



**The effect of rangeland degradation on  
gastro-intestinal parasite infections of Ankole  
cattle in the Mutara Rangelands, Rwanda**

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gastro-intestinal parasite infections of Ankole  
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By

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A dissertation submitted in partial fulfillment of requirements for  
the degree of MASTER of Science in Biology

In the College of Science and Technology

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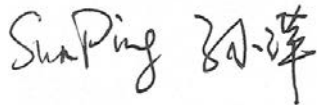
June, 2017

## DECLARATION

I declare that this dissertation has not been previously accepted in substance for any degree and is not being concurrently submitted in candidature for any degree.

I declare that this Dissertation contains my own work except where specially acknowledged. For the collection of the data presented, I have adhered to the Guidelines for the Use of Animals in Research and to the laws of Rwanda.

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Handwritten signature of Sun Ping in cursive script, followed by the Chinese characters 孙萍.

08/06/2017

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## ABSTRACT

The distribution of gastrointestinal (GI) parasites across landscapes is known to be closely related to the spatial distribution of hosts. In gastrointestinal parasites with environmental life stages, the dynamics of the parasite can also be affected by geophysical and ecological components of the environment. This is particularly relevant for domestic livestock species, which are kept across a range of different habitat types with varying quality, and are thus exposed to a wide range of environmentally robust parasite species. In my study, I examined the effect of environmental and anthropogenic parameters on the prevalence and intensity of GI parasites across a free-ranging stock of Ankole cattle in the Mutara rangelands of northeastern Rwanda. Prevalence and intensity of each parasite type (i.e., ‘strongyle-type’ nematodes, *Strongyloides* spp., *Monezia* spp., and coccidian *Eimeria* spp.) were used as dependent variables. I assessed 16 ecological and anthropogenic factors related to land-use form, climate and conservation-political history. I found the prevalence and intensity of *Eimeria* spp. had a positive relationship with vegetation-related effects (grass biomass, herb and grass frequency, tree canopy cover). The risk of *Eimeria* spp. infections was significantly higher in wet season than in dry season. By contrast the intensity of ‘strongyle-type’ nematodes was higher in dry than in wet season, and was negatively related to grass biomass and positively to soil compaction, suggesting that ‘strongyle-type’ nematode infections increase with increasing degradation (increased soil compaction and low grass biomass). Moreover, ‘strongyle-type’ nematode prevalence and intensity were negatively correlated with goat/sheep density, indicating a ‘dilution effect’ of GI infections between domestic livestock species.

## **KEY WORDS**

Domestic livestock, Landscape changes, Coccidian infections, 'strongyle-type' nematodes, Dilution effect, Climate, Vegetation

## LIST OF SYMBOLS AND ACRONYMS

AIC	Akaike Information Criterion
ANOVA	Analysis of variance
BIC	Bayesian information criterion
cm	Centimeter
cm <sup>2</sup>	Square centimeter
cm <sup>3</sup>	Cubic centimeter
Df	Degree of freedom
e.g.	For example
EPGs/OPGs	Eggs/Oocysts Per Gram
i.e.	That is
ID	Identity
GI	Gastro-Intestinal
GR	Game Reserve
km	Kilometer
Km <sup>2</sup>	Square kilometer
Log	Logarithm
LMM	Linear Mixed Model
m	Meter
NP	National Park
PCA	Principal Component Analysis
PCs	Principal Components
REML	Restricted Maximum Likelihood Estimation
SD	Standard Deviation
SE	Standard Error
SPSS	Statistical Package for the Social Science

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# 1 Introduction

About 25% of the earth's terrestrial surface is covered by rangelands with extensive pastoral systems. Between 100 and 200 million people throughout the world rely on pastoralism, an important economic and cultural way of life based on keeping domestic livestock such as cattle, goats and sheep (Rodriguez, 2008; CBD, 2010). Many pastoralists can be found in dry and sub-humid lands in the Middle East, South and East Asia, South America, Africa and Europe (CBD, 2010). In sub-Saharan Africa, approximately 16% of the human population depends on this form of livelihood (WISP, 2008; CBD, 2010; Holechek et al., 2017). Even though with great diversity in pastoral systems, pastoralists are always characterized by low human population densities, high mobility, and a high dependency on traditional ecological knowledge (CBD, 2010; Behnke et al., 2011; Turner et al., 2016). Moreover, pastoralist communities ensure the stability of ecosystems through the fertilization of rangelands (Qu et al., 2016), by maintaining natural vegetation and soils (Ren et al., 2012), capturing carbon (Davies and Nori, 2008), reducing soil erosion, facilitating the soil water holding capacity (Homewood and Rodgers, 1984) and by providing habitat for wildlife (Averbeck, 2006; Averbeck et al., 2012). Despite these significant contributions to the environment, pastoralists are often socially, economically and politically marginalized (CBD, 2010). Pastoralists are considered to be responsible for land degradation, based on the assumption that 'overgrazing' as a consequence of 'overstocking' (exceeding the carrying capacity) is positively related to land degradation ( i.e., increasing erosion, soil compaction and loss of plant cover; Thornes, 2007, but see Perevolotsky and Seligman, 1998).

However, causes of rangeland degradation are manifold, including human factors such as the overuse of natural resources (deforestation and overgrazing) and agricultural mismanagement (FAO, 2003; Rota et al., 2009), but also climatic conditions such as droughts or floods. Depending on the climatic characteristics of a rangeland ecosystem, grazing can have both, a positive and a negative impact on

rangeland vegetation and soils (Milchunas and Lauenroth, 1989; Calvosa et al., 2009; Fox et al., 2012).

African rangelands are nowadays often characterized by dramatic alterations of landscape structure, with a predominance of few(er) vegetation types as a result of human activities such as livestock (cattle and goats) grazing and subsistence agriculture, which are typically accompanied by a loss of biodiversity (du Toit et al., 2010). Unlike most other African countries, 90% of Rwanda is covered by man-made landscapes, with the highest population density in sub-Saharan Africa, and a very low urbanization rate of about 6-9% (Vande weghe and Vande weghe, 2011). Integrating environment and sustainable natural resources management principles, is one of the underlying strategies to counter act the increasing loss of biodiversity and to improve people's livelihoods, especially in rangeland habitats where pastoralism dominates and a semi-natural savannah is still prevailing.

The Mutara rangelands in north-eastern Rwanda are inhabited by a large ancient pastoralist community. The Mutara is part of the Akagera ecosystem, consisting the degazetted parts of the former Akagera National Park (NP), the former Mutara Game Reserve (GR) and three pastoralist communities from adjoining sectors that were never protected. The Rwandan civil war (1991-95) had devastating effects on wildlife and severe consequences on the Akagera NP and the Mutara GR (Kanyamibwa, 1998; Plumptre et al., 2007). After the period of political turmoil, the Mutara GR and large parts of the former Akagera NP were devoted to grazing for about 0.7 million cattle of refugees returning from neighboring countries (Kanyamibwa, 1998; Williams and Ntanyonbya, 1999). Today, pastoral and agro-pastoral farming systems dominate in the Mutara, accounting for a third of Rwanda's human population and for 85% of the country's cattle. Ankole cattle make a significant contribution to food security and income generation of many resource-poor families in the Mutara rangelands (MINAGRI, 2007). Twenty years after the conservation status had changed, large parts of the Mutara rangelands experienced severe landscape changes through overexploitation and environmental degradation. Grasslands were put under the plough, trees were felled, bush cleared and wildlife largely disappeared from the

degazetted areas (Schoene, 2003; Apio et al., 2015). The Mutara rangelands were severely overstocked with cattle, and agriculture and urbanization led to a severe degradation or even the loss of original savannah vegetation (CIRAD, 2002). To mark land-ownership, the remaining rangelands (app. 13% of the original area; Wronski et al., 2017) are increasingly divided by life fences comprising *Euphorbia tirucalli* and lately the invasive, introduced shrub *Lantana camara* (Wronski et al., 2017). Other adverse effects of overstocking with cattle and goats in the Mutara, include soil erosion and compaction (CIRAD, 2002), bush-encroachment (Vande weghe, 1990), and the loss of biodiversity (Kanyamibwa, 1998; Plumptre et al., 2001).

Environmental degradation of rangelands is also suspected to increase the prevalence of zoonotic diseases and the emergence of previously well controlled parasitic infections (FAO, 1999; Smolinski et al., 2003). The exchange of potentially pathogenic parasites between domestic and wild hosts, for example, presents a real but incompletely defined risk to the health of African cattle populations (Grootenhuis, 1999). Veterinary monitoring is an integral part of livestock management and forms an empirical basis for eco-system health in rangelands (Graczyk, 2002). Among endo-parasites and infectious diseases, helminthiasis (especially gastrointestinal nematodes) is regarded a major emerging health threat to livestock and humans (WHO, 1979; Stear et al., 1997; Mas-Coma et al., 2008). Like all organisms, parasites are embedded in complex interactions with both their abiotic and biotic environments (Poteet, 2006). Due to environmental and landscape changes in a degrading rangeland, wildlife and domestic livestock species experience new challenges and interactions, that provide new opportunities for parasite and pathogen exchange (Karesh et al., 2012; Murray and Daszak, 2013). Numerous studies have shown that human induced habitat and landscape changes enhance helminth species richness and abundance (Gillespie et al., 2005; Bull et al., 2006; Wells et al., 2007; Gillespie and Chapman, 2008; Rohr et al., 2008; Püttker et al., 2008; Raharivololona et al., 2009; Chaisiri et al., 2010). Studies on rodents associated with human modified habitats suggest that elevated disease risks might be related to changing rangeland conditions (Chaisiri et al., 2010; Froeschke and Matthee, 2012). Recently, a research on rodents in Southeast

Asia reported that micro-parasite diversity (viruses, bacteria and protozoans) was positively associated with flat, agriculturally modified land (Bordes et al., 2013). A study on gastro-intestinal parasite infections of livestock in a degraded rangeland in Pakistan reports on overgrazing due to high stocking rates. Overcrowding resulted here in vegetation degradation and the introduction of new strains of livestock diseases and heavy helminth infections among local cattle (Taj et al., 2014).

