ENVIRONMENTAL DRIVERS OF PARASITIC NEMATODE DYNAMICS IN WILD UNGULATES IN THE SERENGETI NATIONAL PARK

by

BASIL CHIRAYE SENSO

(Under the Direction of Ricardo Holdo)

ABSTRACT

Parasite infections in host populations frequently display seasonal patterns that can shape host behavior, fitness, and population dynamics. Despite recognition that seasonality plays a key role in infection dynamics across numerous host-parasite systems, the drivers of seasonal infection dynamics for different parasite life histories are often unknown. This lack of system-specific understanding restricts our ability to predict when and why parasite infections and their cascading effects on host populations will have the greatest impact. We investigated how seasonality and its associated environmental variables are related to the infection intensity of two parasitic nematodes with contrasting life cycle strategies: strongyle nematodes (direct life cycle) and lungworms (indirect life cycle). We conducted the study in two free-ranging ungulate species in Serengeti National Park, Tanzania: Coke's hartebeest (Alcelaphus buselaphus) and topi (Damaliscus lunatus). We found a high prevalence of both parasites, with strongyle nematodes occurring in 95.5% of hartebeest and 93.1% of topi, and lungworms occurring in 100% of hartebeest and 99.7% of topi. Strongyle infection intensity peaked in the wet season but showed no strong association with precipitation, temperature, or animal density at the likely time of infection. In contrast, lungworm intensity peaked in the dry season and was associated negatively

with precipitation and positively with animal occupancy. Our results highlight the importance of interactions between parasite life cycle and environmental variables in shaping seasonal infection patterns. Identifying when parasite intensities are highest is critical for predicting when hosts are under the greatest ecological pressure due to parasitism.

INDEX WORDS: Parasite seasonal dynamics, Gastrointestinal nematodes, Lungworms, Alcelaphine, Tropical savanna

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B.S., Sokoine University of Agriculture, Tanzania, 2020

A Thesis Submitted to the Graduate Faculty of The University of Georgia in Partial Fulfillment of the Requirements for the Degree

MASTER OF SCIENCE

ATHENS, GEORGIA

2025

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August 2025

ACKNOWLEDGEMENTS

I would like to express my deepest gratitude to my advisory committee, Dr. Ricardo Holdo, Dr. Jason Donaldson, and Dr. Vanessa Ezenwa, for their invaluable guidance, support, and feedback throughout my academic program. Their mentorship has been instrumental in shaping my growth as a researcher and scholar. I am also grateful to the members of Dr. Holdo's lab group (2024-2025) for their insightful comments and discussions, as well as the Odum School of Ecology community at the University of Georgia for fostering a collaborative and inspiring academic environment.

I extend my sincere thanks to Jeremiah Sarakikya, Norbert Munuo, Megan Gomes, Jumapili Chenga, and Merito Katei for their field support, and to Aidan Trentinus, Hussein Adam, Peace Sabuni, and Mary Zebedayo for their help in the lab. I am particularly thankful to Dr. T. Michael Anderson for providing the camera trap data, which was critical to this research. I also acknowledge the research support provided by collaborators at the University of Glasgow, whose expertise and resources greatly enhanced this study.

I thank Dr. Emmanuel Masenga, the Tanzania Wildlife Research Institute (TAWIRI), Tanzania National Parks (TANAPA), and the Tanzania Commission for Science and Technology (COSTECH) for granting research permits and providing field logistical support, which made this work possible. Finally, I would like to acknowledge the financial support provided by the USDA NIFA grant #2021-67015-33407, which funded this research.

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CHAPTER 1

ENVIRONMENTAL DRIVERS OF PARASITIC NEMATODE DYNAMICS IN WILD UNGULATES IN THE SERENGETI NATIONAL PARK[1]

[1]Basil Chiraye Senso, Jason Donaldson, T. Michael Anderson, Aidan Trentinus, Vanessa Ezenwa, and Ricardo Holdo. To be submitted to the International Journal for Parasitology.

1. INTRODUCTION AND LITERATURE REVIEW

Parasites play a crucial role in ecosystems by influencing host behavior and increasing vulnerability to predation (Dobson, 1988; Hudson et al., 1992; Packer et al., 2003; Poulin, 1994), as well as altering host fitness by reducing host fecundity or increasing mortality, thereby impacting host population dynamics (Hudson et al., 1998; Tompkins et al., 2002). However, parasite dynamics are shaped by a complex interplay of external environmental drivers such as precipitation, temperature, resource availability, and host density, with seasonality playing a fundamental role in infection patterns (Altizer et al., 2006; Habig et al., 2021; Kołodziej-Sobocińska, 2019; Poulin, 2020). Understanding why seasonal infection patterns manifest and how they change across different host-parasite systems is key to understanding when parasites should matter most to ecosystem function.

Seasonal precipitation is essential for maintaining moist conditions, which are required for the survival and development of free-living stages of some parasites. For example, gastrointestinal nematodes (commonly strongyle nematodes, Family Trichostrongylidae) and lungworms (Family Protostrongylidae) are two major groups of parasitic nematode infecting mammals that persist in the external environment (e.g., dung, soil, pasture) for a significant portion of their life cycles (Taylor et al., 2015). Trichostrongylids (hereafter referred to as ‘strongyles’) have a direct life cycle requiring only one host. Female adult worms lay eggs in the gut which are passed in the host feces and hatch into first-stage larvae (L1), which then undergo two molts to become the infective third-stage larvae (L3). L3 must survive on the pasture until they are ingested by a grazing host, where they then penetrate the gut lining, molt further, and

mature into adult worms (Fig. 1). Protostrogylids (hereafter referred to as 'lungworms'), on the other hand, have indirect life cycles whereby female adult parasites in the bronchi produce eggs that hatch into L1, which are coughed up, swallowed, and passed in host feces. L1 penetrates an intermediate host such as terrestrial gastropod, where they develop into L2 then L3. Infection occurs through the ingestion of infected gastropods. After ingestion, larvae penetrate the intestinal wall and migrate via the circulatory system reaching the lungs where they mature (Fig. 2). These groups of parasites, rely on moist conditions for eggs hatching, larvae development, preventing desiccation and facilitating the motility of larvae from dung to pasture (O'Connor et al., 2007, 2006; Stromberg, 1997; Wang et al., 2014).

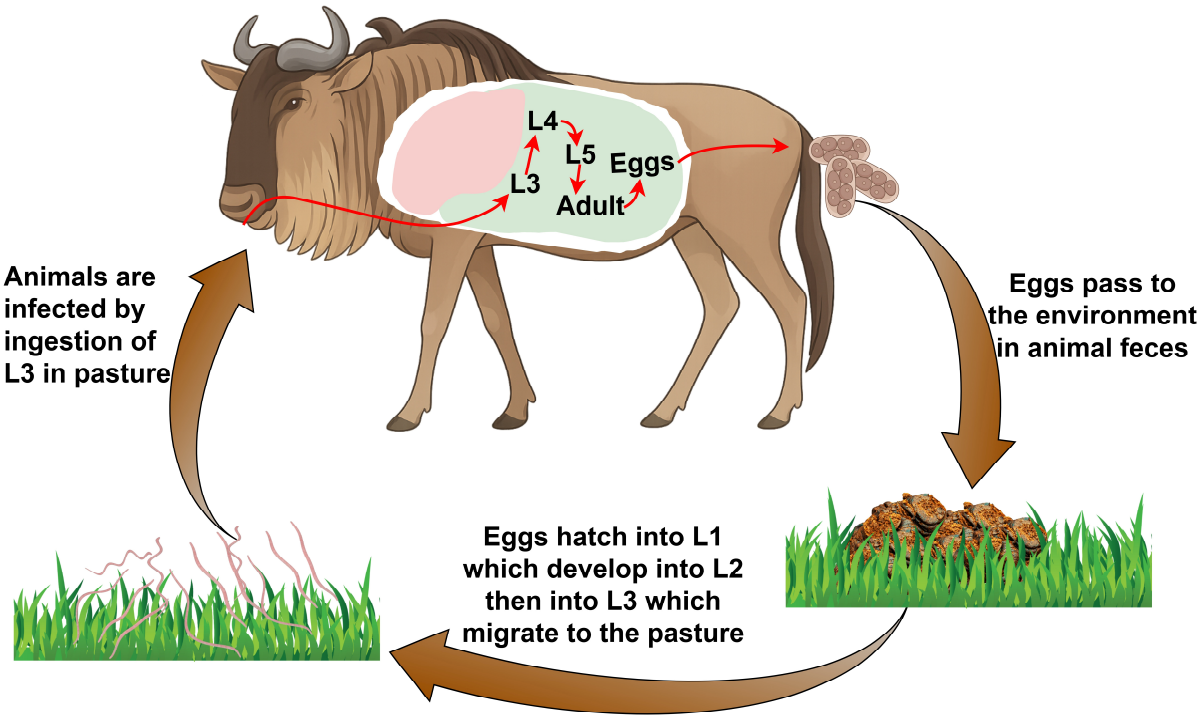

Figure 1: The life cycle of strongyle nematodes in ungulate host. The diagram illustrates the parasite's development from ingestion of infective larvae by the host, through maturation and egg production within the gastrointestinal tract, to the release of eggs in feces and subsequent development into infective larvae in the environment.

