of environmental parasites in savanna ecosystems. Therefore, understanding microclimate effects of vegetation (trees) on environmental parasites has wider implications in economic, health and biodiversity conservation purposes. Thus, our study suggests savanna trees, and herbivore grazing, interact across seasons in ways that modify the development, survival and availability of environmental parasites, helping to generate heterogeneity in infection risk across ecosystems.

4. Infection dynamics in livestock amidst wildebeest migration in the Serengeti drylands

4.1 Abstract

Globally, the extent to which different parasite species are infectious to various hosts remains an important topic in epidemiology particularly for emerging infectious diseases. Furthermore, in many species-rich tropical settings, we poorly understand the degree to which different host species share parasites with one another. Thus, the overall effect of wildlife on livestock health remains uncertain. Here, we examine the spatiotemporal changes of gastrointestinal nematode infections in three livestock species—goats, sheep, and cattle—subjected to different management practices at the eastern and western boundaries of the Serengeti ecosystem, in relation to wildebeest migration. In each region, livestock from two villages were sampled, one of which was exposed to wildebeest during the annual migration, the other remaining unexposed. Livestock were sampled at two time points – before and after/during the migration period. We used McMaster technique and both PCR and sanger sequencing of the ITS2 locus to capture livestock infection intensity and worm species composition amid wildebeest migration in two regions of the Serengeti ecosystem, Tanzania. Our study found the following: (1) Opposite effects of region on worm communities in goats and cattle, where in goats the wet region (West) had higher faecal egg count than the dry region (East), while in cattle the dry region (East) had higher faecal egg count than wet region (West). (2) Region also interacted with migration status and wildebeest exposure in goat, where overall, we found higher faecal egg counts in post wildebeest migration in wet region (West) compared to post wildebeest migration in dry region (East), but the effects seem to be mediated by exposure to wildebeest. (3) We observed lower faecal egg count in area exposed to wildebeest migration compared to area not exposed to wildebeest migration. (4) When we analysed worm strongyle species diversity, we found differences between hosts and timepoints. Goats had lower diversity at the post wildebeest migration timepoint compared to pre wildebeest migration timepoint as well as in areas grazed by the wildebeest compared to areas not grazed by the wildebeest. Yet, in areas grazed

by wildebeest, we also observed an increase of worm diversity post wildebeest migration compared to areas not grazed by wildebeest. For cattle we also found lower worm diversity during post wildebeest migration compared to pre wildebeest migration and similarly we found significant lower diversity in areas grazed by wildebeest compared to areas not grazed by wildebeest. Our results show a mixture of benefits and harms on livestock worm species composition and infection intensity amid wildebeest migration, suggesting outcome of interaction between wild and domestic ungulate in our ecosystem is context dependant, and could be underlaid by temporal, geographical, and cultural factors.

4.2 Introduction

African savannas are home to millions of individuals from diverse wild and domestic ungulate species (Du Toit & Cumming, 1999; Gifford-Gonzalez, 1998; Pranzini et al., 2024) that form coupled human and natural ecosystems. Increasing anthropogenic activities have led to changes of ecological processes such as wildlife migration and shrinking of ecosystems, resulting in more interactions between humans, livestock and wildlife within a more limited space (Otuoma et al., 2009; Pozo et al., 2021; Veldhuis et al., 2019). The increased human, livestock and wildlife interactions escalate conflicts between conservation interests and livestock production (Pozo et al., 2021; Ravenelle & Nyhus, 2017). For example, wildlife-livestock interactions take the form of livestock de-predation by wild-carnivores, crop raiding by wild-herbivores, retaliatory killing of wildlife by humans, illegal grazing of livestock inside of protected areas and illegal hunting of wildlife for meat and disease transmission between wildlife and domesticated animals (Angela et al., 2014; Felix et al., 2022; Kissui et al., 2019; Matungwa et al., 2024; Musika et al., 2021; Nyahongo et al., 2005; Pozo et al., 2021). While most research on conflict between wild and domesticated ungulates focuses on the negative consequences of competition for food and water (Kimuyu et al., 2017; Pozo et al., 2021) and diseases (Benka, 2012; Cleaveland et al., 2005; Gortázar et al., 2007; Muhanga, 2025), in some cases these interactions can be beneficial to either wildlife or humans (Odadi et al., 2011).

In many landscapes, domesticated and wild ungulates have common grazing areas and water points (Fynn et al., 2016; Kimuyu et al., 2017), the use of which causes frequent overlap in time and/or space causing the potential for resource competition and disease transmission (Gifford-Gonzalez, 1998; Homewood & Rodgers, 1991). Strong interactions between domesticated and wild ungulates cause a variety of conflicts among stakeholders due to competing interests (Homewood & Rodgers, 1991; Veldhuis et al., 2019). Mitigation efforts can be limited due to poor understanding of the ecological mechanisms driving spatial overlap between domesticated and wild ungulates, and hence conflicts might amplify (Miller et al., 2013; Pozo et al., 2021). For example, despite evidence of resource partitioning and facilitation between livestock and wildlife herbivores in African savannas (Augustine et al., 2011; Bell, 1971; Kimuyu et al., 2017), it is widely assumed the net effect of resource sharing between wildlife and livestock is negative due to competition (Gordon, 2018). Furthermore, understanding the effects of this overlap is difficult because of movements of both livestock and wildlife (Ekwem et al., 2021, 2023; Tyrrell et al., 2017). Therefore, there is an urgent need to understand how domesticated and wild ungulates interactions vary in space and time, and how they shape productivity and fitness components of individual animals (Gordon, 2018; Gortázar et al., 2007; Miller et al., 2013; Pozo et al., 2021).

In many regions of the world, wildlife harbor a variety of parasites (bacteria, viruses and macroparasites) that can infect livestock upon contact, hence facilitating the transmission of infectious diseases across species boundaries (Barone et al., 2020). For instance, many wild bovines such as wild bison (*Bison bison*) and African buffalo (*Syncerus caffer*) continue to introduce *Brucella spp* that infect cattle and cause brucellosis (Cossu et al., 2025; Dohna et al., 2014). Wildlife population abundance and the level of contact between wildlife and livestock are key factors that influence the diversity of parasites shared between them, as well as the prevalence and intensity of infectious diseases in livestock (Caron et al., 2013; Cleaveland, Kusiluka, et al., 2001). For generalist parasites such as Gastrointestinal Nematodes (GIN), successful transmission between host species depends on the availability of susceptible hosts relative to the survival of free-

living infectious stages of the parasite (Mijele et al., 2016; Morgan et al., 2004a). In arid ecosystems, the availability of the free-living infectious stages of GIN parasites increases with rainfall and high humidity conditions (Fynn et al., 2016; Morgan et al., 2004b); thus, weather conditions cause fluctuations of parasite abundance as well as host abundances.

Globally, the extent to which different parasite species are infectious to various hosts remains an important topic in epidemiology particularly for emerging infectious diseases. Previous studies have reported that approximately 75% of emerging pathogens are also zoonotic pathogens (Taylor et al., 2001). Furthermore, around 61% of all human pathogens are capable of infecting animals, and 44% are known to infect wildlife specifically (Cleaveland et al., 2005; Cleaveland, Laurenson, et al., 2001; Taylor et al., 2001). Lastly, 54% of known livestock pathogens are also known to infect wildlife (Cleaveland, Laurenson, et al., 2001). These cross-species transmissions between wildlife and livestock, are arguably important in reducing development of anthelmintic resistance in parasites due to their ability of offering refugia (Brown et al., 2022). Therefore, livestock using shared grazing areas with wildlife may either benefit or be harmed from such interactions. These dynamics suggest that wildlife migration not only may alter the abundance of infectious larvae in pastures, but also development of worm's drug resistance in livestock, thereby influencing the infection burden in livestock across different locations along migration routes (Mijele et al., 2016; Walker & Morgan, 2014).

As established in my first two chapters, the net impact of migratory wildlife such as wildebeest on infection risk of resident hosts—whether beneficial or harmful—depends on factors that affect the availability of parasites on pasture, such as migration intensity, duration, and prevailing weather conditions. Furthermore, in many species-rich tropical settings, we poorly understand the degree to which different host species share parasites with one another. Thus, the overall effect of wildlife migration on livestock health remains uncertain. Here, we examine spatiotemporal change of GIN infection of three livestock species – goats, sheep and cattle – that have been subjected to different management practices at the

boundary of the Serengeti Ecosystem. I had the following objectives, for each livestock species: (1) to compare the intensity of infection via faecal egg counts of gastrointestinal strongyle nematodes (GIN) before and after the wildebeest migration in two regions of the Serengeti and (2) to compare changes in the composition, richness and diversity of GIN species across two regions and time periods.

Wildebeest migration and livestock movement in the Serengeti Ecosystem, East Africa, is primarily driven by the need to search for green pasture, which is determined by rainfall (Boone et al., 2006; Fynn et al., 2016; Holdo et al., 2009; Leweri et al., 2021; Morgan et al., 2004b). Indeed the scope for interactions between wildebeest and livestock in the Serengeti is high: over 25% of the geographical range of the 1.2 million strong population of migratory wildebeest in Serengeti overlaps with areas grazed by livestock (T.A. Morrison, personal communication), and aerial census of livestock suggest that over 2 million cattle, sheep and goats live within 20km of the boundary of the core protected areas (TAWIRI, 2016). In shared grazing areas within the Serengeti Ecosystem (Ekwem et al., 2023), wildlife and livestock spread parasite eggs via dung deposition and create pools of infectious larvae which may be shared among hosts (Mijele et al., 2016; Morgan et al., 2004b). Yet, due to the hyperabundant and highly mobile behaviour of wildebeest there is a strong grazing intensity which may remove infectious larvae (McNaughton, 1983, 1985; Mijele et al., 2016; Sinclair, 1975, 1985), and a voluminous dung deposition which may reduce the effect of anthelmintic resistance by introducing naïve parasites in shared grazing areas (Brown et al., 2022). To my knowledge, molecular characterisation of the GIN community in Serengeti ungulates has not been performed, although several studies have used morphological identification of adults from various wild ruminant species to characterise community composition (Mijele et al., 2016; Sinclair, 1977).

Given results from Chapters 2 and 3, where L3 densities were higher on pasture under wet conditions than dry conditions, we hypothesized that: (1) the wetter region (West) provides more favourable environmental conditions for the development and survival of L3 (*c.f.* Chapters 2 & 3); as a result, livestock in this

region are likely to ingest a higher abundance of L3 from the pasture, leading to increased infection levels in the wetter region (West) compared to those in the drier region (East). We therefore expected all livestock to have comparatively higher strongyle FEC in the West than in the East, regardless of timepoint, host species or migration exposure (Climate Hypothesis = H1). (2) Given this climatic effect, we hypothesised that wetter areas would be more strongly affected by wildebeest due to wildebeest having relatively large capacity for modifying grass height through grazing (*c.f.* Chapter 2), in wet areas (West) compared to dry areas (East). Based on experimental results from Chapter 3, I predicted higher concentrations of L3 parasites in wet areas following this grazing because of better conditions for egg and larvae survival and emergence (Region x Migration Status Hypothesis = H2). (3) Further, we hypothesised that wildebeest also induce changes in livestock infection intensity and/or parasite species richness and diversity via transport and/or trophic effects (Migrant Effects Hypothesis= H3). Several outcomes from this hypothesis are possible. First, migrating wildebeest may transport new infectious larvae to livestock areas and thereby increase infection intensity (*c.f.* Chapter 2), and diversity of parasites in livestock. Secondly, wildebeest may impose strong trophic effects through grazing and alter the microclimatic conditions in ways that reduce survival and development of parasites (*c.f.* Chapters 2 & 3) and therefore decrease infection intensity in livestock. Lastly, wildebeest may directly remove infectious parasites on pasture via the "hoovering effect" (*c.f.* Chapter 2) and thereby decrease infection intensity in livestock. To note, the two trophic effects above do not have clear predictions in terms of their potential direction or magnitude of impacts on parasite diversity, so were not considered in the analysis (4) Finally, we hypothesised that goats and sheep will have overall greater faecal egg counts than cattle (Host Species Hypothesis = H4), as established in previous work from other systems (Mahieu, 2013).

4.3 Materials and methods

4.3.1 Study area

The study was conducted in four villages adjacent to Serengeti National Park (Fig. 4-1). Two villages, Arash and Piyaya, were on the Eastern side of the ecosystem in

the Ngorongoro District, and two villages, Robanda and Mugumu, were on the Western side in Serengeti District (Fig. 4-1). Hereafter we refer to the East and West sides as “Region”. The Eastern region of the Serengeti is characterized by lower rainfall and shorter grasses (Fig. 4-2), while the Western region of the Serengeti is characterized by higher rainfall and taller grasses (Anderson & Talbot, 1965; Reed et al., 2009). While communities in both the Eastern and Western sides are involved in livestock keeping (Ekwem et al., 2023), the ethnic background, and culture, differ between areas and shape the nature of livestock practices. The Eastern side is mainly occupied by the Maasai tribe that practice semi nomadic pastoralism, while the Western side is mainly occupied by the Bantu tribes such as Kuria, Ikoma, Nata, that practice agropastoralism (Christiansson & Tobisson, 1989; Ekwem et al., 2023).

