Water sources aggregate parasites, with increasing effects in more arid conditions

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Abstract

Shifts in landscape heterogeneity and climate can influence animal behavior and movement in ways that profoundly alter disease transmission. Amid accelerating climate and land use changes, it is increasingly important to identify and monitor hotspots of increased animal activity and overlap where disease transmission is likely to occur. Water sources that are foci of animal activity have great potential to promote disease transmission, but there has been very little work to quantify this, nor any comparison across a range of hosts and climatic contexts. In the case of fecal-oral parasites, water resources can aggregate large groups of many different host species in small areas, concentrate infectious material, and function as disease hotspots. This may be exacerbated where water is scarce and for species that require frequent drinking water access.

Working in an East African savanna, we show via experimental and observational methods that water sources increase the density of wild and domestic herbivore feces and thus, the concentration of fecal-oral parasites in the environment, by up to two orders of magnitude. Our results show that this effect is amplified in drier areas and following periods of low rainfall, creating dynamic and heterogeneous disease landscapes across space and time. In addition, we show via camera trapping methods that herbivore grazing behaviors that expose them to fecal-oral parasites are often increased at water sources relative to background sites, thereby creating landscape hotspots of potential disease transmission. Critically, this effect varies markedly by herbivore species, with strongest effects observed for two large, water-dependent animals that are of critical concern for conservation and development: elephants and cattle.

When water availability is reduced – a global pattern that is increasing amid climate changes and growing anthropogenic water use – risk of parasite exposure may increase substantially, posing multiple threats to critical taxa. These findings are important for understanding shifting parasite dynamics for several threatened wildlife species and for pastoral livelihoods in response to changing water supply due to climate changes.

Introduction

Climate change is predicted to lead to dryland expansion over half of the globe's land by 2100 (1), increasing the importance of surface water for wildlife, domestic animals, and the two billion people currently living in water-stressed areas (2). However, water sources have great potential to serve as transmission foci for a range of diseases in a landscape, as they likely concentrate a wide range of hosts in a small area where parasite exposure may be increased (3, 4). In particular, for many parasites that can be transmitted via the environment, landscape heterogeneity can create localized transmission hotspots that have the potential to markedly affect overall parasite exposure risk (5–7).

Water sources can draw animals together, particularly in dry conditions (8–10). For example, water sources drive large elephant aggregations (11) and increase contact rates among cattle herds (12) during

dry periods. However, the degree to which different herbivores gather at water may vary by diet (13), physiology (14), and predation risk (14, 15). Camera trapping work of animal overlaps at watering holes and at baited food stations has shown species-specific increases in contact rates around resources (16, 17, 18) suggesting potential implications for disease transmission. However, there has been no large-scale experimental work measuring the degree to which animals congregate around water relative to their background density, how this may impact disease risk, or how this varies across climatic contexts. Understanding these patterns will provide critical new information about relative parasite risk across contexts and at relevant spatial scales (18). This will be increasingly important given that water manipulation (e.g. changing waterholes, dams, and rivers) is widespread and increasing across the globe, particularly in water limited landscapes.

Resources that attract hosts and increase contacts with other hosts, vectors, or infectious stages in the environment can act as hotspots of parasite risk. While surface water sources are established as hotspots for diseases with obligate water development of parasite or vector (e.g. mosquitoes that must develop in water sources), there is little understanding on the effects of water on density-dependent parasites transmitted via the fecal-oral route. Such parasites are likely to be particularly affected by host congregations around water, and include many medically and economically important gastrointestinal nematodes (order Strongylida) (19). While parasites are important components of health-intact ecosystems (20), and are key to population regulation, many impose significant health threats. Gastrointestinal nematodes often inflict serious morbidity on domestic and wild herbivores (SI Appendix, Table S1 and S2), and, while no study has quantified the global economic losses attributable to these worms, estimates in Europe show 10-50% production losses on farms due to these parasites (21) and growing worldwide concerns of rising resistance of these parasites to treatment (22). Additionally, gastrointestinal worms cause disease in more than 2 billion people worldwide, particularly for those who are experiencing poverty (23). Health impacts from nematodes can be exacerbated by additional stressors: for example, animals with low nutrition can have heavier infections (24) and those with reduced immune function can have increased mortality (25). Thus, shifting host nutrition and immunity due to land use change (26), pollution (27), and climate changes (28) warrant more careful monitoring of parasite infections in wildlife across contexts.

Many gastrointestinal nematodes are transmitted via the fecal-oral route, releasing thousands of parasitic ova into the environment upon host defecation. These parasites develop in the environment before infecting hosts when they drink water or consume food contaminated with infective parasite stages from feces (e.g. Strongylid nematodes (29)). While parasite egg density is often correlated with exposure risk, this pattern can vary if parasite survival varies significantly among sites. For instance, increased parasite egg density near water might not translate to increased parasite exposure risk if reduced vegetation cover near water increases ground temperatures (30) or reduces moisture (31) such that larval mortality is increased; or conversely, if increased moisture from ground water improves survival. In theory, increased time that hosts spend at water should lead to increased dung density (and thus parasites), followed by increased risk of exposure to infective stages via drinking and eating, such that water may create a potentially important hotspot of gastrointestinal parasite risk in a landscape.

However, this putative link between increased host activity and parasite exposure at water sources has only been supported by models (32) and an observational study on red deer (4). In other systems, food resources have been manipulated to study effects on racoon pathogens (17), and carcass sharing among carnivores has been suggested to increase potential for pathogen transmission (33). However, there has been no large-scale experimental work testing the role of water sources in increasing potential for parasite sharing.

While water-driven parasite aggregation likely occurs across a variety of landscapes where water is scarce and concentrated, East African tropical savannas provide an ideal place to investigate this phenomenon, as they are home to a diverse array of wild and domestic herbivores in a largely water limited landscape. In addition to large numbers of ranched cattle (*Bos taurus*), wild African herbivores include many locally or globally declining species such as zebra (*Equus burchelli* and *Equus Grevyi*), giraffe (*Giraffa camelopardalis*), elephant (*Loxodonta africana*), buffalo (*Syncerus caffer*), and impala (*Aepyceros melampus*), all of which are infected by a diverse community of helminths (34). While many parasites are host-specific, substantial parasite sharing occurs even among taxonomically divergent species (35) when those species overlap spatially (36). Notably, several important parasites (e.g. trichostrongyle nematodes; see SI Appendix, Tables S1 and S2 for a list of host-parasite records and pathogenic effects) are shared with closely-related domestic animals or with humans (34, 37). While many parasite sharing links remain uncertain (37), several pose significant health threats to a range of hosts (38, 39) .

