International Journal for Parasitology xxx (xxxx) xxx

Contents lists available at ScienceDirect

International Journal for Parasitology

journal homepage: www.elsevier.com/locate/ijpara

Environmental drivers of parasitic nematode infection in wild ungulates in the Serengeti National Park

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ARTICLE INFO

Article history:
Received 8 July 2025
Received in revised form 11 January 2026
Accepted 13 January 2026
Available online xxxx

Keywords:
Parasite seasonal dynamics
Gastrointestinal nematodes
Lungworms
Alcelaphine
Tropical savannah

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 parasites with different life cycles 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 environmental variables at the likely time of infection are related to the infection intensity of two parasitic nematodes with contrasting life cycles: 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 considering how parasite life cycles interact with environmental variables operating at different temporal scales, as seasonal infection patterns may emerge from processes acting at distinct times relative to parasite development and transmission. Identifying when parasite intensities are highest is critical for predicting when hosts are under the greatest ecological pressure due to parasitism.

1. Introduction

Parasites play a crucial role in ecosystems by influencing host behavior (Dobson, 1988; Poulin, 1994), population dynamics (Hudson et al., 1998; Tompkins et al., 2002), and interactions (e.g., predation) with other species (Hudson et al., 1992; Packer et al., 2003). Parasite infection dynamics are shaped by a mix of external environmental drivers such as precipitation, temperature, relative humidity, resource availability and host density, with seasonality often playing an important role in transmission and infection patterns (Altizer et al., 2006; Habig et al., 2021; Kołodziej-Sobocińska, 2019; Poulin, 2020). Understanding the timing and drivers of seasonal infection patterns across different host-parasite systems is essential for predicting when and where parasites matter most to animal populations and what drives changes in transmission. Despite this importance, few studies have captured parasite infection patterns and their drivers across entire seasonal cycles.

Seasonally varying environmental conditions are particularly relevant to parasites with free-living stages. For example, parasitic nematodes infecting mammals persist in the external environment (e.g., feces, soil, pasture) for a significant portion of their life cycles (Taylor et al., 2015). Survival and development at these stages depend on environmental conditions such as favorable tempera-

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https://doi.org/10.1016/j.ijpara.2026.104772
0020-7519/

ture and moisture (O'Connor et al., 2006; Stromberg, 1997; Van Dijk and Morgan, 2008), which can, in turn influence prevalence and infection intensity in the hosts. In addition to its direct effects on growth and survival of free-living parasite stages, seasonality imposes indirect effects on host density and movement patterns by modifying resource availability (Bohrer et al., 2014; Boone et al., 2006; Winnie et al., 2008), thereby affecting parasite transmission rates. For example, in tropical and subtropical climates, distinct wet (rainy) and dry seasons strongly affect forage availability for herbivores (Abraham et al., 2019; McNaughton, 1985), 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 compared to 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.

The impact of seasonality on parasite transmission should also depend on parasite life cycles. For example, parasites with direct lifecycles (such as gastrointestinal nematodes) are more sensitive to harsh environmental conditions such as temperature extremes because their free-living stages depend entirely on the external 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 harsh environmental conditions such as hot dry conditions (O'Connor et al., 2008, 2006; Rossanigo and Gruner, 1995; Van Dijk and Morgan, 2008; Van Dijk et al., 2009). Conversely, the intermediate hosts of indirectly transmitted parasites 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)). This means that even under the same seasonal conditions, parasites with different life cycles may show different infection patterns and have divergent impacts on host populations.

Here, we studied the seasonality of gastrointestinal nematodes (commonly strongyle nematodes, Family Trichostrongylidae) and lungworms (Family Protostrongylidae) in two closely related large ungulate hosts—Coke's hartebeest (*Alcelaphus buselaphus cokii*) and topi (*Damaliscus lunatus jimela*)—in a highly seasonal savannah ecosystem, the Serengeti National Park, Tanzania. Trichostrongylids (hereafter referred to as 'strongyles') have a direct life cycle requiring a single host called the definitive host where sexual reproduction of the parasite occurs (Taylor et al., 2015). 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 (Supplementary Fig. S1). Protostrogylids (hereafter referred to as 'lungworms'), on the other hand, have indirect life cycles requiring an intermediate host in addition to the definitive host (Taylor et al., 2015). Female adult parasites reside in the bronchi where they produce eggs that hatch into L1, which are coughed up, swallowed, and passed in host feces. L1 penetrates an intermediate host such as a gastropod, where they develop into L2 then L3. Infection of the definitive host occurs through the ingestion of infected gastropods during grazing. After ingestion, larvae penetrate the intestinal wall and migrate via the circulatory system reaching the lungs where they mature (Supplementary Fig. S2). These groups of parasites, rely on external environmental conditions for egg 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).