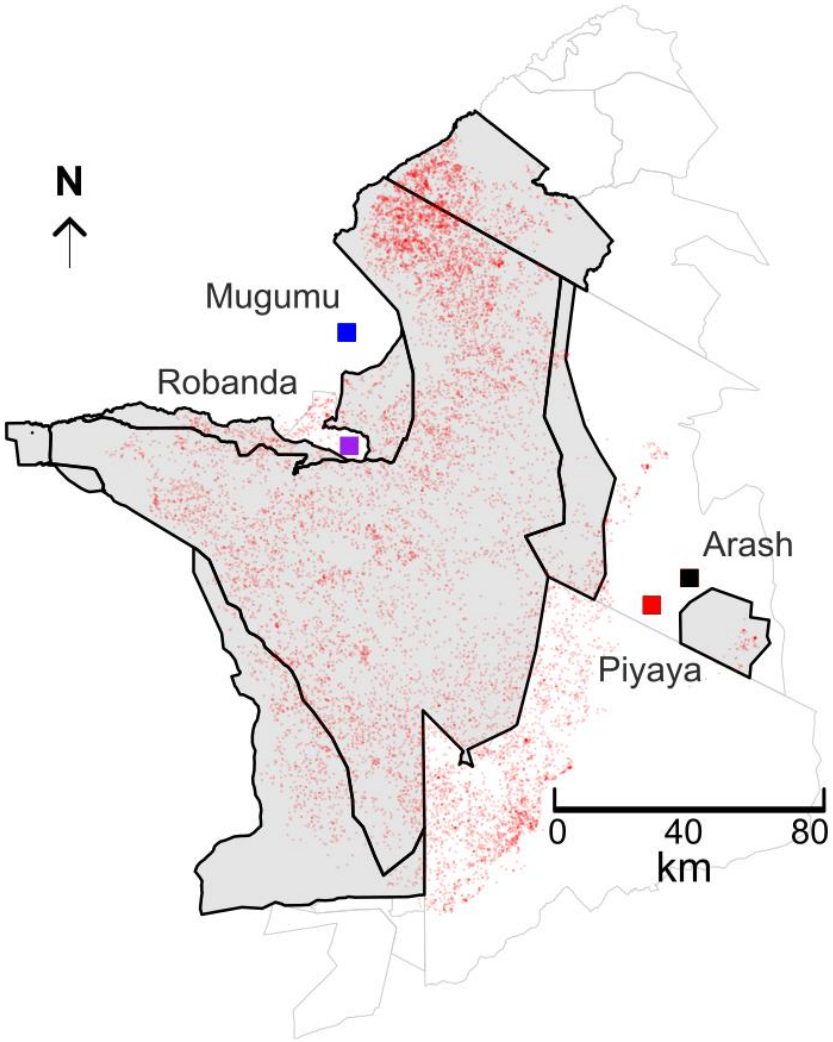

Figure 4 - 1: Exposure to wildebeest in different village amid wildebeest migration in Serengeti ecosystem.

Wildebeest migration in Serengeti ecosystem in East Africa (red points represent GPS trajectory of collared wildebeest from 2021 to 2022). Square boxes represent villages involved in the study, where Eastern region villages are presented in a red square box (Piyaya - exposed to wildebeest migration) and a black square box (Arash - not exposed to wildebeest migration), while Western Region villages are presented in a purple square box (Robanda - exposed to wildebeest migration) and a blue square box (Mugumu - not exposed to wildebeest migration). Thick black line represents boundary of the core protected areas (grey shaded areas) where there are no human settlements, thin grey line represents boundary of the protected area that allows human settlements.

4.3.2 Study design

Our study captured livestock infection intensity of goats, sheep, and cattle before and after wildebeest migration through a before-after-control-impact design (Fig. 4-2). One village from each region was exposed to wildebeest (Piyaya and Robanda), while one village from each region acted as a control just outside of the range of migratory wildebeest (Arash and Mugumu). Each village was sampled on two occasions; before, and after, the wildebeest migrated through the area (Fig. 4-2). I used the term "pre-migration" to refer to initial round of samples collected before wildebeest migrated through the region, and the term "post-wildebeest" migration to refer to the second round of samples collected after wildebeest migrated through the region. The term applied to both villages within the region, regardless of wildebeest exposure. We relied on long term monitoring by the Serengeti Biodiversity Programme to track the wildebeest movements using GPS collars (n=33), enabling us to approximately time the sampling of livestock before versus after the migration, and to understand which areas were exposed to wildebeest and which were not (Fig. 4-1).

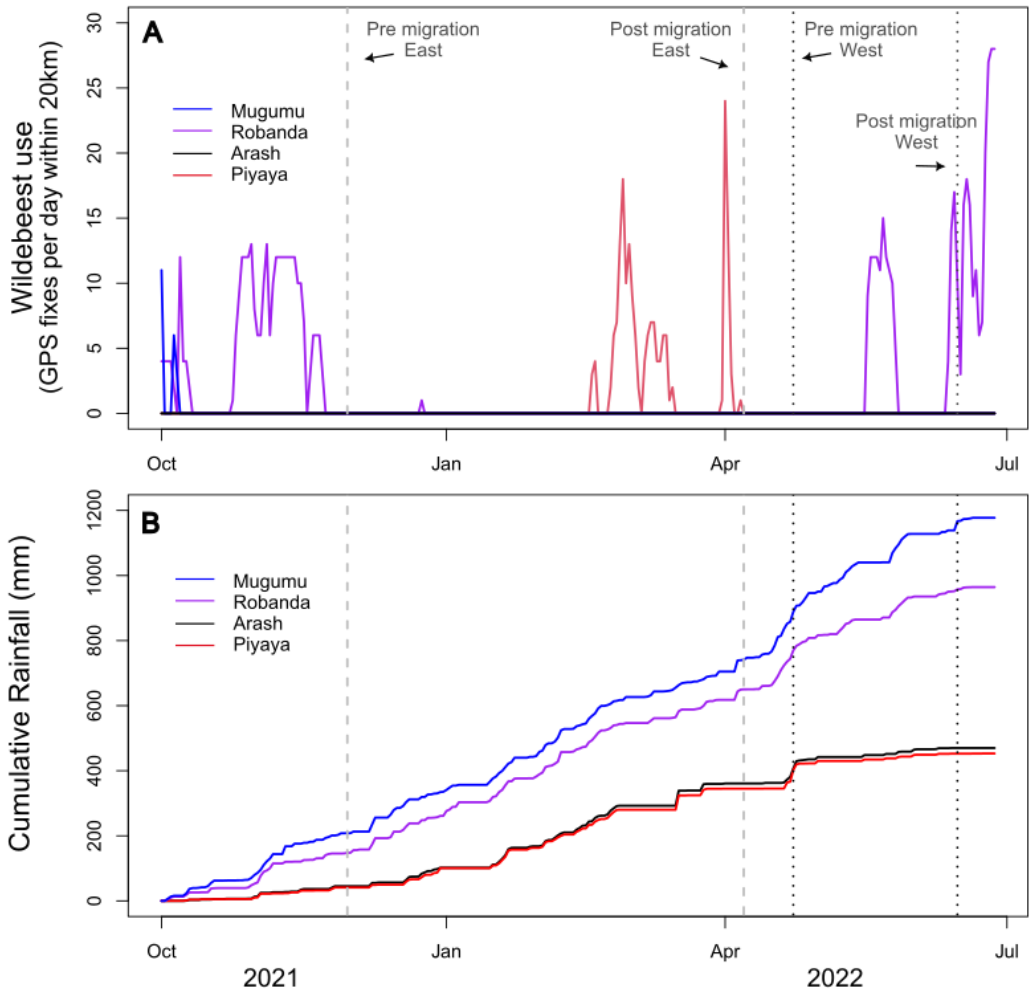

Figure 4 - 2: Survey design of livestock sampling based on wildebeest migration and geographic differences of the regions in Serengeti National Park.

(2: A) Temporal trends in GPS collared wildebeest within 20km of the four sampling villages relative to the before and after surveys of livestock species infection in the East and West regions of Serengeti ecosystem. 20km was selected for illustrative purposes to reflect usage by wildebeest herds, the spatial extent of which are dynamic and can span tens of kilometres. Dashed lines indicate pre and post wildebeest migration sampling period in Eastern region, while dotted lines indicate pre and post wildebeest migration sampling period in Western region. Wildebeest migration in Eastern region (red = Piyaya and black = Arash) and Western region (blue = Mugumu and purple = Robanda) between October 2021 and July 2022. (2: B) Temporal trends in cumulative rainfall in Eastern region (red = Piyaya and black = Arash) and Western region (blue = Mugumu and purple = Robanda) between October 2021 and July 2022.

Following consent to participate in the study, five households in each village were sampled before the wildebeest migration. In each household, we collected faecal samples from six goats, six sheep and six cattle of any age/sex to make the total number of samples for each livestock species to be 30 in each village on each sampling occasion. The same households were revisited after the wildebeest migration, although not necessarily the same individual animals were sampled. Dung was collected either directly from the rectum of the animal, or after watching the animal defecate. Effort was made to avoid any contamination from nearby dung piles. Furthermore, questionnaires were completed by each household, to collect information on livestock condition, grazing areas, and anti-parasitic treatments. The livestock samples and related data were collected prior to, and post wildebeest migration in each region i.e., November 2021 and March 2022 for East Region, and April 2022 and June 2022 for West region. All collected faecal samples were stored at 3-8 ^{o}C and moved to the laboratory within five days from collection date. Once arrived at the laboratory, all the faecal samples (from 720 individuals) were given a laboratory ID and strongyle eggs were counted using a 1:50 sensitivity modified McMaster method (Ezenwa, 2003).

Thereafter, faeces from animals from the same household were pooled together and mixed per host species and cultured for ten days in the 'culture cupboard' under room conditions (shelf covered by loose cloth to prevent direct light and watered after two days). After culture, the 3rd stage larvae from each sample were Baermannised, picked and placed on Whatman Flinders Technology Associates, i.e. "FTA", cards (Table 4-1), and exported to UK for molecular speciation.

Table 4 - 1: Number of L3 livestock samples collected from villages in Serengeti ecosystem

Summary of number of livestock individuals involved in coproculture per host species in each village and the associated number of L3s that were detected during speciation of pre and post migration samples, where BO stands for cattle, CP stands for goats, and OV stands for sheep.

Village	Host species	Total No. of host Individuals		No. of L3s identified to species/genus		Region	Wildebeest exposure
		Pre	Post	Pre	Post		
Arash	BO	7	4	0	0	East	Control
Arash	CP	11	8	41	350	East	Control
Arash	OV	14	10	242	344	East	Control
Sub-total	All host spp	32	22	283	694		
Piyaya	BO	6	6	59	0	East	Wildebeest
Piyaya	CP	14	12	183	394	East	Wildebeest
Piyaya	OV	18	18	91	539	East	Wildebeest
Sub-total	All host spp	38	36	333	933		
Mugumu	BO	5	5	59	53	West	Control
Mugumu	CP	18	17	274	615	West	Control
Mugumu	OV	16	20	222	222	West	Control
Sub-total	All host spp	39	42	555	890		
Robanda	BO	5	5	70	81	West	Wildebeest
Robanda	CP	15	16	307	239	West	Wildebeest
Robanda	OV	16	16	216	409	West	Wildebeest
Sub-total	All host spp	36	37	593	729		

Faecal samples were coprocultured from 282 individuals of three host species (cattle, goats and sheep), and a total of 10,111 L3s were harvested and stored on FTA cards. The number of larvae identified to species/genus level from each village and region of the Serengeti ecosystem and stored in FTA cards are presented in Table 4-1.

4.3.3 DNA extraction of larvae from FTA cards

We extracted DNA from all larvae that were stored on FTA cards. A lysate master mix buffer was prepared inside the hood by mixing 3000 µl of Direct PCR lysis reagent (Cell) (Viagen, Biotech), 150 µl of 1M DTT (Invitrogen), and 30 µl of Proteinase K 100 mg/ml (Thermo Fisher Scientific) per 100 wells of a plate. Then 30 µl of master mix was dispensed in each well of a PCR plate. FTA disc samples (approximately 2 mm diameter) from dried GIN samples impregnated on FTA cards were punched out using a Harris Uni-Core (Pat No 7093508-2.00) and the paper discs transferred to individual wells of a PCR plate. The Harris Unicore Punch was cleaned between each punch by rinsing the tip with 100% absolute ethanol (AnalaR NORMAPUR) followed by DEPC water (Ambion) to minimize cross contamination of strongyles samples. Care was taken to make sure each disc sample was submerged in lysis buffer, then each PCR plate was vortexed for 5 min, and then left on bench for another 5 min before centrifugation at 2500 rpm for 1 min, and then run on PCR machine at 60 °C for 2 h then 85 °C for 45 min to denature the proteinase K. Then 1:4 dilution was prepared by transferring 4 µl of the crude lysate to 12 µl of DEPC water, and both plates were then stored at -80 °C.

4.3.4 Identification of worm species by PCR method

All goat and sheep larvae in FTA cards were analysed by PCR of the ITS-2 locus, with exception of a few worms which were also sequenced following identification using generic strongyle primers, but without confirmation of species by PCR. For cattle, larvae from three bomas were speciated through PCR, and representative samples from all remaining bomas were speciated through Sanger sequencing. We adopted and modified a multiplex PCR method by Bisset et al., (2014). All PCRs were performed in a Mastercycler thermal cycler using a 12.5 µl reaction volume containing 1 µl of the 1:4 diluted lysate, 0.06 µl GoTaq G2 Flexi polymerase 5 U/µl (Promega), 2.5 µl 5X GoTaq G2 Flexi buffer (green), 1.25 µl 25 mM MgCl2, 0.25 µl of dNTPs (each 10 mM) (Promega cooperation), 1.5 pmol of each 10 uM primer (both ITS2GF and ITS2GR primers), combined with either of the following reaction sets: cattle samples targeted *Haemonchus spp.*, *Cooperia oncophora* and *Trichostrongylus axei* having 5 pmol HacoFd3, 3 pmol CoonRv1, and 5 pmol TraxFd1

primers (Bisset et al., 2014). While for small ruminant (goat and sheep) the reaction targeted *Haemonchus spp.*, *Cooperia curticei* and *T. axei* having 5 pmol HacoFd3, 7 pmol CocuFd3 and 5 pmol TraxFd1 (Table 4-2). All primers were obtained from Eurofins Genomics. A touchdown PCR protocol was used as follows: 94 °C for 2 min, followed by 12 cycles of 94 °C for 15 s, 60 °C (−0.5 °C/cycle) for 15 s and 72 °C for 30 s, followed by 25 cycles of 94 °C for 15 s, 54 °C for 15 s and 72 °C for 30 s, with a final elongation step of 72 °C for 7 min. PCR products were visualized using SYBR® Safe (Life Technologies) in a 2.5% agarose gel (NBS Biologicals Ltd).