In this study, we asked: **1) To what extent do water sources concentrate hosts, feces, and fecal-oral parasites across herbivore species?** Implementing a two-year experiment in an East African tropical savanna (Figure 1A,D), we expected that water removal and replenishment would respectively decrease and increase density of water-dependent herbivores and their feces; and, based on parasite eggs in dung, parasite density in the environment. Using additional data on herbivore grazing behavior, we then asked **2) To what extent are water sources parasite exposure hotspots across herbivores?** We combined herbivore grazing behaviors measured from camera traps with parasite density measurements to compare total exposure estimates near water and matrix sites for four parasite mortality scenarios: equal mortality in the environment at water and matrix sites, and half, double, and ten times higher mortality rates near water. We expected that parasite density patterns would drive relative exposure results, with strongly aggregating herbivores showing elevated exposures near water, even with dramatically increased parasite mortality. We then asked: **3) How does the concentration of herbivore activity, herbivore dung, and parasite density at watering holes vary across rainfall contexts?** Using observational data from water sources spread across a broad rainfall gradient (Figure 1A) and over three years of sampling, we tested our hypothesis that herbivores, their dung, and parasite density would be more concentrated near water following periods of low rainfall and in more arid areas, and that effects would be strongest results for highly water-dependent animals.

Methods

Research was conducted at two mixed wildlife and cattle ranching properties in Laikipia county, central Kenya: Ol Pejeta Conservancy and Mpala Research Centre (Figure 1).

Experimental system: At Ol Pejeta Conservancy (0.0043° S, 36.9637° E), we established five experimental sites, each with one pair of water pans (10 pans total) and 1 'dry' (no-pan) site (Figure 1A). Matrix site coordinates were randomly selected from a range of locations 1km from the experimental water pan and at least 1km from any other water source. One of the two water pans (located 0.4 - 1km apart at each site) was drained (experimental pan) for one year and then refilled, while one remained filled throughout the experiment (filled pan) (Figure 1B and C). We measured herbivore activity via camera traps and dung surveys. Camera traps were used to verify elevated herbivore activity patterns suggested by dung density, as dung density does not necessarily indicate increased herbivore exposure risk to parasites. Cameras ran for 709 trap nights during dry season months from August 2016 - August 2018. Full camera trapping methods are provided in the SI Appendix, Figs. S1 and S2, Table S3. We performed dung surveys at each site once before draining water from each experimental pan in October 2016. We repeated dung surveys at each pan and matrix site (every 3 months, $n = 5$ resurveys during the experiment) before refilling in January 2018 and resurveying ($n = 3$ surveys post refill). Surveys were performed along six 150m transects extending radially outward from the water source (or matrix site center). A 1m² quadrat was placed every 10m ($n = 16$ quadrats per transect), and volume of all large mammalian herbivore dung was estimated and classified as 'fresh' (≤ 3 days) or 'old' (> 3 days) (see SI Appendix, Fig. S3, Table S5 for detailed dung volume measurement methods). After a drought in June 2017, quadrats were laid on both sides of the transect to increase sampling area, and density was calculated by averaging across the two quadrats.

Observational system: To investigate herbivore abundance, dung density, and parasite density across climatic conditions, we extended sampling protocols to an additional 20 man-made dams (and associated matrix sites) at Mpala Research Centre (0.283° N, 37.867° E) ($n = 17$, described in (67)) and Ol Pejeta Conservancy ($n = 3$). While experimental pans were confined to one rainfall zone (~ 700 mm/yr), these additional 20 water sources spanned a 460 - 760 mm/year rainfall gradient (Figure 1D), marking a transition from sub-desert scrub to grass/tree savanna (68). We included paired matrix sites 1km from the dam and at least 1km from any other water source. From April - September 2017, one camera was placed at each dam and matrix site for one month (387 trap nights) (full methods provided in SI Appendix and Table S4). Dung surveys were conducted using experimental system methods, except that quadrats were laid on only one side of the transect. Five surveys were conducted from November 2015 – October 2017 at all sites at Mpala; two surveys were repeated at the Ol Pejeta Dams during November 2015 and September 2016.

Photograph analysis: We uploaded camera trap photographs to a citizen science website (<https://www.zooniverse.org/projects/gtitcomb/parasite-safari>) where volunteers assisted in classifying images by counting animals that were present, drinking, and/or grazing. Image processing methods and validation are reported in SI Appendix, Fig. S1 and S2.

Parasite detection: We estimated parasite eggs in the environment (eggs/m²) as the product of median fecal egg counts (eggs/g) by the physical density of fresh dung for each species (g feces/cm³) and the volume of fresh dung in the environment (cm³/m²). Dung density calculations are detailed in SI Appendix and Table S5. To quantify average parasite density, we conducted fecal egg counts (FECs) on fresh herbivore dung samples (n=131) collected across multiple years and locations at Mpala (Figure 1B, Appendix 4) using the mini-FLOTAC protocol (4g feces in Sheather's sugar solution) (69). To contextualize FECs, we conducted a literature search of reported FEC values for focal herbivores. Our values fell within ranges reported throughout East and Southern Africa (Figure 1B, SI Appendix and Table S6).

We also measured parasite eggs at all sites by subsampling surface soil (< 1cm depth) from the water's edge ("0m Wet"), dry soil next to the water ("0m Dry"), and 50m from the center of the matrix site ("1km Dry"). We sieved (2 mm grain) and filtered 4g soil from each of five transects to create a homogenized 20g composite sample (n = 175 at Ol Pejeta; n = 232 at Mpala). For wet soils, we combined 5g from five locations (25g total) and calculated dry weight using a replicate composite sample. We followed a sedimentation-floatation protocol (70), using 0.1% Tween 80 to wash soil, and Sheather's sugar as a floatation solution to isolate eggs. We counted all unhatched and intact strongyle-type eggs that rose to the cover slip following 15 minutes of centrifugation at 500g. For wet soil samples, we used dry soil weight to calculate dry soil epg.

Analyses:

Experimental System

Herbivore activity: We compared total, grazing, and drinking activity (daily individual*seconds) at filled and experimental pans recorded from camera traps using GLMMs with either a negative binomial or Tweedie error structure. The appropriate error structure was determined using both AICc comparisons and residual diagnostics using the *DHARMA* package (71). We tested for significance of the interaction between experiment status (pre, during, or post) and treatment (filled or drained) for each herbivore species using X² tests. Site (n = 5) and month (n = 7) were included as random effects.

Dung and parasite density: We compared parasite and dung density (eggs/m² and cm³/m² respectively) at filled and experimental pans using generalized linear mixed hurdle models with zero-inflation and Gaussian conditional components. Density was cube-root transformed to meet residual assumptions (determined using the *DHARMA* package) for all models (elephants, cattle, zebra, giraffe, and buffalo), except for impala, which was log-transformed. Zebra dung densities reflect both *Equus grevyi* and *Equus quagga*, as their dung is indistinguishable.