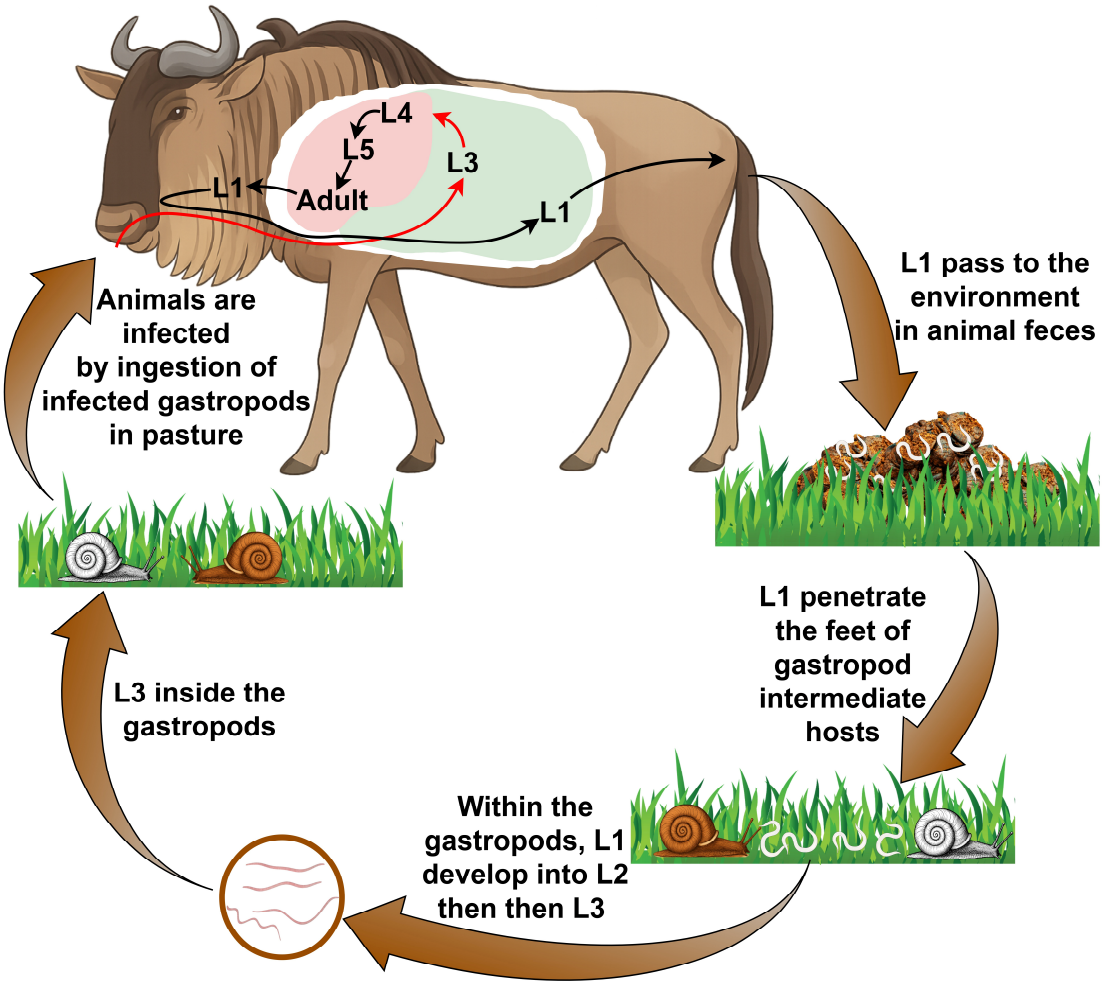

Figure 2: The life cycle of lungworms in ungulate host. The diagram illustrates the parasite's development from ingestion of infective larvae, either free-living or within an intermediate host such as a terrestrial gastropod. After ingestion, larvae penetrate the intestinal walls and migrate via the circulatory system to the lungs, where they mature and produce eggs that hatch into L1, which are then coughed up, swallowed, and passed in host feces. L1 development to the infective stage occurs either directly in the environment or indirectly within the gastropod intermediate hosts.

Seasonality also shapes resource availability for host species, which in turn affects host density and movement patterns (Bohrer et al., 2014; Boone et al., 2006; Winnie et al., 2008) with repercussions for parasite transmission. For example, in tropical and subtropical climates, distinct wet (rainy) and dry seasons (Norton-Griffiths et al., 1975; Pereira et al., 2024; Sinclair et al., 2007) strongly affects forage availability for herbivores, which can disperse more widely in the wet season when food is abundant than in the dry season when resource scarcity forces animals to congregate around limited resources, including water (Macandza et al., 2012; Saltz et al., 2023). This should change parasite infection risk when higher herd densities in the dry season increase the chance of exposure to shared parasites than when herds are widely dispersed (Thurber et al., 2011; Titcomb et al., 2021). Furthermore, seasonal nutritional stress, which is more pronounced in dry periods due to declining forage availability and quality, can compromise immune function and increase host susceptibility to infections (Ezenwa, 2004; Shearer and Ezenwa, 2020). These patterns highlight the importance of examining specific mechanisms when investigating how seasonal drivers influence parasite dynamics in animal populations.

Temperature on the other hand influences parasite survival and development by regulating the physiological processes of both parasites and their intermediate hosts (Kutz et al., 2013, 2005). Free-living parasite stages are particularly sensitive to temperature fluctuations, as their viability outside the host depends on thermal thresholds that determine survival and infectivity (Van Dijk and Morgan, 2008). Warmer temperatures can accelerate parasite eggs development, hatchability and larval survival, while extreme temperatures can limit development and increase mortality (O'Connor et al., 2006; Van Dijk and Morgan, 2008). However, the influence of temperature on parasite survival and development is highly variable, as different

species exhibit distinct thermal tolerances and adaptations to their respective environments (Aleuy et al., 2023; Aleuy and Kutz, 2020; O'Connor et al., 2006).

The impact of seasonality on parasite transmission may also depend on parasite life cycle strategies. Some studies suggest that changes in environmental conditions should have more impact on parasites with indirect lifecycles because there are higher probabilities that some of their obligate hosts would go extinct due to disruption of their natural habitats (Dobson et al., 2008; Rohr et al., 2011). For instance, Wood et al. (2023) investigated a century-long record of parasite abundance in marine fish and found significant declines in parasite taxa, particularly those with complex life cycles involving three or more hosts. These declines were strongly associated with rising sea surface temperatures, suggesting that climate change may disproportionately affect parasites with indirect lifecycles by disrupting the stability and availability of their required host species (Wood et al., 2023). It has been shown, however, that parasites with direct lifecycles, such as gastrointestinal nematodes, are more sensitive to environmental changes because their free-living stages depend entirely on the environment for development (Molnár et al., 2013). These parasites tend to exhibit rapid development in favorable conditions, but their free-living stages are vulnerable to environmental extremes such as hot dry conditions (O'Connor et al., 2006). Conversely, the intermediate hosts of indirectly transmitted parasites like lungworm can extend the survival of free-living parasite stages in the environment by providing temporal buffers (Hoberg, 2010; Molnár et al., 2013). Intermediate hosts such as gastropods are also more effective than free-living parasites at moving to microhabitats that regulate ambient environment conditions, allowing parasites to avoid environmental extremes (reviewed in Aleuy and Kutz (2020)).

Here, we studied the seasonality of strongyles and lungworms in two closely related large ungulate hosts—Coke's hartebeest (*Alcelaphus buselaphus cokii*) and topi (*Damaliscus lunatus jimela*)—in a highly seasonal savanna ecosystem, the Serengeti National Park, Tanzania. Wild ungulates serve as effective models for understanding host-parasite interactions in complex, real-world environments because of their broad geographic distribution, diversity, and abundance of species (Jolles and Ezenwa, 2015). Likewise, the broad host range of Trichostrongylid and Protostrongylid nematodes across ungulate species (Moulton and Sachs, 1970; Ortlepp, 1962; Van Wyk and Boomker, 2011; Walker and Morgan, 2014), makes these parasites an ideal starting point for understanding how parasite life cycle interacts with seasonality to drive variation in infection patterns across host populations. Our first objective was to understand how the burdens of two parasites with different life cycles differ seasonally. Our second objective was to identify specific environmental variables (precipitation, temperature and animal density) associated with variation in infection patterns. Finally, our third objective was to explore potential mechanisms underlying these relationships, including assessing how environmental conditions may influence host exposure and susceptibility through changes in resource availability, grass height, or animal density (Fig. 3).