We focused on wild ungulates because they serve as effective models for understanding host-parasite interactions in complex, real-world environments due to 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 intensities 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. 1).

2. Materials and methods

2.1. Study site

We conducted this study in the Serengeti National Park ("Serengeti" hereafter), which ranges between 33.9°E to 35.3°E and 3.3°S to 1.4°S in northern Tanzania. Serengeti is part of the Serengeti-Mara Ecosystem, spanning approximately 25,000 km^2 (Fig. 2a) within the savannah 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., 2015). Mean annual precipitation ranges from less than 500 mm in the southeastern short-grass plains to over 1,000 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. 2b). 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 prey (Anderson et al., 2016; Beaudrot et al., 2020; Swanson et al., 2015). Mean precipitation in the grid during the wet (November to May) and dry (June to October) 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 (Supplementary Fig. S3). To attain broad sampling across space and to avoid oversampling certain locations, we divided the grid into seven regions, which we visited monthly to collect animal fecal samples. In addition, we used 14 camera-trap sites (between 1 and 4 sites per region) where we collected grass samples monthly (Fig. 2b). Throughout the study, we monitored all 151 camera traps monthly to assess animal occupancy.

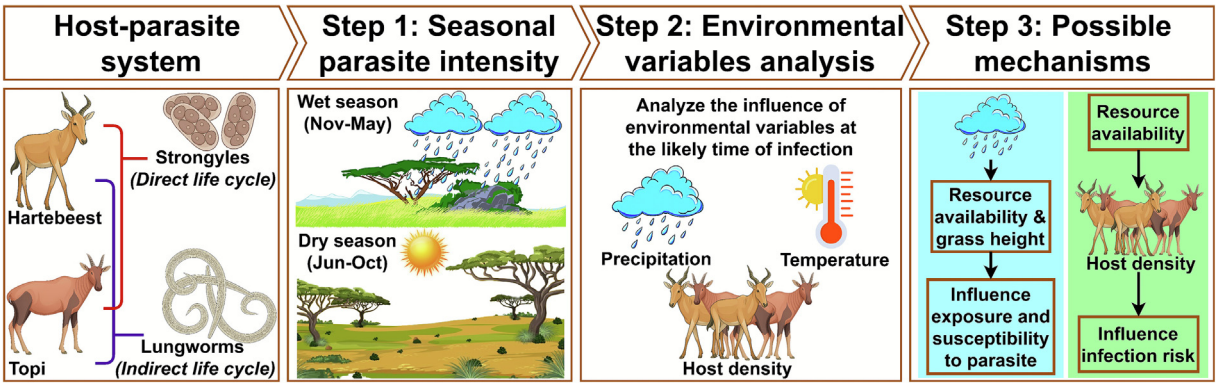

Fig. 1. The conceptual framework of the study examining seasonal patterns and environmental drivers of parasite infection intensity in wild ungulates. The study focused on two ungulate species and two parasite groups.