We tested the effect of experiment status (pre, during, and post) on differences between dung density at filled and experimental pans, assuming a significant interaction between status and treatment in either the conditional or zero-inflated components of the model signified changes due to water manipulation.

We also included outward distance from water (log-transformed) as a fixed effect, while period (n = 10) and site (n = 5) were random effects. We also analyzed the log-ratio of dung density for all dung and parasites summed together as exponentiating the log-ratio provides an intuitive estimate of relative dung and parasite density. These models follow a similar structure as negative binomial GLMMs and have qualitatively similar results; they are presented in full in SI Appendix Tables S9 and S10.

We also compared dung density between matrix sites and filled pans to explore the possibility for underlying variation in the system as a driver of patterns seen. While dung density for most species differed at water sources compared to matrix sites, and was more than eight times higher (at the 0m mark) summed across species, only impala dung density changed at filled pans compared to matrix sites throughout the experimental period, indicating that in almost all cases, significant results were likely a result of changes to experimental pans only (SI Appendix Table S12).

Parasites in soil: We used a negative binomial generalized linear mixed model to test whether soil parasite egg densities in 1) dry soil next to drained and filled water pans and 2) wet and dry soils together differed by experiment status. We used another negative binomial GLMM to test whether dry soil parasite density differed between water pans and non-water matrix sites. We included site (n = 5) and period (n = 10) as random effects in all models.

Total transmissions: For parasites with infectious stages in the environment, parasite exposures per unit time and space can be thought of as the product of parasite density in the environment, the rate at which each host consumes parasites, and the density of hosts in the environment (72). We combined data on parasite density from herbivore dung with herbivore grazing data to estimate total parasite exposures for each herbivore species at permanently filled water pans and matrix sites for each of the five locations. We combined these with four different parasite mortality scenarios: .

$$Exposure\ Ratio = \frac{H_w \times P_w}{H_m \times P_m} \times M$$

Where H is the density of grazing behaviors (individual seconds per 100m² covered by each camera with a 50 degree angle and 15m detection distance) at water (w) or matrix (m), P is the density of eggs in the environment from dung, and M is the ratio of parasite mortality at matrix sites relative to water. We calculated the exposure ratio for low (M = 2), equal (M = 1), high (M = 0.5) or very high (M = 0.1) mortality scenarios near water relative to matrix sites. We used a GLMM with a Tweedie error structure to model the ratio of total parasite exposures using herbivore species and site type (water source or matrix) and their interaction as fixed effects, and location (n = 5) as a random effect. We performed post-hoc tests of pairwise differences between water sources and matrix sites for each species, using the Holm method to control for multiple comparisons (n = 6).

Observational System

To understand how rainfall impacted herbivore activity, dung, and parasite density, we used camera trap, dung count and parasite data collected at paired water and matrix sites for the same species as in our experimental analyses.

Herbivore activity: We compared total (i.e. animal presence, regardless of behavior) and grazing activity (daily individual*seconds) for all herbivores at water sources and matrix sites, again using GLMMs with either a negative binomial or Tweedie error structure. We tested for interactions between site type (water or dry) and MAP and prior 30-day rainfall, including random effects for site ($n = 17$). MAP values were derived from (73), and prior rainfall data were available from Mpala's long term rainfall monitoring project (74).

Dung and parasite density: To understand differences in dung and parasite density at water sources compared to matrix sites, we again used zero-inflated Gaussian hurdle models with a cube-root transformation to test interactions between water presence and prior 30-day rainfall, MAP, and outward distance, including random effects for site ($n = 20$) and period ($n = 5$). We again analyzed the log-ratio of dung density dung and parasites summed together, which provided qualitatively similar results (SI Appendix Table S11).

Parasites in soil: Finally, we used a negative binomial GLMM to test whether soil parasite egg densities differed among sample type (wet soil, dry soil next to the water's edge, and dry soil 1km from water). We included location ($n = 20$) and period ($n = 5$) as random effects.

Total exposures: We computed total exposures using the same methods used for the experimental system: we combined parasite density data with herbivore grazing behavior and four different parasite mortality scenarios for each of 12 different locations with sufficient camera trapping data. We used a GLMM with a Tweedie error structure to model the ratio of total parasite exposures using herbivore species and site type (water source or matrix) and their interaction as fixed effects, and location ($n = 12$) as a random effect. We performed post-hoc tests of pairwise differences between water sources and matrix sites for each species, using the Holm method to control for multiple comparisons ($n = 6$).

All analyses were performed in R 4.0.1 (75).

Results

Together, our results from both experimental and observational systems showed that parasite density was greatly elevated at water sources, but that this varied by herbivore species. Notably, cattle and elephants drove variation in parasite eggs from dung, due to their high biomass, high infection intensity, and high degree of aggregation at water (Figure 2: A, B, C, SI Appendix Fig. S6). Importantly, drier contexts drove increased aggregations and parasite density near water.

Q1: To what extent do water sources concentrate hosts, their feces, and fecal-oral parasites across herbivore species?

Water removal from five ~25,000 liter pans resulted in significantly reduced total, grazing, and drinking activity (measured via camera traps) at experimental water sources relative to filled water sources for elephants and cattle. While drinking activity was significantly reduced for all animals together, the 46% drop (i.e. a two-fold reduction) in total activity at experimental pans was only marginally significant ($t = -1.62$, $p = 0.1$ for the drained x during interaction, SI Appendix, Tables S7, S8, Fig. S4). Interestingly, total, grazing, and drinking activity increased when water was replenished such that it even trended higher compared to pre-experimental levels ($t = 2.27$, $p = 0.02$ for the drained x post interaction, SI Appendix, Tables S7, S8). The interaction between experimental status and treatment was not an important parameter for models of buffalo, zebra, giraffe, or impala activity. However, after pans were refilled, zebra and buffalo activity was significantly higher at experimental pans relative to other phases of the experiment ($p = 0.03$, $p = 0.01$ for total activity, $p = 0.09$ and $p < 0.001$ for grazing, $p = 0.01$ and $p < 0.001$ for zebra and buffalo respectively; SI Appendix, Tables S7, S8).

Dung density at filled water sources relative to experimental water sources increased when water was drained for all animals together and herded cattle and elephants separately (Table 2). This effect was largest for elephants: when experimental pans were drained, dung density was over six times higher at filled pans (in the area closest to water), while it was no different pre-draining or post-refilling ($t = 2.88$, $p = 0.004$ for increased probability of zeros for the drained x during interaction, Table 2). We found a similar pattern for cattle, as dung aggregation at filled pans was over three times higher during the drained period (at the 0m mark), but not during the 'pre' phase ($t = 3.09$, $p = 0.002$ for the increased probability of zeros for the drained x during interaction, Table 2). While cattle dung density was significantly lower at drained pans relative to filled pans after refilling, this effect was substantially reduced. Since cattle and elephants accounted for the largest proportion of dung density (> 50%, Figure 1B), this drove a similar pattern for total dung. However, we detected no effect of water draining for zebra, impala, or giraffe considered separately, and buffalo dung density was slightly higher at experimental sites after refilling.

