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

Houssein Samwel Kimaro [a,b,*], Jennifer Mclntyre [a], Vanessa O. Ezenwa [c], Ricardo M. Holdo [d], Jason Donaldson [e], J. Grant C. Hopcraft [a], Thomas A. Morrison [a]

[a] School of Biodiversity, One Health and Veterinary Medicine, University of Glasgow, UK
[b] College of African Wildlife Management, Mweka, Tanzania
[c] Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT 06511, USA
[d] Odum School of Ecology, University of Georgia, Athens, GA 30602, USA
[e] Nicholas School of the Environment, Duke University, Durham, NC 27708, USA

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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 gastrointestinal nematodes (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 the 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.

1. 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 and 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 and Poulinb, 1995; Donaldson et al., 2024; Patterson and 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 and Hoye, 2014; Donaldson et al., 2024). Trophic effects can involve consumer-resource interactions that directly suppress parasites spread

* Corresponding author at: School of Biodiversity, One Health and Veterinary Medicine, University of Glasgow, UK.
E-mail addresses: 2715776k@student.gla.ac.uk, kimaro.martin@yahoo.com (H.S. Kimaro).

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between two host species when one host consumes parasites (Fig. 1), or infected hosts, and removes them from an area i.e., direct trophic effects (Bauer and 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 and 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 specialization 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 magnitude of trophic effects. For example, the arrival of large herds or the prolonged stay of migratory ungulates in an area can introduce a larger number of parasites (transport effect) and alter vegetation through herbivory and trampling (trophic effects). In parasites with environmental life stages, such as gastrointestinal nematodes (GIN), these vegetation changes may concentrate or dilute the abundance of parasites (Bauer and 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).

The trophic effects of migratory herbivores on fecal-oral transmitted parasites could be complex and depend on climatic conditions and grazing intensity (Figs. 1 and 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 and Todd, 1964; van Dijk and Morgan, 2011). Subsequent grazing by dense herds of migrants should affect the infection risk for other hosts in three possible ways (Figs. 1 and 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) 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). 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). 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

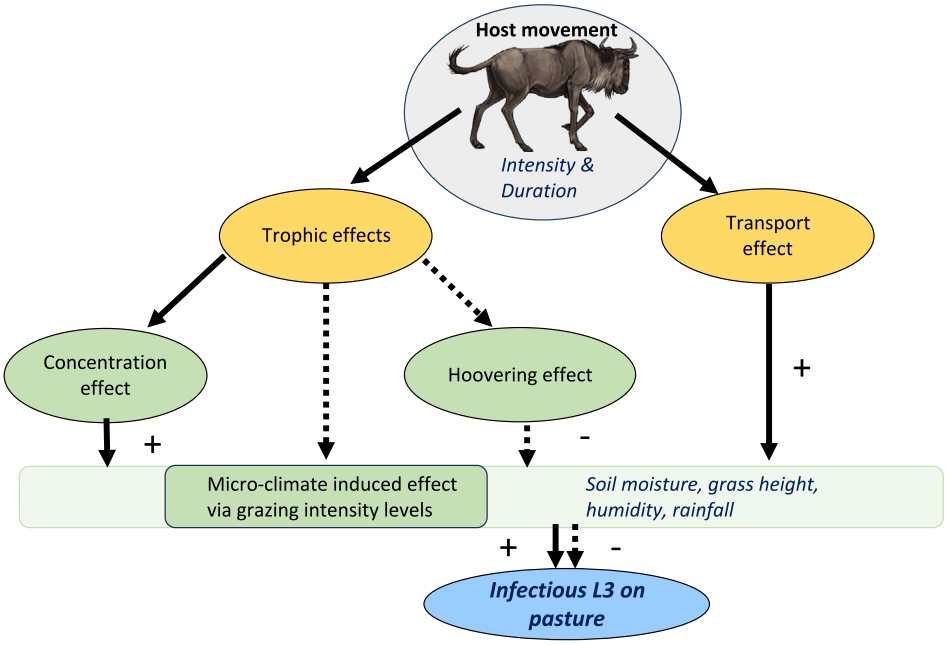

Fig. 1. A conceptual framework of the direct and indirect ways that host movement, via variation in intensity and duration, can modify infectious L3 abundance in the environment. Yellow boxes represent the two main effects of host movement i.e., transport and trophic effects. Green boxes represent three 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. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