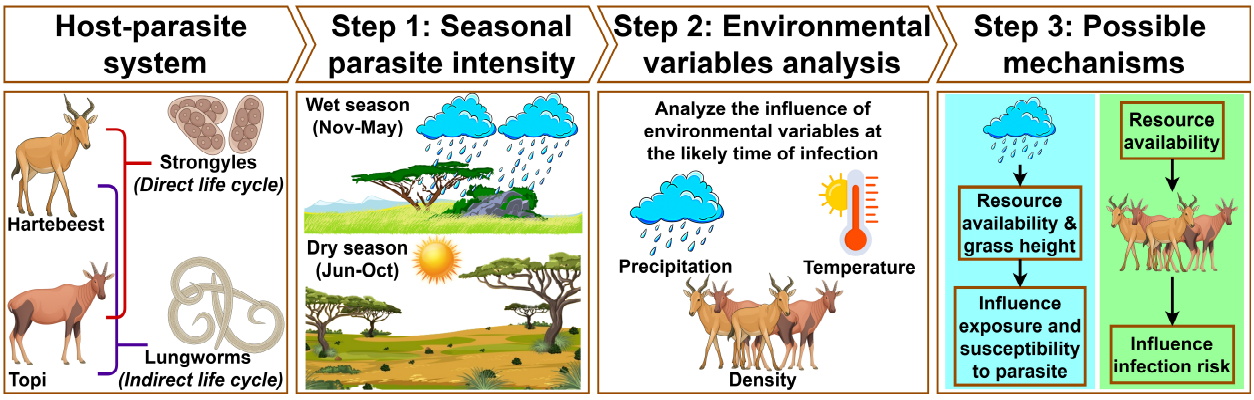

Figure 3: Conceptual framework of the study examining seasonal patterns and environmental drivers of parasite infection intensity in wild ungulates.

2. MATERIALS AND METHODS

Study site

This study was conducted in the Serengeti National Park ("Serengeti" hereafter) located between 33.9°E to 35.3°E and 3.3°S to 1.4°S in northern Tanzania. Serengeti is the ~25000 km^2 section of the Serengeti-Mara Ecosystem (Fig. 4a), which falls within the savanna biome (Sinclair et al., 2007). The most abundant grazing herbivores in Serengeti include blue wildebeest (*Connochaetes taurinus*), plains zebra (*Equus quagga*), Thomson's gazelle (*Eudorcas thomsonii*), African buffalo (*Syncerus caffer*), Coke's hartebeest (*Alcelaphus buselaphus cokii*) and topi (*Damaliscus lunatus jimela*) (Anderson et al., 2016; Beaudrot et al., 2020; Hopcraft et al., 2010). Mean annual precipitation ranges from less than 500 mm in the southeastern short-grass plains to over 1000 mm in the northwestern woodlands (Mahony et al., 2021; Norton-Griffiths et al., 1975).

Our core study area was the long-term Snapshot Serengeti (SS) camera trap grid located within the central Serengeti (Fig. 4b). The SS grid covers an area of 1,000 km^2 and comprises 151 camera traps deployed since 2010 to evaluate spatial and temporal dynamics of large predators and their preys (Anderson et al., 2016; Beaudrot et al., 2020; Swanson et al., 2015). Mean precipitation in the grid during the wet and dry season was 108.1 mm and 20.1 mm, respectively, with March 2023 being the wettest (172.2 mm) and July 2023 the driest (4.3 mm) months over the course of our study (Fig. 5). To attain broad sampling across space and to avoid over-sampling certain locations, we divided the grid into seven regions, which we visited monthly to collect animal fecal samples. In addition, we had 14 camera trap sites (between 1 and

4 sites per region) where we collected pasture samples monthly (Fig. 4b). Throughout the study, we monitored all 151 camera traps monthly to assess animal occupancy.

Our study is part of a broader project initiated in 2021 aiming to investigate how animal movement, particularly wildebeest migration, influences parasite transmission dynamics in the Serengeti ecosystem. The project includes five ungulate species: migratory blue wildebeest, and resident (non-migratory) species—topi, hartebeest, African buffalo and Grant's gazelle. The focal parasite group for the project is gastrointestinal nematodes due to their ability to infect multiple ungulate hosts (Walker and Morgan, 2014). For this study, we focus specifically on topi and hartebeest because of their close phylogenetic relationship to wildebeest (Georgiadis, 1995; Vrba, 1979) and because preliminary lab observations revealed that, in addition to gastrointestinal nematode eggs, lungworm larvae were commonly recovered from the fecal samples of these two species.

Sample collection

Fecal samples were collected to quantify parasite prevalence, infection intensity, and mean parasite abundance in the population. Sampling was carried out monthly by driving within the long-term Snapshot Serengeti (SS) camera trap. Individual animals of target species were observed until they defecated, at which time the observer drove over to the animal's location to collect a fresh sample. Only samples with a high degree of certainty of being fresh and from the species observed were collected. We collected at least 3 to 6 fecal samples per animal species per region within the grid. Samples were collected into zip-lock plastic bags, labeled, and put in a cooler box with icepacks. Date and time of collection, individual's location (longitude and latitude), group size, group ID (individuals from the same species and location) and when possible, the animal's sex was recorded. Sampling in all regions took approximately 7 to12 days,

with each region visited at most three times a month. Over the course of the entire study, 652 samples were collected, 334 from hartebeest and 318 from topi (Fig. 4b).

Pasture samples were collected monthly following the protocol as described in (Donaldson et al., 2023), modified from (Hansen and Perry, 1994). The samples were used to measure the percentage of grass leaf moisture as a proxy for host resource availability and quality. Resource availability can influence animal distribution and density (Bohrer et al., 2014; Winnie et al., 2008), impacting host exposure to parasites (Donaldson et al., 2023; Thurber et al., 2011). Additionally, resource quality can affect host body condition, which in turn influences host susceptibility to parasites (Ezenwa, 2004). Throughout the study period, a total of 168 pasture samples were collected.

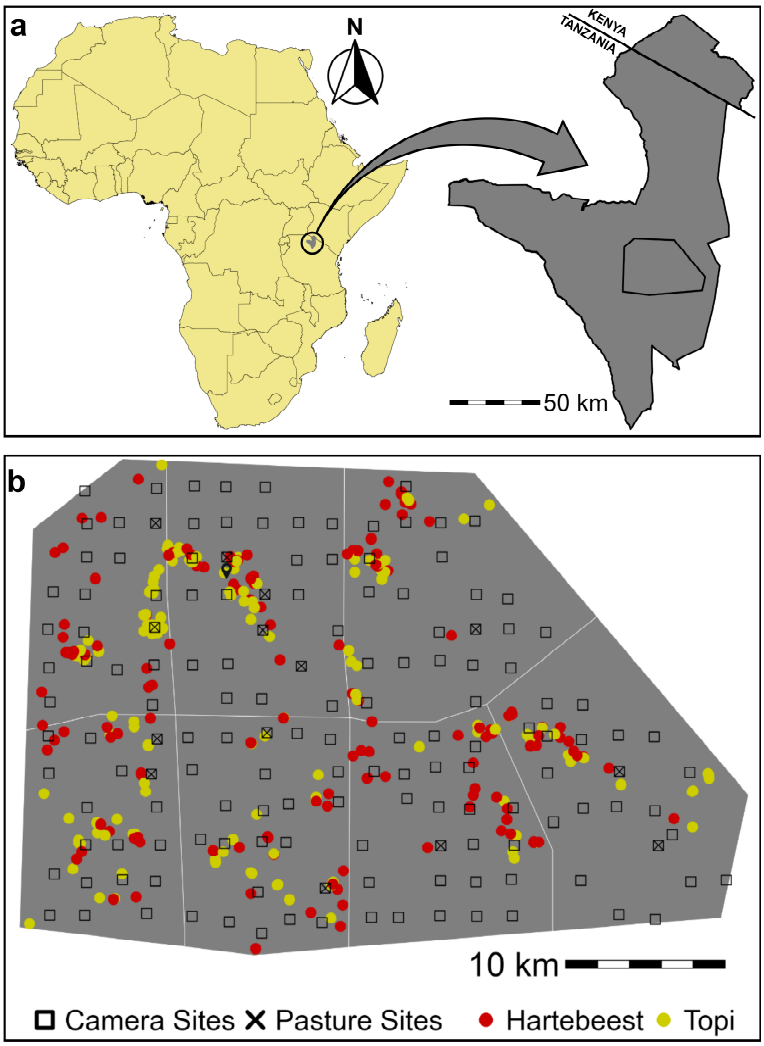

Figure 4: Study area in the Serengeti-Mara Ecosystem. (a) The ecosystem spans the Serengeti National Park in Tanzania and the Maasai Mara National Reserve in Kenya. The polygon in central Serengeti National Park marks the location of the Snapshot Serengeti (SS) camera trap grid. (b) A detailed view of the Snapshot Serengeti (SS) camera trap grid, showing 7 regions, 151 camera trap sites (black squares), 14 pasture samples collection sites (black squares with an x mark), 334 hartebeest fecal samples collection locations (red points), and 318 topi fecal samples collection location (yellow points). The black marker indicates the Serengeti Wildlife Research Centre laboratory, where all samples were processed.

Parasitological analysis

Samples were processed within 24 hours of collection. To quantify strongyle nematode egg output, we used a modified McMaster fecal egg counting technique (Ezenwa, 2003), and recorded the burden as strongyle eggs per gram of feces (EPG, hereafter "EPG"). To quantify the lungworm output, fecal samples were examined for the presence of the lungworm stage-one larvae (L1, hereafter "L1") using the beaker-modified Baermann technique (Snyder et al., 2015), then recorded as lungworm larvae per gram of feces (LPG hereafter "LPG"). EPG and LPG are the estimates of infection intensity in individual host species. For each host species and parasite group we also estimated prevalence as a proportion of infected individuals and mean parasite abundance as the total number of parasites counts (EPG or LPG) divided by the total number of hosts examined.