Generally, there seems to be a positive relationship between helminth prevalence, intensity and abundance, and the fragmentation of habitats, the agriculturally used area and the density of human settlements (Gillespie et al., 2005; Gillespie and Chapman, 2008; Chaisiri et al., 2010; Lane et al., 2013). Heterogeneous landscapes are often the result of human habitat transformations and land use activities influence the host and parasite community (Reisen, 2010). Land use changes were identified to be a major driver of emerging infectious diseases (e.g., Smolinski et al., 2003; Patz et al., 2004; Keesing et al., 2010). While studies on infectious diseases in humans—and their intermediate hosts—in urbanized landscapes are numerous, comparative studies on the dynamics of pathogen interactions of wild and domestic animals in anthropogenically disturbed landscapes are rare (Bradley and Altizer, 2007; Chaisiri et al., 2010).

I expected these adverse environmental changes to have a negative effect on the parasite burden of Ankole cattle in the Mutara rangelands, i.e., on the intensity and prevalence of strongyle type nematodes, *Strongyloides*, *Monezia*, and coccidia. In my study I asked what ecological factors influenced the observed gastro-intestinal (GI) parasite patterns of Ankole cattle—data that may provide useful information about the impact of environmental degradation on the health of pastoralists and their livestock. I first asked whether habitat destruction, i.e., the percentage proportion of ranches to subsistence agriculture (rangeland/field ratio) has a negative impact on the intensity and prevalence of GI parasite infections in Ankole cattle (Lane et al., 2013; Froeschke and Matthee, 2012; McFarlane et al., 2012, Cardoso et al., 2016). Second, I asked whether the conservation–political history, i.e., the time being off conservation, has a negative impact on the GI parasite burden. Within the host community, intrinsic factors

could also be a major aspect facilitating parasite infections. In this case, high GI parasite infections should correspond with high cattle density, large group size (Taylor et al., 2007; Bowman, 2009) or a low adult/juvenile ratio within the study population (Bowman, 2009). I further asked whether the factors relating to changes in the climate regime of the Mutara affect the GI parasite burden. I expected parasite intensity and prevalence to increase with increasing rainfall (Bowman, 2009). Furthermore, I proposed that vegetation changes caused by deforestation and overgrazing translate directly into changes in the micro-climate ( i.e., increased evaporation and lower humidity) and the soil composition ( i.e., increased soil compaction and lower humidity; Schnürer et al., 1986; Taylor et al., 2007; Bowman, 2009), and are thus expected to facilitate the spread of GI parasites (Morgan et al., 2006). I expected parasite intensity and prevalence to increase with increased biomass in the herbaceous layer ( i.e., grass and herb frequency, above ground monocotyledonous biomass), with decreased deforestation ( i.e., percentage cover of trees and shrubs), and with a low degree of soil compaction ( i.e., an increase in soil porosity and water holding capacity, fewer incidences of soil erosion). Finally, I expected a potential cross-infection between goats/sheep and cattle, i.e., increased goat/sheep density translates into higher GI parasite burden in cows.



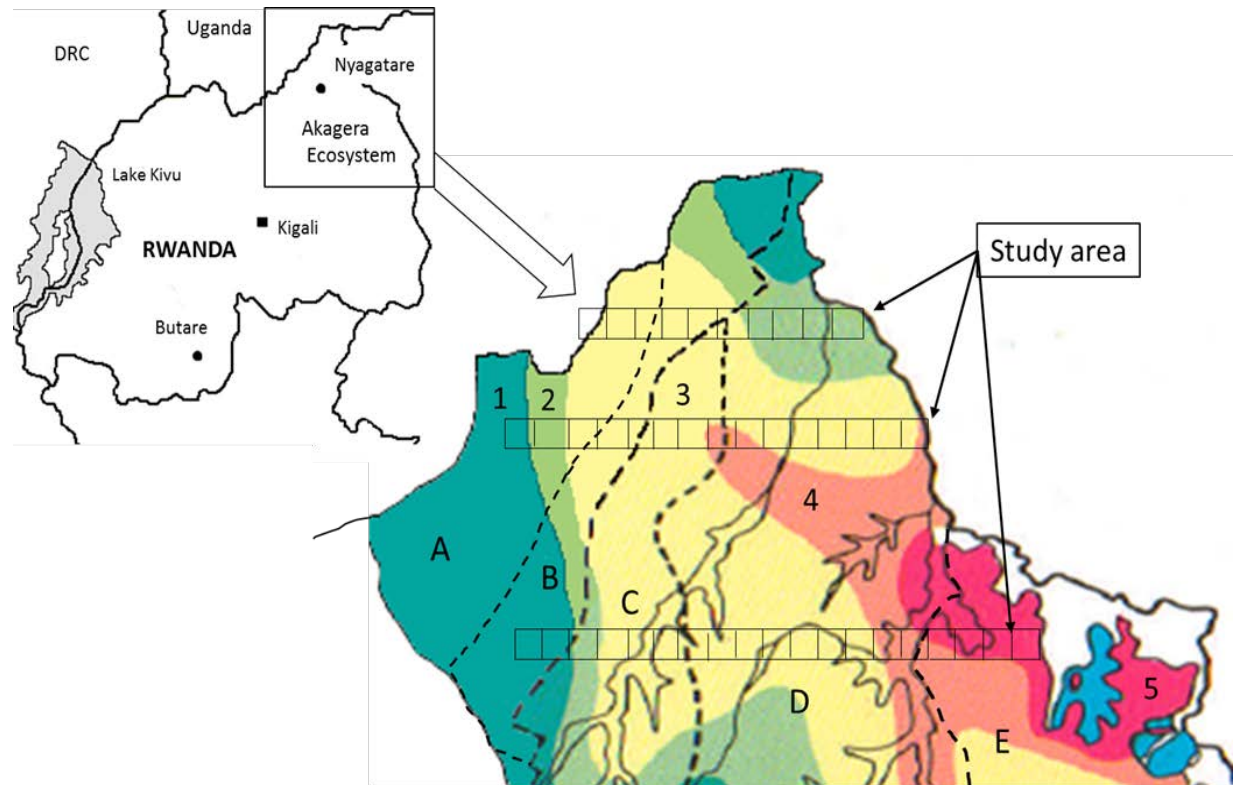
## 2 Material and methods

### 2.1 Study area

The Mutara rangelands are situated in north-eastern Rwanda (Figure 1, as below) and form the Akagera Ecosystem together with Karagwe in Tanzania and the Ankole grasslands in south-western Uganda. The Mutara covers most parts of the District of Nyagatare and comprises of vast open grasslands and savannah woodlands that are predominantly used for grazing cattle. The woody vegetation is dominated by *Senegalia senegal*, *A. polycantha*, and *Combretum* species, while grasslands are mostly composed of gramineous species such as *Bracharia* sp., *Hyparrhenia filipendula* and *Sporobolus pyramidalis* (Vande weghe, 1990). In July 1935 most areas of the Mutara rangelands were protected by Royal Belgian decree (Vande weghe, 1990), and the Akagera NP and the Mutara GR were officially established. Between 1973 and 1990 the western parts of the Mutara GR were opened for development projects, livestock breeding schemes and the army (Vande weghe, 1990). Following the civil war and genocide (1990–1995), the remaining Mutara GR and the western half of Akagera NP were also degazetted, reducing the protected area from an initial surface area of 2,800 km<sup>2</sup> to about 1,200 km<sup>2</sup> (Williams and Ntayombya, 1999, 2001; Vande weghe and Vande weghe, 2011). Areas west of the Muvumba River, i.e., Rwempasha, Tabagwe and Rukomo Sectors were never protected but also included in my analysis. Sampling was carried out along three transect belts across the Mutara rangelands, covering four different zones of conservation-political history from the international border with Tanzania (or the border of the new Akagera NP) in the East to the international border with Uganda (or the Byumba Escarpment) in the West (Figure 1).

One transect belt is situated in the South (S1°26'59 E30°10'05 to E30°32'59), one in the center (S1°17'06 E30°10'05 to E30°32'59) and a third in the North (S1°10'50 E30°17'36 to E30°30'07). Each transect was divided into quadrants measuring 2.5 × 2.5 km (10 in the North, 15 in the center, 15 in the South) in which data collection

was carried out. Transect belts and quadrants were determined using GARMIN MapSource and coordinates were transferred to a Garmin GPS III, ensuring proper orientation in the field.



