RESEARCH ARTICLE

Direct and indirect effects of fire on parasites in an African savanna

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Abstract

1. Fires in grassy ecosystems consume vegetation and initiate high-quality re-growth, which results in pyric herbivory when mammalian grazers concentrate feeding in recent burns. For environmentally transmitted parasites with transmission mechanisms linked to vegetation structure, fire should exert direct effects on parasites, as well as indirect effects resulting from subsequent enhanced herbivory, which can affect parasite input and exposure to environmental conditions.

2. We combined an experimental manipulation with observational data in the Serengeti National Park to investigate the direct and indirect effects of fire on parasites. We assessed the direct effects of fire by measuring changes in parasitic nematode larvae in the grass layer before and after fire on paired experimental burned and control plots. To investigate indirect effects linked to pyric herbivory, we sampled herbivore dung, grass biomass, ground temperature and larval densities every month for 5 months following fire in seven pairs of burned and unburned monitoring plots. Finally, to assess if fire-driven changes to larval densities affected host infection burdens, we collected faecal samples from a key host, Grant's gazelle (*Nanger granti*), each month for 5 months to estimate within-host parasite burdens.

3. Fire killed all larvae and increased grazer dung inputs by 40% for 2 months following fire. Dung inputs after fire led to larval parasite recolonization of burned patches, but intense herbivory kept grass short and larval densities were associated with changes in ground temperature linked to grass biomass and ambient temperature. Grant's gazelles had lower parasite burdens when sampled in areas with higher compared to lower burned area fraction.

4. Fire and pyric herbivory change the densities of larval parasites in the environment and divide the landscape into burned and unburned regions with distinct infection risks for local herbivores.

5. The indirect effects quantified here represent a novel finding with major implications for all grazing systems impacted by fire.

1 | INTRODUCTION

Fires in savannas and grasslands facilitate mammalian herbivore grazing by removing dead and moribund vegetation and initiating high-quality regrowth (Archibald & Bond, 2004; Van de Vijver et al., 1999). Fire-driven changes to the vegetation layer concentrate herbivores on recently burned patches in a magnet effect termed 'pyric herbivory' (Fuhlendorf et al., 2009), a phenomenon that has been documented in Australia (Reid et al., 2022), North America (Allred et al., 2011), Asia (Thapa et al., 2022) and Africa (Archibald & Bond, 2004) in both livestock and wildlife. Fire and subsequent herbivory can drive changes in grass community composition (Koerner & Collins, 2014), create heterogeneity in vegetation structure (Donaldson et al., 2018), impact tree–grass interactions (Donaldson et al., 2022) and drive long-term changes in animal distributions (Burkepile et al., 2016). These outcomes of pyric herbivory also have important implications for parasites, which are strongly impacted by changes in host density (Arneberg, 2001), host resource availability (Hall et al., 2009) and habitat structure (Sehgal, 2015). Yet, despite well-documented fire-grazing interactions and the resulting potential for fire to have complex effects on parasite dynamics, prior work has focused almost exclusively on the direct impacts of fire on parasite densities (Scasta, 2015). Conversely, the role of indirect fire–herbivore interactions on infectious diseases remains a largely unexplored problem of increasing importance within the numerous systems where fire is a dominant driver (Albery et al., 2021).

For parasites with life stages that occur in the external environment (e.g. vegetation, soil), fire can directly impact parasite survival and decrease local parasite densities (e.g. ticks; Goodenough et al., 2017, horn flies; Scasta et al., 2012). In contrast, pyric herbivory concentrates mammalian herbivore hosts on burn patches and has the potential to facilitate the spread of parasites for which direct or indirect contact is a primary mode of transmission (Manlove et al., 2022). Pyric herbivory also fundamentally alters vegetation structure by cropping grass short for extended periods of time (Donaldson et al., 2018; Sensenig et al., 2010), creating habitat conditions that are less suitable for the development and survival of free-living stages of many environmentally transmitted parasites (Morgan & van Dijk, 2012; Van Dijk et al., 2009; Van Dijk & Morgan, 2008; Waruiru et al., 1998). Thus, understanding the impact of fire on parasite dynamics requires linking the direct effects of fire on parasite survival with potential indirect effects on parasite development and transmission.