Environmental data

Data extraction processes were conducted using R v. 4. 4. 2 (R Core Team, 2024). We categorized seasons as wet (November-May) and dry (June-October) based on established precipitation patterns in the Serengeti (Mahony et al., 2021; Norton-Griffiths et al., 1975). This seasonal division matched the monthly precipitation data across all 151 camera trap locations (Fig. 3). We used the *chirps* package (de Sousa et al., 2020) to collect the Climate Hazards group Infrared Precipitation with Stations (CHIRPS) data, a daily precipitation data set with a 0.05° spatial resolution (Funk et al., 2015).

For each dung sample collection point we collected mean daily precipitation (mm/day) from CHIRPS, mean daytime land surface temperature (°C) and total animal occupancy data. Daytime land surface temperature data ("LST_Day_1KM" band) were retrieved from two MODIS satellites, Aqua ("MYD21A2" product for afternoon LST) and Terra ("MOD21A2"

product for morning LST) using *MODISTools* package (Hufkens, 2023), then calculating the average. Camera trap data from 151 sites were used to generate daily animal occupancy data, defined as the number of animal images for each individual species captured per day, which is used as a proxy for animal density. Only images of the same species taken at least 10 minutes apart at the same site were kept to reduce double-counting (Palmer et al., 2017). Using the *gstat* package (Gräler et al., 2016; Pebesma, 2004), we performed Inverse Distance Weighting (IDW) interpolation with an inverse distance power (idp) of 1 to estimate animal occupancy (log transformed) for each host species at each dung collection point (Fig. 6). For all environmental and animal occupancy covariates, we calculated mean or summed values over a time window corresponding to our best estimate of the time from when animals likely ingested the infective stages in the environments to the point of adult egg or larval production. We assumed that the period from ingestion to collection was 2-4 weeks for strongyle nematodes and 5-10 weeks for lungworms (Taylor et al., 2015).

For pasture sample collection sites, we recorded monthly animal occupancy for each study species, grass height (cm), grass wet weight (on day of collection) and grass dry weight (after drying for at least 10 days). Percentage grass leaf moisture was calculated as [(wet weight − dry weight) / wet weight] × 100 %. We also extracted the mean daily precipitation (mm/day) for each site two weeks before pasture collection to evaluate its influence on grass height, grass moisture, and animal occupancy.

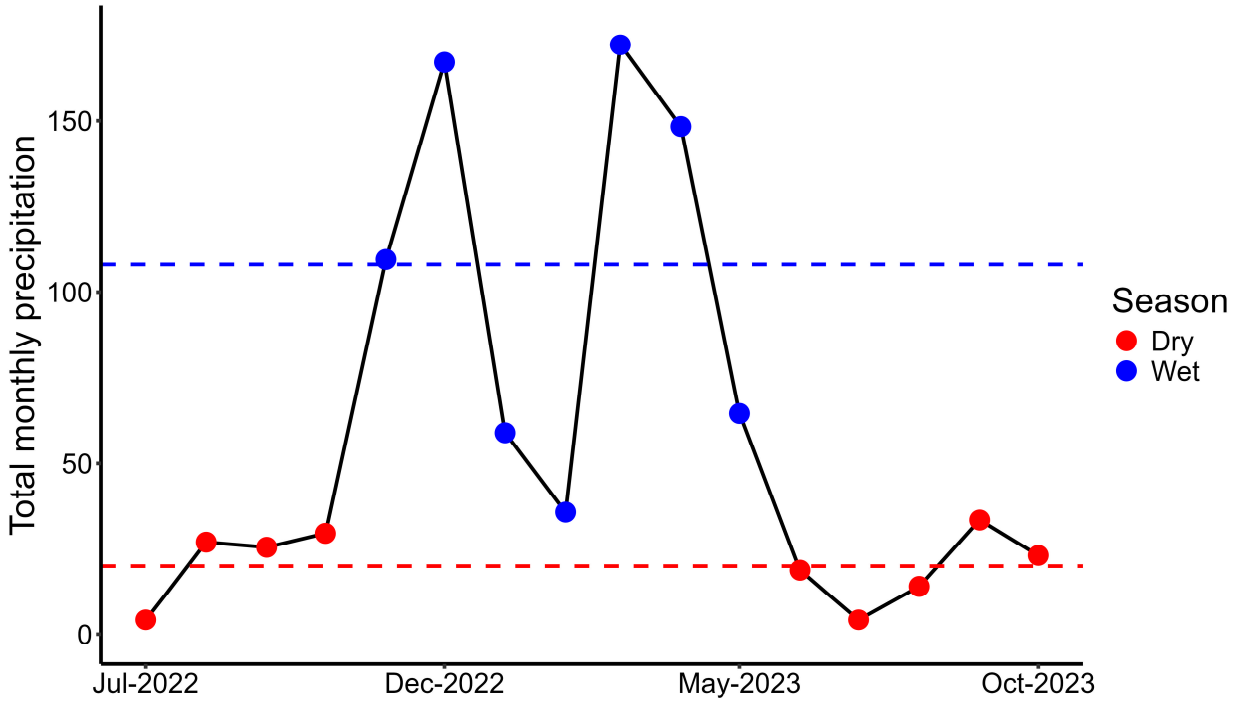

Figure 5: Precipitation trend in the Snapshot Serengeti (SS) grid from July 2022 to October 2023, covering the study duration (October 2022 to September 2023). Each point represents the monthly precipitation averaged across all the CHIRPS cells within the SS grid. The dashed lines represent the seasonal mean precipitation in the grid.

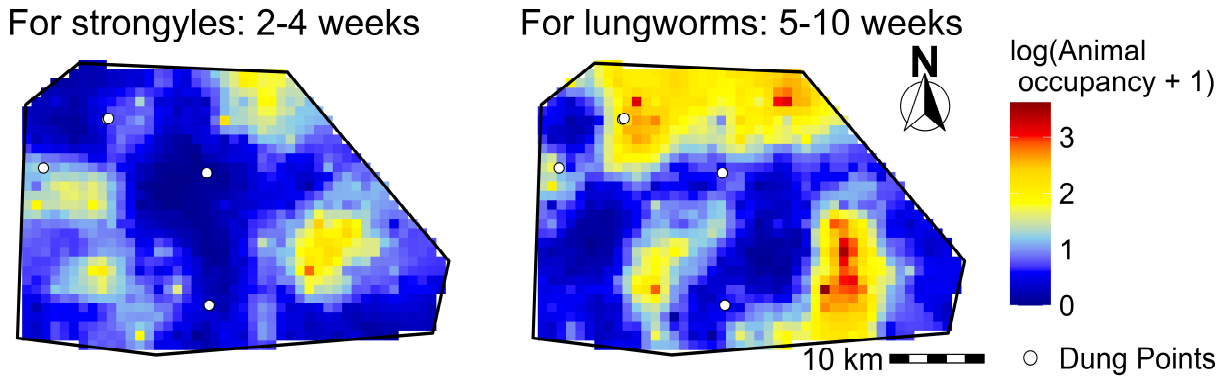

Figure 6: Example of IDW interpolated occupancy values corresponding to hartebeest fecal samples collected on 5th December 2022. The heatmaps represents hartebeest occupancy in the whole study area during the likely time of infection by parasites.

Statistical analysis

To evaluate the influence of environmental factors on parasite infection rates, we performed a series of analyses using R software v. 4. 4. 2 (R Core Team, 2024). We compiled the following datasets: fecal strongyle EPG count, fecal lungworm LPG count, season, mean daily precipitation 2-4 weeks and 5-10 weeks before sample collection, mean daytime temperature 2-4 weeks and 5-10 weeks before sample collection, log transformed total animal occupancy 2-4 weeks and 5-10 weeks before sample collection, and animal group ID. We log transformed the response variables: log(lungworm LPG + 1) for lungworm infection and log(strongyle EPG + 1) for strongyles infection, then fit linear mixed models (LMM hereafter "LMM") using the *glmmTMB* package (Brooks et al., 2017). Log transformation reduced the skewness of the response variables making the distribution closer to normal (Fig. 7). A value of 1 was added to avoid taking the logarithm of zero (which is undefined) accounting for the observations with zero parasite counts.

We first assessed the overall effect of season by fitting LMM for each parasite group and host species with the season as a predictor variable and animal group ID as a random effect which accounted for the individual samples from the same species, collected on the same date and location. Second, we assessed the influence of environmental variables (precipitation, temperature and animal occupancy) collected at the likely time of infection. Before fitting the models, we checked for the presence of multicollinearity among the predictors using variance inflation factor (VIF) analysis. Separate models for each ungulate species and parasite group were fitted in several combinations: single predictor, two predictors in additive and interactive models, and all predictors in an additive model. All models included the animal group ID as a random effect. Then, we compared these models for each ungulate host species and parasite

group using Akaike's Information Criteria (AIC), selecting the best-fitting model *i.e.*, the one with the lowest AIC score (Sakamoto et al., 1986). All selected models were checked for the presence of spatial autocorrelation using Moran's I test. We recognized that both spatial and temporal autocorrelation could potentially be present in residuals, but we focus on spatial autocorrelation because the time series had many missing values and is therefore difficult to examine for temporal autocorrelation.

In cases where associations were observed between parasites and environmental variables, we explored the underlying processes. These include associations between precipitation and grass height, precipitation and animal food availability, and food availability and animal density. We compiled monthly summed animal occupancy for each study species, mean daily precipitation (mm/day) for two weeks before pasture sample collection, grass height (cm), and percentage grass leaf moisture data from 14 pasture sampling sites. We then fit a LMM of grass height (cm) as a function of precipitation, a LMM of grass leaf moisture as a function of mean precipitation, and a generalized linear mixed model (GLMM) of monthly animal occupancy as a function of grass leaf moisture, assuming a negative binomial distribution. Both models included pasture sites as a random effect.