**Figure 1** The Akagera Ecosystem in Rwanda: study area (forty 2.5 x 2.5 km quadrants) extending along two 37.5 km and one 25 km transect lines across the Mutara Ranchlands from East to West. Areas of conservation-political history and eco-climate (modified from Vande weghe, 1990; Wronski et al., 2017) are: (A, west) Mutara rangelands, never protected, (B, central west) Mutara Game Reserve, degazetted between 1971-90, (C, central) Mutara Game Reserve, degazetted in 1997, (D, central east) Akagera National Park, degazetted in 1997, (E, east) new Akagera National Park; (1, dark green) below Byumba Escarpment (900-1000 mm annual rainfall), (2, light green) higher Mutara (800-900 mm), (3, yellow) lower Mutara (700-800 mm), (4, orange) drier Mutara (600-700 mm), (5, pink) drier Kagera (500-600 mm).

## 2.2 *Assessment of gastro-intestinal parasite prevalence and intensity*

### *(Dependent variables)*

#### 2.2.1 *Fecal sampling method*

From October 2015 to August 2016, thirty fecal samples (15 in dry season, 15 in wet

season) were collected in each of the 40 quadrants, immediately after a focal animal was seen defecating. Fecal samples were collected regardless of the time of the day or weather conditions but where possible at the same day within the same quadrant. Since immature cows, young calves and pregnant adults show highest egg counts (Waruiru et al., 2000), only Ankole cattle females (preferably pregnant) and their calves were sampled. Exotic Frisians or hybrids with Ankole cattle were ignored. Prior to sample collection it was ensured that focal animals were not treated by anti-helminthics within the last 6 months and that all animals experience similar living conditions, e.g. overnight kraaling. Samples were collected from as many different groups as possible (3-6 groups) but from within the same quadrant. Fecal samples (app. 30 g per individual) were placed into labeled polythene containers, and preserved in 5-10% formalin until further processed (Morgan et al., 2006). Additionally, I recorded date, time, quadrant ID, age class (adult, yearling, calve), position (using Garmin GPS III), and number of animals in the group.

### 2.2.2 *Parasite isolation, identification and quantification*

A total of 1200 (30×40) fecal samples were processed in the laboratory at the University of Rwanda (Nyagatare Campus) to determine the prevalence and intensity (eggs/oocysts per gram feces, EPGs/OPGs) of gastro-intestinal tract (GI) parasitic infections. The prevalence of parasite eggs and oocysts were defined as described by Margolis et al. (1982), i.e., the number of hosts infected with a certain parasite divided by the total number of hosts examined. Simple Flotation and McMaster techniques were employed to isolate and count helminths (nematodes and cestodes) eggs as well as coccidian oocysts, following procedures described in Hansen and Perry (1994) and Zajac and Conboy (2012). I refrained from using FLOTAC (Cringoli et al., 2010) due to financial constraints and the fact that the use of FLOTAC resulted in similar EPGs/OPGs than McMaster (Rinaldi et al., 2010). Ten grams of feces were crushed, mixed with 140 ml of saturated NaCl solution and filtered. Aliquots of the filtrate were transferred into two chambers of a McMaster egg counting apparatus,

filling each chamber at a time. Eggs/oocysts were identified and counted using a microscope at 10 x magnification. Counts of each egg/oocyst type from both chambers were summed and multiplied by the factor 50 to calculate the number of eggs/oocysts per gram of feces (Hansen and Perry, 1994). The identification of helminth (nematode and cestode) eggs and protozoan oocysts was carried out using keys provided by Hansen and Perry (1994), Foreyt (2001), Zajac and Conboy (2012), and Hendrix and Robins (2012). A check list of helminths parasites from the gastro—intestinal tract of African mammals (including cattle) by Round (1968) and Taylor et al. (2007) also aided identification. A check list of helminth parasites from the gastro—intestinal tract of African mammals (including cattle) by Round (1968) and Taylor et al. (2007) also aided identification.

### 2.3 *Ecological predictor variables (Independent variables)*

#### 2.3.1 *Conservation-political history and eco-climate*

Assignment of quadrants to different zones of conservation-political history and eco-climate followed Vande weghe (1990) and Wronski et al. (2017, Figure 1). Ten quadrants were located in parts of the Mutara rangelands that were never protected, six in the Mutara GR (degazetted between 1973 and 1990), eight in the Mutara GR (degazetted in 1997), and 16 in the former Akagera National Park (degazetted in 1997). Eco-climatic zonation is based on rainfall data obtained before 1990 by Vande weghe (1990). Three quadrants were located in the wettest zone along the Buyumba Escarpment (900-1000 mm annual rainfall), six in the higher Mutara rangelands (800-900 mm), and 26 in the lower Mutara (700-800 mm), and five in the drier parts of the Mutara (600-700 mm). For statistical analysis, different zones of conservation-political history and eco-climate were coded using integer numbers from one to four.

### 2.3.2 *Cattle density*

Overstocking with domestic livestock is held accountable for increasing rates of infectious diseases and helminth infections in cattle (Pandey et al., 1993; Swai et al., 2006; Gupta et al., 2012; Taj et al., 2014). However, overcrowding often causes soil compaction and thus leads to changes in the plant community. A reduction of plant cover increases surface evaporation, therefore lowers humidity and reduces the survival of helminths larvae in the vegetation (Taylor et al., 2007; Bowman, 2009). Density data of local Ankole cattle, goats and sheep in 40 quadrants across the Mutara rangelands from Wronski et al. (2017) were used to assess the effect of overstocking on Ankole cattle GI parasite burden, i.e., three walking transects were established (two 1.5 km and one 0.5 km long) to count the number of Ankole cattle in each quadrant. Transect counts were conducted once in dry season and once in wet season. For distance sampling analysis the perpendicular distance was determined for each cattle encounter, i.e., the direct distance between the transect line and the animal or group of animals, using a *Bushnell Yardage ProX 500* range finder. To estimate cattle densities, I employed the software DISTANCE vs. 6.0 (Thomas et al., 2005, 2010). Making full use of the power of AIC (Akaike Information Criterion) and information theory, I included ‘goats and sheep’, which were also counted but not used in this study, into the population estimate. I first explored the full data set to determine the best fitting model, i.e., the detection function with the lowest AIC. Raw distances were binned into 3 or 4 intervals (avoiding cut points that coincide with multiples of 10) and truncated at 25-350 m to eliminate outliers from the model. All other binning intervals or truncations that resulted in smaller, i.e., significant  $\chi^2$  values, were omitted. Subsequently, I split the overall data set into four groups (cattle dry, cattle wet, sheep & goat dry, sheep & goat wet), rerunning the analyses with the same settings as established above.

### 2.3.3 *Group size and age ratio*

Intrinsic parameters, such as the group size of the investigated individual, as well as the age ratio in that group are important factors when exploring GI parasite prevalence and intensity in domestic livestock (Taylor et al., 2007; Bowman, 2009). I established the group size for each individual from which fecal samples were taken. Furthermore, the age ratio, i.e., the number of adults ( $\geq 24$  months of age) divided by the number of calves (0-6 months) and yearlings (6-24 months) in that group was also established.

### 2.3.4 *Degree of grassland fragmentation*

Cattle ranches (semi-natural grassland) and fields for subsistence agriculture are the two major land use forms prevailing in the Mutara rangelands. The degree of grassland fragmentation was set as 100% grassland, as part of Akagera NP were used for ranching prior to the designation as a national park in 1934. To determine the degree of rangeland transferred into agricultural land, i.e., the destruction of grassland, the rangeland/field ratio was measured. Location fixes for each change from a field to a ranch and vice versa were taken whilst walking transects established to count cattle (see Wronski et al., 2017). Later location fixes were plotted using BASE CAMP software (Garmin) to measure the distance between each point and assign each distance to either ranch or field. Rangeland/field ratios were expressed as proportions of fields or rangeland cover (km field or rangeland/total transect length).

### 2.3.5 *Soil compaction and erosion*

Soil compaction can be related to overstocking with domestic livestock but also to urbanisation and changes in the land use system (Doichinova et al., 2006). It was described to have an indirect impact on the prevalence and intensity of GI infections in domestic livestock species (see above). I assessed the degree of soil compaction using water-holding capacity and soil porosity as determined in Wronski et al. (2017), i.e., a

standardized soil volume of 261.25 cm<sup>3</sup> (23.75 cm<sup>2</sup> x 11 cm) was collected at ten locations in each quadrant and transferred to the laboratory to obtain wet and dry weight. Soil water holding capacity and soil porosity (aeration porosity) were calculated following procedures described in Wilke (2005). Assuming the density of water is 1 g per cm<sup>3</sup> and particle density is 2.65 g per cm<sup>3</sup>, soil water holding capacity was calculated by the mass of water when saturated (mass of water + mass of air), divided by the mass of dry soil. Soil porosity was calculated using the air filled pore volume (height of air \* surface area) divided by the bulk volume of soil (container volume). Calculations of both parameters were averaged to obtain one value for each quadrant. Whilst walking transects established to count cattle (see Wronski et al., 2017), I established the degree of erosion expressed as the number of erosion incidences per 3.5 km walked.

### 2.3.6 *Woody plant cover*

I assessed the percentage canopy cover of woody vegetation (trees and shrubs) in the Mutara rangelands. Lush, woody vegetation creates shade and thus reduces evaporation. Decreased humidity is reported to reduce the survival of infectious helminth larvae in the vegetation (Taylor et al., 2007; Bowman, 2009). The degree of canopy cover of trees and shrubs was measured 40 times ( i.e. 20 times in the wet, 20 times in the dry season) in each quadrant using the line intercept method (Kent and Coker, 1992). Percent cover was sampled by recording the length of intercept for each plant type along a stretched tape by measuring the distance between starting and ending point of the vegetation. Intercept lengths were summed and divided by the total tape length, resulting in the percent cover for trees and bushes along the transect line. To determine the direction of the tape and the starting point, a random procedure was applied prior to each measure. Percentage proportions were averaged to obtain one value for each quadrant (data from Wronski et al., 2017).