In this study, we use gastrointestinal nematodes (GINs) that infect large mammalian herbivores as a model system for exploring the role of fire and subsequent pyric herbivory on parasite dynamics in a savanna system with a diverse wild mammalian grazer community. We focus on 'strongyle' nematodoes (Order: Strongylida; Superfamily: Trichostrongyloidea), which are ubiquitous parasites of wild and domestic ruminants. Eggs of adult strongyle parasites are typically shed in host faeces and hatch as first-stage larvae within the faecal mass, before leaving as third-stage larvae within days to weeks (Levine, 1968). Third-stage larvae ('L3' hereafter) migrate onto vegetation to await ingestion by a susceptible host and are highly sensitive to environmental conditions (Morgan & van Dijk, 2012). The environmental stages of GIN parasites that can be exposed to fire and climate allow us to evaluate both direct and indirect effects of fire on parasite dynamics. We focus on three specific hypotheses related to the direct, indirect and combined effects of fire on environmental stages of GIN parasites: (**H1**) fire kills the environmental stages of parasites (a direct effect) and locally 'cleanses' vegetation; (**H2**) the shedding of parasites in burn scars linked to pyric herbivory (an indirect effect) drives recovery of parasites in post-burn grass regrowth; and (**H3**) fire and subsequent herbivory keep grass short (i.e. it removes microhabitats) and change parasite exposure to environmental conditions and survival of environmental stages of parasites on burned relative to unburned patches (an indirect effect). To understand whether fire-driven changes in environmental parasite densities would scale-up to impact host infection outcomes, we also tested a further hypothesis: (**H4**) herbivores feeding in regions with high availability of burned grass will have distinct parasite burdens compared to those feeding in regions with low availability of burned grass.

2 | MATERIALS AND METHODS

2.1 | Study site

We conducted the study within the central Serengeti National Park ('Serengeti' hereafter), Tanzania, between July 2022 and February 2023. This area receives a mean annual rainfall of 650 mm and is dominated by open grasslands, with tree canopy cover consistently below 20% (Reed et al., 2009). A wide range of free-ranging indigenous mammalian grazers occur in this region (Swanson et al., 2015) and show a strong preference for feeding on recent burns (Eby et al., 2014; Wilsey, 1996). The average fire return time in our study region is 4 years, with management fires burned by Tanzanian National Parks (TANAPA) during the dry season (June–August) to improve forage quality and limit risk to infrastructure.

2.2 | Direct effect of fire on L3 densities

To test the direct impact of fire on GIN L3s in the environment (**H1**), we set up four blocks of paired 3×3 m control and fire treatment

plots resulting in a total of eight plots at the Serengeti Wildlife Research Centre. We set up exclosures around plots 3 months prior to any treatments to ensure large mammalian herbivores had been excluded. We avoided the effects of faecal contamination from outside plots by removing grass outside exclosure fences and excluding grass within 50 cm from the edge of the exclosure from sampling, effectively reducing each plot size to 2 × 2 m. Paired plots were within 4 m of one another with blocks 20 m apart. To ensure strongyle L3 were present, we seeded plots with blue wildebeest (*Connochaetes taurinus*) faecal samples. Samples were collected from 24 wildebeest, and for each sample the number of strongyle eggs per g faeces (epg) was determined using a modified McMaster egg counting technique as described in (Ezenwa, 2003). Individual faecal piles were then combined into a single sample and mixed thoroughly before being cultured for 3 days to improve larval emergence (O'Connor et al., 2006). We split the post-culture sample into equal weight portions (357 g) and added three portions to each plot. This equated to a dung pile density of 0.75/m², tailored to match the mean densities of wildebeest dung observed in five 100 × 2 m belt transects measured when collecting dung from free-ranging wildebeest herds. Peak L3 emergence in East African savanna systems is estimated to be between 14 and 20 days (Waruiru et al., 1998). We therefore waited 14 days after faecal samples were added before sampling. Following Ezenwa (2004), we sampled L3s on grass by randomly clipping grass above 2 cm height within the plots until a 16.51 × 8.25 cm sealable bag was filled. Grass clippings were collected no closer than 20 cm from dung piles between 09:00 and 11:00 h. Once collected, grass was soaked in 10.0 L of water with detergent for 24 h, and nematode L3s were extracted as described in Hansen and Perry (1994). L3s were then stained for 1 h with Lugol's iodine, counterstained with sodium thiosulphate and examined under 40× magnification. Larvae were distinguished into two groups based on morphology and staining patterns: free-living nematodes and parasitic nematodes. Grass clippings were air-dried and weighed to calculate total parasitic L3/kg dry matter (DM). We set fire to treatment plots following initial pasture sampling in October 2022. Fire temperatures were measured every s with thermocouples placed at ground level in all corners of the burned plots. During burn application, all thermocouples recorded temperatures in excess of 100°C for at least 5 s and the mean maximum recorded temperature was 273°C. Peak herbivore utilization of burn patches generally occurs when rainfall initiates regrowth (Eby et al., 2014). We therefore waited until rainfall-initiated grass regrowth (21 days) before post-burn grass sample collections were repeated.

2.3 | Pyric herbivory effects on L3 densities

To assess both the indirect effect of concentrated host densities on dung inputs and subsequent strongyle L3 density within burn scars (**H2**), and the combined fire and pyric herbivory effect on vegetation and L3 dynamics (**H3**), we monitored plots at 14 sites within the long-term Snapshot Serengeti (SS) camera trap grid

(Anderson et al., 2016; Swanson et al., 2015). We waited for management burns to conclude in August 2022 and selected seven camera trap sites burned during management fires that had paired unburned camera sites within 5 km. Starting in September 2022, we measured GIN L3 density, herbivore dung inputs, standing grass biomass and temperature at ground level within permanent 25 × 43 m monitoring plots at each of the 14 camera sites. To measure L3 density on grass within each monitoring plot, we sampled along two separate 50-m W-shaped transect lines (Hansen & Perry, 1994). Along each transect, we clipped three randomly selected grass samples every 5 m, which resulted in 60 clipped samples per transect, each filling a 3.79-L sealable bag. Grass was clipped 2 cm above the soil surface and at least 20 cm from dung piles. Transects ran from the northernmost and southernmost corners to the adjacent corners of monitoring plots and were sampled between 09:00 and 11:00 h. Grass samples were returned to the laboratory and soaked in 15.0 L of water with detergent for 24 h before nematode larvae were extracted and parasitic L3 quantified as described above.