Total parasite density (order Strongylida) – estimated as the product of dung volume in the environment, dung physical density, and median fecal egg count for each species – was three times higher at filled pans compared to experimental pans during the experiment but was no different before or after ($t = -2.93$, $p = 0.003$ for the drained x during interaction, Table 2, Figure 3, see SI Appendix Fig. S7 for species-specific responses).

Finally, parasite egg counts in dry soil near water pans were relatively low but consistent across treatments throughout the experiment (X^2_2 for status x treatment = 0.14, $p = 0.93$), suggesting that water removal did not substantially affect dry soil parasite density. However, after including eggs found in wet soils, density was 16 times higher at filled pans during the experiment, but not significantly different before or after (based on dry weight, X^2_2 for status x treatment = 9.30, $p = 0.01$), since wet soils were not present at drained pans. Additionally, soil egg density in dry soils around both pan treatments averaged 4.5 times that at non-water sites (X^2 for treatment = 5.58, $p = 0.02$).

Q2: To what extent are water sources parasite exposure hotspots across herbivores?

Combining dung parasite density results (Figure 2: A, B, C) with herbivore grazing behaviors showed that total parasite exposures for cattle and elephants were more than an order of magnitude higher near water if parasite mortality was equivalent at water and matrix sites (Figure 2: D, E, F). For the observational system, parasites of buffalos and elephants showed the strongest increase in total estimated exposures near water (85 and 39 times respectively, $p = 0.09$ and 0.002), with parasites of all other species except impala also trending higher. The strong results for buffalo were driven by the very low levels of buffalo observed grazing at matrix sites. With increasingly more conservative assumptions about parasite mortality differences across site types (assuming higher mortality of parasites near water), this effect diminished, such that at our most conservative assumptions (10x higher parasite mortality near water) only buffalo, elephants, and cattle had elevated estimated parasite exposures at water, although this increase was not statistically significant (Figure 2F).

For the experimental system comparisons between permanently filled water sources and matrix sites, parasite exposure was elevated near water for cattle, elephants, zebra, and impala (143, 67, 20, and 8 times higher respectively, $p < 0.001$ for all but impala for which $p = 0.005$). This remained significantly elevated (14 times and 7 times higher) for cattle and elephants, even in the scenario when parasite mortality between egg and infection was 10 times greater near water ($p < 0.001$, $p = 0.002$ respectively; Figure 2F).

Q3: How does herbivore activity, herbivore dung, and parasite density at watering holes vary across rainfall contexts?

Total herbivore grazing activity measured from camera traps was twice as high at water sources compared to matrix sites ($t = 2.51$, $p = 0.01$ for all species together), and it was significantly elevated for elephants, and marginally elevated for buffalo and zebra (Figure 2E). We found no significant interaction between mean annual precipitation (MAP) and animal grazing at water although both predictors were important separately (SI Appendix Table S9). This was likely due to the short deployment duration and low statistical power, as activity declined with increasing annual precipitation at both matrix sites and water sources, and it tended to be further elevated near water in drier areas (SI Appendix Table S9, Fig. S5). For all species except impala, grazing activity trended higher at water compared to matrix sites.

MAP and prior rainfall were important parameters in cattle, elephant, zebra, and total dung density models (Table 2, SI Appendix Fig. S8). In dry locations (~ 460 mm/year) close to water and following no rainfall, cattle dung density was three orders of magnitude higher at water relative to matrix sites, but this elevated density decreased as MAP and outward distance increased. This pattern was also strong for elephants: in dry areas following periods of no rainfall, elephant dung was approximately ten times higher close to water, but this effect weakened as MAP and outward distance increased (Table 2, SI Appendix Fig. S8). Zebra dung density was no different between water and matrix sites when there was little prior rainfall or low MAP, and we even observed potential aversion to water during the wettest periods in high MAP areas. Impala dung density was also slightly elevated near water in low-rainfall locations but depressed near water in wet conditions. We observed slightly higher dung density levels at watering holes

relative to matrix sites for buffalo and giraffe in low-rainfall conditions, and there was a significant interaction between MAP and prior rainfall for giraffe (Table 2, SI Appendix Fig. S8).

Critically, outward distance from water, MAP, and prior rainfall all modulated parasite density at water sources compared to matrix sites. In areas where MAP was lowest (450 mm/year) and prior 30-day rainfall was 0mm, parasite egg density from dung was estimated to be more than 150 times higher than matrix sites in the closest area to water. This effect decreased sharply as MAP, prior rainfall and outward distance increased (MAP: $t = 3.40$, $p = 0.001$; prior rainfall: $t = 5.06$, $p < 0.001$; distance: $t = 3.01$, $p = 0.003$, Table 2; Figure 4).

In our negative binomial model of eggs found in soil, parasite densities differed significantly based on water proximity ($X^2_3 = 135.7$, $p < 0.001$). Parasites (eggs per 20 grams dry soil) were more than two orders of magnitude higher in damp soil (based on dry weight, mean $\pm$ SE = 31.1 ± 8.0), and four times higher in dry soil (1.02 ± 0.35), near the water's edge compared to locations 1 km from water (0.26 ± 0.13) (SI Appendix Fig. S9).

Discussion

Utilizing experimental and observational datasets we show that water sources strongly concentrate herbivores, herbivore dung and parasite egg density, with increasing effects in dry conditions with low prior rainfall and low MAP. Effects were greatest for cattle and elephants which drove patterns in total dung and estimated parasite density due to the high relative abundance of dung and average parasite fecal egg count. However, all species showed at least some negative interaction between dung density at water sources and annual or recent rainfall, suggesting that fecal-oral parasite density at water sources will be elevated in drier conditions for all species.

Q1: Water sources strongly increase parasite density for some herbivores

Experimental findings showing strong reductions in total dung density and estimated parasite density with water removal were driven by two globally important species: cattle and elephants. Weaker responses for other herbivores likely demonstrate differing balances of resource requirements, predation risk, and parasite exposure risk.

Both elephants and cattle are highly water dependent (40, 41) compared to other animals in our study. Elephants can quickly alter their movements in response to water availability (42). Cattle, whose movements are typically dictated by humans, reflect the rapid ability for humans and their livestock to adapt to changes in water distribution. In contrast, lower water removal responses for other herbivores may be explained by foraging and water-seeking tradeoffs. If forage quantity or quality is reduced near water, some species may drink and depart, rather than stay and forage near water (43). In another study in this system, understory height, grass and forb cover were reduced near water (Titcomb *in press*), consistent with findings in other systems (44). For large water-dependent grazers, such as zebra and buffalo, foraging requirements might limit their ability to consume sufficient material near water (43).