### 2.3.7 *Above ground monocotyledonous biomass*

To assess the degree of ‘overgrazing’, the above-ground monocotyledonous (grass) biomass was determined following methods described in Steinman and Lamberti (1996). Above ground grass matter was cut in twenty 50 x 50 cm plots (10 in the wet, and 10 in the dry season) arbitrarily in each quadrant. Samples were processed in the laboratory by measuring the wet weight and then drying the grass sample to a constant dry weight. For ash free dry weight (digestible biomass excluding water and minerals), the dried material was oxidized (ashed) in a muffle furnace at high temperature and re-weighed (data from Wronski et al., 2017).

### 2.3.8 *Grass and herb frequency*

Grass and herb frequencies were measured 20 times in each quadrant (10 times in the wet, and 10 times in the dry season) following methods described in Kent and Coker (1992). A 0.9 × 0.9 m sampling rectangle was laid arbitrarily on the ground and the presence of grass or herbs in each sampling grid recorded to establish the fraction of grids containing grass or herbs (data from Wronski et al., 2017).

## 2.4 *Statistical analysis*

In all cases, measurements were averaged across samplings to obtain one value for each quadrant and for each season. For statistical analysis all absolute data, i.e., fecal egg and oocyst counts, as well as cattle and goat/sheep density, cattle group size, soil water holding capacity, soil erosion and above ground monocotyledonous biomass were log-transformed ( $\log_{10}(x+1)$ ) to stabilize variance before analysis. Subsequently, I arcsine (square root)-transformed all relative data such as the GI parasite prevalence, the rangeland/field ratio, percentage canopy cover of shrubs and trees, soil porosity as well as grass and herb frequencies. Subsequently, I applied z-transformation to the entire data set to normalize data dimensionality. Thirteen explanatory variables were then subjected to a factor reduction (Principal Component Analysis, PCA) using the



varimax rotation option. The five resulting principle components (explanatory PCs) with an Eigenvalue  $> 1.0$ , explained 66.07% of the total variance (Table 2), and were used as explanatory variables in my statistical analyses.

By using a univariate linear mixed model (LMM, SPSS version 22.0), I was able to test what factors influence the prevalence and intensity of GI parasites of Ankole cattle in the Mutara rangelands. I first explored the full data set to determine the best fitting model, i.e., the model adequacy with the lowest Bayesian information criterion (BIC). I included three categorical, explanatory variables (season, eco-climate, and conservation-political history) as fixed factors and five explanatory PCs as covariates. Random intercepts were specified for each quadrant (subject-quadrant ID with random intercepts specified). Furthermore, I included all two-way interactions between fixed factors and covariates, and between all covariates in the initial model. In my reduced model, non-significant interaction terms were removed using a step-wise backwards elimination procedure if  $P > 0.1$  (all excluded terms:  $F < 2.524$ ,  $P > 0.118$ ). The resulting data-sets for independent, categorical variables (two levels of season: dry and wet; four levels of eco-climate: Buyumba Escarpment, higher Mutara-, lower Mutara- and drier Mutara rangelands; and four levels of conservation-political history: never protected, Mutara GR degazetted before 1991, Mutara GR degazetted in 1997, and former Akagera NP) were tested for differences using a either independent t-test or Mann-Whitney U test for seasonal differences, or a One-way ANOVA (Kruskal Wallis ANOVA) for differences between zones of varying eco-climatic or conservation-political history. To avoid over-interpretation of my results, I tested the robustness of statistically significant effects in my LMMs via post-hoc non-parametric Spearman rank correlations with those factors contained in the respective significant explanatory PCs (axis loadings  $> |0.50|$ ; Table 2).

### 3 Results

#### 3.1 General

During this study, I detected eggs of strongyle-type nematodes *Haemonchus*, *Ostertagia*, *Trichostrongylus* (Trichostrongylidae); *Oesophagostomum* (Strongyloidae); *Cooperia* (Cooperidae) and *Bunostomum* (Ancylostomatidae) in the feces of Ankole cattle. Apart from ‘strongyle-type’ nematode eggs, other nematode eggs such as *Strongyloides* (Rhabditidae), *Nematodirus* (Trichostrongylidae) and *Trichuris* (Trichuridae) were also counted. The latter two were found in only a few individuals (*Nematodirus* spp.: 2 females; *Trichuris* spp.: 8 juveniles) and were therefore omitted from my statistical analysis. Eggs or oocysts of gastrointestinal parasites belonging to other taxonomic groups such as the cestode *Moniezia* (Anoplocephalidae) or the protozoan coccidian *Eimeria* spp. (Eimeridae) were also recorded and statistically analysed.

Significant seasonal differences were unrevealed for the intensity of coccidian (*Eimeria* spp.) oocysts (higher in wet season) and ‘strongyle-type’ nematode eggs (lower in wet season; Table 1). Also, the prevalence of *Eimeria* spp. significantly increased during wet seasons, while *Strongyloides* spp. and *Monezia* spp. did not show any seasonal variation (Table 1). The same was true for conservation-political history: only *Eimeria* spp. prevalence was significantly higher in zones that lost their conservation status in 1997 (Table 1).

**Table 1** Differences in the prevalence and intensity of four parasite types (‘strongyle-type’ nematodes, *Eimeria* spp., *Strongyloides* spp. and *Monezia* spp.) within three fixed factors, i.e., season (dry, wet), eco-climate zones (Byumba escarpment, high Mutara, low Mutara, dry Mutara) and zones of conservation-political history (never protected, Mutara GR 1991, Mutara GR 1997, Akagera NP 1997).

Intensity	Season	mean	SE	test	N	T/F	<i>p</i>
strongyle	dry	1.590	±0.478	Independen t t-test	40	2.019	<b>0.047</b>
	wet	1.372	±0.487		40		
<i>Eimeria</i> spp.	dry	1.185	±0.476	Independen t t-test	40	-3.723	<b>&lt;0.001</b>
	wet	1.579	±0.471		40		

<i>Strongyloides</i> spp.	dry wet	0.130 0.135	±0.146 ±0.216	Mann-Whitney U test	40 40	-0.832	0.405
<i>Monezia</i> spp.	dry wet	0.099 0.097	±0.146 ±0.153	Mann-Whitney U test	40 40	-0.075	0.940
<b>Prevalence</b>	<b>Season</b>	<b>mean</b>	<b>SE</b>	<b>test</b>	<b>N</b>	<b>T/F</b>	<b>p</b>
strongyle	dry wet	1.006 0.940	±0.216 ±0.256	paired t-test	40 40	1.260	0.211
<i>Eimeria</i> spp.	dry wet	0.708 1.002	±0.156 ±0.216	paired t-test	40 40	-6.965	<b>&lt;0.001</b>
<i>Strongyloides</i> spp.	dry wet	0.188 0.202	±0.167 ±0.191	Mann-Whitney U test	40 40	-0.184	0.854
<i>Monezia</i> spp.	dry wet	0.159 0.183	±0.189 ±0.188	Mann-Whitney U test	40 40	-0.551	0.581
<b>Intensity</b>	<b>Eco-climate</b>	<b>mean</b>	<b>SE</b>	<b>Test</b>	<b>N</b>	<b>T/F</b>	<b>p</b>
strongyle	Byumba Mutara high Mutara low Mutara dry	1.361 1.546 1.510 1.215	±0.191 ±0.563 ±0.476 ±0.528	One-way ANOVA	6 12 52 10	1.015	0.391
<i>Eimeria</i> spp.	Byumba Mutara high Mutara low Mutara dry	1.231 1.303 1.434 1.280	±0.387 ±0.571 ±0.491 ±0.605	One-way ANOVA	6 12 52 10	0.520	0.670
<i>Strongyloides</i> spp.	Byumba Mutara high Mutara low Mutara dry	0.569 0.104 0.138 0.189	±0.657 ±0.142 ±0.203 ±0.157	Kruskal-Wallis ANOVA	6 12 52 10	2.629	0.453
<i>Monezia</i> spp.	Byumba Mutara high Mutara low Mutara dry	0.129 0.039 0.100 0.187	±0.180 ±0.086 ±0.144 ±0.227	Kruskal-Wallis ANOVA	6 12 52 10	5.851	0.119
<b>Prevalence</b>	<b>Eco-climate</b>	<b>mean</b>	<b>SE</b>	<b>Test</b>	<b>N</b>	<b>T/F</b>	<b>p</b>
strongyle	Byumba Mutara high Mutara low Mutara dry	0.938 0.994 0.993 0.817	±0.035 ±0.280 ±0.229 ±0.237	One-way ANOVA	6 12 52 10	1.369	0.259
<i>Eimeria</i> spp.	Byumba Mutara high Mutara low Mutara dry	0.735 0.803 0.866 0.947	±0.207 ±0.224 ±0.251 ±0.179	One-way ANOVA	6 12 52 10	1.027	0.385
<i>Strongyloides</i>	Byumba	0.131	±0.151	Kruskal-W	6	2.529	0.470