We counted herbivore dung inputs at each monitoring plot by walking three parallel 43 × 2 m belt transects and recording the number of dung piles from each herbivore species. We measured the environmental conditions on each plot by non-destructively estimating grass biomass at 20 points along a 50-m W-shaped transect line using a disc pasture metre (DPM; Zambatis et al., 2006) calibrated to our study sites. The transect line started at the northernmost corner and ran to the adjacent corner of each plot. In the centre of each plot, we placed a thermocouple that recorded ground-level temperature every hour, and took a DPM measurement above the thermocouple every month. Within the SS grid, we measure ambient temperature and humidity at five weather stations.

2.4 | Burned area effects on host parasite burdens

To assess if differences in L3 densities in burned and unburned grass resulted in differences in the parasite burdens of host animals foraging in regions with a high or low burned area fraction (**H4**), we quantified the GIN burdens of Grant's gazelles (*Nanger granti*). Grant's gazelles are a resident herbivore species found commonly within the SS grid (Swanson et al., 2015) that actively select for burned patches (Eby et al., 2014). We collected faecal samples from 21 Grant's gazelles each month. Sampling occurred at least 10 days after L3 sampling and was carried out by dividing the SS grid into seven regions and collecting three samples from different individuals in each region, every month. To assess if other known drivers of strongyle burdens in herbivores dampen or amplify effects of burning, we recorded the herd size (number of animals within a group) and sex of sampled individuals. Each faecal sample was collected in a sealable bag and kept at 4°C until processing (all counts occurred within 24 h of collection). Strongyle egg output in faeces was quantified using a modification of the McMaster egg counting technique (Ezenwa, 2003). We used

faecal egg counts as a proxy for an individual's parasite burden since they reflect a combination of the number, size and fecundity of the worm population within a host (Gasbarre et al., 2001).

Grant's gazelles within our study region have well-defined home ranges approximately 5 km in diameter (Walther, 1972). We therefore assumed that the individuals we sampled were regularly foraging within 2.5 km of the area in which they were sampled and that area burned within their home range represented the availability of burned grass. To link gastrointestinal parasite burdens to the availability of area burned within Grant's gazelle core area, we used NASA's $MOD_{09}GQ$ to create an 8-day fire product using algorithms previously generated specifically for the Serengeti (Anderson et al., 2020). We then used location data for each faecal sample to calculate the proportion of burned area within a 2.5 km radius.

2.5 | Data analysis

To measure the direct impact of fire on L3 (**H1**), we fit a linear mixed effects model (LMM) using the lme4 (Bates et al., 2015) package in R v 4.01 (R Core Team, 2021). We square-root transformed L3 data to improve model fit and modelled it as a function of fire treatment (burn or no-burn), time (pre- and post-fire) and their interaction, with block and plot being treated as random effects.

We assessed the effects of fire on dung inputs by herbivores and subsequent impact on L3s (**H2**) by fitting two GLMMs using the lme4 package (Bates et al., 2015). We first fit a GLMM with a Poisson distribution with herbivore dung as a function of fire treatment (burn or no-burn), month sampled and their interactions, with pair (paired burned and unburned plots) and sampling plot as random effects (Bates et al., 2015). Next, we fit a GLMM with the same model structure but with L3/kg dry matter as the response variable.

To identify how fire and herbivory impacted available microhabitats and subsequently L3 survival (**H3**), we first fit a LMM with standing grass biomass g/m^2 as the response and fire treatment (burn or no-burn), sampling month and their interactions as the fixed effects, and pair and plot as the nested random effects. We compared the ground temperature over the study period to fire treatment by fitting a LMM with ground temperature as a function of fire treatment and pair representing the random effects. Next, we calculated Δ L3 as the difference in log-transformed L3 densities between monthly samples and fit a linear model with Δ L3 as a function of herbivore dung/m^2, ground temperature (°C) and fire treatment. We used ground temperature as a covariate to represent microhabitat conditions as it captures the combined effects of standing grass biomass and changes in ambient temperature. Moreover, ground temperature exhibited a strong correlation (CC = −0.8) with humidity during our study and therefore represents multiple microhabitat features that can affect L3 survival (Morgan & van Dijk, 2012). We calculated ground temperature as the mean temperature at ground level over the 14-day period (peak emergence time of larvae; Waruiru et al., 1998) prior to each sampling event. Thermocouples were exposed to damage from animals, and occasionally failed. In these cases, we used the relationship between the difference in weather station (ambient) and ground temperature and standing grass biomass to derive ground temperature using grass biomass measurements and temperature readings from the nearest weather station. Finally, we calculated the coefficient of variation (CV) for L3 found in equal sample sized bins of grass biomass.