Table 4 - 2: Primers used for speciation of nematode larvae from cattle, goat and sheep, based on method provided by Bisset et al., (2014).

Nematode species	Primer name	Primer sequence	T_a (^{0}C)	Product size (bp)
Haemonchus spp.	HacoFd3	CATGTATGGCGACGATGTTCT	55	90 bp
Cooperia oncophora	CoonRv1	CTATAACGGGATTTGTCAAAACAGA	53	173 bp
Trichostrongylus axei	TraxFd1	CAAATATTGTGATAATTCCCATTTTAGTTT	53	236 bp
Cooperia curticei	CocuFd3	TAATGGCATTTGTCTACATTGGTTC	53	252 bp
Strongyle	ITS2GF	CACGAATTGCAGACGCTTAG	54	370–398 bp
Strongyle	ITS2GR	GCTAAATGATATGCTTAAGTTCAGC	54	370–398 bp

4.3.5 Speciation of worm species by Sanger sequencing

For cattle larvae samples, we sequenced the ITS-2 locus of 16 worms per boma from the West region, making a PCR plate of 80 positive samples from five bomas per wildebeest migration period per village. Thus, I had a total of four plates from the two villages of the West i.e., one plate per wildebeest migration season per village. I also sequenced two plates worth (one plate per host species) of unknown worm species (positive only with generic strongyle primers) from goat and sheep

samples. For each of these unknown larvae from goat and sheep, worms were selected at random across and within samples. All these samples were identified and marked in a paperwork prior to laboratory work. A standard protocol of Phusion™ High Fidelity DNA polymerases, 2U/µL, (F534S Thermo Scientific™) as specified in the reagent kit was adopted. All PCRs were performed in a Mastercycler thermal cycler using a 50 µl reaction volume containing 0.5 µl of Phusion polymerase 2 U/µl (Thermo scientific), 10 µl of × GC buffer, 1 µl of dNTPs 10 mM each, 2.5 pmol of each primer (both forward and reverse generic primers). We then added 2.5 µl of 1:20 DNA lysate in each well with PCR master mix, with exception of two wells left as negative controls. Phusion PCR was run using protocol as follows: 98 °C for 30 s, followed by 35 cycles of 99 °C for 7 s, 61 °C for 15 s and 72 °C for 15 s, followed by final elongation step of 72 °C for 7 min. PCR products were visualized using SYBR® Safe (Life Technologies) in a 2% agarose gel. Samples considered to be positive with strongyles were sent for sequencing at Genewiz.

4.3.6 Bioinformatic analysis of sanger sequencing results

Fasta files quality from Sanger sequencing were checked by inspecting fluorescent signal peaks for each nitrogenous base from a chromatogram. We retained sequences with clear non-overlapping peaks, no heterozygous peaks and total read length ≥40 base pairs after quality trimming. Following this, sequences were then analysed through the NCBI data base (version 2.16 and 2.17, available at BLAST: Basic Local Alignment Search Tool) using web blast to identify worm species. Briefly, sequences were uploaded into the NCBI BLASTN tool, and the Nematoda (taxid:6231) used to search the *nematoda* dataset. Results were manually examined; the hit with the highest percentage identity and lowest expected value (e-value) in the database was accepted as the correct species, providing other conditions were also met. These included the need for the length of the hit to cover the majority of the sequence (accession length), and cross check the sequence ID details. Species or genus was assigned based on their highest taxonomic resolution by using percentage identity scores (the highest percentage score for identified species/genus ranged from 78.8% to 100%). If two species had the same percentage identity score, I used accession length and expected value i.e., picked the identity of the one with the highest accession length and lowest e-value. Where there was

more than one species returned, without a clear species identity based on unmatched percentage score and accession length, results were reported at genus level only.

All identified worm species from PCR method and Sequencing method were combined into one data master file, prior to statistical analysis. Sanger sequencing allowed us to identify samples to genus or species level, while through PCR method samples were identified to genus, species, or as strongyle.

4.3.7 Statistical analysis

For faecal egg counts (FEC), we fitted a generalized linear mixed model (GLMM) using a negative binomial distribution for the response variable; *Strongyle* counts. Predictor variables included '*Migration Status*', a binary variable indicating whether the sample was collected before or after the migration period of the region; '*Age*', the host animals age, a categorical variable indicating whether the host animal was an adult, or juvenile; '*Drug Treatment'*, indicating the host species had been treated with anthelmintic drug less than a month before faecal sample collection and '*Region*' (East/West). In the general model, we also included an interaction between '*Migration Status*' i.e., sampling time point based on wildebeest migration period and '*Wildebeest Exposure*' (i.e., exposed vs. not exposed to wildebeest migration), as well as an interaction between '*Migration Status*' and '*Region*' (East vs. West). To account for repeated sampling, we incorporated '*Household/Boma*' as a random intercept.

To test the different hypotheses suggested earlier in our introduction, we developed four models, each testing a separate hypothesis, and used Likelihood Ratio Tests (LRTs) to compare between complex and simple models, and we report coefficients from top models or model of particular hypothesis tested.

To test for the effect of *Region* on livestock FEC (H1), we compared a model with and without the main effect of *Region*. We also tested for the effect of *Region* and *Migration Status* on livestock FEC, where we compared a model with and without the interaction between *Region* and *Migration Status* (H2). To test for the effects

of wildebeest on livestock FEC (H3), we compared a model with and without the interaction between *Migration Status* and *Wildebeest Exposure*.

To test for the effect of *Host species* on FEC (H4), we fit a generalized linear mixed model (GLMM) using negative binomial distribution with strongyle FEC as a function of host species (cattle, goat and sheep), *Migration Status*, *Age*, *Drug Treatment*, interaction of *Migration Status* with both *Wildebeest Exposure* (exposed to wildebeest migration or not exposed to wildebeest migration), as well as *Region* (East/West), and used *Household/Boma* as random intercept. We employed a Tukey contrast test in the "*mcp*" package with fitted model above to analyse a pairwise comparison of host species differences. This allowed us to assess the host species effect on FEC (H4).

For worm species richness (number of worm species per household) and diversity index (Shannon Weiner), we used a similar, but simplified, modelling approach - where for sheep and goats we compared models with and without interaction between *Migration Status* and *Wildebeest Exposure* to test for the effect of migrants on livestock. Whereas for cattle we developed a single simple model to test for the effect of *Migration Status* and *Drug Treatment* on livestock samples of Western region only. Again, we report the coefficients from the top model for each host species but use LRTs for hypothesis testing in goat and sheep. Diversity of worms were analysed though vegan package, and Shannon Weiner was used as a measure of diversity index.

We visually assessed for model fit using QQ plot simulated residuals by plotting observed against expected values, and found the distribution was appropriate for our data set. We used R-studio version 2022.12.0+253 and R version 4.2.1 to do all the analysis (R core Team 2021).

4.4 Results

4.4.1 Effect of Region and Migration status on livestock faecal egg counts

Our study found strong effects of both region and migration status on livestock infection intensity between the East and West Serengeti ecosystem (Fig. 4-3 and Fig. 4-4). We have found mixed support for the climate hypotheses (H1) across host species. In goats, we found a Region effect (X^2 = 3.643, Df = 1, p = 0.0563) where the West Region had higher FEC than the East region (Z = 1.971, p = 0.0487, Fig. 4-3). In contrast, a sheep model found no effect of region on FEC (X^2 = 1.2173, Df = 1, p = 0.2699), while in cattle, Region had a significant effect (X^2 = 7.0578, Df = 1, p = 0.0078), with the West region having a lower FEC count than the East region (Z = -2.79, p = 0.00527, Fig. 4-4).

For our second hypothesis (H2) exploring the interaction between migration status and region, we again observed mixed results across host species. In goats we found an effect of interaction between migration status and region (X^2 = 9.3443, Df = 1, p = 0.0022, Fig. 4-3, Table 4-3), where in the West region there was an increase of FEC between pre and post-wildebeest migration period, while the opposite was found in the East region, where there was a decrease of FEC between pre and post-wildbeest migration period. In overall, the West region had significantly higher FEC in the post wildebeest migration period compared to East region (Z = 3.102, p = 0.00192). In contrast, we found no effect of the interaction of migration status and region on FEC in sheep (X^2 = 0.4184, Df = 1, p = 0.5177), nor cattle (X^2 = 1.4486, Df = 1, p = 0.2288).

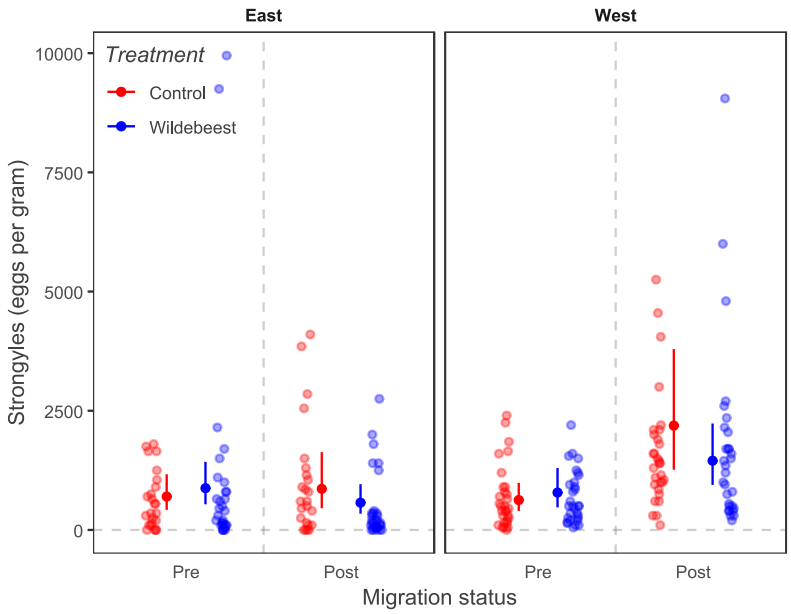

Figure 4 - 3: Effects of region and migration status on goat FEC

Region and migration status effects on goat FEC, where the goats from West region had higher FEC than from East region, and post wildebeest migration in West region had higher FEC than post wildebeest migration in Eastern region. The heavy dots with standard error bars represent predicted average ± SE values from the best model in goat (Table 4-3), while light dots represent observed FEC data. The red colour represents FEC from goats exposed to wildebeest migration, while the blue colour represents FEC from goats not exposed to wildebeest migration.

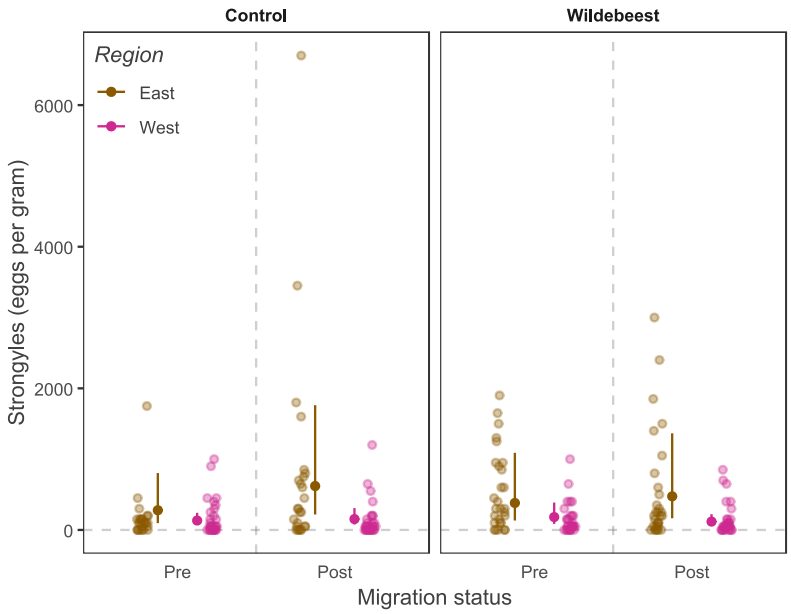

Figure 4 - 4: Effect of region on cattle FEC

Region effect on cattle FEC, where cattle from East region had higher FEC than cattle from West region. The heavy dots with standard error represent predicted average ± SE values from the best model in cattle (Table 4-3), while light dots represent raw FEC count data. The brown colour represents FEC counts from cattle in Eastern region, while the pink colour represents FEC from cattle in Western region.

4.4.2 Livestock infection burden depends on host species, migrants' effects and livestock husbandry

We found effects of migration status and wildebeest exposure (H3) on FEC in goats (X^2 = 0.2394, Df = 1, and p < 0.001), sheep (X^2 = 9.7272, Df = 1, and p <0.001) and cattle (X^2 = 4.2081, Df = 1, and p < 0.001). In areas where wildebeest graze, goats had lower FEC following wildebeest exposure compared to areas where there were no wildebeest grazing at the same time point (Z = -1.672, p = 0.0945, Fig. 4-5). Secondly, we found in areas where wildebeest graze, sheep also had lower FEC during post wildebeest migration compared to those in areas where there were no wildebeest grazing at the same time point (Z = -3.161, p = 0.00157, Fig. 4-6). For cattle, the significant effect of wildebeest exposure on FECs reduction was mediated by the migration status (Z = -1.691, p = 0.090).

Our result from the overall model, that involved all host species shows livestock infection (FEC) depends on host species (H4), where we found goat (Z = 8.471, p <0.001) and sheep (Z = 8.205, p = <0.001) had higher FEC than cattle, and no difference in FEC between goat and sheep (Z = -0.090, p = 0.996).

We also observed mixed effects of drug treatment and age in three host species. We found no effects of age nor drug use in goats (Table 4-3), but in sheep we found effects of drug treatment, where sheep treated with drug had lower FEC than sheep that were not treated with drug (Fig. 4-6 and Table 4-3), and no effect of age. In cattle, we found significant effects of age, and no effect of drug treatment (Table 4-3).