spp.	Mutara high	0.156	±0.173	allis	12		
	Mutara low	0.204	±0.184	ANOVA	52		
	Mutara dry	0.249	±0.170		10		
<i>Monezia</i> spp.	Byumba	0.181	±0.225	Kruskal-W	6	4.560	0.207
	Mutara high	0.096	±0.150	allis	12		
	Mutara low	0.180	±0.193	ANOVA	52		
	Mutara dry	0.262	±0.186		10		
<b>Intensity</b>	<b>Conservation political history</b>	<b>mean</b>	<b>SE</b>	<b>Test</b>	<b>N</b>	<b>T/F</b>	<b>p</b>
strongyle	Never protected	1.291	±0.437	One-way	20	1.799	0.154
	Mutara GR 1991	1.405	±0.527	ANOVA	12		
	Mutara GR 1997	1.613	±0.486		16		
	Akagera NP 1997	1.564	±0.495		32		
<i>Eimeria</i> spp.	Never protected	1.275	±0.445	One-way	20	1.060	0.371
	Mutara GR 1991	1.232	±0.474	ANOVA	12		
	Mutara GR 1997	1.471	±0.499		16		
	Akagera NP 1997	1.462	±0.559		32		
<i>Strongyloides</i> spp.	Never protected	0.194	±0.155	Kruskal-W	20	1.632	0.652
	Mutara GR 1991	0.157	±0.187	allis	12		
	Mutara GR 1997	0.081	0.133	ANOVA	16		
	Akagera NP 1997	0.158	0.225		32		
<i>Monezia</i> spp.	Never protected	0.069	±0.113	Kruskal-W	20	2.963	0.397
	Mutara GR 1991	0.055	±0.115	allis	12		
	Mutara GR 1997	0.154	±0.216	ANOVA	16		
	Akagera NP 1997	0.108	±0.143		32		
<b>Prevalence</b>	<b>Conservation political history</b>	<b>mean</b>	<b>SE</b>	<b>Test</b>	<b>N</b>	<b>T/F</b>	<b>p</b>
strongyle	Never protected	0.883	±0.172	One-way	20	2.003	0.121
	Mutara GR 1991	0.970	±0.264	ANOVA	12		
	Mutara GR 1997	1.080	±0.264		16		
	Akagera NP 1997	0.973	±0.241		32		
<i>Eimeria</i> spp.	Never protected	0.772	±0.241	One-way	20	3.249	<b>0.026</b>
	Mutara GR 1991	0.735	±0.197	ANOVA	12		
	Mutara GR 1997	0.929	±0.180		16		
	Akagera NP 1997	0.915	±0.248		32		
<i>Strongyloides</i> spp.	Never protected	0.194	±0.155	Kruskal-W	20	0.765	0.858
	Mutara GR 1991	0.161	±0.206	allis	12		
	Mutara GR 1997	0.172	±0.164	ANOVA	16		
	Akagera NP 1997	0.218	±0.191		32		
<i>Monezia</i> spp.	Never protected	0.130	±0.171	Kruskal-W	20	7.117	0.068
	Mutara GR 1991	0.073	±0.136	allis	12		
	Mutara GR 1997	0.230	±0.219	H test	16		
	Akagera NP 1997	0.205	±0.188		32		

### 3.1.1 Prevalence

Eight univariate Linear Mixed Models (LMM) with restricted maximum likelihood estimation (REML), revealed that the prevalence and intensity of ‘strongyle-type’ nematodes, *Strongyloides* spp. and coccidian *Eimeria* spp. were significantly affected by several environmental variables, while the prevalence and intensity of *Moniezia* spp. had no significant relationship with any independent variable (Table 3, 4). ‘Strongyle-type’ nematode prevalence was significantly affected by the explanatory PC2, which received axis loadings ( $>|0.50|$ ) from goat/sheep density, soil porosity and water holding capacity (Table 2). Prevalence was also significantly related to eco-climate (Table 3). *Strongyloides* prevalence was significantly affected by PC1 and PC3. Explanatory PC1 received high axis loadings ( $>|0.50|$ ) from cattle density, the adult/juvenile proportion, cattle group size and the rangeland/field ratio (Table 2), while PC3 received high axis loadings ( $>|0.50|$ ) from erosion and tree canopy cover (Table 2). *Strongyloides* prevalence also showed a significant relationship with the conservation-political history of the Mutara rangelands (Table 3). The prevalence of coccidian *Eimeria* spp. was affected by conservation-political history, season, and the interaction term ‘eco-climate  $\times$  PC5’ (Table 3). Explanatory PC5 received high axis loadings ( $>|0.50|$ ) from herb and grass frequencies (Table 2).

**Table 2** Axis loadings of five principal components (explaining 66.03 % of the total variance), resulting from principal component analysis of thirteen independent variables (see above) collected 40 quadrants along three transect belts across the Mutara rangelands. PC loadings  $> |0.5|$  are shown in bold font type.

Explanatory variable	PC1	PC2	PC3	PC4	PC5
Eigenvalue	3.15	1.71	1.45	1.16	1.12
Percent variance	24.26	13.13	11.18	8.92	8.58
Cattle density	<b>0.850</b>	0.092	0.004	0.045	-0.123
Age ratio	<b>0.743</b>	-0.032	0.057	-0.119	-0.026
Group Size	<b>0.690</b>	-0.170	0.312	-0.329	-0.021
Rangeland/field ratio	<b>0.567</b>	-0.105	0.435	0.155	0.018
Soil porosity	-0.084	<b>0.831</b>	-0.012	-0.071	-0.337
Water holding capacity	-0.178	<b>0.690</b>	-0.211	0.084	0.215
Goat/sheep density	0.182	<b>0.638</b>	0.122	0.225	0.234
Erosion	0.043	0.111	<b>0.761</b>	-0.247	0.076

Tree canopy cover	0.237	-0.175	<b>0.735</b>	0.138	-0.138
Shrub canopy cover	-0.054	-0.006	0.046	<b>0.766</b>	-0.005
Monocotyledonous biomass	-0.018	0.252	-0.305	<b>0.593</b>	0.147
Herb frequency	-0.289	0.124	0.024	0.152	<b>0.833</b>
Grass frequency	0.333	-0.073	-0.191	<b>-0.517</b>	<b>0.587</b>

**Table 3** Results of univariate LMMs using the prevalence of four parasite types as dependent variables, eco-climate, conservation-political history and season as fixed factors and five explanatory PCs as covariates. Interaction terms were excluded if  $P > 0.1$ .

Fixed effects	<i>F</i>	<i>df</i> <sub>1</sub> , <i>df</i> <sub>2</sub>	<i>p</i>
<b>'Strongyle-type' nematodes</b>			
<b>Eco-climate</b>	<b>4.410</b>	<b>3, 34.942</b>	<b>0.010</b>
<b>Conservation-political history</b>	2.822	3, 32.107	0.054
<b>Season</b>	0.239	1, 45.910	0.628
<b>PC1</b>	2.552	1, 41.830	0.118
<b>PC2</b>	<b>6.151</b>	<b>1, 65.521</b>	<b>0.016</b>
<b>PC3</b>	2.009	1, 43.522	0.163
<b>PC4</b>	1.496	1, 46.341	0.227
<b>PC5</b>	0.258	1, 52.380	0.613
<b>Covariance parameters</b>	<b>Estimate</b>	<b>SE</b>	
<b>Residual</b>	0.635	0.149	
<b>Intercept</b>	0.142	0.141	
<b><i>Strongyloides</i> spp.</b>			
<b>Eco-climate</b>	2.028	3, 67	0.118
<b>Conservation-political history</b>	<b>3.022</b>	<b>3, 67</b>	<b>0.036</b>
<b>Season</b>	0.134	1, 67	0.716
<b>PC1</b>	<b>8.168</b>	<b>1, 67</b>	<b>0.006</b>
<b>PC2</b>	0.172	1, 67	0.680
<b>PC3</b>	<b>5.253</b>	<b>1, 67</b>	<b>0.025</b>
<b>PC4</b>	0.047	1, 67	0.829
<b>PC5</b>	0.698	1, 67	0.406
<b>Covariance parameters</b>	<b>Estimate</b>	<b>SE</b>	
<b>Residual</b>	0.952	0.164	
<b>Intercept</b>	0.000	0.000	
<b><i>Monezia</i> spp.</b>			
<b>Eco-climate</b>	2.226	3, 67	0.093
<b>Conservation-political history</b>	1.349	3, 67	0.266
<b>Season</b>	0.514	1, 67	0.476
<b>PC1</b>	1.948	1, 67	0.167
<b>PC2</b>	1.418	1, 67	0.238
<b>PC3</b>	0.773	1, 67	0.383
<b>PC4</b>	0.007	1, 67	0.936

<b>PC5</b>	0.382	1, 67	0.539
<b>Covariance parameters</b>	<b>Estimate</b>	<b>SE</b>	
<b>Residual</b>	0.941	0.163	
<b>Intercept</b>	0.000	0.000	
<hr/>			
<i>Eimeria</i> spp.			
<b>Eco-climate</b>	1.191	3, 64	0.320
<b>Conservation-political history</b>	<b>3.054</b>	<b>3, 64</b>	<b>0.035</b>
<b>Season</b>	<b>32.414</b>	<b>1, 64</b>	<b>0.000</b>
<b>PC1</b>	0.299	1, 64	0.586
<b>PC2</b>	0.001	1, 64	0.970
<b>PC3</b>	0.212	1, 64	0.647
<b>PC4</b>	2.232	1, 64	0.140
<b>PC5</b>	3.479	1, 64	0.443
<b>Eco-climate × PC5</b>	2.988	3, 64	<b>0.038</b>
<b>Covariance parameters</b>	<b>Estimate</b>	<b>SE</b>	
<b>Residual</b>	0.492	0.870	
<b>Intercept</b>	0.000	0.000	

### 3.1.2 Intensity

Unlike prevalence, ‘strongyle-type’ nematode intensity was significantly affected by the explanatory PC2 and PC4. Explanatory PC4 received high axis loadings ( $>|0.50|$ ) from shrub canopy cover, grass biomass and grass frequency (Table 2). ‘Strongyle-type’ nematode intensity was also significantly related to eco-climate (Table 4). *Strongyloides* spp. intensity was only affected by the interaction term of explanatory ‘PC1 × PC4’ (Table 4). Intensity of coccidian *Eimeria* spp. had a strong relationship with the explanatory PC3 and the interaction term of ‘conservation political history × PC3’ (Table 4). It was also strongly affected by the interaction term of ‘ecoclimate × PC5’ (Table 4). Additionally, *Eimeria* spp. intensity was affected by seasonal differences (Table 4).