To assess whether there were differences in the infection burdens of Grant's gazelle sampled in regions with high or low availability of burned area (**H4**), we first fit a GLMM with strongyle egg count as the response and proportion burned area, herd size and sex (male/female) as fixed effects, with sampling region as the random effect, assuming a Poisson distribution for the response variable. Then, to assess differences in strongyle egg counts of gazelles over time, we took the proportion of area burned within a 2.5 km radius of dung sample locations and split samples into 'high' or 'low' monthly burned area with equal sample sizes. We then fit a GLMM assuming a Poisson distribution with burned area bin, sampling month and their interaction as the main fixed effects and sampling region representing the random effect.

3 | RESULTS

3.1 | Direct effect of fire on L3 densities

We recovered no surviving strongyle L3s in experimentally burned plots 21 days after fire (Figure 1). L3 densities were driven by a fire treatment × time interaction and did not change significantly in unburned plots over the same period (mean = 387.6 L3/kg, SE = 119.83) despite similar levels of pre-fire strongyle L3s in grass between control (mean = 580.6 L3/kg, SE = 150.45) and burned (mean = 440.3 L3/kg, SE = 89.46) plots (Table 1).
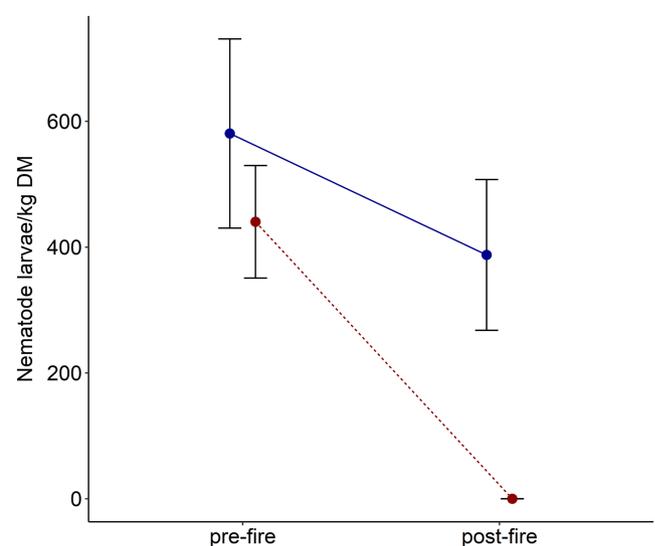
FIGURE 1 Density (mean ± SE) of free-living gastrointestinal nematode third-stage larvae (L3) per kg of dry matter (DM) within paired fire (dashed red line) and control (solid blue line) treatments in experimental plots in the Serengeti National Park.

TABLE 1 Results of factorial ANOVAs for the effects of fire treatment (burn vs. no-burn), and pre- and post-treatment (time) on parasitic L3 densities in experimental plots (A), the effects of fire treatment (burn vs. no-burn), and sampling month on herbivore dung densities (B) and parasitic L3 densities in monitoring plots (C), the effects of herbivore dung piles, ground temperature and fire on changes in gastrointestinal nematode stage 3 larvae (Δ L3; D), and (E) the effects of fire treatment (burn vs. no-burn) on temperature measured at ground level.

Variable	df	F	p
(A) Parasitic L3s			
Fire treatment	1	0.83	0.363
Time	1	2.42	0.119
Fire treatment×Time	1	14.33	<0.001
(B) Herbivore dung			
Fire treatment	1	0.44	0.508
Sampling month	4	258.69	<0.0001
Fire treatment×Sampling month	4	39.25	<0.0001
(C) Parasitic L3s			
Fire treatment	1	100.53	<0.0001
Sampling month	4	358.01	<0.0001
Fire treatment×Sampling month	4	251.52	<0.0001
(D) Δ L3			
Herbivore dung	1	2.23	0.143
Ground temperature	1	5.89	0.019
Fire treatment	1	3.09	0.085
Herbivore dung×Ground temperature	1	1.82	0.184
(E) Ground temperature (°C)			
Fire treatment	1	57.91	<0.0001

3.2 | Pyric herbivory effects on L3 densities

A fire treatment×month interaction drove changes in herbivore dung densities (Table 1), and herbivores (as indexed by dung counts) actively selected for burned patches in the landscape after the first rainfall in late September (Figure 2a). Average dung inputs on burn plots were 40% higher than on unburned plots during October and November, before decreasing to match unburned plots in December and January (Figure 2a). Increased dung meant that L3 densities were also impacted by a fire treatment×month interaction (Table 1). L3 densities recovered quickly after fire (Figure 2b) on burned plots. Ultimately, L3 densities on burns were higher (mean=106.4 L3/kg, SE=47.91) than nearby unburned plots (mean=81.7 L3/kg, SE=28.23) by October (~2 months since fire), but decreased in November (mean=28.2 L3/kg, SE=20.48) to less than half those recorded in paired unburned plots (Figure 2b) before recovering to match unburned plots for the remainder of the study.