Browsers, such as giraffe and impala are less water dependent as their digestive systems allow for better water retention (45). Lack of suitable browse near heavily impacted water sources may explain why giraffe dung is not substantially elevated at water. Finally, species-level differences in defecation behavior may also explain observed variation. For example, impala tend to defecate in middens, which have been shown to increase density of surrounding infective larvae themselves (46). If middens are independent of water location, then dung density is unlikely to tightly correlate with water proximity.

Elevated predation risk at water sources (13, 47) may also explain lower aggregation levels for certain herbivores. This explanation is parsimonious with our results given that the large body size of elephants affords some protection from predation (48) and in this system cattle move exclusively with human protection, reducing both predation risk and the ability of animals to respond to that risk. Heightened risk for smaller herbivores (48) may explain why impala, which are strongly constrained by predators (49), had little dung accumulation near water, despite having moderate water requirements (43). Indeed, our camera trapping data showed more than twice as much carnivore activity at water sources at both Mpala Research Centre and Ol Pejeta Conservancy than at matrix sites. It thus seems likely that predators may indirectly influence herbivore fecal-oral parasite exposure via a landscape of fear.

Q2: To what extent are water sources parasite exposure hotspots across herbivores?

Our results suggest that water sources are hotspots of parasite exposure (and thus, transmission), especially for parasites of highly water-dependent species, such as elephants and cattle. While this corresponded to increased parasite egg density patterns, it was also influenced by increased herbivore grazing behavior near water (Table S7 and S8). Indeed, despite several studies documenting severe vegetation loss around water in highly arid conditions (50), water sources can also promote grazing lawns attractive to herbivores that may increase parasite exposure (Titcomb *in press*). Furthermore, our results show that microclimatic conditions at water sources would need to induce at least 10 times higher parasite mortality for total transmissions to be only modestly elevated compared to matrix sites for highly water dependent species (Figure 2F, Table S13 and S14). This may be unlikely, given that nematodes often migrate through soil to optimize the balance between increasing survival and increasing transmission probability, and can often avoid severe surface conditions (30). Indeed, moist conditions near water may mitigate parasite desiccation. Consistent with this, our finding that damp soil, as opposed to dry soil, had higher egg density could reflect increased input from dung, increased egg survival, and/or delayed hatching. The relatively low parasite egg density and lack of treatment effect in dry soils indicates that larvae likely develop and disperse into soil and surrounding vegetation quickly, where their survival and probability of infecting a host also likely varies by parasite species.

In addition to microclimate influences on parasites, broader climate changes will affect parasite survival in the environment to varying degrees depending on parasite-specific resilience to changing temperatures and ability to adapt (51). Specific parameters are unknown for most of the wildlife parasites in this system, but future modelling work may be able to explore the extent to which variation in survival, development, and dispersal will allow for more nuanced predictions across parasites and hosts, in

addition to extensions for a wide variety of other pathogens transmitted via the fecal-oral route, including enteric viruses, intestinal protozoa, and bacteria. This is especially true given that our relative transmission calculations accounted for transmission via grazing only; for many of these additional pathogens that also spread via drinking, water sources will further amplify parasite exposure.

While these study results have clear implications for parasitism within individual herbivore species, the consequences of total increase in parasite density on other species will depend on interspecific parasite sharing. While parasite identifications were not possible from morphological analysis, literature reviews indicate that all hosts share at least one parasite with at least one other host species (34). However, elephants rarely share nematode parasites with other species (34), indicating that the strong implications of water in concentrating elephant parasites are likely largely confined to elephants. However, cattle share multiple gastrointestinal helminths with many species (37), and their strong aggregations at water may increase parasite exposure for other nearby foraging or drinking animals. Given that cattle comprise approximately one half of all herbivore biomass in the broader region (52), even a small degree of overlap in parasite sharing may substantially affect parasitism in other wildlife (18). This may be another way in which human domination of landscapes increases threats to wildlife. However, cattle anthelmintic treatment has the promise to reduce shared helminth transmission, and could alleviate parasite sharing risk in areas where this is of conservation concern, although increasing anthelmintic resistance is a growing issue (22).

Q3: Reduced MAP and prior rainfall concentrate dung and parasites around water

Observational results expand upon experimental findings, showing that lower recent rainfall and MAP can further concentrate animal dung around water. While effects varied by species, elephant, cattle, giraffe, and buffalo dung was concentrated more strongly at water sources in areas of low MAP, suggesting that density of their fecal-oral parasites increases when water is limiting. Furthermore, several species were dependent on short-term rainfall – during dry periods (< 50mm rain over 30 days), giraffe, buffalo, zebra, and impala dung was elevated at water, suggesting a shifting tradeoff between water requirements and forage and/or predation risk. Indeed, the context of water limitations may explain why these animals demonstrated lower (or no) aggregation levels at our experimental site, which was located in an area of higher annual rainfall (Figure 1A). Together, these results suggest that climatic context can alter fecal-oral parasite dynamics at water sources for these species. While future annual rainfall projections in our study region are mixed (53), local models predict seasonal long rain reductions (54). Globally, increased temperatures (55), broadscale aridification (1), and increased competition for water with humans (56) may drive certain wildlife to congregate more strongly at water, likely increasing fecal-oral parasite exposure.

Costs of certain nematode infections for many host species is non-trivial. For instance nematode infections in elephants, a species classified as vulnerable by the IUCN, are common (SI Appendix Table S2), and at least one study identified parasitism and starvation as likely causes of death for 38 young elephants that died during a period of severe drought in Kenya (57), underscoring the importance of

incorporating likely changes in parasite infection risk as part of conservation planning for management of this species amid changing environmental conditions. Large strongyles that infect equids, including endangered Grevy's zebra, can cause severe effects, including colic and death, and while nematode pathology in wildlife is not well understood, a wide array of trichostrongyles and hookworms cause substantial economic losses for livestock (58) (SI Appendix Table S1 and S2).

In addition to direct impacts on animal health, parasite aggregation may have indirect impacts on animal behavior and fitness, much as predators may impose fitness costs to prey through the 'landscape of fear' that, at population level, often exceed the fitness costs of direct predation. Recent work has focused on the ability for "landscapes of disgust" to facilitate host avoidance of parasites (59, 60). Parasite avoidance behavior may complicate our findings if animals can detect parasites in water or the environment. For example, other studies have shown fecal avoidance in feeding dik-dik (a small antelope) (61) and elephants and lemurs seeking water (62, 63). These studies suggest that in certain cases, the costs of parasite exposure may alter animal behavior and foraging.