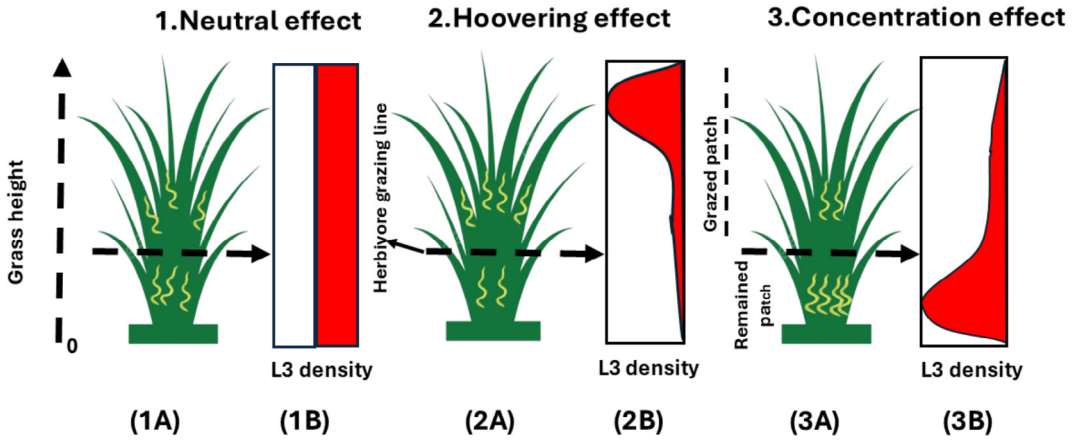

Fig. 2. Conceptual framework showing the interplay between grazing and parasite distribution in grass patches that can result in three possible trophic effects: (1A, 1B) Neutral effects, (2A, 2B) Hoovering effects and (3A, 3B) Concentration effects. Larvae distribution is depicted as yellow squiggles and red frequency distribution, while the grazing depth is depicted by the horizontal arrow. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

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.

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 gastrointestinal nematode. 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. 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. Materials and methods

2.1. 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 subtropical 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 and 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 and 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.

2.2. 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 × 3 m in size (Appendix S1). Treatments and L3 sampling occurred in the central 2 × 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. 3 and Table 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. 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 2 × 2 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 2 × 2 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

