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Mixed-host aggregations and helminth parasite sharing in an East African wildlife–livestock system

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ABSTRACT

Parasitic infections transmitted between livestock and wildlife pose a significant risk to wildlife conservation efforts and constrain livestock productivity in tropical regions of the world. Gastrointestinal helminths are among the most ubiquitous parasites, and many parasites within this taxon can readily infect a wide range of host species. Factors shaping bidirectional transmission of parasites in wildlife–livestock systems are understudied. In this study, we investigate the prevalence and diversity of helminth infections in an East African community of wild and domestic ungulates. We also identify pairs of host species between which transmission may be possible based on shared parasite taxa, and explore the role of multi-host aggregations in shaping patterns of parasite sharing. Helminth taxa detected included *Trichostrongylus*, *Trichuris*, *Paramphistomum*, *Skrjabinema*, *Strongyloides*, *Strongylus* spp., and other strongyle-type nematodes. We found that nearly 50% of individuals harbored at least one species of helminth, but certain species, such as zebra and impala, exhibited higher prevalence than others. High canopy feeders, like giraffe, had lower prevalence than hosts feeding at medium and low foraging heights. For helminths, patterns of parasite sharing likely emerge from shared space use, which is mediated in part by mixed-species aggregations. The frequency with which host species associated together in mixed-species aggregations was positively correlated with the number of parasite taxa shared. We suggest that variation among species in their tendency to form mixed-species aggregations creates heterogeneity in transmission opportunities, and consequently, parasite sharing across ungulate species. These results enhance our understanding of the role of spatiotemporal relationships among host species in shaping parasite communities in mixed wildlife–livestock grazing systems.

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1. Introduction

Parasitic infections are a concern for many wildlife populations and are a growing issue for both conservation

biologists and livestock owners (Cleaveland et al., 2000; Haydon et al., 2002; Kock, 2005; Osofsky, 2005; Delahay et al., 2009). Approximately 77% of livestock pathogens are multi-host (Cleaveland et al., 2001), and pathogens shared among livestock and wild ungulates may have adverse effects on both populations. Indeed, most endangered species at risk from disease acquire their pathogens from domestic populations (Altizer et al., 2003), and wildlife serve as a reservoir for many economically important livestock diseases (Wambwa, 2005; Michel and Bengis,

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2012). Pathogen transmission is of particular concern in sub-Saharan Africa because of the close proximity of wildlife to livestock and the high prevalence and diversity of pathogens (Cleaveland et al., 2005; Wambwa, 2005). Despite the potential importance of wildlife in pathogen transmission dynamics, many parasitological studies focus on domestic species while the potential for wildlife and livestock to share parasites is largely overlooked.

Gastrointestinal helminths are among the most ubiquitous parasites worldwide (Petney and Andrews, 1998). In central Kenya, helminth prevalence in cattle can approach 90% (Waruiru et al., 2000). These parasites can play a role in regulating wildlife populations (Gulland, 1992), and have been shown to have detrimental health effects on wildlife and domestic animals, such as impaired growth and development (Falvey and Bambridge, 1975; Stein et al., 2002). In domestic ruminants, infections can depress growth rates by >25%, reduce fecundity and milk yields by 30%, and increase risk of mortality (Carles, 1992; Thumbi et al., 2013a; Thumbi et al., 2013b). Thus, helminths are an important factor limiting livestock productivity. In free-ranging wild ungulates, infected animals have been shown to have lower body mass, reduced fecundity, and higher mortality rates (Gulland, 1992; Stein et al., 2002). In addition, helminths have strong effects on immune function and, consequently, host responses to secondary infections (Graham et al., 2007; Ezenwa and Jolles, 2011). For example, African buffalo (*Syncerus caffer*) are less able to tolerate bovine tuberculosis infection if co-infected by helminths (Jolles et al., 2008), and buffalo treated with anthelmintic drugs exhibit altered immune function relevant to tuberculosis infection (Ezenwa et al., 2010).

Interspecific transmission of helminths via fecal–oral mechanisms readily occurs between sympatric ungulates (Sachs and Sachs, 1968; Preston et al., 1979; Waruiru et al., 1995). However, in order to accurately quantify transmission risk at the wildlife–livestock interface, we need to better understand factors that impact interspecific transmission dynamics (Osofsky, 2005). Within a single species, it has been well documented that patterns of contact and interaction among conspecifics are crucial factors determining transmission patterns (Coté and Poulin, 1995; Altizer et al., 2003). Generally, higher levels of interaction create transmission opportunities among conspecifics (Altizer et al., 2003; Godfrey et al., 2009; VanderWaal et al., 2014a), and parasite prevalence, intensity, and diversity are correlated with intraspecific variation in group size (Hoogland, 1979; Brown and Brown, 1986; Rubenstein and Hohmann, 1989). In addition, neighboring social groups often harbor unique arrays of gastrointestinal microbes (Freeland, 1979; Degnan et al., 2012). Despite extensive research effort on how grouping behavior impacts transmission risk within a single species, the role of multi-species aggregations in creating opportunities for sharing multi-host parasites, such as helminths, has been minimally explored. Among sympatric ungulates, transmission opportunities between species are mediated by patterns of space use and aggregation (Ezenwa, 2003; VanderWaal et al., 2014b). Ezenwa (2003) demonstrated that individual ungulates living in areas with high bovid species diversity were infected by a greater number of parasite taxa,

perhaps because the diversity of closely related hosts created opportunities for parasite sharing or host-switching. In addition, ungulate species with higher levels of spatial contact with heterospecifics were more likely to be infected with strongyle-type nematodes, suggesting that indirect contact via shared space use generates interspecific transmission opportunities (Ezenwa, 2003). However, the role of mixed-species aggregations in shaping parasite communities remains less clear, and the importance of such spatiotemporal contact in African ecosystems where both cattle and wildlife are present has not yet been examined.