Fire treatment had a significant effect on ground temperature (Table 1) which was on average 1.7°C higher on burned compared
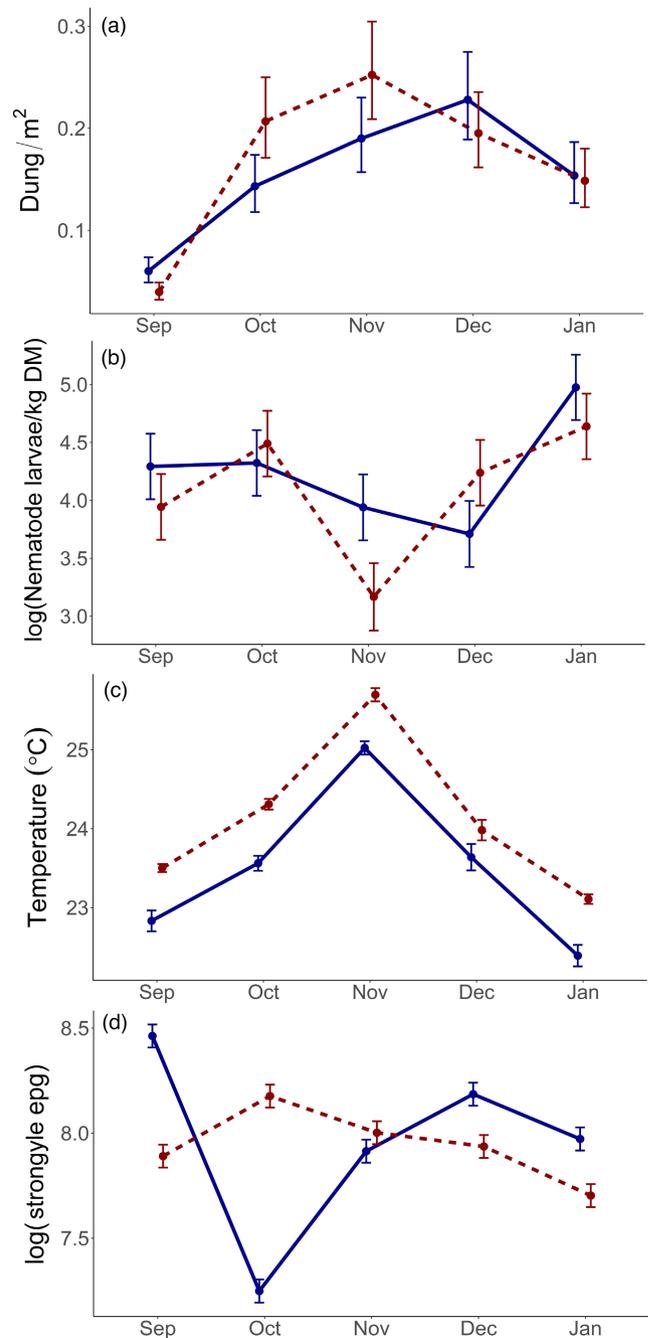
FIGURE 2 Dung piles per m² (a), Gastrointestinal nematode free-living larvae per kg dry matter (DM) estimated from grass clipping (b), ground temperature in degrees Celsius (c), and strongyle eggs per gram from faecal samples of Grant's gazelle (*Nanger granti*) collected in areas with high (red dashed line) or low (blue solid line) proportion of burned grass (d) for the period of September 2022 to January 2023 in the Serengeti National Park. Dung densities, nematode larvae and ground temperature were measured in seven-paired burned (red dashed line) and control (blue solid line) monitoring plots. Values represent marginal means and standard errors from GLMMs.