Notably, several study conclusions are based on average fecal egg count (FECs) measurements to estimate fecal-oral parasite density and transmission opportunities. While this assumption allowed us to ask questions at a larger scale, seasonality can affect FECs for different host and parasite species in different directions, and many studies have shown seasonal variation in herbivore FEC (24, 64, 65). Any consistent seasonal deviation in infection intensity could dampen or heighten the effect of water. Studies have found both increases and decreases in FECs over rainfall seasons and droughts for the herbivore species examined in this study. However, previous work from this study site found that drought was associated with increased FECs for six of nine bovid species (24), with no species showing decreases. Thus, our results may be a conservative estimate of the impacts of drought on parasite egg aggregation in the environment, but this may be offset by increases in parasite mortality due to desiccation. These nuances underscore the importance of future work investigating combined host and parasite responses to ongoing climate changes.

Conclusion

This study shows that water sources cause large scale – up to 150-fold – increases in helminth parasites that are expelled into environment compared to background density during the driest conditions, although the effects vary strongly across herbivore species. Accounting for herbivore grazing behavior and parasite survival scenarios revealed that this increase in parasite density translates to increases in total parasite transmissions near water, except in severe circumstances when parasite mortality is more than an order of magnitude higher at water and for less water-dependent species. Critically, we show that climatic context greatly modifies patterns of parasite density, with stronger levels of parasite concentration in rainfall-limited times and locations. This suggests that water management - for both human and domestic animal use - is an important way in which humans influence wildlife parasite dynamics. This influence will likely only increase as water becomes increasingly scarce and livestock biomass continues to increase regionally (52) and globally (66). Cumulatively, these findings highlight

multiple potential pathways in which humans can affect wildlife parasitism and behavior via climate change and domestic animal management.

Declarations

Acknowledgments

This study was conducted on land originally occupied by different indigenous people including pastoralists, hunter-gatherer and earlier human communities. During British colonial rule and continued adjudication in independent Kenya, land in Laikipia was converted to commercial and group ranches, communal lands, and conservation areas. Mpala's land and resources are managed by a board of trustees including international and Kenyan institutions focused on a mission of science, education, conservation, and community outreach. We thank Ol Pejeta Conservancy, Mpala Research Centre, and Kenya Wildlife Service for facilitating this work. Fieldwork for this project is permitted under the Kenyan National Commission for Science, Technology, and Innovation (NACOSTI/P/16/0782/10585) and Kenya Wildlife Service (KWS/BRM/5001). GCT was supported by the National Science Foundation Graduate Research Fellowship (1650114) and National Geographic Society Early Career grant (EC-33R-18). This work was also supported by NSF DEB 1556786 awarded to HSY. We are grateful to Michelle Long, Edward Trout, and Valerie Lensch for additional field assistance, and we are especially thankful to the many thousands of citizen science volunteers on the Zooniverse platform. Finally, we give our sincere thanks to Vanessa Ezenwa for feedback that improved this manuscript.

Author Contributions

GT designed the study, conducted field and lab work, performed analyses, and wrote the paper. JM, JH, IR, and DB conducted field and lab work and provided feedback on the paper. HY assisted with study design and writing the paper. All authors approved the final manuscript.

Competing Interests

The authors declare no competing interests.

Data Availability

Datasets and code for analysis are currently available in draft version at: <https://portal-s.edirepository.org/nis/mapbrowse?packageid=edi.116.1>. All data and code will be made publicly available on the main EDI site upon publication.

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Tables

Table 1. Coefficients are presented for both the conditional and zero-inflation components of the models (“Cond”, and “Zero”). Parameters signifying a decline in density at experimental pans “During” or “Post” experiment are bordered by a solid line. When dung density increased with outward distance (a pattern contrary to our expectations), parameters are bordered by a dotted line. The intercept corresponds to 0m from water prior to conducting the experiment (“Pre”).