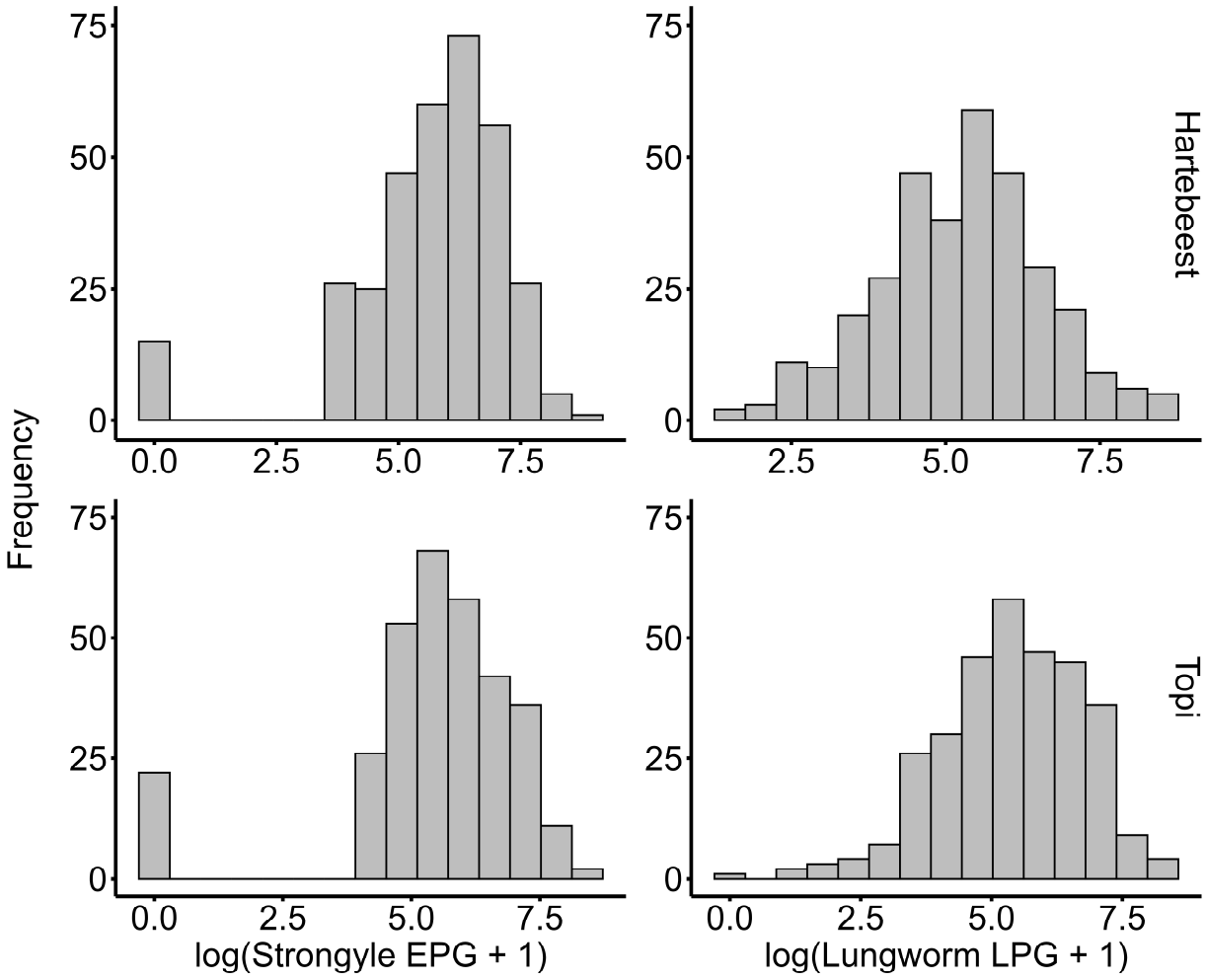

Figure 7: Histograms of log-transformed parasite infection intensity for hartebeest and topi. The first column shows strongyle infection intensity, and the second column shows lungworm infection intensity.

3. RESULTS

Strongyle nematode eggs were detected in 95.5% of hartebeest samples (n = 334) and 93.1% of topi samples (n = 318), with mean infection intensities (mean ± standard error [se]) of 616 ± 39 EPG and 509 ± 34 EPG, respectively. Lungworm first-stage (L1) larvae occurred in 100% of hartebeest and 99.7% of topi samples, with mean infection intensities (mean ± se) of 434 ± 38 LPG and 452 ± 33 LPG, respectively. Parasite infection intensity was strongly associated with season in both host species. Strongyle infection intensity was high during the wet season and low during the dry season, but we observed the opposite for the lungworms where infection intensity was high in the dry season (Table 1, Fig. 8).

Table 1: Parameter estimates for the relationship between parasite infection intensity and season for hartebeest and topi in Serengeti National Park.

Host species	Parasite	Season (Wet)		
		Estimate	Std. Error	P-value
Hartebeest (n = 334)	Strongyle	0.53	0.21	0.012
	Lungworm	-0.53	0.20	< 0.01
Topi (n = 318)	Strongyle	0.73	0.23	< 0.01
	Lungworm	-0.41	0.21	0.049

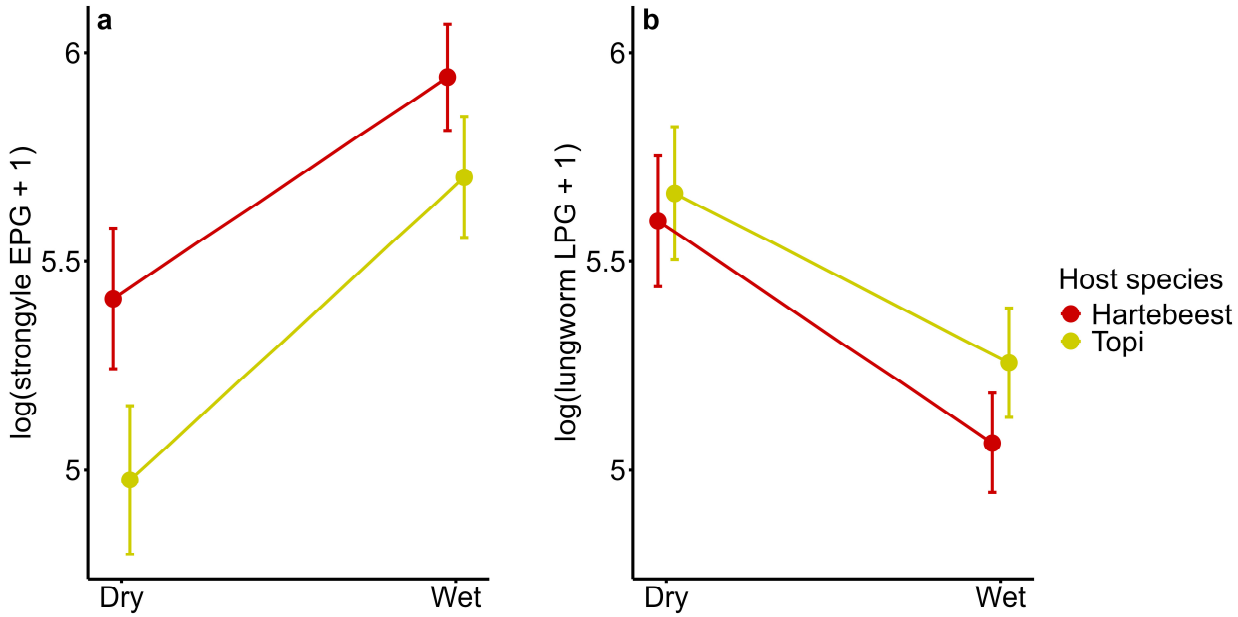

Figure 8: Parasite infection intensity as a function of season. Point represents the mean value, and the error bar is the standard error.

For each helminth parasite group in each host species, variance inflation factor (VIF) indicated no evidence of multicollinearity among predictor variables. Model selection indicated that no environmental predictor (precipitation, temperature, or occupancy) at the likely time of infection was strongly associated with strongyle infection intensity in either host species (Table 2, Fig. 9). The best-fitting model for hartebeest included temperature alone, but its explanatory power was comparable to the intercept-only model (ΔAIC = 1.9). Similarly, for topi, the intercept-only model had the lowest AIC, indicating that addition of any predictor did not improve model fitness.

Table 2: Model performance summary for predicting strongyle nematode infection intensity in hartebeest and topi. The response variable is log(Strongyle EPG + 1). PRCP and TEMP represent mean daily precipitation (mm) and mean daytime temperature (°C), respectively, averaged over a 2 to 4 week window prior to fecal sample collection. OCC is the log-transformed summed animal occupancy (log[x + 1]) over the same period. K is the number of model parameters. All models include animal group as a random effect.