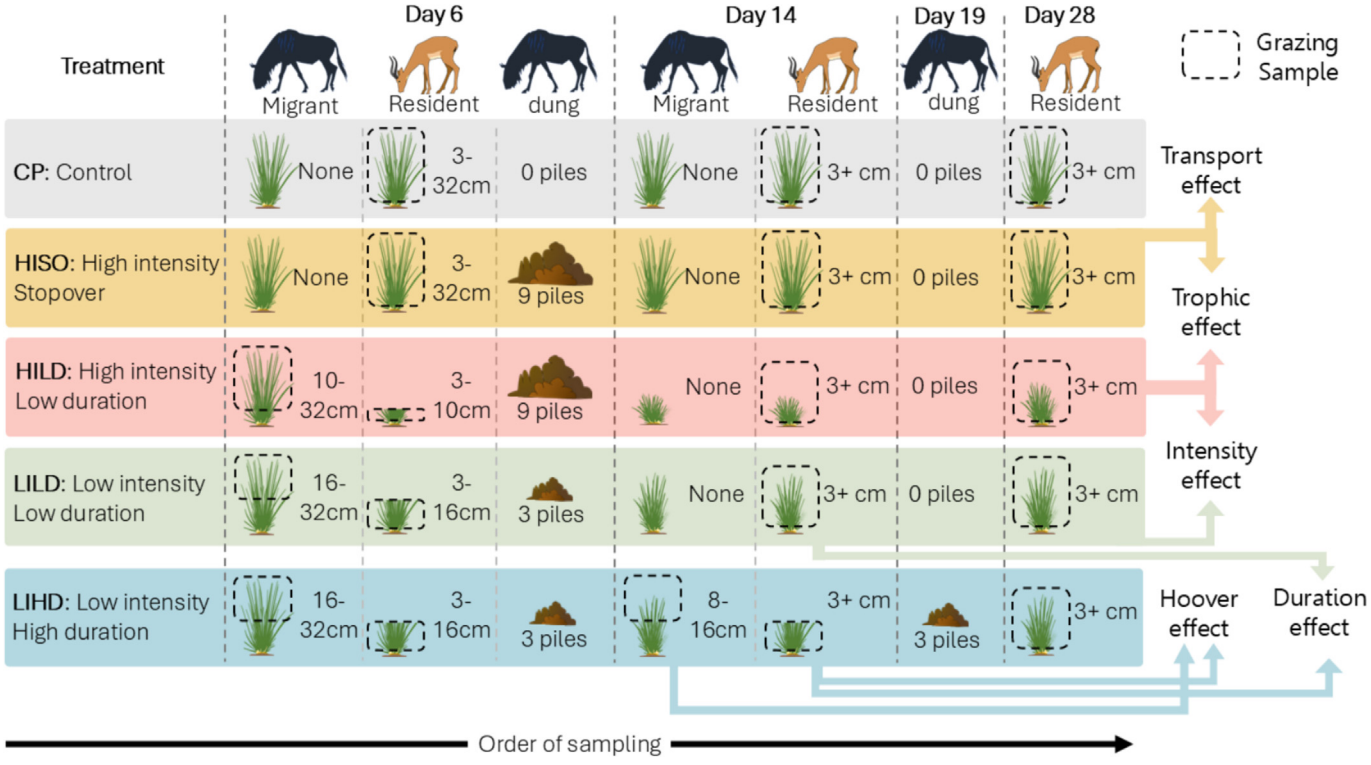

Fig. 3. Experimental design of the simulated grazing and dung addition and their impacts on the abundance of 3rd stage larvae (L3) of ruminant gastrointestinal nematodes in pasture. The experiment allowed testing of five separate effects through comparisons of different treatments, as indicated on the 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.

Table 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 and 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

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 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. 3). We used a random number generator to identify random *x*–*y* locations within the inner 2 × 2 m 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.

2.4. 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. 3 and Table 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 and Owen-Smith, 2002; McNaughton, 1976), then clipped the bottom part of the grass to form a "resident exposed" sample (Gwynne and 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. 3 and Table 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.

2.5. 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 and 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× 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.

2.6. 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.

2.7. 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 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).

2.8. 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.

3. Results

3.1. 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. 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. 4, Table 2, Appendix 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. 4 and Table 3). *Post-hoc* tests showed that on Day 14, there was a significant difference between all treatments (Table 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 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 3, Appendix 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 3, Appendix S6).

3.2. 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, Fig. 5), suggesting a hoovering effect from migrants (Fig. 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, Fig. 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, Fig. 5).