**Table 4** Results of univariate LMMs using the intensity of four parasites as dependent variables, eco-climate, conservation-political history and season as fixed factors, and five explanatory PCs as covariates. Interaction terms were excluded if  $P > 0.1$ .

<b>Fixed effects</b>	<b>F</b>	<b>df<sub>1</sub>, df<sub>2</sub></b>	<b>p</b>
<b>‘Strongyle-type’ nematodes</b>			
<b>Eco-climate</b>	<b>3.473</b>	<b>3, 34.995</b>	<b>0.026</b>
<b>Conservation-political history</b>	1.278	3, 31.610	0.299
<b>Season</b>	2.557	1, 43.677	0.117
<b>PC1</b>	2.281	1, 43.077	0.138
<b>PC2</b>	<b>8.477</b>	<b>1, 63.448</b>	<b>0.005</b>
<b>PC3</b>	1.204	1, 44.545	0.279

<b>PC4</b>	<b>4.756</b>	<b>1, 48.413</b>	<b>0.034</b>
<b>PC5</b>	0.004	1, 49.167	0.950
<b>Covariance parameters</b>	<b>Estimate</b>	<b>SE</b>	
<b>Residual</b>	0.540	0.128	
<b>Intercept</b>	0.208	0.142	
<hr/>			
<i>Strongyloides</i> spp.			
<b>Eco-climate</b>	1.772	3, 34.747	0.171
<b>Conservation-political history</b>	1.335	3, 31.868	0.280
<b>Season</b>	0.821	1, 47.979	0.369
<b>PC1</b>	1.374	1, 37.496	0.249
<b>PC2</b>	1.682	1, 64.211	0.199
<b>PC3</b>	0.425	1, 45.998	0.518
<b>PC4</b>	0.058	1, 49.722	0.811
<b>PC5</b>	0.872	1, 54.136	0.355
<b>PC1 × PC4</b>	<b>5.230</b>	<b>1, 56.953</b>	<b>0.026</b>
<b>Covariance parameters</b>	<b>Estimate</b>	<b>SE</b>	
<b>Residual</b>	0.867	0.202	
<b>Intercept</b>	0.107	0.173	
<hr/>			
<i>Monezia</i> spp.			
<b>Eco-climate</b>	1.542	3, 67	0.212
<b>Conservation-political history</b>	0.593	3, 67	0.622
<b>Season</b>	0.280	1, 67	0.598
<b>PC1</b>	1.525	1, 67	0.221
<b>PC2</b>	0.060	1, 67	0.807
<b>PC3</b>	0.681	1, 67	0.412
<b>PC4</b>	0.086	1, 67	0.770
<b>PC5</b>	0.879	1, 67	0.352
<b>Covariance parameters</b>	<b>Estimate</b>	<b>SE</b>	
<b>Residual</b>	1.018	0.176	
<b>Intercept</b>	0.000	0.000	
<hr/>			
<i>Eimeria</i> spp.			
<b>Eco-climate</b>	1.817	3, 31.535	0.164
<b>Conservation-political history</b>	1.377	3, 30.935	0.268
<b>Season</b>	<b>4.341</b>	<b>1, 46.802</b>	<b>0.043</b>
<b>PC1</b>	1.745	1, 34.110	0.195
<b>PC2</b>	2.082	1, 60.903	0.154
<b>PC3</b>	<b>4.536</b>	<b>1, 49.728</b>	<b>0.038</b>
<b>PC4</b>	0.582	1, 41.161	0.450
<b>PC5</b>	0.001	1, 45.122	0.979
<b>Conservation-political history × PC3</b>	<b>3.369</b>	<b>3, 45.584</b>	<b>0.026</b>
<b>Eco-climate × PC5</b>	<b>4.713</b>	<b>3, 39.480</b>	<b>0.007</b>
<b>Covariance parameters</b>	<b>Estimate</b>	<b>SE</b>	
<b>Residual</b>	0.654	0.167	



<b>Intercept</b>	0.006	0.131
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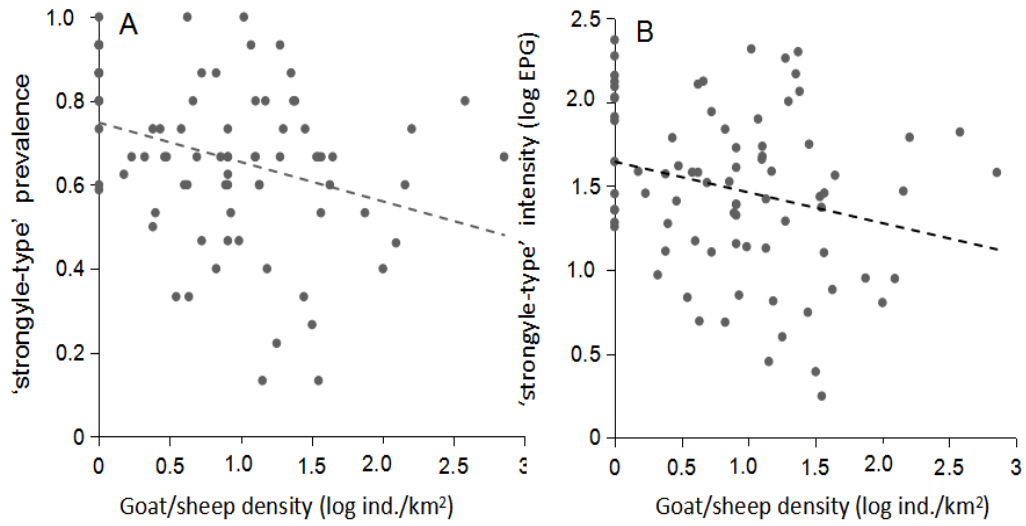
### 3.1.3 Post-hoc analysis

I used post-hoc analyses based on Spearman’s rank correlations (Table 5) to test the robustness of the effects detected in the mixed models. The prevalence of miscellaneous ‘strongyle-type’ nematode parasites in Ankole cattle was negatively correlated with goat/sheep density (Figure 2a). While the prevalence of the nematode *Strongyloides* had no significant correlation with any ecological independent variables. The prevalence of coccidian *Eimeria spp.* was positively correlated with grass and herb frequency (Figure 3a, b). The intensity of ‘strongyle-type’ nematode was highly negatively correlated with soil porosity (Table 5, Figure 4a), water holding capacity (Table 5, Figure 4b), goat/sheep density (Table 5, Figure 2b) and monocotyledonous biomass (Table 5, Figure 3f). Shrub canopy cover showed marginally non-significant negative relationship ( $r = -0.219, p = 0.051$ ; Table 5). Monocotyledonous biomass was positively correlated with *Strongyloides* intensity (Table 5, Figure 3c). The intensity of Coccidian *Eimeria spp.* was positively correlated with incidences of soil erosion, herb frequency (Table 5, Figure 3d), tree canopy cover (Table 5, Figure 3e)