Estimate ±SE t (P-value)	All		Elephant		Cow		Zebra		Buffalo		Impala (log)		Giraffe		Parasites	
	Cond	Zero	Cond	Zero	Cond	Zero	Cond	Zero	Cond	Zero	Cond	Zero	Cond	Zero	Cond	Zero
Intercept	5.77	-2.92	5.41	0.01	5.19	-0.88	3.80	3.00	4.20	0.83	0.50	1.63	0.92	2.91	36.49	-2.97
Status = Pre	±0.87	±0.67	±0.91	±0.59	±0.63	±0.63	±0.79	±0.79	±0.57	±0.79	±0.49	±0.72	±0.47	±0.78	±5.56	±0.67
Treat = Filled	6.65	-4.34	5.97	0.01	8.24	-1.39	4.78	3.80	7.36	1.05	1.02	2.25	1.95	3.72	6.56	-4.44
Distance = 0	(<0.001)	(<0.001)	(<0.001)	(0.99)	(<0.001)	(0.16)	(<0.001)	(<0.001)	(<0.001)	(0.29)	0.31	(0.02)	(0.05)	(<0.001)	(<0.001)	(<0.001)
During	-0.83	0.36	-0.54	0.35	-1.08	-0.81	-0.86	0.30	-0.06	1.14	-0.81	0.44	0.08	-0.04	-5.63	0.48
	±0.93	±0.66	±0.97	±0.60	±0.66	±0.60	±0.66	±0.69	±0.60	±0.79	±0.49	±0.69	±0.35	±0.68	±5.89	±0.67
	(0.37)	(0.59)	(0.58)	(0.56)	(0.10)	(0.18)	(0.19)	(0.66)	(0.92)	(0.15)	0.03	(0.52)	(0.82)	(0.96)	(0.34)	(0.47)
Post	-0.82	-0.07	-1.63	-0.66	-1.23	-1.68	-1.17	1.04	-0.54	1.93	-0.87	0.51	0.06	-0.15	-6.37	0.03
	±0.98	±0.71	±1.00	±0.63	±0.70	±0.64	±0.71	±0.73	±0.69	±0.88	±0.39	±0.73	±0.37	±0.71	±6.21	±0.71
	(0.40)	(0.92)	(0.11)	(0.29)	(0.08)	(0.01)	(0.10)	(0.16)	(0.43)	(0.03)	0.03	(0.49)	(0.87)	(0.84)	(0.31)	(0.97)
Drained	0.27	0.52	-0.56	-0.38	-0.38	-0.06	0.63	0.85	-0.02	-0.67	-0.13	1.44	-0.09	0.57	0.81	0.49
	±0.29	±0.46	±0.57	±0.39	±0.33	±0.35	±0.37	±0.36	±0.38	±0.41	±0.55	±0.58	±0.37	±0.57	±2.17	±0.45
	(0.35)	(0.26)	(0.32)	(0.33)	(0.25)	(0.86)	(0.09)	(0.02)	(0.95)	(0.11)	0.81	(0.01)	(0.81)	(0.32)	(0.71)	(0.27)
Outward Distance	-0.30	0.22	0.01	0.37	-0.18	0.41	-0.06	-0.73	-0.07	0.25	-0.03	-0.17	0.09	-0.23	-1.28	0.24
	±0.04	±0.07	±0.07	±0.05	±0.04	±0.05	±0.12	±0.09	±0.06	±0.06	±0.09	±0.08	±0.07	±0.10	±0.30	±0.06
	(-0.001)	(0.001)	(0.94)	(-0.001)	(-0.001)	(-0.001)	(0.62)	(-0.001)	(0.25)	(-0.001)	0.71	(0.03)	(0.23)	(0.02)	(-0.001)	(-0.001)
During; Drained	-1.01	0.62	0.17	1.33	-0.05	1.20	-0.41	0.58	-0.52	0.19	0.37	-0.85	0.08	-0.14	-7.09	0.64
	±0.33	±0.50	±0.69	±0.46	±0.36	±0.39	±0.42	±0.41	±0.47	±0.49	±0.59	±0.63	±0.39	±0.62	±2.42	±0.48
	(0.002)	(0.22)	(0.81)	(0.004)	(0.89)	(0.002)	(0.33)	(0.16)	(0.27)	(0.70)	0.53	(0.17)	(0.83)	(0.82)	(0.003)	(0.19)
Post; Drained	-0.66	0.28	1.13	0.94	-0.03	0.90	-0.57	0.33	-0.91	-1.40	-0.06	-1.00	-0.10	-0.45	-4.53	0.29
	±0.34	±0.54	±0.65	±0.45	±0.36	±0.41	±0.48	±0.46	±0.59	±0.68	±0.62	±0.66	±0.40	±0.64	±2.53	±0.52
	(0.06)	(0.60)	(0.08)	(0.04)	(0.92)	(0.03)	(0.23)	(0.47)	(0.13)	(0.017)	0.92	(0.13)	(0.80)	(0.48)	(0.07)	(0.57)
σ^2_{new}	0.04	0.04	0.00	0.08	0.06	0.27	0.01	0.46	0.09	0.40	0.00	0.10	0.02	0.26	3.69	0.04
σ^2_{prior}	0.68	0.24	0.59	0.22	0.31	0.24	0.31	0.33	0.16	0.40	0.03	0.29	0.05	0.26	26.60	0.25
σ^2_{random}	2.78	2.78	2.85	2.85	1.48	1.48	1.87	1.87	1.11	1.11	1.60	1.60	0.34	0.34	156.85	156.85
R^2_M	0.102		0.084		0.111		0.084		0.155		0.078		0.045		0.084	
R^2_C	0.286		0.209		0.289		0.218		0.309		0.158		0.201		0.232	
N = 1440																

Table 2. Coefficients are presented for both the conditional and zero-inflation components of the hurdle models (“Cond”, and “Zero”). Parameters signifying a negative relationship between density and each covariate are shaded in blue (as hypothesized), while a positive relationship is shaded in orange (contrary to expectations). The intercept corresponds to dung and parasite density at matrix sites when distance and prior rainfall are zero and MAP is the lowest level observed (450 mm/yr).