Response	Model	K	Δ AIC
Hartebeest (n = 334)	TEMP	4	0.0
	OCC + TEMP	5	0.9
	PRCP + TEMP	5	1.8
	Intercept-only	3	1.9
	OCC	4	2.5
	PRCP + OCC + TEMP	6	2.6
	OCC × TEMP	6	2.8
	PRCP × TEMP	6	2.8
	PRCP	4	3.6
	PRCP + OCC	5	4.4
	PRCP × OCC	6	6.4
Topi (n = 318)	Intercept-only	3	0.0
	PRCP + TEMP	5	0.2
	PRCP × OCC	6	0.6
	TEMP	4	0.6
	PRCP	4	1.5
	OCC	4	1.7
	PRCP × TEMP	6	1.8
	PRCP + OCC + TEMP	6	2.2
	OCC + TEMP	5	2.6
	PRCP + OCC	5	3.1
	OCC × TEMP	6	4.5

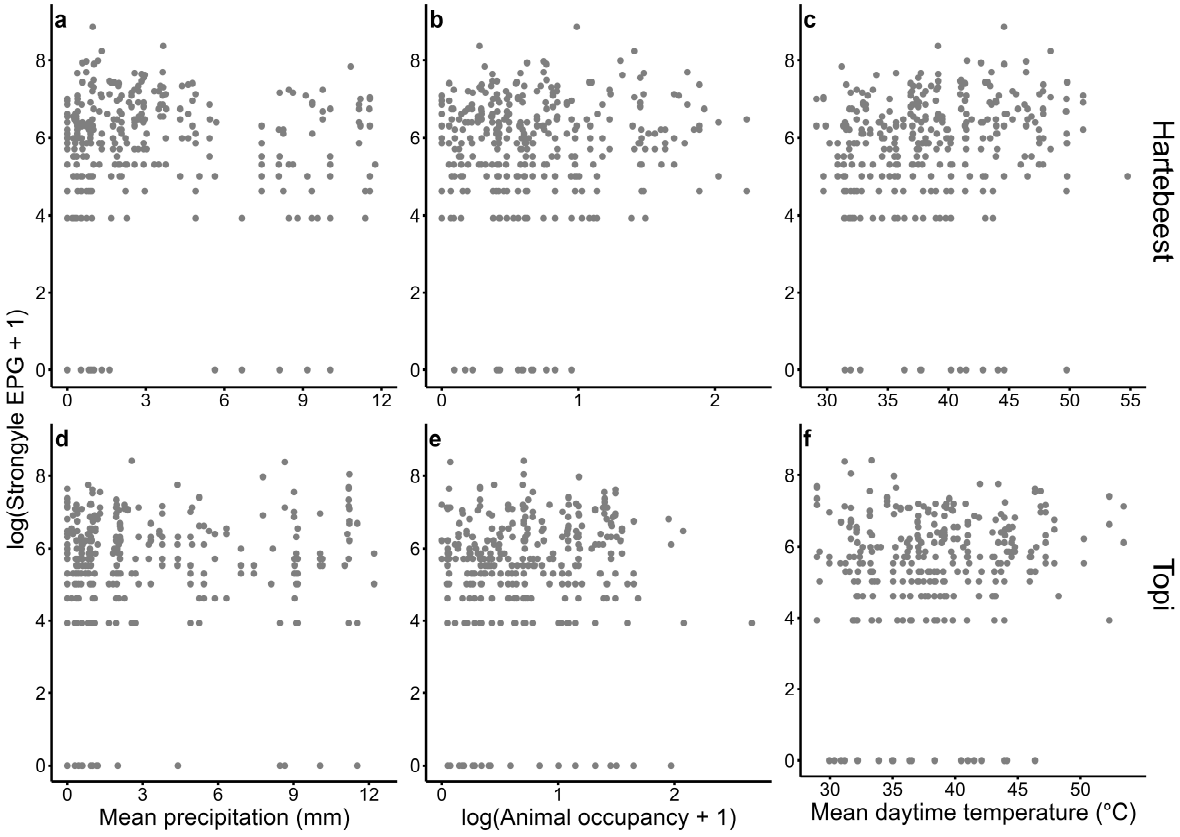

Figure 9: Strongyle nematode infection intensity as a function of precipitation (a, d), animal occupancy (b, e) and temperature (c, f) in hartebeest (a-c) and topi (d-f). The grey points represent observed raw data.

In contrast to strongyle nematodes, lungworm infection intensity was associated with environmental factors. The best-supported model for both hartebeest and topi were additive models that included precipitation and animal occupancy as predictors (Table 3, Fig. 10). For hartebeest, precipitation was negatively associated with lungworm intensity (Fig. 10a), while occupancy was positively associated with lungworm intensity (Fig. 10b). Similarly, for topi, precipitation was negatively associated with lungworm intensity (Fig. 10d), whereas occupancy was positively associated (Fig. 10e). No effect of temperature was detected (Fig. 10c&f). Spatial autocorrelation analysis using Moran's I indicated no clear spatial structure in the residuals of the best-fitting lungworm infection models (Fig. 11).

Table 3: Model performance summary for predicting lungworm infection intensity in hartebeest and topi. The response variable is log(Lungworm LPG + 1). PRCP and TEMP represent mean daily precipitation (mm) and mean daytime temperature (°C), respectively, averaged over a 5 to 10 week window prior to fecal sample collection. OCC is the log-transformed summed animal occupancy (log[x + 1]) over the same period. K is the number of model parameters. All models include animal group as a random effect.

Response	Model	K	Δ AIC
Hartebeest (n = 334)	PRCP + OCC	5	0.0
	PRCP + OCC + TEMP	6	1.0
	PRCP × OCC	6	1.3
	PRCP	4	2.1
	PRCP + TEMP	5	3.0
	PRCP × TEMP	6	5.0
	OCC + TEMP	5	6.9
	OCC × TEMP	6	6.9
	TEMP	4	7.5
	OCC	4	8.6
	Intercept-only	3	9.2
Topi (n = 318)	PRCP + OCC	5	0.0
	OCC	4	0.8
	PRCP + OCC + TEMP	6	1.2
	PRCP × OCC	6	1.9
	OCC + TEMP	5	2.7
	OCC × TEMP	6	4.3
	PRCP	4	9.7
	Intercept-only	3	9.9
	PRCP + TEMP	5	11.7
	TEMP	4	11.8
	PRCP × OCC	6	12.9

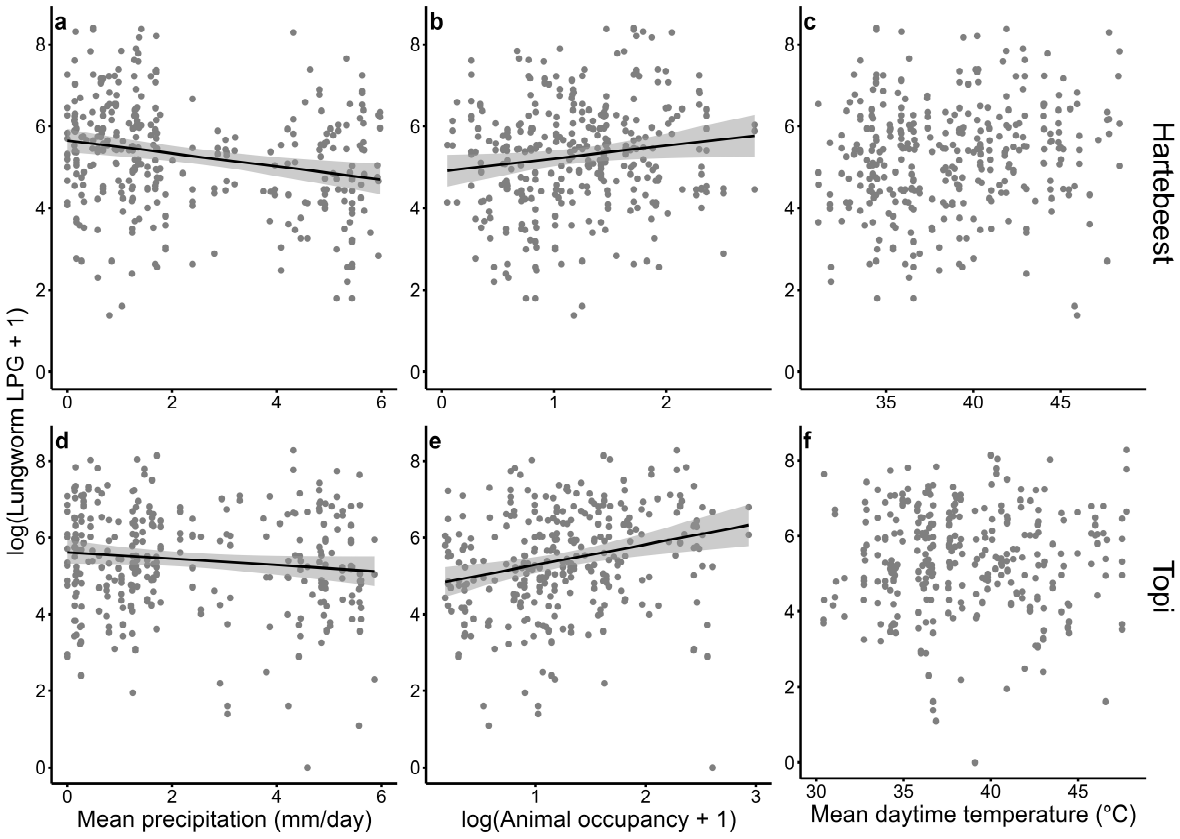

Figure 10: Lungworm infection intensity as a function of precipitation (a, d), animal occupancy (b, e) and temperature (c, f) in hartebeest (a-c) and topi (d-f). The grey points represent observed raw data, and the solid black lines are the predicted regression lines from the best-fit models, which include precipitation and animal occupancy. For predictions involving precipitation, occupancy was held at the mean value, and vice versa. The grey shaded region indicates the 95% confidence interval for the predicted lines.