to unburned plots. The highest mean daily ground temperature (mean=25.7°C, SE=0.08) was recorded on burned plots in November (Figure 2c) when L3 densities on burn plots declined (Figure 2b).
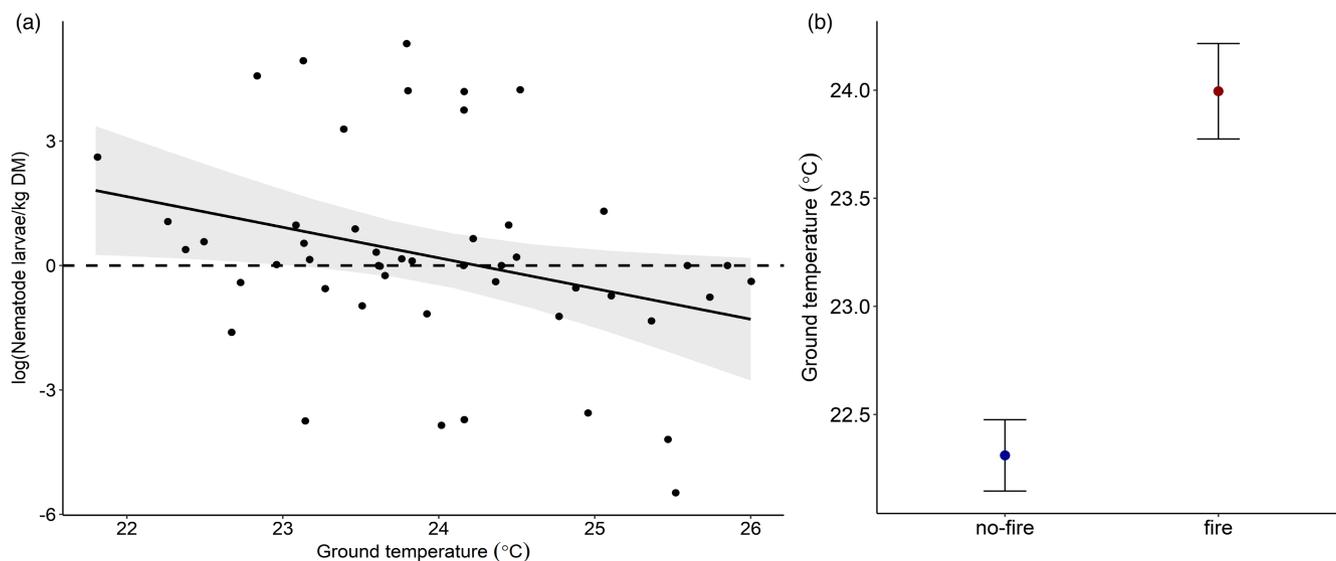
FIGURE 3 Relative change in free-living gastrointestinal nematode third-stage larvae (L3) per kg dry matter as a function of the temperature (°C) measured at ground level (a), and temperature measured at ground level (mean ± SE) as a function of fire treatment (b) in fire (red) and no-fire control (blue) monitoring plots between July 2022 and January 2023 in the Serengeti National Park. Relative change (a) above the dashed line indicates an increase in L3 and the solid line represents linear model predictions with the shaded area the 95% confidence intervals.

TABLE 2 Results of factorial ANOVAs for the response of strongyle eggs per gram of Grant's gazelle (*Nanger granti*) dung samples to (A) gazelle herd size, sampled animal sex and proportion of area burned within 2.5 km radius of sample location, and (B) the binned proportion of area burned (high burned area vs. low burned area) within 2.5 km radius of sample location and month of sample collection.

Variable	df	F	p
(A) Strongyle eggs per gram			
Herd size	1	2303.90	<0.0001
Sex	1	625.94	<0.0001
Proportion burned	1	6072.38	<0.0001
(B) Strongyle eggs per gram			
Binned proportion burned	1	1262.01	<0.0001
Sampling month	4	8440.11	<0.0001
Binned proportion burned × Sampling month	4	12,465.42	<0.0001

We found that Δ L3 across all plots decreased significantly with increasing ground temperature (Table 1; Figure 3). L3 were predicted to increase when mean ground temperature was below ~24.5°C and decline above that temperature (Figure 3). There was no effect of dung density, fire nor the interaction with ground temperature on Δ L3 (Table 1). Fire treatment was the only significant driver of standing grass biomass (Appendix S1: Table S1). Unburned plots had fivefold greater grass biomass (mean = 314.2 g/m², SE = 14.02) than burned plots (mean = 66.8 g/m², SE = 6.81), regardless of monthly changes in rainfall (Appendix S1: Figure S1), and the CV of L3 densities was highest when grass biomass was below 143.6 g/m² (Appendix S1: Figure S2).

of burned area. Gazelle parasite burdens were also significantly higher when sampled animals were found in larger herds and significantly lower in male than female animals (Table 2). There was a significant proportion burned area × month interaction effect (Table 2; Figure 2d), where strongyle burdens of gazelles found in areas with low burned area peaked ~1 month after fire in September (mean = 4250.0 epg, SE = 769.92), while gazelles sampled in the same period within regions of higher burned area had significantly lower strongyle burdens (mean = 2933.9 epg, SE = 332.27). In October, faecal egg counts of gazelle found in low burn areas collapsed to levels below those in high burned areas before increasing in December and January (Figure 2d).

3.3 | Burned area effects on host parasite burdens

The proportion of area burned had a significant effect on Grant's gazelle strongyle burdens (Table 2), with parasite burdens decreasing when gazelles were sampled in areas with higher proportions