Estimate ±SE t (P-value)	All		Elephant		Cow		Zebra		Buffalo		Impala		Giraffe		Parasites	
	Cond	Zero	Cond	Zero	Cond	Zero	Cond	Zero	Cond	Zero	Cond	Zero	Cond	Zero	Cond	Zero
(Intercept)	3.86	-0.88	4.59	0.63	3.32	1.89	3.51	1.52	4.17	4.22	1.18	2.22	1.51	1.85	46.09	-2.72
MAP= 4.5	±0.49	±0.40	±0.60	±0.58	±0.37	±0.58	±0.38	±0.53	±0.50	±0.93	±0.26	±0.51	±0.19	±0.42	±8.03	±0.74
Dist= 0	7.85	-2.22	7.62	1.09	8.86	3.23	9.20	2.90	8.31	4.55	4.59	4.36	8.09	4.42	5.74	-3.69
Rain= 0	(<0.001)	(0.027)	(<0.001)	(0.28)	(<0.001)	(<0.001)	(<0.001)	(<0.001)	(<0.001)	(<0.001)	(0.00)	(<0.001)	(<0.001)	(<0.001)	(<0.001)	(<0.001)
MAP	-0.33	0.45	-0.22	0.95	0.20	0.72	-0.01	0.32	-0.04	-1.19	-0.17	0.00	-0.17	0.36	-4.04	0.43
	±0.20	±0.12	±0.29	±0.31	±0.14	±0.24	±0.15	±0.25	±0.18	±0.28	±0.10	±0.23	±0.10	±0.23	±1.31	±0.11
	-1.68	3.83	-0.74	3.08	1.42	2.98	-0.05	1.27	-0.20	-4.24	-1.67	0.02	-1.61	1.54	-3.09	3.78
	(0.092)	(<0.001)	(0.46)	(0.002)	(0.16)	(0.003)	(0.96)	(0.20)	(0.84)	(<0.001)	(0.10)	(0.98)	(0.11)	(0.12)	(0.002)	(<0.001)
Water	3.14	-2.43	2.33	-2.70	1.03	-3.03	-0.01	-0.05	0.11	-1.73	-0.46	-2.15	-0.29	-0.99	34.12	-4.73
	±0.43	±0.37	±0.67	±0.44	±0.40	±0.48	±0.56	±0.47	±0.54	±0.62	±0.37	±0.74	±0.27	±0.47	±8.06	±0.85
	7.38	-6.61	3.48	-6.19	2.60	-6.31	-0.03	-0.11	0.20	-2.80	-1.23	-2.92	-1.06	-2.09	4.23	-5.68
	(<0.001)	(<0.001)	(0.001)	(<0.001)	(0.009)	(<0.001)	(0.98)	(0.91)	(0.84)	(0.005)	(0.22)	(0.003)	(0.29)	(0.036)	(<0.001)	(<0.001)
Distance	0.06	0.01	0.24	0.01	-0.03	-0.18	-0.09	-0.03	0.08	0.16	-0.06	-0.09	0.04	0.01	0.53	0.00
	±0.07	±0.05	±0.12	±0.07	±0.07	±0.08	±0.07	±0.06	±0.10	±0.11	±0.05	±0.10	±0.04	±0.07	±0.48	±0.05
	0.91	0.12	1.93	0.11	-0.37	-2.15	-1.23	-0.39	0.86	1.38	-1.18	-0.92	1.04	0.20	1.10	-0.05
	(0.36)	(0.91)	(0.053)	(0.91)	(0.71)	(0.032)	(0.22)	(0.70)	(0.39)	(0.17)	(0.24)	(0.36)	(0.30)	(0.84)	(0.27)	(0.96)
Rain	-1.41	0.74	0.38	1.59	0.00	1.09	-0.10	0.60	-0.52	1.64	-0.35	-0.55	0.00	-0.23	-9.70	0.80
	±0.27	±0.21	±0.44	±0.28	±0.27	±0.31	±0.29	±0.27	±0.27	±0.35	±0.16	±0.40	±0.13	±0.27	±1.93	±0.20
	-5.21	3.54	0.86	5.63	0.01	3.48	-0.36	2.25	-1.93	4.73	-2.24	-1.37	-0.01	-0.87	-5.04	4.12
	(<0.001)	(<0.001)	(0.39)	(<0.001)	(0.99)	(0.001)	(0.72)	(0.02)	(0.054)	(<0.001)	(0.025)	(0.17)	(0.99)	(0.38)	(<0.001)	(<0.001)
MAP: Water	-0.38	0.45	0.10	0.41	-0.36	0.16	-0.11	0.21	-0.23	0.41	0.18	0.45	0.22	0.56	-3.01	0.47
	±0.19	±0.15	±0.36	±0.22	±0.17	±0.21	±0.22	±0.19	±0.20	±0.24	±0.18	±0.37	±0.13	±0.22	±1.36	±0.14
	-2.00	3.04	0.29	1.84	-2.13	0.76	-0.52	1.12	-1.15	1.74	0.98	1.21	1.70	2.52	-2.20	3.40
	(0.045)	(0.002)	(0.77)	(0.065)	(0.034)	(0.45)	(0.61)	(0.26)	(0.25)	(0.08)	(0.33)	(0.23)	(0.09)	(0.012)	(0.028)	(0.001)
Distance: Water	-0.49	0.18	-0.50	0.31	-0.12	0.44	0.01	-0.17	-0.06	0.10	0.01	0.12	0.04	-0.05	-3.15	0.21
	±0.09	±0.07	±0.14	±0.09	±0.08	±0.10	±0.11	±0.10	±0.12	±0.14	±0.07	±0.14	±0.06	±0.10	±0.62	±0.07
	-5.68	2.48	-3.55	3.56	-1.52	4.58	0.05	-1.70	-0.52	0.70	0.14	0.89	0.80	-0.56	-5.08	3.01
	(<0.001)	(0.013)	(<0.001)	(<0.001)	(0.13)	(<0.001)	(0.96)	(0.090)	(0.60)	(0.48)	(0.89)	(0.38)	(0.42)	(0.58)	(<0.001)	(0.003)
Rain: Water	-0.05	1.23	-0.72	0.15	-0.33	0.27	0.15	0.95			0.41	1.58	-0.19	0.87	-0.37	1.18
	±0.32	±0.25	±0.52	±0.32	±0.31	±0.36	±0.38	±0.33			±0.22	±0.62	±0.18	±0.33	±2.32	±0.23
	-0.16	4.99	-1.37	0.46	-1.07	0.76	0.39	2.86			1.88	3.07	-1.04	2.63	-0.16	5.06
	(0.87)	(<0.001)	(0.17)	(0.64)	(0.28)	(0.45)	(0.69)	(0.004)			(0.060)	(0.002)	(0.30)	(0.012)	(0.87)	(<0.001)
σ_{Site}	0.43	0.19	0.09	0.74	0.10	0.50	0.12	0.65	0.00	0.64	0.20	0.35	0.00	0.48	2.63	0.20
σ_{Period}	0.69	0.67	0.33	0.73	0.25	0.80	0.13	0.69	0.30	1.49	0.00	0.26	0.00	0.25	4.79	0.68
σ_{Residual}	2.08	2.08	1.91	1.91	0.91	0.91	1.18	1.18	0.95	0.95	0.56	0.56	0.55	0.55	15.43	15.43
R^2_{M}		0.128		0.032		0.042		0.010							0.128	
R^2_{C}		0.244		0.062		0.119		0.031							0.226	
N = 2816																

Figures

Figure 1

Experimental and observational study sites were located in central Kenya. A) We used five pairs of experimental water pans (blue and green dots) with matched matrix sites (gray dots) at Ol Pejeta Conservancy (OPC) and 20 pairs of observational dams (blue triangles) and matrix sites (gray triangles) at OPC and Mpala. B) Schema of sampling transects that radiated outwardly from both water pans and dams. C) Sites were consistently utilized by both wildlife and domestic animals as measured by camera traps. D) Experimental pans were filled and surveyed at the beginning of the study (“Pre”, $n = 1$) before being drained (“During”, $n = 5$) and refilled (“Post”, $n = 3$).

Figure 2

Measurements of parameters used to calculate parasite density in the environment and to estimate the degree to which parasite exposures are elevated near water relative to matrix sites. A) Fecal egg counts measured in this study (green triangles) compared to those reported in studies across the African continent (mean of individual studies in blue; studies weighted by sample size in red). B) Average dung density contributed by each major species in both experimental (OPC) and observational systems (Mpala). C) Comparisons of estimated parasite eggs contributed by each species at permanent water sources (either dams or pans) and matrix sites (calculated from both experimental and observational datasets) show considerable consistency across species. Estimates from the experimental system compare filled pans only to matrix sites. Note that both graphs are visualized on the log₁₀ scale. D) Four

scenarios of parasite mortality at water sources relative to matrix sites, ranging from an assumption of reduced mortality (Low) due to potential increases in ground moisture, to an assumption of greatly increased mortality (Very High) due to decreases in vegetation cover.. E) Herbivore grazing activity at water sources and matrix sites for both experimental and observational systems. Note that both graphs are visualized on the log10 scale. F) Relative number of parasite exposures at water relative to matrix sites for each species and parasite mortality scenario from panel D. Significant ($p < 0.05$) and marginally significant ($p < 0.1$) differences after multiple comparison corrections are bordered by solid and dotted lines respectively.

Figure 3

Log ratio of parasite density at filled water pans relative to experimentally drained water pans throughout the experiment (pre-draining, during experiment, and post-refilling). Points and lines that lie above 0 indicate increased density at filled pans relative to experimental pans. Points show averages at each 10m outward distance interval. Species-specific figures illustrating zero-inflated data are available in SI Appendix Fig. S7.

Figure 4

Visualized log ratio of parasite density at watering holes relative to matrix sites across differing levels of mean annual precipitation, prior rainfall, and outward distance. Points and lines that lie above 0 indicate increased density at water relative to matrix sites. Points represent averages for each value of MAP, prior rainfall, or outward distance. Species-specific figures illustrating zero-inflated data are available in SI Appendix Fig. S8.

Supplementary Files

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