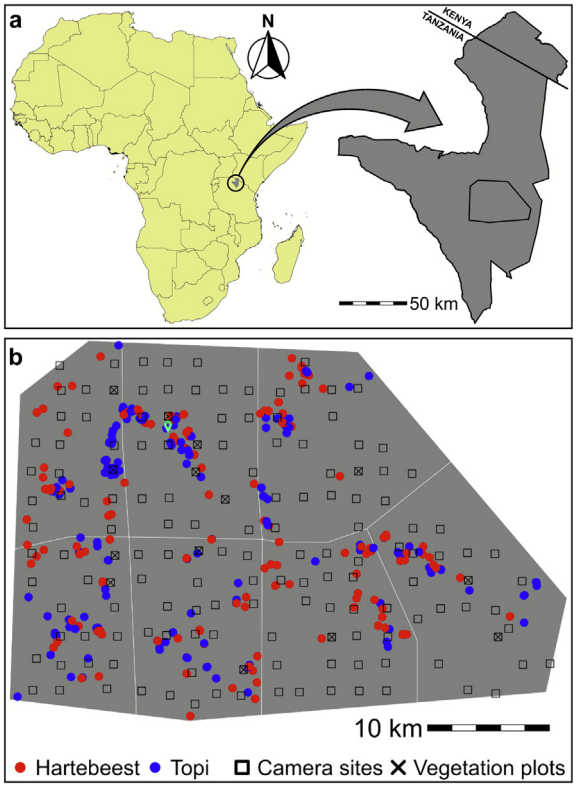

Fig. 2. Study area in the Serengeti-Mara Ecosystem: a) Serengeti National Park in Tanzania and the Maasai Mara National Reserve in Kenya. The polygon in central Serengeti marks the location of the Snapshot Serengeti (SS) camera trap grid. b) Detailed view of the SS grid, showing sampling regions, camera trap sites (black squares), grass samples collection sites (black squares with an 'x' mark), hartebeest fecal samples locations (red points), and topi fecal samples location (blue points). The green marker indicates the Serengeti Wildlife Research Centre laboratory, where all samples were processed. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.2. Sample collection

Sample collection occurred between October 2022 and September 2023. We collected fecal samples to quantify strongyle and lungworm infections in our two host species. We carried out monthly sampling by driving along established roads within the long-term Snapshot Serengeti (SS) camera trap, following a prescribed rotation through the seven sampling regions. Animals of our host species were located and observed until they defecated, at which time the observer drove over to the animal's location to collect a fresh sample. We collected 3–6 fecal samples per animal species per region within the grid. To account for potential non-independence among samples from the same species, collected on the same date and location, we assigned each sample to an animal group ID. Over the course of the entire study, we collected 652 samples, 334 from hartebeest and 318 from topi (Fig. 2b). According to the census conducted in 2010 by the Tanzania Wildlife Research Institute (TAWIRI), estimated populations are approximately 11,354 hartebeest and 35,512 topi across the entire park ~12,930 km^2 (TAWIRI, 2010). Our 1,000 km^2 study area represents ~7.73% of the park's area. Assuming relatively uniform distribution, we estimate that roughly 877 hartebeest and 2,745 topi may have used the study grid during the sampling period. Thus, our sample size represents approximately 38% and 12% of the estimated hartebeest and topi population respectively. We also collected grass samples to measure the percentage of grass moisture content as a proxy for host resource availability and quality following the protocol described in Donaldson et al. (2023). Grass samples were collected monthly across 14 monitored sites (Fig. 2b), with each site sampled once per month, resulting in a total of 168 samples.

2.3. Parasitological analysis

We processed fecal samples within 24 h of collection. To quantify strongyle intensity, we used a modified McMaster fecal egg counting technique (Ezenwa, 2003), and calculated parasite intensities in units of strongyle eggs per g of feces (EPG). To quantify the lungworm intensity, fecal samples were examined for the presence of the lungworm stage-one larvae (L1) using the beaker-modified Baermann technique (Snyder et al., 2015), calculated as L1 per g of feces (LPG hereafter "LPG"). We used EPG and LPG as metrics of infection intensity in individual hosts (Byrne et al., 2018; Gasbarre et al., 2001; Roberts and Swan, 1981).

2.4. Environmental data

We obtained and analyzed environmental data with R v. 4. 4. 3 (R Core Team, 2025). 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 (Supplementary Fig. S3). 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). We also retrieved the mean daytime

land surface temperature (LST, in °C) at 1 km spatial resolution from two MODIS satellites, Aqua ("MYD21A2" product for afternoon LST) and Terra ("MOD21A2" product for morning LST) using *MODISTools* package (Hufkens, 2023), and calculating the mean of the two. 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 we used as a proxy for animal density. Only images of the same species taken at least 10 min 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 focal host species at each dung collection point (Supplementary Fig. S4).