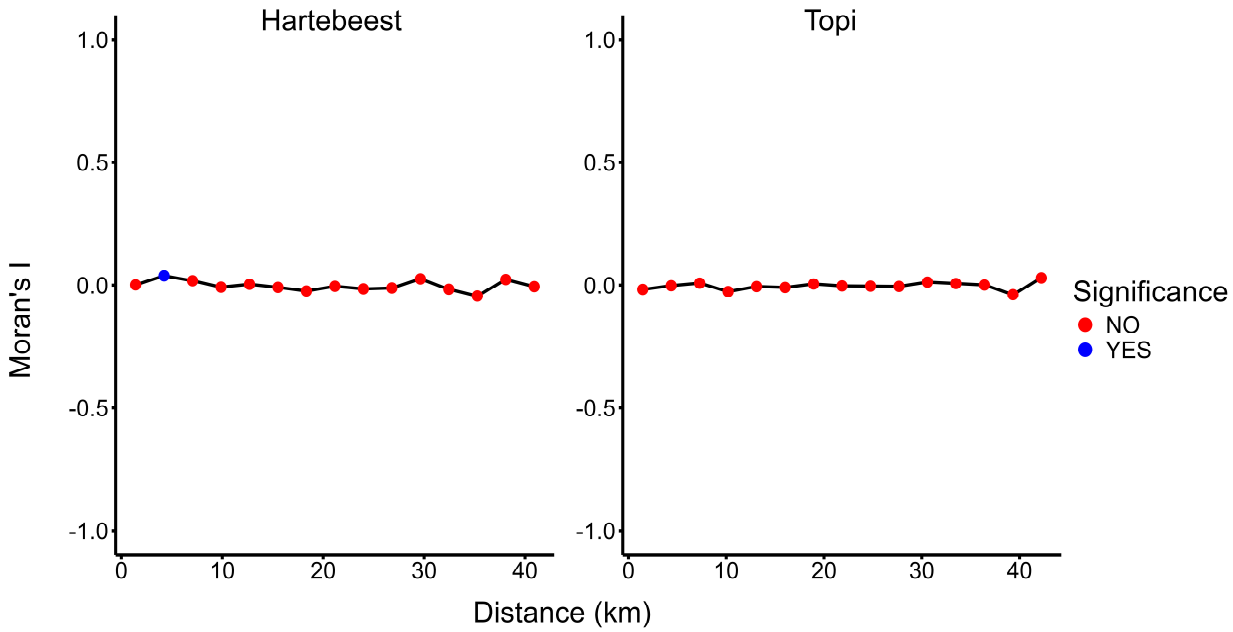

Figure 11: Spatial autocorrelation test results for lungworm infection intensity in hartebeest and topi. Points indicate Moran's I values, and colors reflect statistical significance (blue for significant autocorrelation at $p \leq 0.05$ and red for non-significant autocorrelation). Dashed horizontal lines represent no spatial autocorrelation (Moran's I = 0). Analyses were conducted on residuals from the best-fitting models to assess spatial patterns after accounting for fixed effects (precipitation and animal occupancy) and the random effect of animal group in the linear mixed models.

Analysis of pasture data from 14 monitored sites showed that precipitation was positively associated with both grass height (LMM: estimate ± se: 0.74 ± 0.31, $p = 0.018$; Fig. 12a) and percentage grass leaf moisture (LMM: estimate ± se: 4.25 ± 0.56, $p < 0.001$; Fig. 12b). In turn, grass leaf moisture was positively associated with both hartebeest occupancy (negative binomial GLMM: estimate ± se: 0.0195 ± 0.0069, $p < 0.01$; Fig. 12c) and topi occupancy (negative binomial GLMM: estimate ± se: 0.0174 ± 0.0047, $p < 0.001$; Fig. 12d).

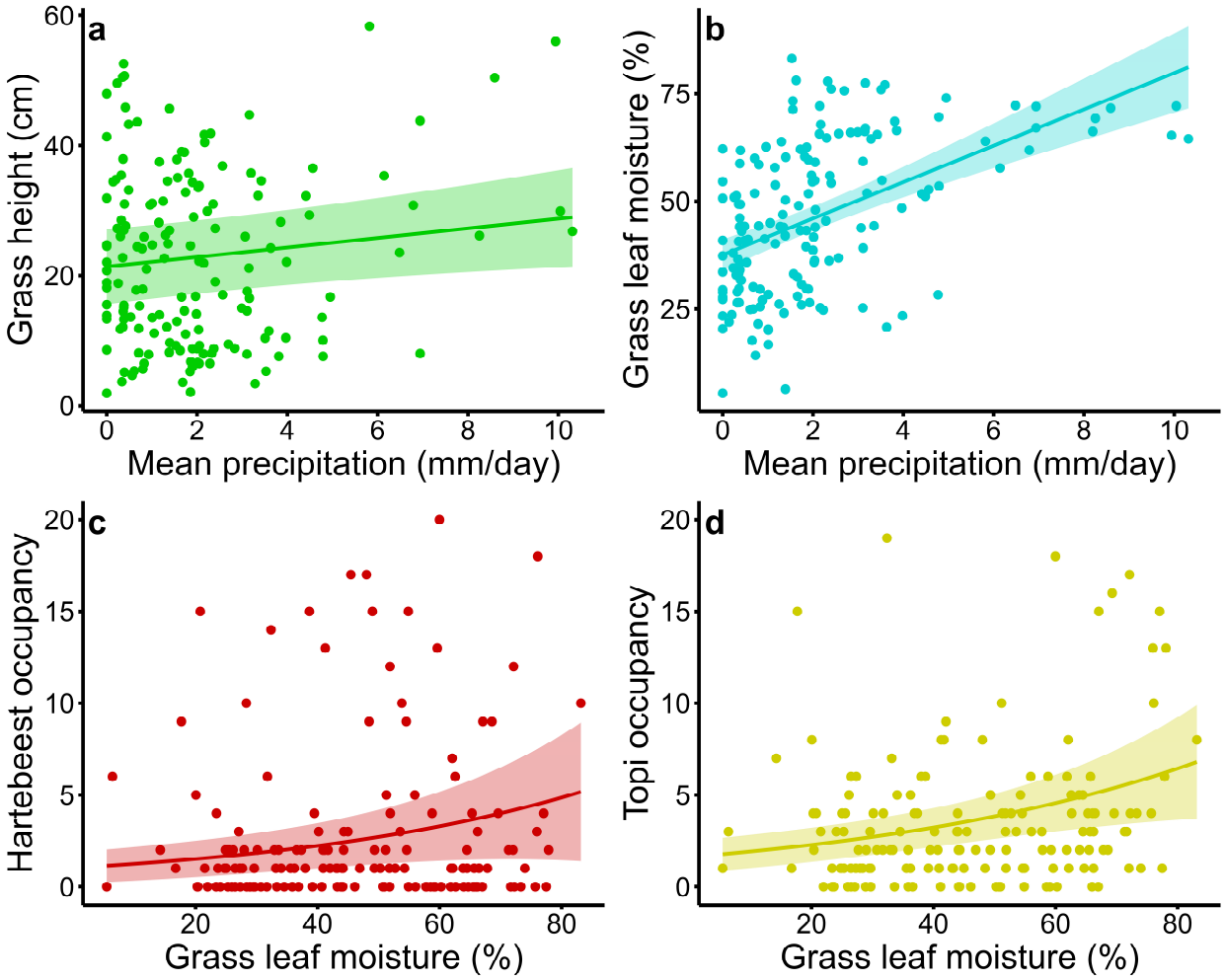

Figure 12: Relationships between (a) precipitation and grass height, (b) precipitation and grass leaf moisture, (c) hartebeest occupancy and grass leaf moisture, and (d) topi occupancy and grass leaf moisture across 14 pasture collection sites monitored monthly during the study period. These analyses assess the potential links between precipitation, grass height, food availability, and animal density.

4. DISCUSSION

Our study investigated the overall effect of seasonality and the influence of precipitation, temperature, and animal density on the infection intensity of strongyle nematodes and lungworms in two closely related ungulate species, Coke's hartebeest (*Alcelaphus buselaphus cokii*) and topi (*Damaliscus lunatus jimela*). We found that both strongyle nematodes and lungworms were highly prevalent in both host species, but strongyle nematode intensities were higher during the wet season in contrast to lungworm intensities which were higher during the dry season. Also, we observed no strong association between strongyle infection intensities and environmental factors at the likely time of infection while lungworm infection intensity was positively associated with precipitation and negatively associated with animal occupancy. These findings suggest that parasite life cycles may be important in shaping parasite responses to environmental drivers in free-ranging ungulates.