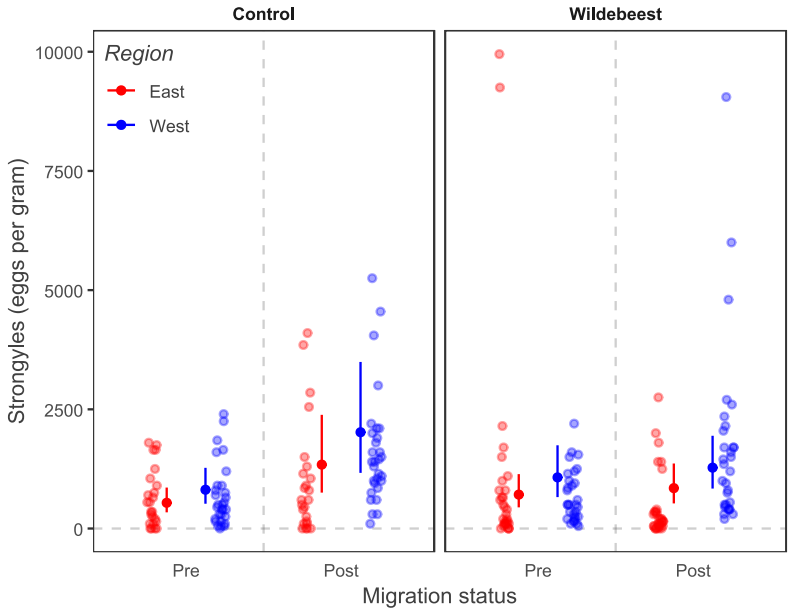

Figure 4 - 5: Effects of herbivore migration on goat FEC

Effects of migratory hosts on goats FEC, where goat had lower FEC during post wildebeest migration in areas exposed to wildebeest migration compared to post wildebeest migration in areas not exposed to wildebeest migration. The heavy dots with standard error represent predicted average ± SE values from the best model in goat (Table 4-3), while light dots represent raw FEC data. The red colour represents FEC from goat in Eastern region, while the blue colour represents FEC from goat in Western region.

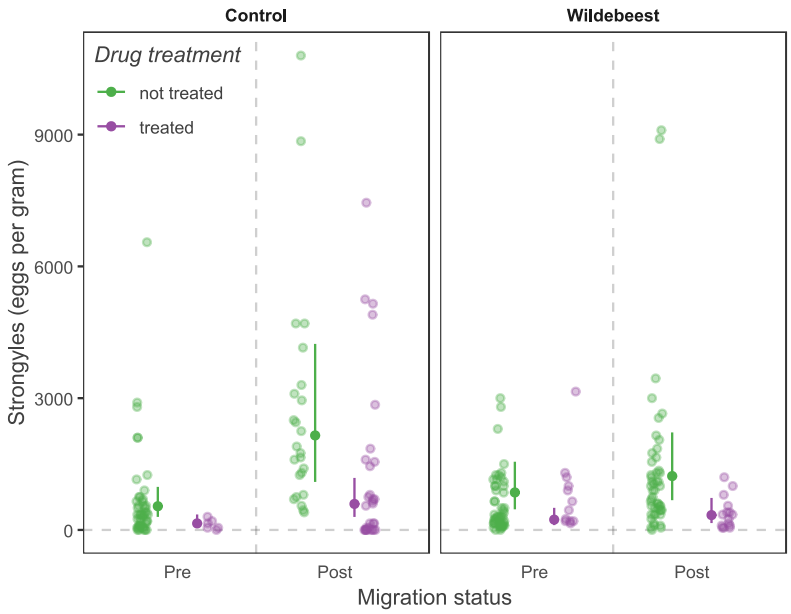

Figure 4 - 6: Effect of herbivore migration and drug treatment on sheep FEC

Effects of migratory hosts and drug treatment on sheep infection intensity, where sheep had lower FEC during post wildebeest migration in areas exposed to wildebeest migration compared to post wildebeest migration in areas not exposed to wildebeest migration as well as sheep treated with drug had lower FEC than sheep not treated with drug. The heavy dots with standard error represent predicted average ± SE values from the best model in sheep (Table 4-3), while light dots represent raw FEC data. The green colour represents FEC from sheep not treated with drug, while the purple colour represents FEC from sheep treated with drug.

Table 4 - 3: Summary results of best model in three livestock species.

Host species	**Goats**			**Sheep**			**Cattle**		
Treatment/Coefficient	**Estimate**	**SE**	**P-value**	**Estimate**	**SE**	**P-value**	**Estimate**	**SE**	**P-value**
Intercept	2.613	0.243	<0.0001	2.337	0.289	<0.0001	1.871	0.443	<0.0001
MigrationPost	0.170	0.344	0.622	1.443	0.278	<0.0001	0.567	0.319	0.075
Wildebeest Exposure: Wildebeest	0.180	0.263	0.494	0.474	0.410	0.248	0.254	0.348	0.731
MigrationPost:Wildebeest ExposureWildebeest	-0.536	0.343	0.118	-1.069	0.338	0.002	-0.719	0.425	0.091

MigrationPost:RegionWest	1.0393	0.3350	0.002	-	-	-	-	-	-
RegionWest	-0.097	0.269	0.718	-	-	-	-1.069	0.3830	0.005
AgeJuvenile	0.056	0.377	0.883	0.433	0.338	0.200	-0.569	0.321	0.077
Drug treatmentTreated	-0.101	0.253	0.689	-1.293	0.270	<0.0001	0.274	0.362	0.449

4.4.3 Patterns of worm community composition across cattle, goats and sheep

We found a total of 23 worm 'types' from the three livestock species using a combination of PCR and Sanger sequencing (Table 4-4), of which 22 worm species/taxa were identified to species (17) or genus level (5), and remaining one represented a group of unknown strongyle species. In goats, we found a total of ten worm species/taxa: (1) HC 87%, (2) CC 2.6%, (3) TC 1.7%, (4) TA 1.7% (5) TV 0.0168%, (6) TP 0.084%, (7) BT 0.084%, (8) US 0.084%, (9) TS 0.042% and (10) Tec 0.042%, while the remaining unknown strongyles represented 6.5% (Table 4-4). In sheep, we found a total of six worm species/taxa: (1) HC 88%, (2) TA 1.75%, (3) CC 1.6%, (4) TC 1%, (5) OC 0.175%, and (6) TS 0.088%, while unknown strongyles represented 7.48% (Table 4-4). In cattle, we found a total of 16 worm species/taxa: (1) HC 39%, (2) TA 15%, (3) TC 11%, (4) HL 9%, (5) CS 7%, (6) CP 6%, (7) CE 2%, (8) HS 1%, (9) CO 0.9%, (10) CL 0.09%, (11) BP 0.9%, (12) BT 0.6%, (13) OS 0.6% (14) OR 0.3% (15) OC 0.3% and (16) HI 0.3%, while unknown strongyles represented 2% (Table 4-4).

Only three worm species – *Haemonchus contortus* (HC), *Trichostrongylus colubriformis* (TC) and *Trichostrongylus axei* (TA) – were found to infect all three livestock species. We found goats and sheep shared two worm species/taxa, *Cooperia curticei* (CC) and *Trichostrongylus spp*, while goat and cattle shared one species, *Bunostomum trigonocephalum* (BT). In goats, we found four worm species/taxa which were limited to goat only: *Trichostrongylus vitrinus* (TV), *Trichostrongylus probolurus* (TP), *Uncinaria spp* (US) *and Teladorsagia circumcincta* (Tec). We also observed sheep and cattle shared only one species, *Oesophagastomum columbianum* (OC), and no worm species that were limited to sheep only. Lastly, we found ten worm species/taxa limited to cattle only: *Haemonchus longistipes* (HL), *Cooperia spp* (CS), *Cooperia pectinata* (CE), *Haemonchus spp* (HS), *Cooperia oncophora* (CO), *Cooperia spatulata* (CL), *Bunostomum phlebotomum* (BP), *Oesophagostomum spp* (OS), *Oesophagostomum radiatum* (OR), and *Haemonchus similis* (HI). For the goats and sheep, we have called all

Haemonchus positive worms as *Haemonchus contortus*. Although this is the expected predominant *Haemonchus* parasite in these small ruminants, we cannot say with 100% certainty that all those identified by PCR were *Haemonchus contortus* as the primers would amplify at least three species of *Haemonchus*. Nevertheless, only *Haemonchus contortus* was found by sanger sequencing.

Table 4 - 4: Identified worm species from livestock versus worms previous reported to be found in wildebeest.

Identified worm species/taxa and their respective percentages per host species in goat, sheep and cattle (grey table), against a list of previously reported worm species from wildebeest (white table).

No:	Livestock worm species	Goat	Sheep	Cattle	Previously reported worm species from wildebeest in the literature
1	*Haemonchus contortus* (HC)	86.93	87.83	39.44	*Haemonchus contortus*, *Haemonchus placei*, *Haemonchus bedfordi*, *Trichostrongylus thomasi*, *Oesophagastomum columbianum*, *Agriostomum gorgonis*, *Cooperia connochaeti*,
2	Strongyle (S)	6.5	7.48	2.17	
3	*Cooperia Curtei* (CC)	2.61	1.62	0	
4	*Trichostrongylus colubriformis* (TC)	1.73	1.05	11.49	
5	*Trichostrongylus probolurus* (TP)	0.08	0	0	
6	*Trichostrongylus spp* (TS)	0.04	0.09	0	
7	*Trichostrongylus vitrinus* (TV)	0.17	0	0	

8	*Teladorsagia circumcincta* (Tec)	0.04	0	0	*Galgeria pachyscelis*, *Trichostrongylus axei*, *Trichostrongylus colubriformis*, *Trichostrongylus falculatus*, *Dictyocaulus bedfordi*, *Protostrongylus etoshai*, *Cooperia fulleborni*, *Trichostrongylus rugatus*, *Pneumostrongylus calcaratus*, *Protostrongylus african*, *Setaria pultoni*
9	*Haemonchus longistipes* (HL)	0	0	9.32	
10	*Haemonchus spp* (HS)	0	0	1.24	
11	*Oesophagostomum spp* (OS)	0	0	0.62	
12	*Trichostrongylus axei* (TA)	1.73	1.75	15.22	
13	*Bunostomum phlebotomum* (BP)	0	0	0.93	
14	*Bunostomum trigonocephalum* (BT)	0.08	0	0.62	
15	*Cooperia spatulata* (CL)	0	0	0.93	
16	*Cooperia punctata* (CP)	0	0	6.52	
17	*Cooperia spp* (CS)	0	0	7.45	
18	*Uncinaria spp* (US)	0.08	0	0	
19	*Cooperia pectinata* (CE)	0	0	2.17	
20	*Cooperia Oncophora* (CO)	0	0	0.93	
21	*Haemonchus similis* (HI)	0	0	0.31	
22	*Oesophagastomum columbianum* (OC)	0	0.18	0.31	
23	*Oesophagostomum radiatum* (OR)	0	0	0.31	

Haemonchus contortus was the dominant strongyle GIN infecting all three host species in all four villages (Fig. 4-7). Small ruminants were infected with a higher proportion of *Haemonchus spp* than cattle. The proportion of

Haemonchus spp over other worm species appears to be larger during post wildebeest migration timepoints compared to their proportion during pre-wildebeest migration timepoints in all villages except Piyaya (Fig. 4-7). In Arash (no wildebeest grazing), the proportion of *Haemonchus contortus* over other worm species was higher in sheep than goat in the pre-wildebeest migration period (Fig. 4-7).

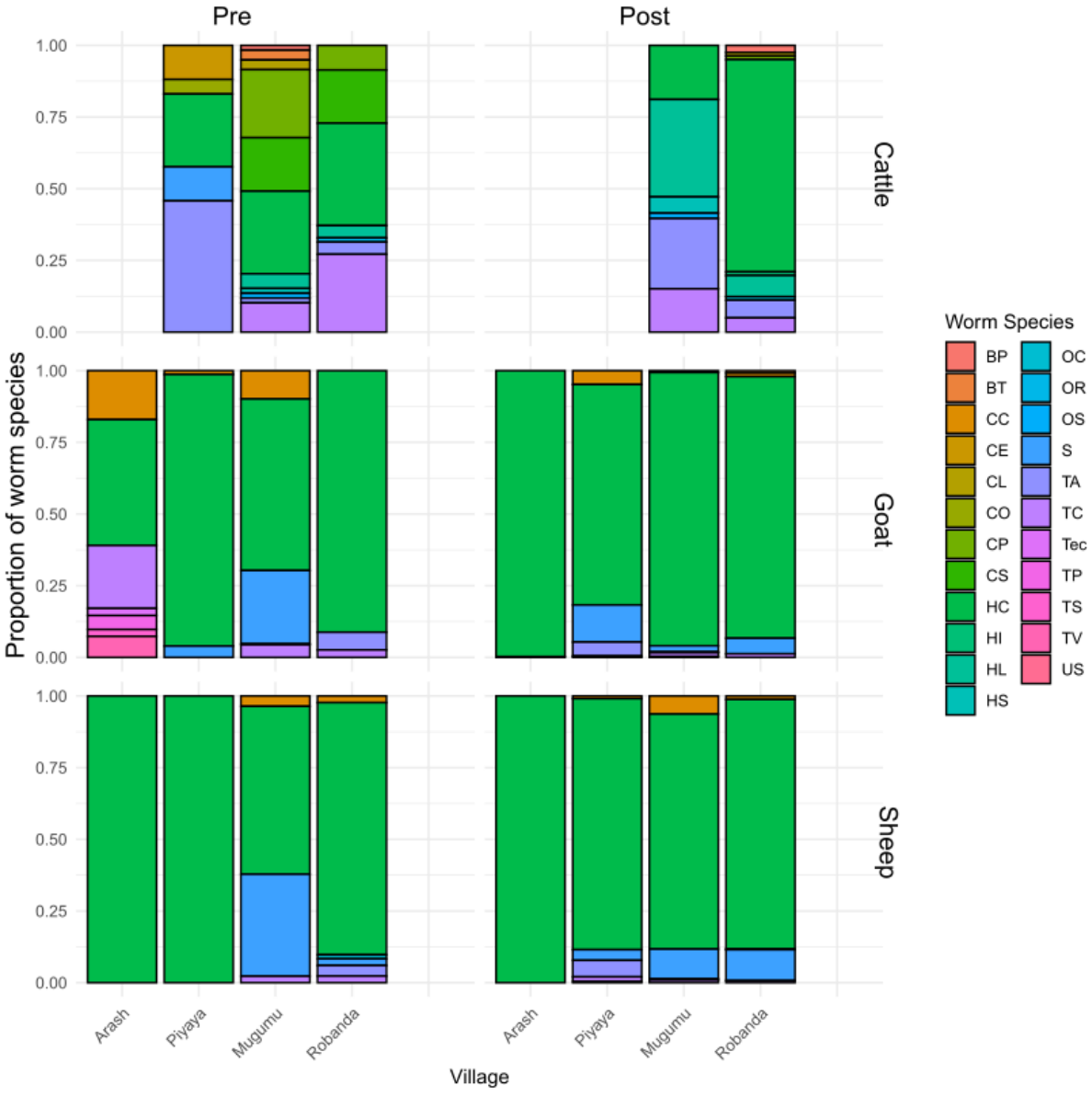

Figure 4 - 7: Worm species/tax proportions in livestock from villages amid wildebeest migration

Worm species/taxa proportion in three livestock (goat, sheep and cattle) across four villages during pre and post wildebeest migration. The green colour, comprising the

largest proportion across all goat and sheep villages, represents proportion of the predominant *Haemonchus contortus*, while the blue colour (e.g. common in Mugumu pre migration period in goats and sheep), represents the proportion of the unknown strongyle, (*c.f*. Table 4-4 for the full names of all worm species identified).