For each dung sample collection point we obtained mean daily precipitation (PRCP) from CHIRPS, mean daytime land surface temperature (TEMP) and summed animal occupancy (OCC) data. For all environmental variables, 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 egg or larval production by adult parasites. We assumed that the period from ingestion to parasite shedding was 2–4 weeks for strongyle nematodes and 5–10 weeks for lungworms (Taylor et al., 2015).

For grass sample collection sites, we recorded monthly animal occupancy values 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 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 grass sampling to evaluate its influence on grass height, grass moisture, and animal occupancy.

2.5. Statistical analysis

We performed all analyses using R v. 4. 4. 3 (R Core Team, 2025). First, we tested for the effect of season on log-transformed values of our two response variables: log[LPG + 1] and log [EPG + 1]). Log transformation reduced the skewness of the response variables and stabilized the variance, making the distribution approximately normal (Fig. S5). Second, we assessed the influence of environmental variables (precipitation, temperature and animal occupancy) at the likely time of infection on EPG and LPG. In both cases, we fit separate models for each parasite and host species, using linear mixed models (LMMs) implemented with the *glmmTMB* package (Brooks et al., 2017), treating animal group ID as a random effect. Before fitting the second set of models, we checked for the presence of multicollinearity among the predictors using variance inflation factor (VIF) analysis, and tested models with either a single predictor, two predictors in additive and interactive models, or all predictors in an additive model. We compared model fit using Akaike's Information Criteria (AIC) (Sakamoto et al., 1986). We tested the best-fitting model in each group for residual spatial autocorrelation using Moran's I. We recognize that both spatial and temporal autocorrelation could potentially be present in residuals but focused on spatial autocorrelation because the time series had many missing values, precluding the estimation of temporal lag effects.

In cases where we observed associations between parasites and environmental variables, we explored the underlying processes. These included associations between precipitation and grass height, precipitation and 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 grass sample collection, grass height (cm), and percentage grass moisture data from 14 monitored sites. We then fit a LMM of grass height (cm) as a function of precipitation, a LMM of grass moisture as a function of mean precipitation, and a generalized linear mixed model (GLMM) of monthly animal occupancy as a function of grass moisture, assuming a negative binomial distribution. Both models included sampling sites as a random effect.

3. Results

We detected strongyle nematode eggs in 95.5% of hartebeest samples (n = 334) and 93.1% of topi samples (n = 318), with mean infection intensities (mean ± se) of 616 ± 39 and 509 ± 34 EPG, respectively. Lungworm L1 occurred in 100% of hartebeest and 99.7% of topi samples, with infection intensities (mean ± se) of 433 ± 38 and 452 ± 33 LPG, respectively. Results from LMMs revealed that parasite infection intensity was strongly associated with season in both host species. Strongyle infection intensity was higher in the wet than in the dry season (hartebeest: p = 0.012; topi: p < 0.01). We observed the opposite pattern for the lungworms, where infection intensity was higher in the dry than in the wet season (hartebeest: p < 0.01; topi: p = 0.049; Fig. 3, Supplementary Fig. S6).

For each helminth parasite group in each host species, variance inflation factor (VIF) analysis indicated no evidence of strong multicollinearity among environmental 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 (EPG) in either host species (Table 1, Fig. 4a-f). 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.

In contrast to strongyle nematodes, lungworm infection intensity (LPG) 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 2). For hartebeest, precipitation was negatively associated with lungworm intensity (Fig. 4g), while occupancy was positively associated with it (Fig. 4h). Similarly, for topi, precipitation was negatively associated with lungworm intensity (Fig. 4j), whereas occupancy was positively associated (Fig. 4k). No effect of temperature was detected (Fig. 4i&l). Spatial autocorrelation analysis using Moran's I indicated no clear spatial structure in the residuals of the best-fitting lungworm infection models (Supplementary Fig. S7).

Since we observed associations between lungworm intensity and both precipitation and animal occupancy, we tested for possible mechanisms explaining these relationships using data from 14 monitored sites. We found that precipitation was positively associated with both grass height (LMM: p = 0.017; Supplementary Fig. S8a) and percentage grass moisture (LMM: p < 0.001; Supplementary Fig. S8b). In turn, grass moisture was positively associated with both hartebeest occupancy (negative binomial GLMM: p < 0.01; Supplementary Fig. S8c) and topi occupancy (negative binomial GLMM: p < 0.001; Supplementary Fig. S8d).