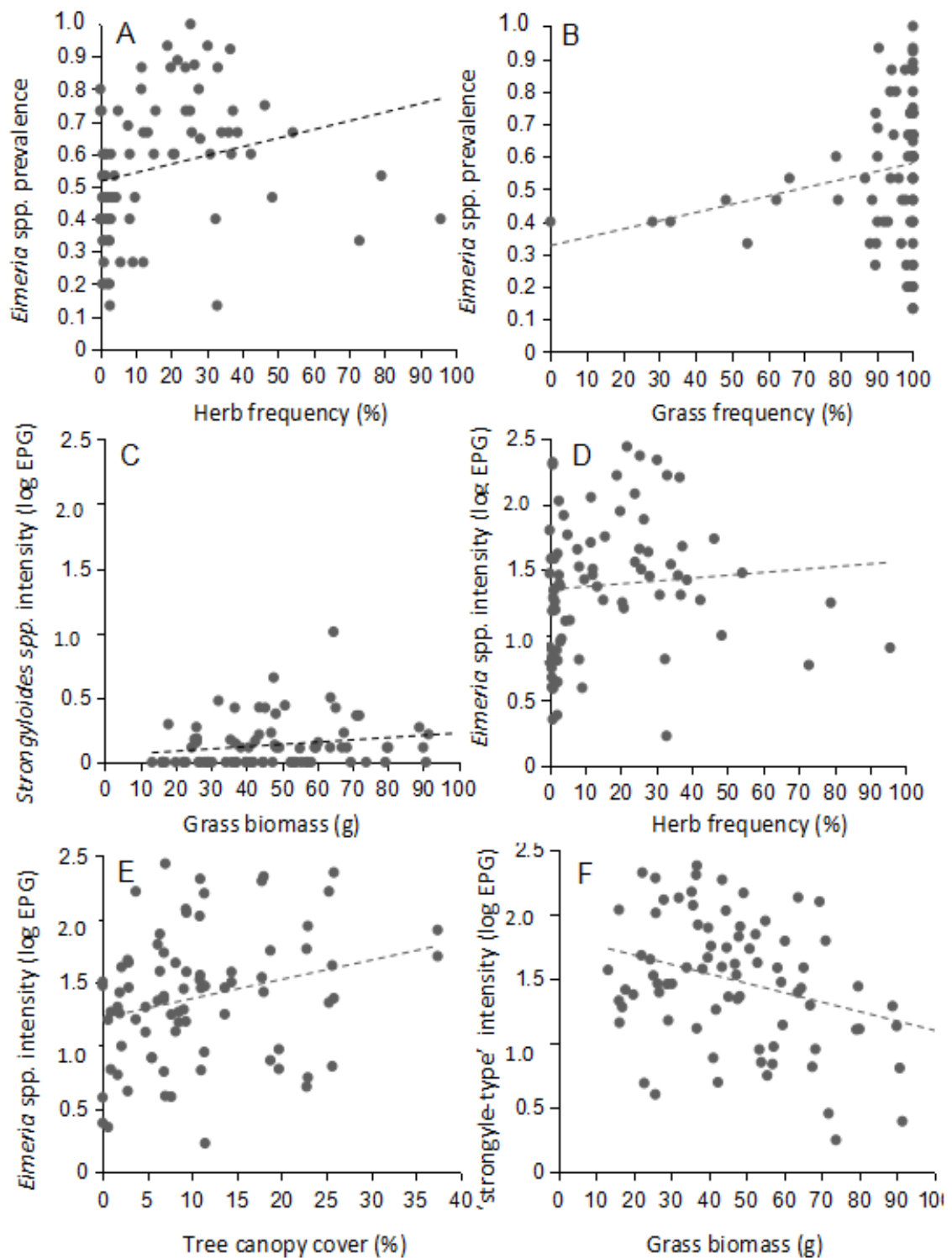
**Table 5** Post-hoc Spearman rank correlations for significant effects (see LMMs, Table 3, 4) between prevalence or intensity of GI parasites and factors with high axis loadings contained in PC1 to PC5 (see Table 2).

<b>‘Strongyle-type’ prevalence</b>				
<b>PC2</b>	Soil porosity	Water holding capacity	Goat/sheep density	
<i>r</i>	-0.119	-0.144	<b>-0.327</b>	
<i>P</i>	0.292	0.201	<b>0.003</b>	
<b><i>Strongyloides spp.</i> prevalence</b>				
<b>PC1</b>	Cattle density	Age ratio	Group size	Rangeland/field ratio
<i>r</i>	-0.149	-0.142	-0.061	-0.124
<i>P</i>	0.186	0.207	0.59	0.272
<b>PC3</b>	Soil erosion	Tree canopy cover		

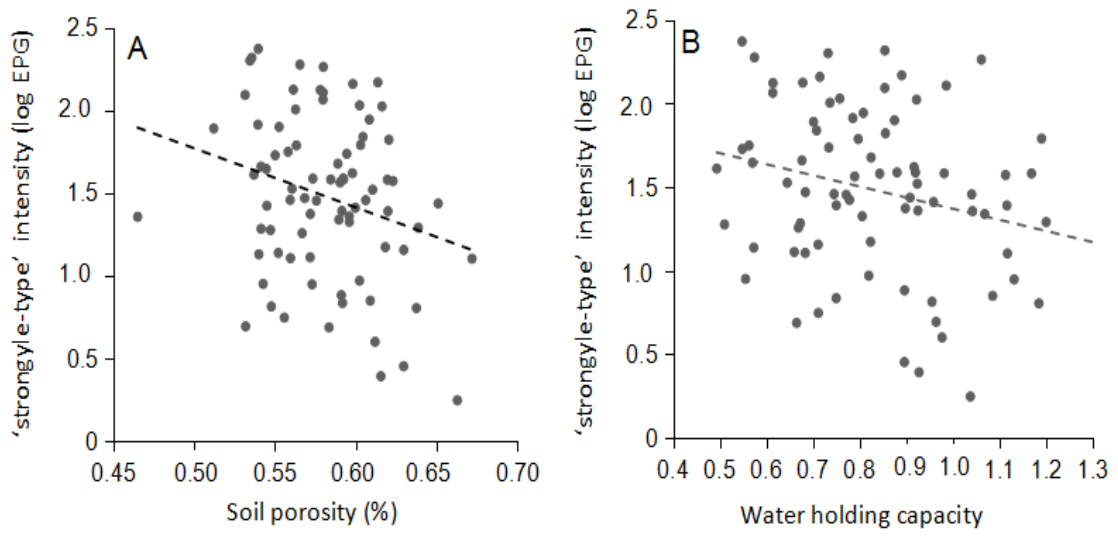
<i>r</i>	-0.104	-0.096		
<i>P</i>	0.358	0.397		
<b><i>Eimeria</i> spp. prevalence</b>				
<b>PC5</b>	Herb frequency	Grass frequency		
<i>r</i>	<b>0.387</b>	<b>0.230</b>		
<i>P</i>	<b>&lt;0.001</b>	<b>0.040</b>		
<b>'Strongyle-type' intensity</b>				
<b>PC2</b>	Soil porosity	Soil water holding capacity	Goat/sheep density	
<i>r</i>	<b>-0.220</b>	<b>-0.247</b>	<b>-0.234</b>	
<i>P</i>	<b>0.050</b>	<b>0.027</b>	<b>0.037</b>	
<b>PC4</b>	Shrub canopy cover	Grass biomass	Grass frequency	
<i>r</i>	-0.219	<b>-0.280</b>	0.002	
<i>P</i>	0.051	<b>0.012</b>	0.986	
<b><i>Strongyloides</i> spp. intensity</b>				
<b>PC1</b>	Cattle density	Age ratio	Group size	Rangeland/field ratio
<i>r</i>	-0.151	-0.181	-0.070	-0.117
<i>P</i>	0.181	0.108	0.537	0.302
<b>PC4</b>	Shrub canopy cover	Grass biomass	Grass frequency	
<i>r</i>	-0.079	<b>0.263</b>	0.007	
<i>P</i>	0.484	<b>0.018</b>	0.951	
<b><i>Eimeria</i> spp. intensity</b>				
<b>PC3</b>	Soil erosion	Tree canopy cover		
<i>r</i>	<b>0.304</b>	<b>0.273</b>		
<i>P</i>	<b>0.006</b>	<b>0.014</b>		
<b>PC5</b>	Herb Frequency	Grass frequency		
<i>r</i>	<b>0.238</b>	0.168		
<i>P</i>	<b>0.034</b>	0.137		



**Figure 2** Goat/sheep-related effects: *post-hoc* Spearman rank correlations for significant effects between 'strongyle-type' prevalence (A), log-transformed 'strongyle-type' intensity (B) of Ankole cattle and goat/sheep density.



**Figure 3** Vegetation-related effects: *post-hoc* Spearman rank correlations for significant effects between *Eimeria* spp. prevalence and herb (A) and grass frequency (B), for significant effects between log-transformed *Eimeria* spp. intensity and grass biomass (C), herb frequency (D) and tree canopy cover (E), and for significant effects between log-transformed 'strongyle-type' intensity and grass biomass (F).



**Figure 4** Soil-related effects: *post-hoc* Spearman rank correlations for significant effects between log-transformed 'strongyle-type' intensity and soil porosity (A) and water holding capacity (B).

## 4 Discussion

My study aimed to identify ecological and landscape-related factors that influence the prevalence and intensity of GI parasite infections of Ankole cattle in a degraded pastoral rangeland ecosystem in north-eastern Rwanda. Interestingly, habitat destruction, i.e., urbanization and the increase of agriculturally used area (rangeland/field ratio), had no direct impact on the health of cattle (Table 5). Although time off-conservation was significantly related to the prevalence of *Eimeria* spp. and *Strongyloides* spp. (Table 3), the effect of conservation-political history was negligible with no significant differences between zones of varying time off-conservation (Table 1). I expected intrinsic factors such as cattle density, group size and the age ratio of the investigated group to have a direct effect on prevalence and intensity of GI parasite infections (Taylor et al., 2007; Bowman, 2009; Zvinorova et al., 2016). However, this was not the case, suggesting that these core effects were covered by environmental and ecological effects that can be attributed to overstocking and overgrazing. For example, large cattle group size may have had a negative effect on GI parasite infections, but the effect was not traceable owed to stronger impacts caused by environmental changes. Despite the general rule that age and group size affect the parasite burden of individuals, other studies have shown that the prevalence of nematode infections can be independent of age (Morgan et al., 2006; Magona and Musisi, 2002) and group size (Morgan et al., 2005).