4 | DISCUSSION

We examined the direct and indirect mechanisms by which fire can affect parasite densities within systems where herbivores concentrate on recent burns, and the implications for parasite burdens in

hosts. Our results show that fire kills infective parasite larvae (L3s) and cleanses burn patches (in line with **H1**), affording herbivores an opportunity after fire to feed in areas with low parasite exposure. In support of **H2**, we found that post-fire pyric herbivory concentrated dung inputs in burn scars and resulted in the recolonization and recovery of L3s on burned grass to match the densities in unburned patches. However, over the entire study period, L3 densities in the grass were determined by ground temperature and not dung inputs and were highly stochastic in burned plots that had lower standing grass biomass and greater exposure to harsh conditions. High dung inputs on burn patches prime the system for L3 recovery, but absolute L3 densities appear to be limited by environmental conditions. Thus, fire and subsequent intensive grazing that removes microhabitats, couple L3 survival to environmental conditions (in line with **H3**). All of these fire-driven effects result in distinct L3 densities on high versus low burn areas and, in support of **H4**, we found that differences in L3 densities translate into distinct parasite burdens in the hosts feeding in areas with high versus low burned grass. These fire-driven parasite dynamics should be relevant in the many grass-dominated systems where there are strong fire–herbivore interactions (Allred et al., 2011; Archibald & Bond, 2004) and potentially play a significant role in driving parasite dynamics in wildlife and livestock hosts on a global scale.

For free-living GIN larvae, exposure to stressful environments and an absence of microhabitats to buffer external stressors is a major determinant of survival and abundance within pasture (Morgan & van Dijk, 2012; Van Dijk et al., 2009; Van Dijk & Morgan, 2008; Waruiru et al., 1998). In line with this, we found that the major impact of pyric herbivory on GIN dynamics is to maintain the structural changes in vegetation that are initiated by fire, and in so doing, expose infective larvae to more extreme temperature, humidity and light fluctuations. Within our system, fire removes L3 from grass and couples recolonizing L3 survival more closely to climate than in unburned areas. Although concentrated herbivore densities and subsequent dung inputs would lead to recovery of L3 levels on burns, our results show that the larvae emerging from the higher numbers of faecal inputs may ultimately be limited in terms of their capacity to survive in heavily grazed (and therefore stressful) areas. This is most clear in November, when we recorded the hottest and driest conditions (Figure 2c) at a time when L3 densities on burn patches collapsed to their lowest level despite high dung deposition (Figure 2a,c). Fire can therefore drive a seasonal mosaic of distinct burned and unburned L3 densities on the landscape that should continue until grass biomass recovers (Figure 4). These differences between burned and unburned patches should be more distinct when
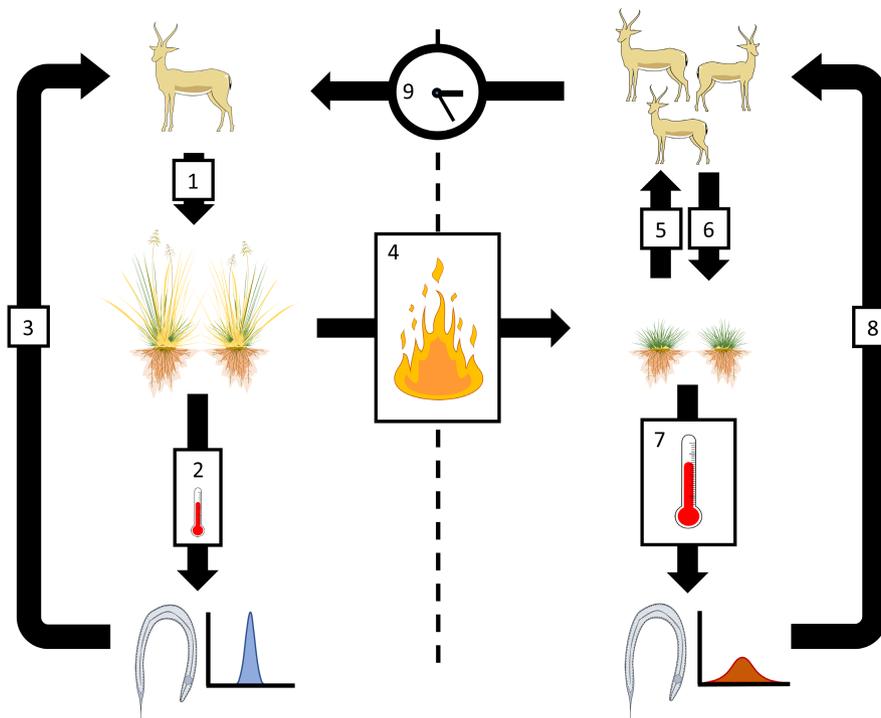
FIGURE 4 Conceptual framework on the role of fire in structuring gastrointestinal nematode (GIN) dynamics in grazing systems. In unburned areas, grazers are dispersed and have a limited capacity to reduce standing grass biomass (1). Standing grass biomass provides a buffer from environmental conditions (e.g. temperature, solar radiation) for emerging larvae (2). GIN parasite burdens in the landscape remain relatively stable and reinfection of hosts may be largely determined by host susceptibility (3). Fire initiates changes in the system by consuming standing grass biomass and initiating fresh regrowth (4). These changes concentrate grazers (5) that maintain grass in a short-cropped state (6) with GIN larval survival in the grass becoming highly stochastic and coupled to environmental conditions at the time that they emerge (7), which ultimately determines the intensity of larval challenge experienced by grazers feeding within burned patches (8). Over time, herbivores stop utilizing burn patches and they should transition back to the dynamics of unburned patches (9) resulting in a shifting seasonal pattern of burned and unburned patches in the landscape.

conditions are harsh and protection from grass cover becomes more important for sensitive parasites. Thus, pyric herbivory effects that manifest via the loss of microhabitats should become increasingly prominent in hot and dry systems or areas with high solar exposure. Conversely, concentrated shedding of parasites in burn patches could be more important at moderate temperatures or in mesic systems where milder conditions link parasite densities more closely to inputs from herbivores.