4. Discussion

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

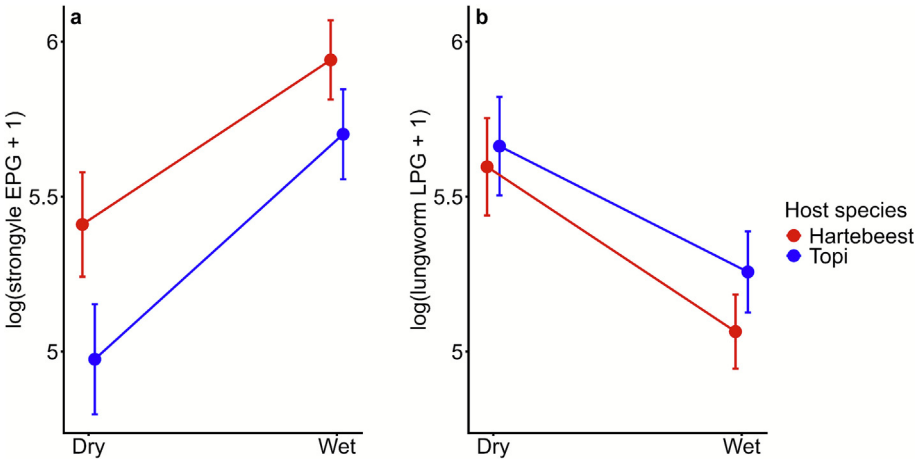

Fig. 3. Infection intensity of a) strongyles and b) lungworms as a function season in hartebeest and topi. Points and error bars are means and standard errors, respectively.

Table 1
Model fits for strongyle nematode infection intensity in hartebeest and topi given by log(Strongyle EPG + 1). All models include animal group ID as a random effect.

Response	Model [a]	K [b]	ΔAIC
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

[a] See main text for variable abbreviations.
[b] K is the number of model parameters.

Table 2
Model fits for lungworm infection intensity in hartebeest and topi given by log (Lungworm LPG + 1). All models include animal group ID as a random effect.

Response	Model [a]	K [b]	ΔAIC
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

[a] See main text for variable abbreviations.
[b] K is the number of model parameters.

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 (Jacquiet et al., 1995; Nalubamba et al., 2012; Turner and Getz, 2010), suggesting that environmental conditions play a key role in the survival and development of the parasite free-living stages (O'Connor et al., 2008, 2007, 2006; Stromberg, 1997). We failed to find associations between strongyle infections and precipitation, temperature, or host density at the likely time of infection in our study which suggests that other mechanisms are driving the seasonal pattern. 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). This mechanism has also been proposed in similar ecological contexts by Turner and Getz (2010).

An important caveat regarding strongyles is that EPG represents an aggregate measure of multiple trichostrongylid genera. The community in hartebeest and topi includes genera such as *Haemonchus*, *Trichostrongylus*, *Cooperia*, *Oesophagostomum*, *Robustostrongylus*, *Agriostomum*, and *Impalaia* (Boomker et al., 1986; Hoberg et al., 2009; Junker et al., 2015; Pester and Laurence, 1974; Reinecke et al., 1988; Waruiru et al., 1995), each with potentially distinct climatic preferences (O'Connor et al., 2006; Rossanigo & Gruner, 1995). The lack of association between strongyle EPG and the environmental variables we measured could therefore reflect offsetting responses across genera where some are favored by higher moisture and others by intermediate conditions thus obscuring correlations with any single measured driver. Despite this complexity, the pronounced wet season elevation in