4.4.4 Wildebeest migration impact on livestock worm species richness and diversity index

Our study found a mixed effect of wildebeest exposure and migration status on species richness of host species (H3 i.e., migrant effect hypothesis). In goats we found effects of wildebeest exposure, and the interaction between wildebeest exposure and migration status, where we found goats had significantly lower worm species richness in areas grazed by wildebeest (Z= -1.917, p = 0.0552). Yet, in contrast, we found strong interaction between migration status and wildebeest exposure in goat, where post wildebeest migration in area grazed by wildebeest, goats had significantly higher worm species richness compared to post wildebeest migration species richness in areas not grazed by wildebeest (Z= 2.358, p = 0.0184). Our study also suggests migrants introduce new worms in areas they visit or increases chance of rare worms to infect sheep, where worm species richness increased in post wildebeest migration in area visited by migrant, predominantly due to the increase in the number of species represented in Piyaya post migration (Z= 1.895, p = 0.0581). And we found no effects in cattle.

For diversity index, we found mixed effects of impact of wildebeest migration effects on worm species Shannon Weiner index (H3 i.e., migrant effect hypothesis). In goats, we found strong effects of migration status, wildebeest exposure and interaction of migration status with wildebeest exposure on Shannon Weiner index; we found significantly lower diversity index in post wildebeest migration period compared to pre- migration period (Z= -2.541, p = 0.01107). We also found that diversity index of worm species in goat decreased significantly in areas where wildebeest graze compared to area

where no wildebeest graze (Z= -1.881, p = 0.0599). Despite this, we found interaction between migration status and wildebeest exposure in goat, increased diversity index of worm species in post wildebeest migration period in areas where wildebeest graze compared to post wildebeest migration period in areas where there were no wildebeest grazing (Z= 2.343, p = 0.01914). While in sheep we found no effect of migration status and wildebeest exposure, p > 0.1. For cattle, considering the west only, we found strong effect of migration status and wildebeest exposure, where we observed significantly lower diversity index in post wildebeest migration compared to pre wildebeest migration (Z= -2.673, p = 0.00751). While for Wildebeest Exposure we found cattle had significantly lower diversity in areas where wildebeest graze compared to areas where wildebeest do not graze (Z= -1.683, p = 0.09229).

4.5 Discussion

Interactions between wildlife and livestock are increasing worldwide, with profound consequences for the epidemiology of infectious diseases. Ungulate migrations, such as those of wildebeest, result in widespread grazing and extensive dung deposition, but the role of wildebeest migration in either increasing or reducing infection risk in livestock and other resident hosts remains poorly understood. This study employed a design that considered livestock GIN infection intensity via a proxy of FEC before and after wildebeest migrated through shared grazing areas, with nearby control areas where wildebeest did not occur, to provide evidence on how livestock infection burden changes amid wildebeest migration in two regions of the Serengeti National Park in Tanzania.

Apart from wildebeest interactions, an important aim of our study was to understand how broad-scale differences in environmental conditions might mediate infection dynamics in livestock. One possibility (H1) was that in wetter areas, livestock infection intensity would be higher because the environmental conditions would promote emergence and survival of free-living stages of larvae (Kimaro, 2025). This pattern was supported in goats,

where the West region had higher FEC than the East region. Contrary to our hypothesis, we observed higher FEC in the East region than the West region in cattle. One possibility is that, as bulk feeders cattle may be more at risk from ingesting high densities of parasites close to the ground in the East region due to shorter grass in that region. A study by Normandeau et al., (2020) also suggested the role of different regional environmental conditions on giant liver fluke infection intensity between elk populations found in Eastern and Western regions of Banff National Park in Canada. The authors reported elk migrants found in eastern region had higher infection intensity than elk migrants in western region. They reasoned that this was due to warmer conditions in eastern region that might have promoted early cercariae production by snail, hence exposing the eastern elk population to longer periods of infective stages on pasture compared to Western. In our study, we also found cattle had a higher diversity of worm species than small ruminants, in both the East and West and so this difference in FEC between regions may have been related to the community of worms that infect cattle and how they respond to environmental conditions. However, we have limited data on worm species in cattle in the East, and so further work would be needed to investigate this hypothesis. Apart from our predicted Climate hypothesis (H1), it is also reported that agropastoralist communities in the West tend to take cattle away from their household during wet season and keep them near to their household during the dry period, whereas the pastoralist communities in East region do the opposite (Ekwem et al., 2021). Such different livestock management strategies might lead to different cattle infection risk between West and East regions, but the clear mechanism for that will need further research.

We were also interested to understand any interactions between region and migration status (H2). We found support for the Region x Migration Status Hypothesis (H2) in goats, in which we observed a larger increase in FEC between pre and post-wildebeest migration period in the West region, while there was a decrease in FEC between pre and post-wildebeest migration period in areas grazed by wildebeest from the East region (*c.f.* Figure 4-3), suggesting an increase of FEC in areas grazed by wildebeest in the West region

and a removal of parasites in areas grazed by wildebeest in the East region. This might be due to regional difference in environmental conditions between West and East regions as discussed in the previous paragraph; it was considerably wetter in the West by the second sampling time point in July, than it had been in the East at the second sampling time point in April (Figure 4 -2). Our results also suggested that FEC may depend on the level of exposure to wildebeest (H3). Notably, we observed lower FEC in areas exposed to wildebeest following the migration compared to areas not exposed, in both goats and sheep. This implies trophic effects are likely the main effect of wildebeest exposure compared to transport effects. Thus, the net effect of wildebeest on livestock could depend on how they modify grass through grazing. These findings suggest that migratory wildlife could be beneficial in livestock production and contribute to managing conflict between wildlife management and livestock production, at least under certain climatic conditions. Our findings should be cautiously interpreted because the study lacked quantitative measures of exposure to wildebeest, as we assumed villages within the long-term range of wildebeest (Robanda and Piyaya) were "exposed" while other control villages were not. Despite these limitations, other studies have found similar effects of wildlife on livestock parasite infection. For example in Botswana, goats exposed to wildlife (wildebeest and zebra) had lower infection compared to goats not exposed to wildlife (Walker et al., 2018). Previously it has been suggested that grazing by wild deer might also remove parasites from pasture for livestock (Barone et al., 2020).

We found that small ruminants (goats and sheep) had higher FEC compared to large ruminants (cattle), and no difference in FEC between goats and sheep, confirming our Host Species Hypothesis (H4). We observed differences between hosts in the effect of anthelmintic treatment and age on FEC. We found anthelmintic drug use in sheep reduced FEC, while no effects were observed in goats and cattle. According to Várady et al., (2011) nematodes develop drug resistance more rapidly in goats than in sheep. Thus, differences in resistance could potentially explain the observed effect of drug in sheep compared to goats. In such scenarios wildlife might be beneficial to livestock by introducing naïve worms, which are more treatable. In cattle, juveniles

(calves and subadults) had significantly lower FEC than adults, which was opposite to results from work in central Kenya where calves and immature animals had higher FEC than adults (Waruiru et al., 2000). The observed opposite effects of calves and immature animals could be due to different livestock practices, where in central Kenya they use intensive zero grazing while in Serengeti-Tanzania they use agropastoral and nomadic pastoralism; hence adults could be exposed to higher infection from grazing in different grazing area in Serengeti Tanzania. Further, in our study area, cattle are a highly valuable livestock compared to goats and sheep, this might trigger different care (possibly through strategic grazing or anthelmintic drug use) between adult and juvenile cattle, and between cattle and small stock (goat and sheep).

We found *Haemonchus contortus* was the dominant strongyle GIN worm infecting all three host species in all four villages. Its proportional abundance increased during the post wildebeest migration period compared to pre wildebeest migration period. However, this finding might have been biased by our larvae sampling approach, where culturing for worm species identification only involved faecal samples with high faecal egg counts. Because *Haemonchus contortus* has high fecundity, samples with high FEC may have been disproportionately infected with *Haemonchus contortus*. Moreover, exclusion of faecal samples with low faecal egg counts might have excluded worm species with lower fecundity. Hence the study findings might have a biased observed composition relative to the true composition of species infecting the livestock hosts. Nevertheless, *Haemonchus contortus* has also been found as a dominant worm species that infects at least six species of livestock and wildlife in other African ecosystems, e.g. Botswana (Walker et al., 2017, 2018).

We found three worm species infecting all three host species. Goats had three worm species and one genus found in goat only, in contrast sheep had no worm species limited to sheep only, whereas cattle had seven worm species found in cattle only. Cattle also had additional worms which had ITS2 sequences not identifiable beyond genus level, which could indicate the presence of other

Haemonchus, Cooperia or *Oesophagostomum* species, or more divergent individuals within the overall parasite populations. Previous reports suggest worm species sharing is determined by diet overlap (Wells et al., 2018); this might explain why cattle had higher number of worm species found in cattle only compared to goats and sheep, as cattle (grazer) feed on bulk of grasses that might increase exposure to infective stages of different environmental parasites compared to sheep, while goats are mixed feeders that can browse and graze.

We also found cattle have a higher diversity of worm species and a more even distribution of worm species abundance compared to goat and sheep. This might be due to different techniques used to speciate the samples, where most of the worm species were speciated primarily though sequencing approach for cattle compared to goats and sheep which were primarily speciated by the PCR method. The PCR method may have introduced some biases or misidentification in species composition measures; I used the ITS-2 region to identify parasites primarily via a multiplex PCR for sheep and goats, for which some of the primers (including *Haemonchus* primers) were specific to genus level only. However, this was supplemented with Sanger sequencing, confirming the presence of *Haemonchus contortus*. If there were mutations in primer binding sites, they might have prevented amplification, and these worms might have not been identified as strongyles, or to species level, at all. For the sequencing analysis, I used ITS-2 sanger sequences with conserved subunit presence, that could potentially have led to misidentification of species, as longer database sequences with conserved subunits may have scored more highly following BLAST than those with shorter database sequences without conserved subunits. Furthermore, there is potential for wildlife to infect livestock with novel distinct species not found in existing genetic databases, which are currently dominated by species known to infect livestock. In the future, this analysis could be redone using phylogenetic analysis and only ITS2 sequences (with conserved rRNA subunit sequences removed) that will help to improve species identification.

When we compared worm species found in our livestock to previous reported worm species infecting wildebeest from literature, we found only three worm species (*Haemonchus contortus, Trichostrongylus axei,* and *Trichostrongylus colubriformis*) were common between wildebeest and all three livestock species, while one worm species (*Oesophagastomum columbianum)* was common between wildebeest, sheep and cattle only. The first three worm species have been previously reported to be zoonotic in nature (Bhat et al., 2023), while *Oesophagastomum columbianum* has been found to be an important worm species infecting livestock in different parts of the world (Hanafiah et al., 2019; Nwosu et al., 2011). However, the described species composition of the livestock from this study came from a sample of 282 individuals of the three livestock species across two regions, four villages and four sampling timepoints, which is a relatively small sample size to generalize patterns of parasite species composition given the large number of livestock found in the ecosystem, the large degree of similarity of parasites shared within households, and the way in which parasites distribute themselves amongst hosts. Therefore, we recommend future studies to increase sample size of livestock bomas (households), over individual animals within households, as this will increase both representation of livestock population and the spatial coverage of the area. This approach may increases the probability of identifying rarer species passed from wildlife to livestock, or identifying differences between areas exposed to wildebeest and those unexposed.

Furthermore, our result shows mixed evidence of the impact of wildebeest migration on livestock worm species/taxa composition in villages, where goats had significantly lower worm species richness in areas grazed by wildebeest compared to areas not grazed by wildebeest (H3). Yet, the interaction between migration status and exposure to wildebeest shows there is significant higher worm species richness in goats during post wildebeest migration in area exposed to wildebeest compared to worm species richness in areas not exposed to wildebeest migration. For sheep, in contrast, we found worm species richness increased significantly during post wildebeest

migration in area grazed by the wildebeest compared to areas not grazed by the wildebeest. The study findings suggest under different conditions, wildlife may be able to introduce or reduce parasites in an area, hence migrant play a key role on livestock health by spreading infectious parasites across habitats in our ecosystems.