The seasonal divergence in infection intensity between strongyle nematodes and lungworms reflects fundamental differences in their life cycles and how they interact with seasonal ecological pressures. The peak of strongyle nematode intensity during the wet season was also observed in other ungulate systems in tropical and sub-tropical climates (Nalubamba et al., 2012; Turner and Getz, 2010), suggesting the influence of environmental conditions on the survival and development of the parasite free-living stages as the plausible mechanism (O'Connor et al., 2008, 2007, 2006; Stromberg, 1997). The lack of strong associations with precipitation, temperature, or host density at the likely time of infection in our study, suggests that other mechanisms may be at play. One explanation is that hosts may shed fewer infective

stages during dry periods due to arrested larval development (hypobiosis)—a phenomenon observed in other ungulate systems (Ndao et al., 1995). However, we acknowledge limitation in our analysis because inference about infection timing based on an assumed 2–4 week lag between exposure and observed parasite load may not fully capture the complexity of parasite development, host exposure and response. For example, we found a noticeable effect on the results when we used the summed occupancy over the entire study duration and categorized occupancy as "low" (≤ median value) vs. "high" (> median value; Fig. 13), whereby parasite infection intensity was consistently higher in high-occupancy areas for both host species and parasite types (Fig. 14). In addition, ongoing work suggests that interactions with migratory species such as blue wildebeest may shape strongyle transmission dynamics. These migrants may contribute to infection patterns in resident species like hartebeest and topi through increased dung deposition while also reducing exposure via removal of infective stages during intensive grazing (Donaldson et al., 2024).

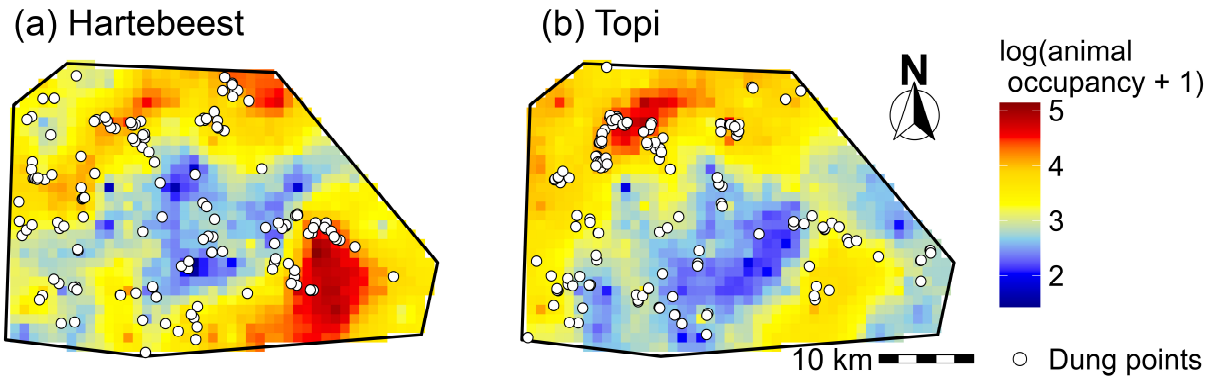

Figure 13: IDW interpolated occupancy values corresponding to (a) hartebeest and (b) topi fecal sample collection points. The heatmaps represent the summed animal occupancy in the whole study area while the white points represent fecal sample collection points during the whole study duration (October 2022 to September 2023).

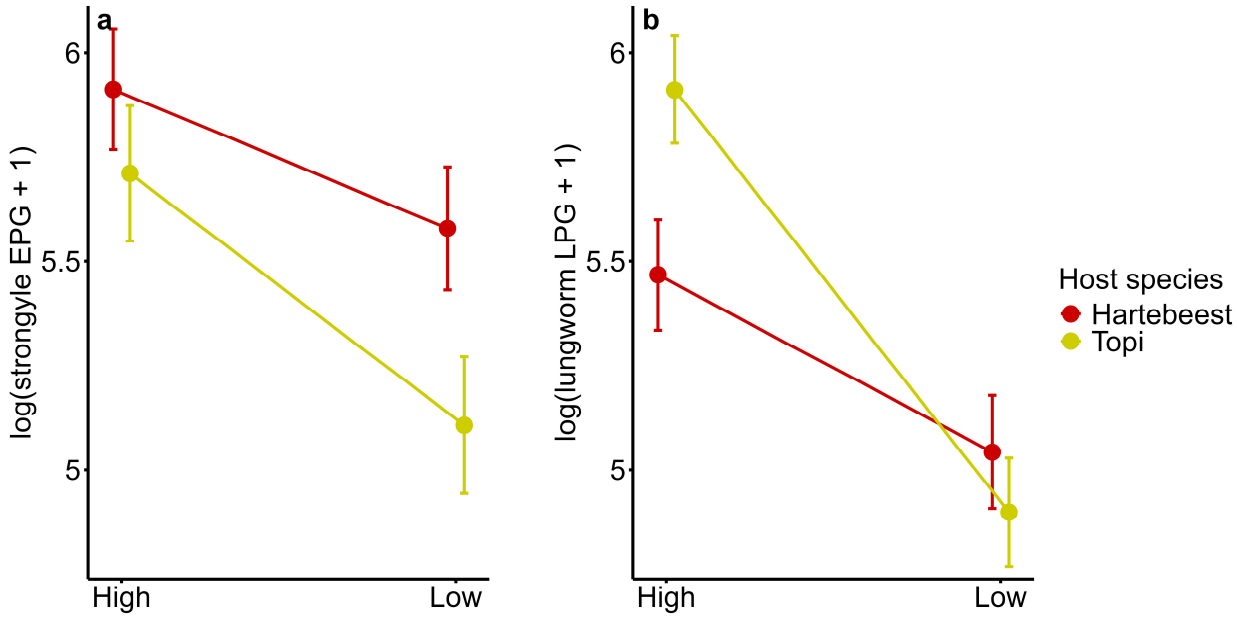

Figure 14: Infection intensity of a) strongyles and b) lungworms as a function of animal occupancy in hartebeest and topi. Point represents the mean value, and the error bar is the standard error.

In contrast to strongyle nematodes, lungworm infection intensity was higher during the dry season and was negatively associated with precipitation but positively associated with animal occupancy. These associations could potentially be explained by different mechanisms. First, it is known that infective stages of lungworm can persist within the intermediate host for the lifetime of gastropod, often exceeding two years (Taylor et al., 2015), suggesting that transmission may occur throughout the year. Thus, increased precipitation may reduce host exposure to infected gastropods, the intermediate hosts of lungworms because higher grass during wet periods could make it less likely that hosts encounter and ingest infected gastropods. In support of this, we found that precipitation was positively associated with grass height. Conversely, in the dry season grazing in short grass may increase host exposure to the infected gastropods. Second, increased precipitation improves forage quality and availability, which enhances host nutritional status and immune function, reducing susceptibility to infection. In support, we observed that

precipitation was positively associated with grass moisture. Increased moisture enhances forage quality, as green, moist vegetation is more nutritious and is preferred by herbivores for its greater palatability and digestibility (McNaughton, 1985; Treydte et al., 2013; Van Soest, 1994). Interestingly, grass moisture was positively associated with animal occupancy, and lungworm intensity increased with animal occupancy. This pattern likely reflects increased dung deposition in areas with higher host density, leading to greater contamination of the environment with parasite stages (Thurber et al., 2011; Titcomb et al., 2021). This, in turn, may increase the likelihood of gastropods becoming infected and transmitting the parasite to hosts.

We found no association between temperature and either strongyle nematode or lungworm infection intensity. This contrasts with findings from temperate and Arctic systems, where temperature strongly influences parasite development, survival, transmission, and infection intensity in the hosts (Filip-Hutsch et al., 2020; Kutz et al., 2013; Van Dijk and Morgan, 2008). In those regions, large seasonal fluctuations in temperature may create conditions that significantly affect parasite dynamics, however the relatively stable thermal conditions in the tropical climates, may not vary enough to significantly impact parasite transmission. Alternatively, the effects of temperature may be masked by the more dominant influences of precipitation, host density or other ecological interactions in this system.

5. CONCLUSION

Our findings highlight the importance of considering both environmental factors and parasite life cycle strategies when studying parasite infection patterns in wildlife populations (Aleuy and Kutz, 2020; Molnár et al., 2017, 2013; Rose et al., 2015). By comparing strongyle nematodes and lungworms, parasites with direct vs. indirect life cycles, we found contrasting seasonal infection patterns whereby strongyle nematode intensities peaked during the wet season and lungworms peaked during the dry season. We also showed the lack of strong associations between strongyle nematode intensity and environmental variables at the likely time of infection suggesting that other mechanisms may shape the pattern of strongyle intensity in our study system, while for lungworms, infection intensity was linked to precipitation and animal occupancy. Clear seasonal peaks in parasite intensity suggest that the effects of parasitism on host fitness such as increased vulnerability to predation, reduced fecundity, or elevated mortality may be most pronounced during specific times of year. Identifying when parasite burdens are highest is critical for predicting when hosts are under the greatest ecological pressure due to parasitism.

AUTHOR CONTRIBUTIONS

Basil Senso contributed to the conceptualization of the study, and led in data collection, analysis, and writing the manuscript.

Ricardo Holdo, Jason Donaldson, and Vanessa Ezenwa supervised the project and provided feedback on all aspects of the study, including conceptual development.

T. Michael Anderson contributed the camera trap data used in the analysis.

Ricardo Holdo, Vanessa Ezenwa, and T. Michael Anderson contributed to the funding acquisition.

Aidan Trentinus assisted with laboratory and field data collection.

All co-authors agree that the work may be included in this thesis.

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