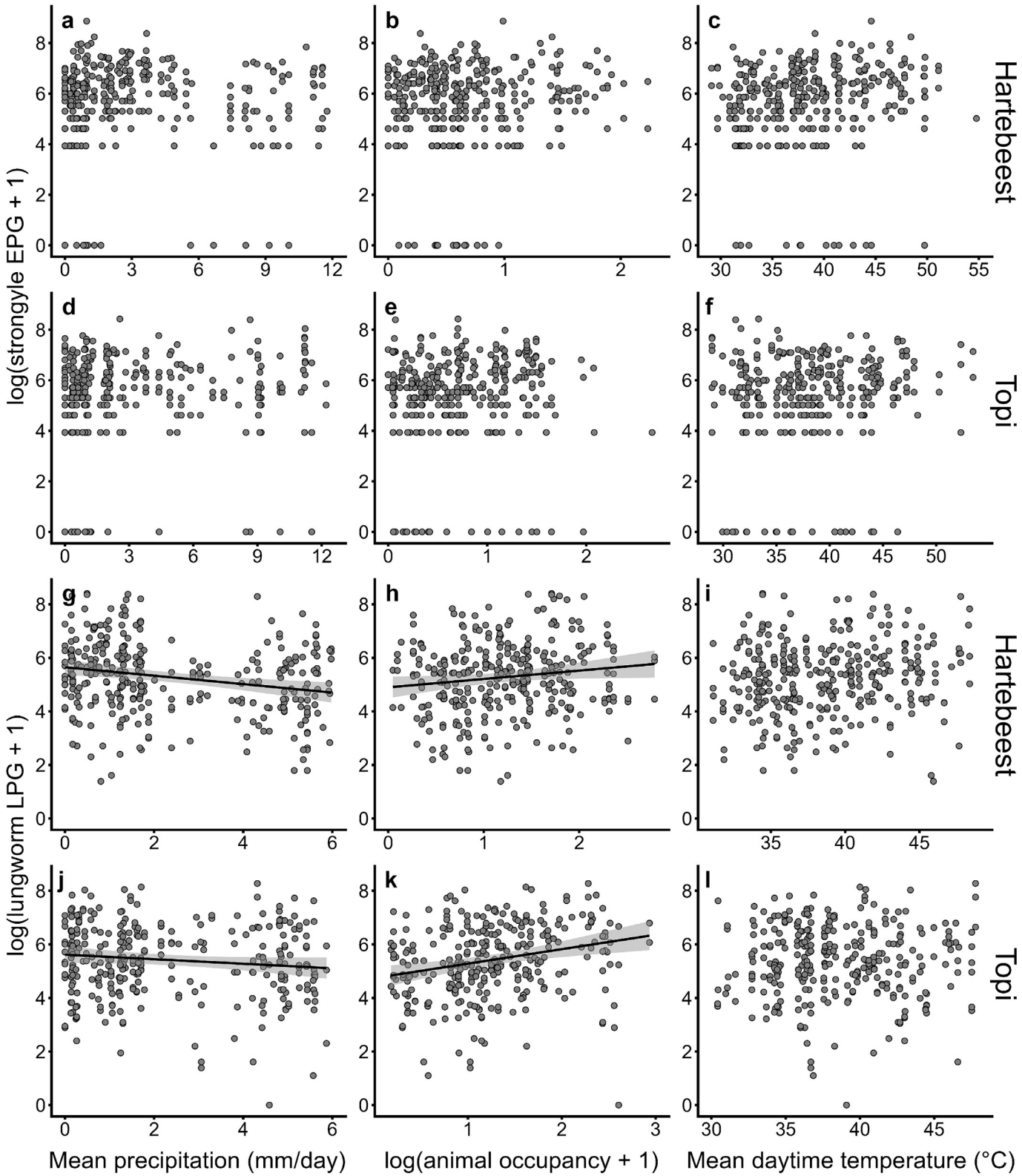

Fig. 4. Strongyle (a-f) and lungworm (g-l) infection intensity as functions of precipitation (a, d, g, j), animal occupancy (b, e, h, k), and temperature (c, f, i, l) in hartebeest (a-c, g-i) and topi (d-f, j-l). Grey points represent individual samples. For lungworm plots, the solid black lines are 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.

EPG indicates that seasonal factors still strongly regulate overall strongyle dynamics, even if the mechanisms are not captured by our aggregate-level environmental models. We also acknowledge that, our 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; Supplementary Fig. S9), whereby parasite infection intensity was consistently higher in high-occupancy areas for both host species and parasite types (Supplementary Fig. S10). 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; Kimaro et al., 2025).