Similarly, our result shows wildebeest migration was associated with different outcomes related to the diversity of worm species in livestock hosts (H3). For goats, we found significantly lower Shannon Weiner diversity indexes during the post wildebeest migration period compared to pre wildebeest migration as well as in areas grazed by the wildebeest compared to areas not grazed by the wildebeest. We also found significant interactions between migration status and wildebeest exposure on worm diversity in goats, where there was a significant increase of worm diversity during post wildebeest migration in area grazed by wildebeest compared to area not grazed by wildebeest. For cattle we found significant lower worm diversity during post wildebeest migration compared to pre wildebeest migration, and we found significantly lower diversity in areas grazed by wildebeest compared to areas not grazed by wildebeest. The changes in worm diversity could be linked to effects of wildebeest in changing density of dominant worm species in post wildebeest migration timepoint as well as in grazed areas.

In our study we explored infection intensity and worm species composition of livestock species amid wildebeest migrations around Serengeti National Park-Tanzania, in relation to their different regional environmental conditions and livestock husbandry. Our results suggest wildebeest migration might impact livestock both positively (reducing infection intensity) and negatively (increasing infection intensity and parasite diversity) in different regions of the Serengeti under different migration status and prevailing region environmental conditions. We found FEC and worm species composition of different livestock species in the Serengeti Ecosystem were associated with contextual factors such as: (1) regional environmental conditions which appeared to be particularly important for goats and cattle, though in opposite

directions. For example, goats had higher faecal egg counts under wet conditions, which aligned with our climate hypothesis (H1), while cattle had higher faecal egg counts under dry condition contrary to climate hypothesis (H1). (2) Exposure to wildebeest and migration status (H2 and H3), where all host species showed a lower faecal egg count during post wildebeest migration period in wildebeest grazing areas compared to areas not grazed by wildebeest. For worm species richness, there was an increase of richness in goat and sheep in areas visited by the wildebeest during post wildebeest migration period (i.e., an interaction between wildebeest exposure and migration status). In contrast, goats had lower species richness in areas exposed to wildebeest migration compared to areas not exposed to wildebeest migration. (3) Livestock species difference (H4), where goat and sheep had higher faecal egg counts than cattle aligning with our hypothesis on host species effects. Furthermore, goats and cattle showed a different association to regional environmental conditions (dry and wet), as explained on first point above.

Other contextual factors that appeared to be important included livestock deworming and age, where (4) sheep were the only species to show sensitivity to farmer-reported anthelmintic drug use. Lastly, (5) we observed an effect of age in cattle on FEC, where juveniles (calves and subadult) had lower FEC than adult, but we observed no effect of age in goats and sheep. Based on our results we conclude that wildlife-livestock interaction amid wildebeest migration shows a mixture of benefits and harms on livestock worm species composition and infection intensity, suggesting outcomes of interaction between wild and domestic ungulate in our ecosystem is context dependant, and could be underlaid by temporal migration dynamics, differences in climatic conditions, and cultural and farming practices of the area.

5. Conclusion

5.1 Synthesis of the study and general discussion

Savannas are well known for being dynamic ecosystems in time and space. While many ecological studies of savannas have focused on understanding how fire, grazing, herbivory and seasonality shape the composition and distribution of species in ecosystems, in this thesis I explored how some of these factors affect parasitism of ungulates at the wildlife-livestock interface.

First, this study found wildlife migration intensity and duration shape infection risk of parasites on pasture that is available to subsequent grazing hosts via dung deposition (transport effects) and grazing (trophic effects). Increasing migration intensity increased L3 density on pasture, but the net effect of migration depended on both the intensity and duration via trophic effects that reduced density of L3s via consumption and/or microclimate effects. For example, in the high migration duration scenario, I found low L3s density due to a combination of migrants' consuming L3s that had self-deposited, and increased exposure of L3s to higher sunlight and temperature due to relatively short grass. Also, I found high migrant intensity with grazing had low density of L3s compared to high migrant intensity without grazing, which suggested shorter grass resulted from heavy grazing exposed L3s to harsher microclimate conditions (higher sunlight and temperature) compared to tall grass in high intensity without grazing. This study suggests that even with large numbers of migrants, L3 infection risk can be quite low in short grass with low humidity, high sunlight or high temperature, which leads to desiccation and low worm survival. The findings from this study underscore the importance of wildlife movement and resource-consumer interactions in shaping disease transmission among different hosts in our ecosystems. Though the study used a migratory species with a very large, and highly aggregated, population of ~1.3 million wildebeest, the distribution of wildebeest in the Serengeti is highly unevenly distributed in space and time, generating considerable scope for variability in their effects on parasites and other hosts. The findings could be applicable in other similar grazing ecosystems with large or dense populations of migratory herbivores, such as Saiga antelope (*Saiga tatarica*) with total population of 2 million in Kazakhstan (IUCN, 2023), white-eared kob

(*Kobus kob leucotis*) with a population of 800,000 in Sudan (Morjan et al., 2018), or migratory elk (*Cervus canadensis*) with population of 8,000 in Yellowstone National Park, United States of America (Vucetich et al., 2005; White et al., 2024). The work is also relevant to areas where there is high aggregation of mobile livestock, such as under large intensive commercial livestock production using rotational grazing, or in traditional pastoralist areas. Moreover, global forces such as climate change, and anthropogenic pressures, such as hunting, road and fences, affect wildlife migration pattern/routes, likely shifting the intensity and duration of space use and trophic interactions in ways that may have consequences for parasites (Cooke et al., 2024; Dybas, 2022; Harris et al., 2009; Harvell et al., 2009; Middleton et al., 2020; Stoellinger et al., 2020). My results provide insight into how changing wildlife migration intensity and duration under these distinct scenarios may affect environmental parasite survival and transmission, as well as disease prevalence across ecosystems.

Secondly, this thesis demonstrated how savanna vegetation such as scattered trees and variable grass heights induced by the herbivore grazing (trophic effects) could further shape landscape infection risk to herbivores via microclimate effects across wet and dry conditions. The study shows how vegetation shade induced by differential herbivore pasture grazing intensity and tree canopies modify fine scale environmental conditions in dry or wet conditions of the year and increase environmental parasite abundance. Such findings help broaden our understanding of the scope of potential impact of climate change (e.g. elevated temperature, increased drought, increased rainfall) on environmental parasites and infectious disease epidemiology at fine spatial scale. Moreover, such findings imply the global trend of increasing woody plant encroachment in savanna ecosystems (Stevens et al., 2017; Venter et al., 2018) might also contribute to changing infectious diseases dynamics (Loss et al., 2022) via increased survival of environmental parasites in different agents such as pasture, dung and soil. Similarly, such findings might contribute to commercial livestock production in tropical savanna areas, as it raises an important question of net cost and benefit of protecting or planting trees in livestock grazing areas. Currently trees are incorporated as a means to maximize livestock production due to their role in protecting animals from heat stress i.e., a positive impact in livestock production (de Sousa et al., 2021; Deniz et al., 2020; De-Sousa et al., 2023; Giro et al., 2019).

In contrast, my study shows trees have a potential associated cost by enhancing survival of free-living stages of environmental parasite and improving microclimate conditions for the infectious L3 GIN stage on the environment. However, my experimental approaches did not directly introduce fresh dung piles into our treatments. Instead, I placed dung piles containing artificially cultured L3s that facilitated recovery of sufficient numbers of L3s to test for the differences among experimental treatments, even if harsh (i.e. arid) weather conditions prevailed during the experimental period. Eggs and L1/L2 larval stages may be more sensitive to changes in microclimate weather conditions than later stages. Desiccation of these earlier lifecycle stages may occur more rapidly, and so it is possible that fewer L3 would have been recovered than we found. Nonetheless, given the strong microclimatic effects observed in our study, I would not expect the relative effects of treatments to have changed substantially if fresh dung piles had been used. Third, this thesis found both positive and negative association between wildlife migration and livestock infection under different contexts of wildlife exposure, climatic conditions and livestock husbandry. Using faecal egg counts as a proxy for infection intensity, this study found wetter regions had higher goat infection intensity, which I attributed to overall favorable environmental conditions that enhance GIN development and survival, while in contrast, cattle had higher infection intensity in the dry region which I thought could be due to higher infection risk per grass bite in short grass. I also found livestock in areas exposed to wildebeest migration had lower infection intensity compared to areas not exposed to wildebeest migration. Hence, the study contributes to understanding different contexts of wildlife-livestock interface on environmental trichostrongylid L3 parasite transmission and disease epidemiology. This finding will be valuable to facilitate and manage wildlife-livestock coexistence by informing practitioners at the wildlife-livestock interface on how and where wildlife can be beneficial or harmful to livestock health.

Overall, this study contributes to a growing body of knowledge on the linkages, direct and indirect, between wildlife migration and infectious diseases (Altizer et al., 2011; Bauer & Hoye, 2014; de Angeli Dutra et al., 2021, 2024; Mijele et al., 2016; Poulin & de Angeli Dutra, 2021), and on the effect climate change, or interaction between climate change and wildlife migration, have on GIN parasitic diseases (Dickinson et al., 2024; Harvell et al., 2009). This study broadens our

understanding of the role of the microclimate on GIN parasitic diseases and contributes to studies of landscape epidemiology (Bonnell et al., 2016; Restrepo et al., 2016; Titcomb et al., 2021; Wang et al., 2018). Furthermore, it contributes to studies of cross species transmission, particularly between migratory wildlife and livestock (Morgan et al., 2007), and studies that cultivate pathways toward wildlife-livestock co-existence (Odadi et al., 2011; Stears & Shrader, 2020; van Dam et al., 2024), particularly from deep understanding of epidemiology of infectious diseases at the wildlife livestock interface (Hassell et al., 2017; Karmacharya et al., 2024; Pal et al., 2025; Ranjan et al., 2025; van Dam et al., 2024).

5.2 Future research

This study has addressed the question of how herbivore movement, weather conditions and vegetation shape infection risk across the savanna ecosystem, but there are still many knowledge gaps. Of these gaps, the most important to fill are (1) to assess changes of pasture larvae abundance during wildebeest migration in shared wildlife-livestock grazing area alongside sampling of both livestock and wildebeest GIN communities in these areas; (2) To assess specificity of parasite shared between wildlife and livestock; (3) To assess if herbivores actively (or unknowingly) balance trade-offs between infection risk on pasture and pasture nutrition/palatability. Thus, to advance our understanding of parasite transmission and infectious disease risk at the wildlife-livestock interface, I recommend the following future study.

5.2.1 Assessing pasture and infectious parasite dynamics in shared wildlife-livestock grazing areas

The study shows that livestock infection changes following wildebeest migration, yet in the current study there was no information on how vegetation conditions (such as grass height and cover) change, nor how the abundance of L3s in pasture changes before and after wildebeest migration in villages next to Serengeti National Park. Thus, the study assumed there is a change of pasture infection risk in shared pasture following wildebeest arrival in villages that would be mediated through both transport and trophic effects and captured in livestock infection intensity after the wildebeest migration. While the assumption is biologically

plausible, it is difficult to directly link impact of wildebeest on livestock infection changes without better understanding the dynamics of parasites on pasture. A follow up study to produce such information will continue to advance our understanding of parasite transmission at the wildlife - livestock interface in different ecosystems. Therefore, I recommend the future study to measure changes of grass height and cover, as well as pasture larvae abundance before and after wildebeest migration in shared grazing areas between wildlife and livestock.

5.2.2 Specificity of shared parasites between wildlife and livestock

This study assessed worm species that infect ruminant livestock (goats, sheep and cattle) in villages next to Serengeti National Park within and near to the path of the wildebeest migration. Among the worm species that were found to infect livestock, I also found worms that have been reported to infect wildebeest from previous literature. However, my thesis did not assess worm species infecting wildebeest, leaving a gap as to whether the same worm species are found in wildebeest in the study area. Yet another remaining important question is whether same population of different nematode species is transmitted between wild and domestic ruminant hosts in Serengeti host, or whether there might be cryptic genetic structure suggesting local adaptation to different host species, or localised transmission patterns among the parasite's populations. Such information would help advance our understanding of infection risk from different host species (Fenton et al., 2015), and their role in spread of resistant parasites within the ecosystem (Brown et al., 2022).

5.2.3 Tradeoff between grass nutrition and parasitism

In the current study, I have shown how different grass height and tree cover change infection intensity in pasture, however it's not clear how the different grass heights or shade availability from tree cover might affect pasture nutrition or palatability and how that might link with herbivore infection risk to impact the net costs or benefits of grazing near or away from mature savanna trees. Therefore, I recommend future work to address this gap, by analyzing grass nutrition contents, and palatability of grasses alongside associated infection levels.

Apart from the three important gaps described above, other relevant interesting research gap on parasite transmission and infection risk in Serengeti ecosystem includes;

5.2.4 Parasite effects on wildlife

In future it will be important to understand how dynamism in parasites, i.e., parasite diversity and infection intensity, translate into health effects in wildlife species. Broadly, we still have little understanding of how parasite infections affect wildlife performance such as movements, habitat selection and reproduction success, such information will advance our understanding of parasite role in shaping population growth and species distribution in ecosystems. Furthermore, it would also be important to understand how livestock affect wildlife health, for instance, do livestock act as reservoirs and source populations of parasites (including resistant population of parasites) to wildlife? Or do they carry parasites from one herd of livestock to another (Ezenwa & Jolles, 2015; Francis & Šlapeta, 2023)?