4. 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-

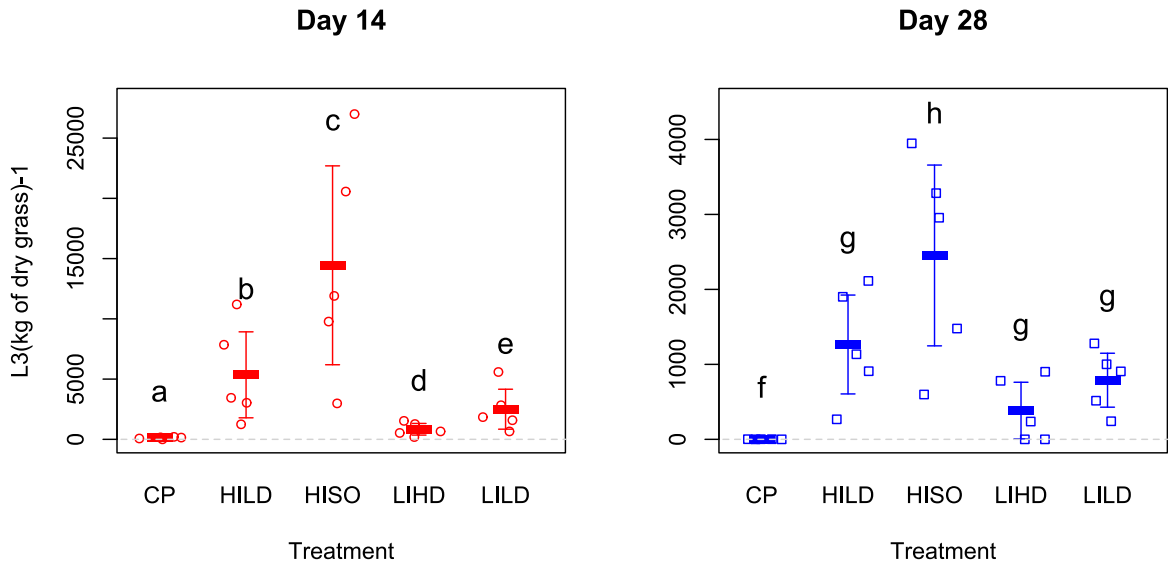

Fig. 4. Observed parasite densities (L3 per kilogram of dry grass biomass) across experimental treatments (CP: Control plot, HILD: High Intensity Low Duration, HISO: High Intensity Stop-over, LIHD: Low Intensity High Duration and LILD: Low Intensity Low Duration) on Day 14 and 28. Bars indicate mean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

Table 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***

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. 5). In the same way, using field grazing experiments, previous studies have reported a large reduction of L3s in pasture (i.e., ≥80 % reduction

Table 3
Post hoc Tukey analysis of differences between treatments on L3 abundance on Day 14 and Day 28 (*c.f.* Fig. 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***	−3.6	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

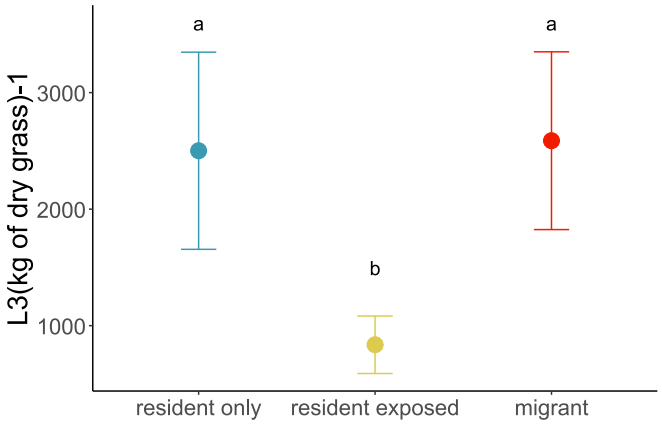

Fig. 5. Mean density (±standard error) of L3 (kg of dry grass)$^{-1}$ across 3 types of pasture samples collected 14 days after experimental dung addition. Resident-only samples (blue) represent parasite conditions when resident hosts graze in an area without any grazing by migratory hosts (c.f. Fig. 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. Fig. 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. Fig. 3, Low intensity high duration treatment on Day 14). Different letters show significant differences among the treatments from post-hoc Tukey tests. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

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). 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 and Sheath, 2008; Moss and 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 and 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 fecal addition (HILD) had shorter grass height (10 cm) than in plots with high intensity fecal 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 fecal 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 and 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. 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), 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. 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). This evidence demonstrates the importance of incorporating trophic effects (Figs. 3 and 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 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 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.

CRediT authorship contribution statement

Houssein Samwel Kimaro: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Jennifer McIntyre:** Writing – review & editing, Supervision, Project administration, Methodology, Formal analysis, Data curation, Conceptualization. **Vanessa O. Ezenwa:** Writing – review & editing, Visualization, Validation, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Ricardo M. Holdo:** Writing – review & editing, Visualization, Validation, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Jason Donaldson:** Writing – review & editing, Validation, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **J. Grant C. Hopcraft:** Writing – review & editing, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Thomas A. Morrison:** Writing – review & editing, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Appendix A. Supplementary material

Supplementary material to this article can be found online at https://doi.org/10.1016/j.ijpara.2025.08.014.

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