The strongyle parasite burdens in Grant's gazelle sampled within high burn areas appeared to track fluctuations in burned plot L3 densities, with burdens low in the month after fire before rising in October following landscape L3 recovery, and declining again in December and January after L3 densities declined in November. The feedback between the reduction of environmental parasite stages by fire to host parasite burdens has been demonstrated for ticks and horn flies in livestock (Scasta et al., 2012). Similar evidence in wildlife systems is rare (Albery et al., 2021). Although our methods for assessing the impact of larval challenge on herbivore parasite burdens is admittedly coarse, it shows that fire acts beyond the initial direct effect and may change host infection rates over longer periods and play an important and under-appreciated role in seasonal host–parasite interactions in wildlife populations (Altizer et al., 2006). The lower parasite burdens found in gazelles feeding in low burn areas in October could be attributed to changes in the mean herd size, which was 35% and 25% of the size of herds sampled 1 month before and those collected in burned areas during the same period respectively. Animals sampled in larger herds in our study had higher parasite burdens, a trend consistent with Grant's gazelle in other systems (Ezenwa & Worsley-Tonks, 2018). Thus, gazelles may have concentrated in large herds on burned patches following September rainfall and left only small, low-density herds with lower infection burdens remaining in unburned areas.

The use of fire by humans to reduce parasite burdens in livestock pasture predates modern commercial farming practices (Trollope, 2011) and continues to be a driver of prescribed burning on rangelands and in wildlife systems (Fyumagwa et al., 2007; Polito et al., 2013). Previous work has shown that fire can remove or reduce parasite densities in the environment for a range of parasites important for animal and human health (Goodenough et al., 2017; Polito et al., 2013; Scasta et al., 2012). Similarly, our work shows that fire is effective at removing GIN larvae from grass, and unlike certain tick species that survive fire through use of refugia (Padgett et al., 2009), we found no evidence that strongyle L3 were able to avoid mortality from fire. In systems where livestock are treated with anthelmintics, the input effects of pyric herbivory may also be reduced and result in longer-term reductions in parasite challenge to susceptible hosts. These impacts should provide an important additional benefit to grazers feeding immediately after fire, when nutrient gains from feeding in fresh regrowth occur concurrently with lower GIN larval challenge at a time of year when forage quality in unburned areas is low, and herbivores are experiencing high nutritional stress (Owen-Smith & Novellie, 1982).

5 | CONCLUSIONS

Previous work on fire effects on parasites have focused on the direct impact of fire on parasite survival (Fyumagwa et al., 2007; Goodenough et al., 2017; Polito et al., 2013; Scasta, 2015; Scasta et al., 2012). Here we have extended this work by showing that concentrated herbivory following fire can lengthen the effects of fire on free-living parasites into the following rainfall season. Thus, fires can create divided landscapes with burned and unburned areas that have distinct infection risks (Figure 4). Importantly, how long fire effects continue to influence patch level parasite densities in savannas each season should depend on the strength of the pyric herbivory effect and the productivity of the system, such that recovery to previous dynamics occurs slower in regions with high herbivore densities and low productivity. Developing a clear understanding of the effects of fire timing and size on herbivore–parasite dynamics and incorporating the seasonal role of fire into herbivore–parasite population models is an important next step in understanding fire's role in infectious disease dynamics more broadly.

AUTHOR CONTRIBUTIONS

All authors conceived the ideas and designed methodology; Jason E. Donaldson, Basil Senso and Aidan Trentinus collected the data; Jason E. Donaldson analysed the data; Jason E. Donaldson led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

CONFLICT OF INTEREST STATEMENT

The authors declare that there is no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.k3j9kd5dr (Donaldson et al., 2023).

STATEMENT OF INCLUSION

Our study brings together authors from a number of different countries, including scientists based in Tanzania where the study was carried out. The study was designed in Tanzania with all authors involved in the study design to ensure that the diverse sets of perspectives they represent were considered from the onset.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Results of factorial ANOVA for the effects of fire (+FIRE vs. −FIRE), and sampling month (MONTH) on standing grass biomass (g/m^2), inferred using a linear mixed-effects model.

Figure S1. Standing grass biomass (mean ± SE) in g/m^2 from burned (red dashed line) and unburned (dark-blue line) monitoring plots in the Serengeti National Park over the period of September 2022 to January 2023. The light-blue shaded area represents monthly rainfall (mm) over the same time period.

Figure S2. The coefficient of variation for gastrointestinal nematode stage 3 larvae recovered from grass pasture in 14 monitoring plots in the Serengeti National Park from different grass biomass (g/m^2) bins.