5.2.4 Traditional pasture management and parasitism

In this study I have shown how variation of vegetation cover can affect survival and abundance of parasites in pasture, therefore in future studies it could be interesting to understand how the traditional pasture grazing and management, such as the Maasai's *Alalili* system (Hezron et al., 2024), modifies infection risk for livestock. This will help to understand how traditional cultural practice shape infection risk of livestock in rangeland areas, and how loss of traditional life might contribute to spread and prevalence of parasite in ecosystem. Maasai's *Alalili* involves protecting a portion of rangeland resources such as forage and water particularly over wet season period from ongoing utilization by the livestock, for future grazing during dry season. As many traditional cultural practices are beginning to change because of both endogenous and exogenous factors, yet they also face further threats from climate change, tenure security, land use change and unsustainable practice, therefore it is important to understand the role of the traditional grazing system in modifying disease risk in rangeland areas.

5.3 Herd management recommendations

Gastrointestinal nematode eggs hatch and develop to infectious L3s stage over the course of a week under optimal conditions. While in practice many livestock keepers will decide where to graze livestock mainly based on forage availability (not infection risk), our study findings offer options to understand where and when to graze based on infection risks and forage availability following exposure to wildlife migration. For instance, the study found that L3 are more abundant on pasture under wet and shade conditions (in shorter grass) than under dry conditions (or wet and long grass). Thus, choosing where to graze livestock should consider the followings: (1) Days since migratory wildlife first arrive/depart, (2) Number of migratory wildlife, (3) Weather conditions since their arrival, (4) Vegetation structure - e.g. presence or absence of trees. More specifically, my study offers a limited livestock grazing management recommendation based on infection risk and the associated pasture availability to livestock in shared grazing areas as follows:

1. During the wet season 0-7 days post departure of migratory wildlife, there might be less concern for pasture availability due to grass regrowth unlike the dry season, as well as lower infection risks in shared grazing areas between wildlife and livestock, except where wildlife have stayed for long periods. Furthermore, while trophic effects may remove parasites from the ecosystem in both short and long stays by migratory wildlife, wildlife also reduce forage for the subsequent grazers that will use the area before grass regrowth. Thus, trophic effects may also impose negative impacts for the subsequent grazers through strong competition of limited forage, though strength of competition or even facilitation will depend on season (Odadi et al. 2011).

2. Seven days after the first arrival of migratory wildlife, eggs deposited by wildlife may have developed to infectious L3 on pasture. Livestock keepers can graze their livestock in shared grazing areas that had short stay and low number of wildlife within 7 – 28 days post departure with lower infection risk compared to shared grazing areas that had longer stay and/or high abundance of wildlife during both dry and wet seasons. While at 7 – 28 days

grass regrowth will compensate wildlife grazing in many shared grazing areas and hence might reduce pasture concerns. While our study offers insight on pasture availability and infection risks following wildlife migration, I recommend future studies quantify how forage availability and nutrition conditions of the pasture change with infection risk by assessing parameters such as carrying capacity of the pasture per area, and minerals (for examples nitrogen, calcium, and potassium) contents of the grasses change amid wildlife migration events.

3. Apart from possible grazing options outlined above, I further recommend carefully planned drug treatment of goats and sheep as they were found to be more infected compared to cattle, and livestock sector could benefit from more monitoring of livestock health.

4. Use of the FAMACHA test (Van Wyk & Bath, 2002) to guide drug treatment decisions, as I found the common and dominant infecting worm species was *Haemonchus spp*. The underlying principle behind FAMACHA test is to treat livestock that have only failed to withstand *Haemonchus spp* infection and develop severe anaemia. The test uses progressive change of conjunctivae colour from red (health condition) to white (severe anaemia) as an indicator of what an animal to treat based on severity of infection observed.

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Appendices

Appendix A: Supplementary materials for chapter 2

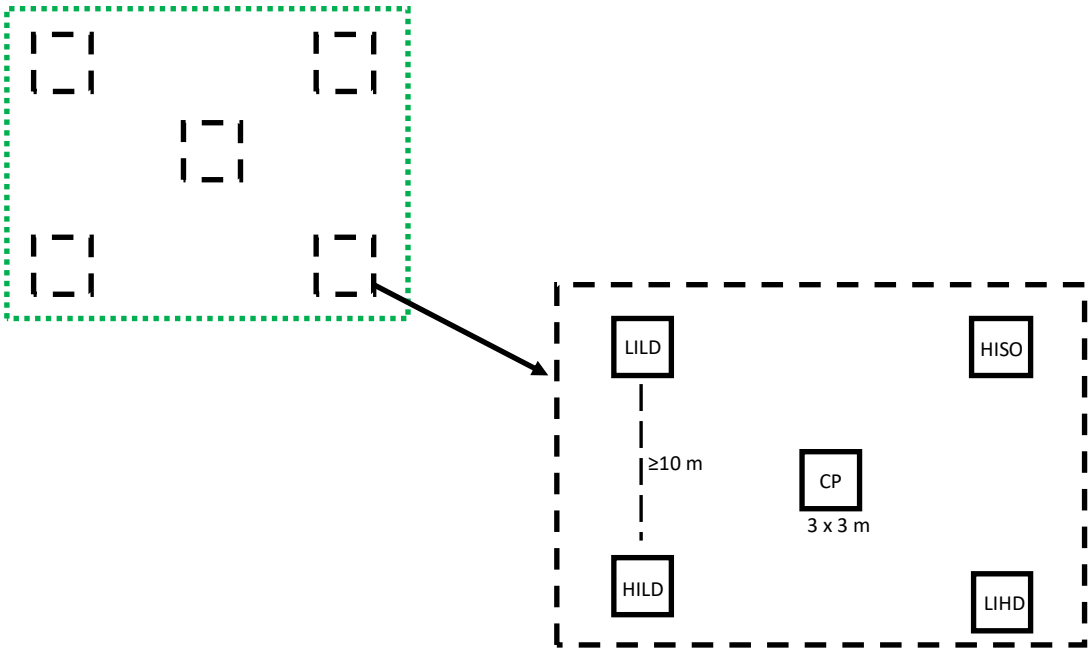


Figure A:S1: Block layout In Seronera Wildlife Research Centre, Serengeti National Park, Tanzania. Dashed lined squares represent five blocks established in our experimental plots, and heavy lined squares represent five treatments plots established in each block.

Figure A:S2: Faecal egg counts for dung piles used in different blocks. No significant differences were detected across blocks, and blocks were included as a random effect in the models of L3 counts.

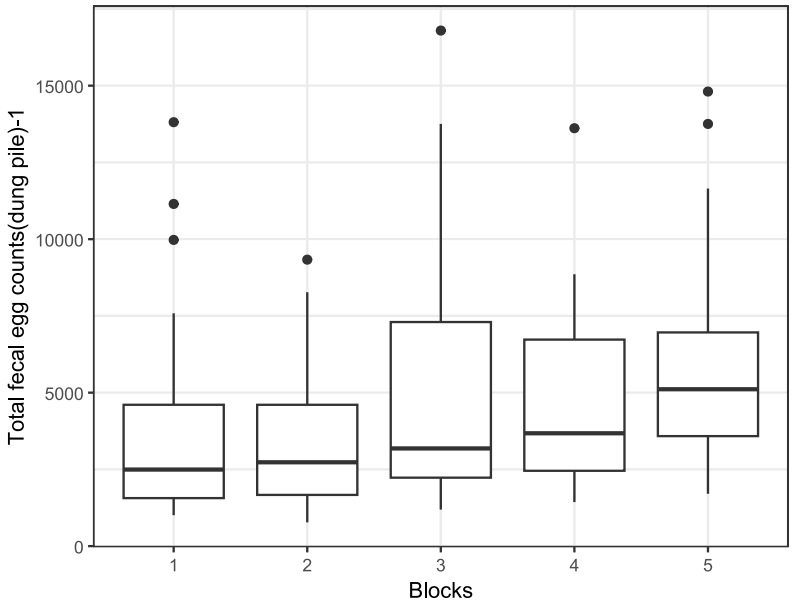


Figure A:S3: Hourly maximum temperature, solar radiation, relative humidity, and soil volumetric water content during the experimental period, recorded by a nearby weather station at the TAWIRI Seronera Wildlife Research Centre.

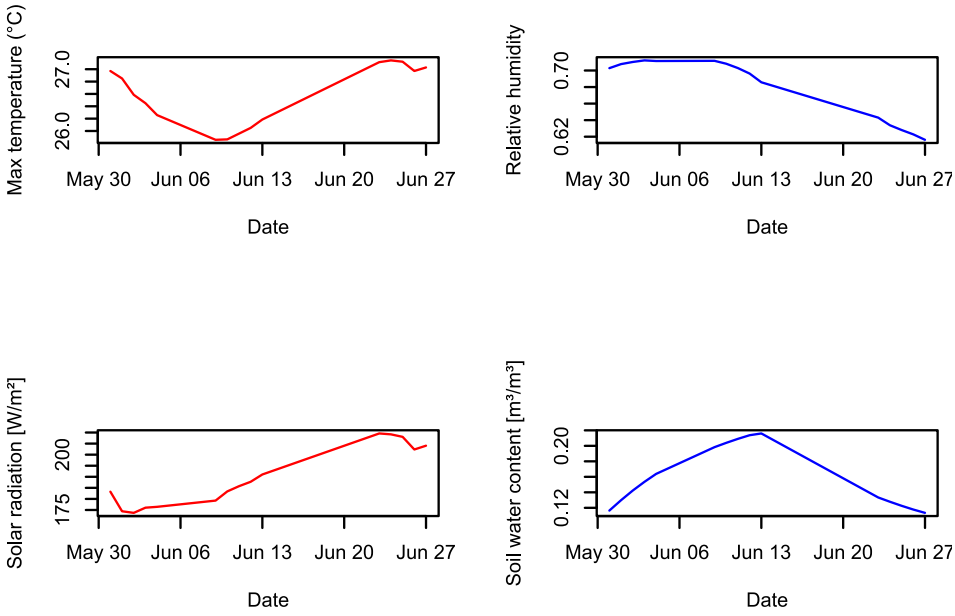


Figure A:**S4:** Mean ± standard error L3 (kg of dry grass)$^{-1}$ of High Intensity Stopover (HISO) treatments i.e., point and line in red color and High Intensity Low Duration (HILD) i.e., point and line blue color. The graph demonstrates how trophic effects of dampen transport effects of GIN in a grass patch.

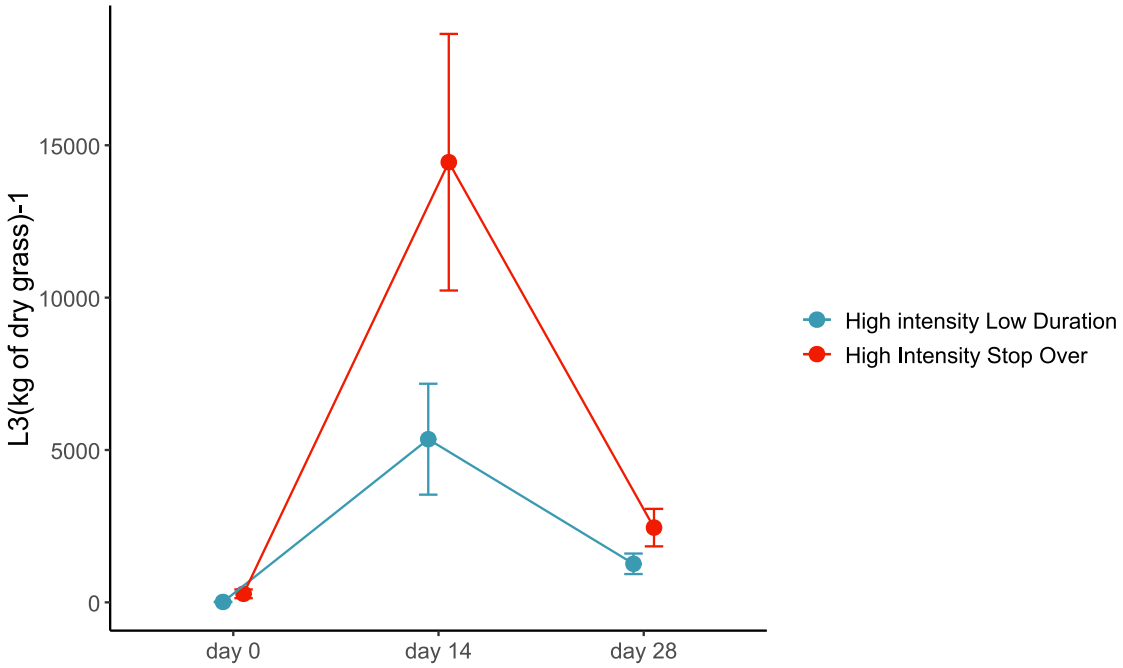


Figure A:S5: L3 (kg of dry grass)$^{-1}$ (mean ± standard error) of High Intensity Low Duration (High dung addition) treatments i.e., point and line in red color and Low Intensity High Duration (Low dung addition) i.e., point and line blue color. The graph demonstrates higher intensities (higher dung deposit by the migrant) increase parasite density in grass compared to Low dung addition.