Beyond wildebeest, the diverse ungulate community in the Serengeti may further modulate parasite dynamics for hartebeest and topi. Generalist trichostrongylids and protostrongylids can infect multiple host species (Ezenwa, 2003; Moulton and Sachs, 1970; Ortlepp, 1962; Van Wyk and Boomker, 2011; Walker and Morgan, 2014). This means that infection pressure on focal hosts could be diluted by some resident hosts removing parasites through intensive grazing or amplified via increased dung deposition, as proposed for migratory wildebeest. For example, high densities of buffalo, Thomson's gazelle, Grant's gazelle or other resident ungulates could increase environmental contamination with infective stages thereby increasing transmission (Ezenwa, 2003). Also, habitat use and grazing succession patterns where different species prefer different grass quality and quantity (Anderson et al., 2024; Donaldson et al., 2025; Murray and Brown, 1993) might partition exposure risk spatially and temporally. Such multi-host dynamics could partly explain the lack of strong environmental associations for strongyles if infection pressure is more strongly driven by total ungulate density and the degree of parasite sharing rather than conspecific density alone.

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. Lungworm infections in hartebeest and topi likely include species such as *Protostrongylus africanus*, *Protostrongylus etoshai*, *Pneumostrongylus calcaratus* and *Pneumostrongylus cornigerus* (Dinnik and Sachs, 1968; Ezenwa, 2003; Moulton and Sachs, 1970). The associations between lungworm infection and precipitation and animal occupancy may be explained by different mechanisms. First, it is known that infective stages of lungworm can persist within the intermediate host for the lifetime of the 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 because taller grass during wet periods lowers the likelihood that hosts encounter and ingest infected gastropods. 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 (Coop and Kyriazakis, 2001; Navarro-Gonzalez et al., 2011). 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 tropical climates may not produce enough variation 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.

For all parasite groups and host species, several methodological considerations should be noted. First, our sampling was designed to examine relative changes in infection intensity across seasons and environmental gradients, not to estimate absolute population means, a task that would require marked individuals. Second, helminth parasites are often highly aggregated within host populations (Shaw et al., 1998). While such aggregation increases variance, our spatially and temporally replicated sampling across many social groups likely captured a representative range of infection intensities for detecting seasonal patterns. Finally, we were unable to account for host age, which can influence parasite burden (Albery et al., 2024; Cattadori et al., 2005). Although we targeted adult-sized animals to reduce extreme age-related effects, substantial variation in parasite intensity can still exist among adults due to differences in acquired immunity, cumulative exposure, and senescence. This undetected age structure may contribute to within-season variance in EPG/LPG. Despite these constraints, the consistent seasonal signals we observed across two host species and two parasite groups support the robustness of our findings regarding the role of seasonality and life history in shaping infection dynamics.

Our findings highlight the importance of considering environmental factors at different time scales and parasite life cycle strategies when studying parasite infection patterns in animal 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. In contrast, lungworm 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 (Hudson et al., 1992), reduced fecundity (Hudson et al., 1998), or elevated mortality (Gulland, 1992) resulting from parasite infection may be most pronounced during specific times of year.

CRediT authorship contribution statement

Basil C. Senso: Writing – review & editing, Writing – original draft, Visualization, Supervision, Methodology, Investigation, Formal analysis, Conceptualization. **Jason E. Donaldson:** Writing – review & editing, Supervision, Project administration, Methodology, Investigation, Formal analysis, Conceptualization. **T. Michael Anderson:** Writing – review & editing, Funding acquisition, Data curation. **Aidan Trentinus:** Writing – review & editing, Investigation. **Vanessa O. Ezenwa:** Writing – review & editing, Supervision,

Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Ricardo M. Holdo:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Formal analysis, Conceptualization.

Acknowledgements

We express our gratitude to Jeremiah Sarakikya, Norbert Munuo, Megan Gomes, Jumapili Chenga, and Merito Katei for their field support, and to Hussein Adam, Peace Sabuni, and Mary Zebedayo for their help in the lab. We also acknowledge the research support provided by collaborators at the University of Glasgow, whose expertise and resources greatly enhanced this study. We thank Dr. Emmanuel Masenga (Director, Serengeti Wildlife Research Center), 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. Finally, we would like to acknowledge the financial support provided by the USDA National Institute of Food and Agriculture grant #2021-67015-33407.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ijpara.2026.104772.

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