Coccidian *Eimeria* spp. prevalence and intensity were significantly affected by seasonal changes in rainfall (Table 1). Both observations were not unexpected, since I predicted parasite intensity and prevalence — at least in ‘strongyle-type’ nematodes and coccidia — to increase with increasing rainfall (Kheysin, 1972; Garcia Romero and Gruner, 1984; Onyali, 1989; Magona and Musisi, 2002). Both taxa need sufficient humidity and moderate temperatures to hatch and disperse within the herbaceous vegetation where moisture remains high unless overgrazed or mowed (Armour, 1980; Barnes et al., 1988; Coyne and Smith, 1992; O’Connor et al., 2007; Blackie, 2014). Surprisingly, ‘strongyle-type’ nematode intensity was also affected by season, but with

higher infections in dry season than in wet season (Table 1). Here rainfall and consequently humidity in the herbaceous layer are generally lower. After defecation, the larval stage (L3) of an infectious nematode is retained within the crusted fecal pat and cannot disperse onto the pasture until sufficient humidity is available (Vlassoff, 1982; Hansen and Perry, 1994). Rainfall but also the degree of evaporation directly affects the humidity in the pasture. Dense herbaceous vegetation and a close tree or shrub canopy reduce evaporation, maintain humidity and therefore provide suitable conditions for the migration of L3 larvae (Angus, 1978; Gibson, 1966; Garcia Romero and Gruner, 1984; Onyali, 1989). I therefore predicted that the degradation of pasture, i.e., soil erosion, reduced grass biomass, changes in the frequency of herbs and grasses or deforestation (cutting trees and clearing bushes) reduce the survival of larvae and thus lower the risk of infection with GI parasites. The prevalence of *Eimeria* spp. as well as the intensity of *Eimeria* spp. and *Strongyloides* spp. were indeed positively related to herb/grass frequency and grass biomass respectively (Table 5, Figure 3a-d). The intensity of *Eimeria* spp. was also positively related to the percentage of tree canopy (Table 5, Figure 3e). However, this pattern was not confirmed for the relationship between the intensity of 'strongyle-type' nematode infections and grass biomass, suggesting that 'strongyle-type' larvae are not adversely affected by overgrazing but rather increase the risk of infection with increasing grassland degradation (Table 5, Figure 3f). Onyali (1989) attributed this phenomenon to the accumulation of cattle around water holes and swamps during the dry season in northern Nigeria. Water holes in the Mutara contain water throughout the year and hence enable grasses to flourish during the dry season. At that time, grazing cattle are concentrated around water holes and troughs, pasture is extremely short and the accumulation of cattle feces leads to increased intensities of GI parasite infections in dry season (Table 1). Coccidian oocysts and *Strongyloides* larvae are more susceptible to dry conditions (Taylor et al., 2007) and may thus not survive in the short, overgrazed pasture.

I expected parasite intensity and prevalence to decrease with increasing soil compaction, i.e., a decrease in soil porosity and water holding capacity will lead to less

humidity in the soil and thus reduces the prevalence and intensity of GI parasite infections (Schnürer et al., 1986). Moreover, soils that hold large amounts of water are less susceptible to leaching losses of nutrients or organic matter. This is because soils with a limited water holding capacity reach saturation much earlier than soils with higher water holding capacity. After a soil is saturated with water, all excess water including nutrients and organic material contained in the soil are leached down the soil profile and become unavailable to plants (Wilke, 2005). Contrary to my prediction, this was not confirmed by my study: both, soil porosity and the water holding capacity of the soil were negatively related to the 'strongyle-type' parasite burden. High water holding capacity or soil porosity translates into a low degree of soil compaction. A well aerated soil keeps moisture and thus provides suitable environmental conditions for L3 larvae (Armour, 1980; Barnes et al., 1988; Coyne and Smith, 1992; O'Connor et al., 2007). In the Mutara rangelands high 'strongyle-type' nematode intensity correlated to low soil compaction (Table 5, Figure 4a, b), suggesting that 'strongyle-type' nematode larvae benefit from grassland degradation and soil compaction. As outlined for low monocotyledonous biomass around water holes during the dry season, the effect of soil compaction on 'strongyle-type' intensity may be explained in the same way, i.e., the accumulation of cattle dung countervails the otherwise negative conditions for larvae. In both cases, i.e., vegetation degradation and soil compaction, 'strongyle-type' nematodes seem to benefit and cause increased rates of infection in cattle, grazing on overgrazed and degraded pastures. On the other hand it was reported that soil compaction increases plant (grass and herb) production. The density of annual grasses on a cattle ranch in Namibia was significantly higher outside experimental cattle exclosures than inside where grazing was prevented (Zimmermann et al., 2009). The increase of annual grasses on trampled sites may be responsible for sucking more water from the soil, resulting in higher grass productivity from trampling (if followed by sufficient rest), and thus explaining the increased survival of 'strongyle-type' nematodes despite increased levels of soil compaction.

The most interesting result of my study is the decrease of 'strongyle-type' nematode infections with increasing goat densities. Both, prevalence and intensity of



strongyle-type infections, decreased with increasing numbers of goats/sheep in the area (Table 5, Figure 2a, b). I expected a potential cross-infection between goats/sheep and cattle, i.e., increased goat/sheep density translates into higher GI parasite burden in cows (Armour et al., 1988). Other authors argued that due to the high degree of parasite-host specificity the risk of cross infection between different taxa of domestic ruminants is negligible (Giudici et al., 1999; Rocha et al., 2008). Due to the relatively high host-specificity of many nematode species, the infectivity of a pasture will be lowered by grazing a second or third host species on the same pasture (Hoste et al., 2003; Marley et al., 2006) and thus diluting the risk of one livestock species being cross-infected by another. This dilution effect was recently proposed as a grazing management system with a sustainable and integrated worm control, especially in tropical environments (Waller, 1997,1999; Muheua and Zimmermann, 2009; d'Alexis et al., 2012). Diversification of livestock species grazed in the Mutara rangelands was already proposed by earlier studies, not only to 'dilute' the risk of cross-infection with GI parasites, but also to reduce the spread of invasive plant species (Wronski et al., 2017) or to diversify income generating measures and improve livelihoods amongst local pastoralist communities (Bariyanga et al., 2016).

## 5 Conclusion

In conclusion, prevalence and intensity of GI parasite infections of Ankole cattle in the Mutara rangelands seems to be determined by vegetation related parameters, the degree of soil compaction and the presence or absence of goat/sheep grazing. Environmental degradation had no obvious impact on the prevalence and intensity of *Monezia* spp. or *Strongyloides* spp., but to a certain degree on the prevalence and intensity of coccidian *Eimeria* spp. and ‘strongyle-type’ nematodes. For coccidia, environmental variables are known to affect the presence and survival of oocysts in the pasture, while ‘strongyle-type’ nematodes seem to benefit from environmental degradation (pasture and soil) and thus increase the risk of GI infestations of Ankole cattle. Coccidian *Eimeria* spp. are known to rest on the availability of moisture in the pasture and are most affected by climate changes. Although, my data do not indicate climate-induced effects on the GI parasite burden, the worldwide increase of GI parasite related diseases in recent years has mainly been attributed to climate change (Mitchell and Somerville, 2005; van Dijk et al., 2008). This is because the survival of free-living larval stages and coccidian oocysts are mainly dependent on temperature and humidity (Armour, 1980; Barnes et al., 1988; Coyne and Smith, 1992; O’Connor et al., 2007; Fox et al., 2012). Recent temperatures in Rwanda have been 2°C warmer than the mean monthly data collected over a period of 29 years (1961 and 1990), while deviations from the long-term average rainfall were recorded, with unusual periods of both high and low rainfall (Loevinsohn, 1994; Kalisa, 2012). Moreover, deviations from the long-term average precipitation in the Mutara resulted in unusual periods of high or low rainfall (Loevinsohn, 1994; Kalisa, 2012). It is anticipated that over the next decade, climate change in the Mutara rangelands will cause even greater extremes of weather conditions, with a general trend towards being drier and warmer. This will probably have a positive impact on cattle grazing by reducing the degree of coccidian infections, but is predicted to enhance ‘strongyle-type’ nematode infections.

In temperate climates, changes have been reported in the incidence, pattern and geographical distribution of helminth infections in ruminant livestock species (Skuce et

al., 2008). It is anticipated that over the next decade, climate change in the Mutara Rangelands will cause greater extremes of weather conditions, with a general trend towards being drier and warmer. This will probably have a positive impact, reducing the degree of coccidian infections, but is predicted to enhance ‘strongyle-type’ nematode infections in the area. Since ‘strongyle-type’ nematode larvae seem to have adopted to dry season conditions it can be expected that the overall prevalence of ‘strongyle-type’ infections in Ankole cattle will increase in the near future. Given that temperatures in the Mutara will increase and precipitation will decrease, increased GIT parasite prevalence in conjunction with droughts and overstocking will lead to higher mortality rates, poorer body conditions and therefore economic losses for pastoralist communities. This in turn might have negative impacts on the sustainable development of the Mutara and will lead to more agriculturally used area and thus to further degradation of rangelands. However, especially for African livestock systems, more information on the helminth burdens of domestic livestock and the environmental (abiotic and biotic) factors that influence the parasite load are needed. Parasite burdens change within different landscapes and between varying degrees of degradation, and more scientifically sound information on the effects of human induced landscape changes on the prevalence and intensity of helminthiases is required to improve our understandings of these relationships and our capacity to introduce land-use policies that improve human and livestock health (Farrell et al., 2013; McFarlane et al., 2013).

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