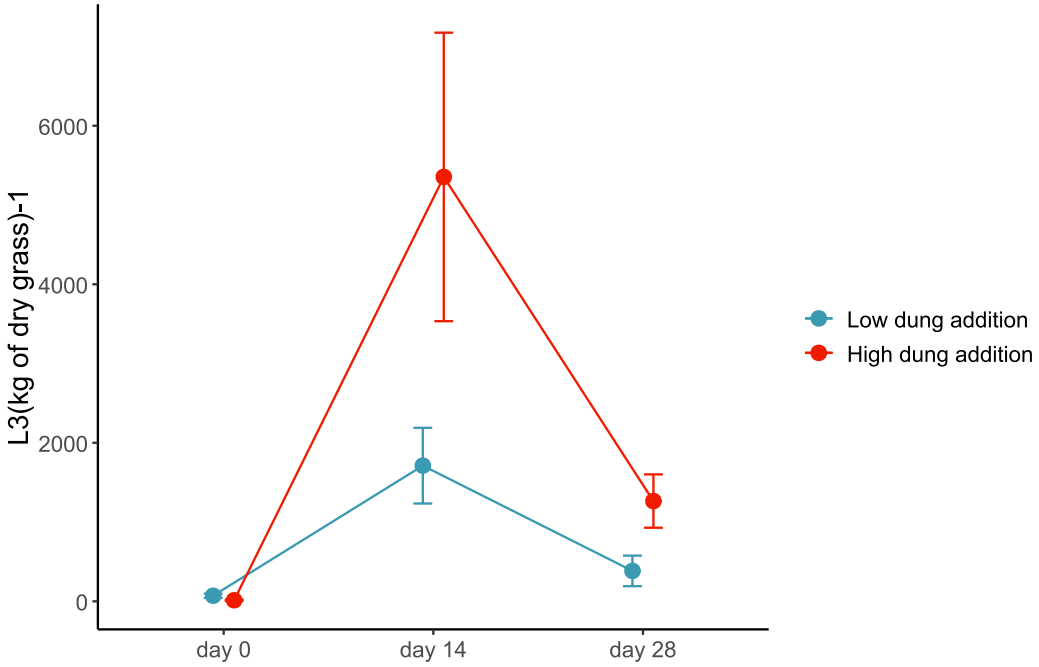
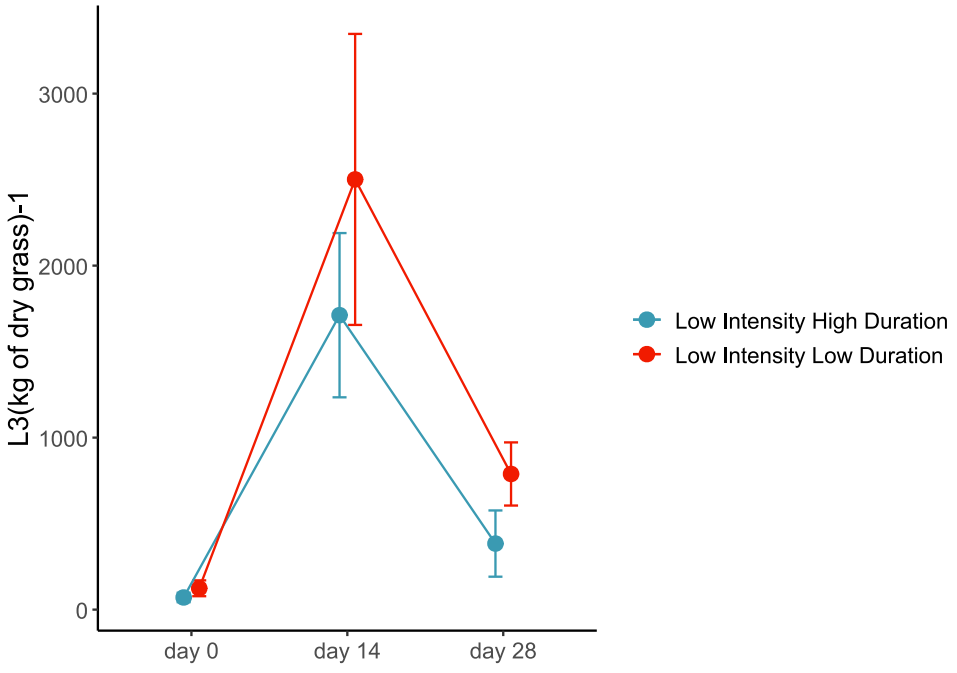


Figure A:S6: Average L3 (kg of dry grass)$^{-1}$ (Mean ± standard error) of Low Intensity Low Duration (LILD) treatments i.e., point and line in red color and Low Intensity High Duration (LIHD) i.e., point and line blue color. The graph demonstrates the impact of long migrant duration on GIN density in a grass patch.



Appendix B: Supplementary materials for chapter 3

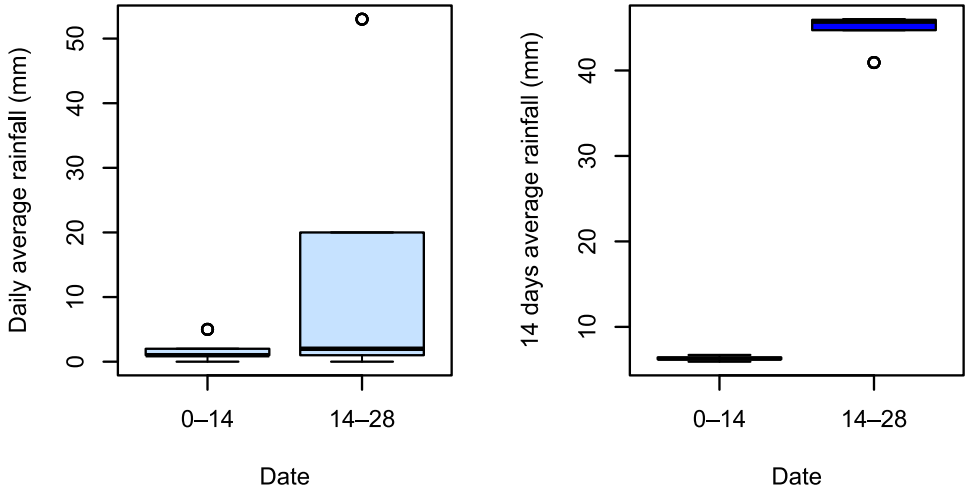


Figure B:S1: Distribution of daily mean rainfall (left) and 14 days average rainfall (right) across the experiment period. Daily mean rainfall represents distribution of average rainfall in 24 hours period across days 0-14 and day 14-28, while 14 days average rainfall represent distribution of average daily rainfall for the previous 14 days for the period of day 0-14 and 14-28.

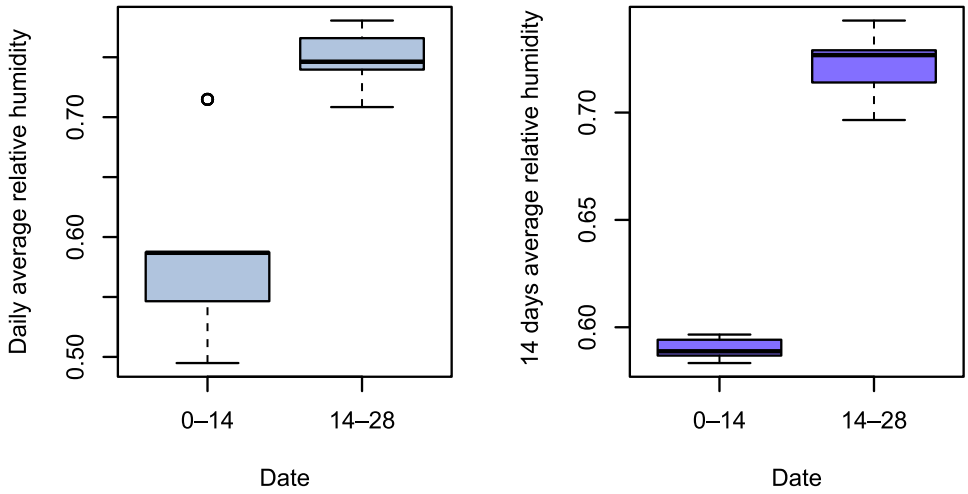


Figure B:S2: Distribution of daily mean humidity (left) and 14 days average humidity (right) across the experiment period. Daily mean humidity represents distribution of average humidity in 24 hours period across days 0-14 and day 14-28, while 14 days average humidity represent distribution of average daily humidity for the previous 14 days for the period of day 0-14 and 14-28.

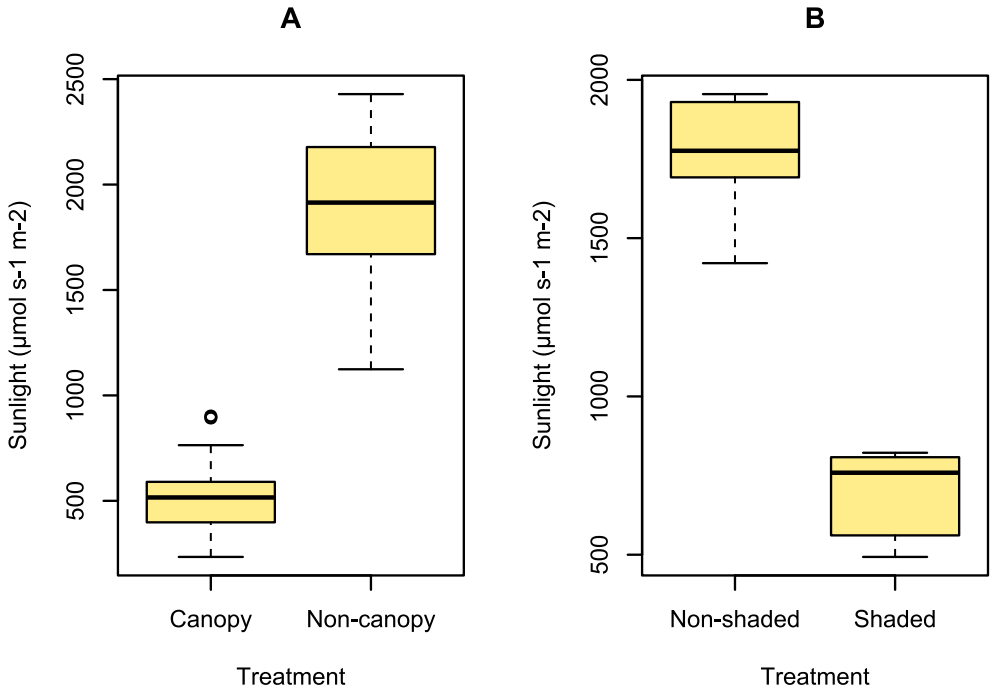


Figure B:S3: Variation of sunlight radiation between area under tree canopy and non-canopy area from field survey (Fig. A). Variation of sunlight radiation between area shaded area and non-shaded area from experiment manipulation (Fig B).

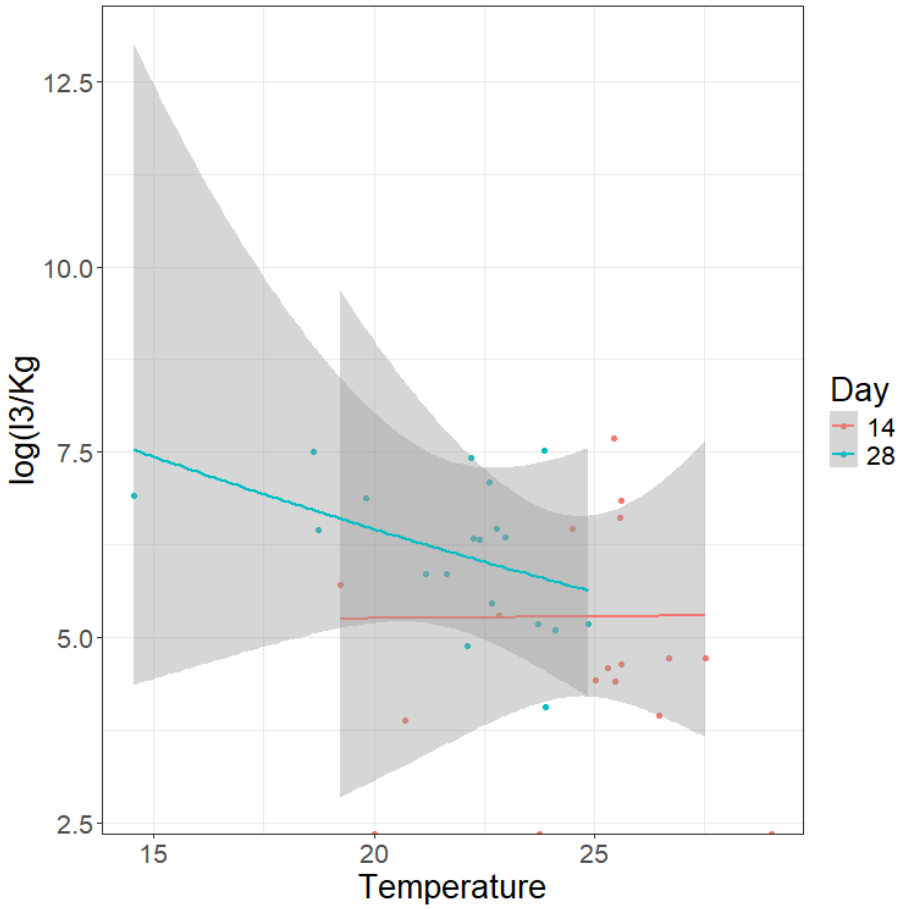
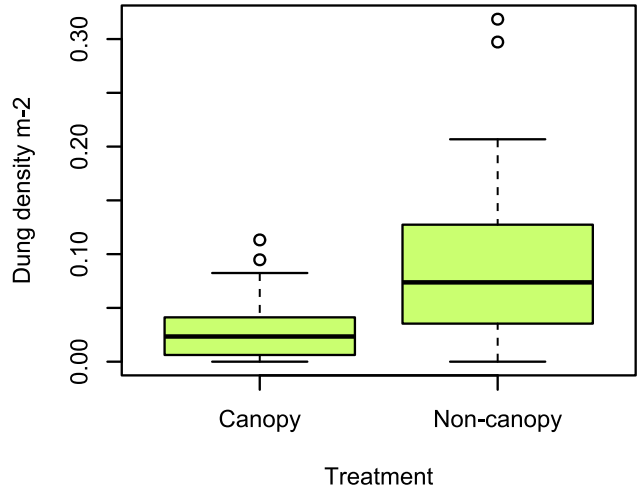


Figure B:S4: Variation of density of larvae recovered during dry and wet conditions, where red line = Day 14 represents recovered larvae during dry conditions, while blue line = day 28 represent recovered larvae during wet conditions. Where x - axis represents average temperature during morning hours (pasture clipping time).



Appendix B:S5: Variation of dung density per sq-meter of ruminant herbivores under tree canopies versus non-canopy areas from a field observational survey in Serengeti National Park, Tanzania.