The objectives of this study were to survey helminth parasites in a mixed system comprised of wild and domestic ungulates in a semi-arid region of Kenya, and to investigate the risk of interspecific transmission at the wildlife–livestock interface. We provide baseline data on helminth prevalence and diversity, and identify pairs of host species between which transmission is possible based on shared parasite taxa. We further explore how mixed-species aggregations contribute to parasite sharing.

2. Methods

2.1. Study site and species

This study was conducted in Ol Pejeta Conservancy (OPC), a 364-km² wildlife reserve and commercial cattle ranch in central Kenya. OPC is a semi-arid savanna ecosystem located on the equator (0° N, 36°56' E), receiving on average 900 mm of rainfall per year (Birkett, 2002). Species included in this study included the African buffalo (*S. caffer*, Conservation status: Least concern), eland (*Taurotragus oryx*, status: Least concern), Thomson's gazelle (*Gazella thomsonii*, status: Near threatened), reticulated giraffe (*Giraffa camelopardalis reticulata*, sub-species status: Lower risk – conservation dependent), Jackson's hartebeest (*Alcelaphus buselaphus jacksonii*, sub-species status: Endangered), impala (*Aepyceros melampus*, status: Least concern), plains zebra (*Equus burchelli*, status: Least concern), and domestic cattle (*Bos indicus*). Cattle were minimally managed and free-ranging within OPC. Cattle shared grazing pastures and water sources with wildlife during the day. Cattle were not routinely de-wormed.

Dietary niche is likely to affect both parasite exposure and the internal environment within the gut (Dehority and Odenyo, 2003; Apio et al., 2006). Ungulate dietary niches lay along a browser/grazer continuum based on the proportion of the diet consisting of grass relative to forbs, leaves, and woody vegetation. Three general dietary guilds are commonly recognized: grazers, browsers, and mixed feeders (Hoffmann and Stewart, 1972; Jarman, 1974). Here, species whose diets consist of >70% grass were defined as grazers, 30–70% grass as mixed feeders, and <30% grass as browsers (VanderWaal et al., 2014b). Values for diet composition were taken from the literature (Hoffmann, 1989; Gagnon and Chew, 2000; Watson and Owen-Smith, 2000; Cerling et al., 2003; Sponheimer et al., 2003; Codron et al., 2007; Copeland et al., 2009). Study species included two browsers (eland and giraffe), four grazers (zebra,

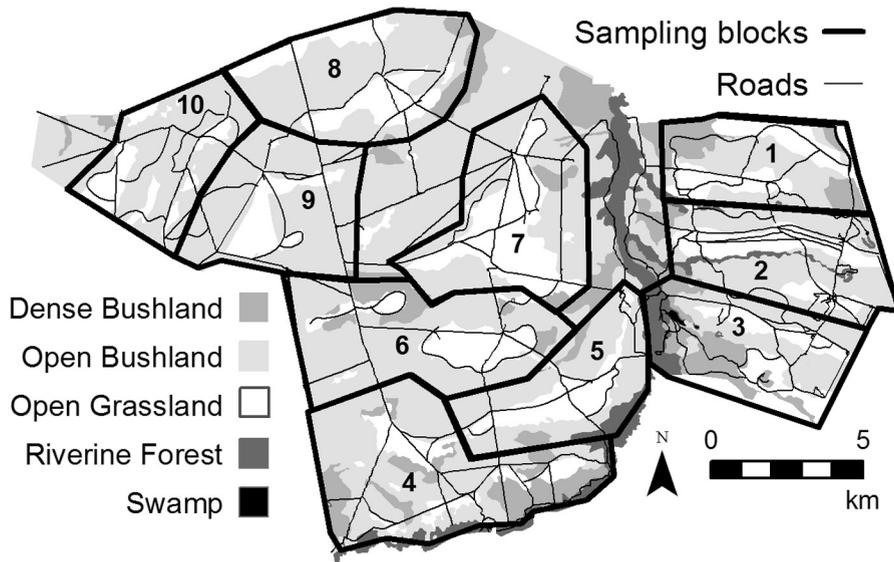


Fig. 1. Map of Ol Pejeta Conservancy depicting habitat types, road network, and sampling blocks.

hartebeest, cattle, buffalo), and two mixed feeders (impala and Thomson's gazelle).

2.2. Fecal collection and analysis

Fecal samples were collected from 213 individuals from eight different ungulate species. All samples were collected between August 28, 2011 and October 7, 2011. Sampling was stratified across ten spatial blocks within OPC (Fig. 1). Spatial blocks were visited once every three days until two samples per species were collected from every block. Not all species could be found in all blocks. Samples were obtained from 15 buffalo, 14 cattle, 18 eland, 97 giraffe, 14 hartebeest, 18 impala, 19 Thomson's gazelle, and 18 zebras. For species with small population sizes (<400 animals: giraffe, hartebeest), caution was exercised to ensure that no individual was sampled multiple times. Each giraffe was individually identifiable as a result of ongoing population monitoring (VanderWaal et al., 2014c). Hartebeest social groups occupied very small, spatially separated territories (~5 km², OPC Ecological Monitoring Department), and we collected only one sample per social group. For all other species, population sizes were very large relative to sample size. On average, only 1.4% (range: 0.22–4.5%) of the total population was sampled. Samples were collected from the ground immediately after defecation was observed. Care was taken to ensure that only portions of feces not in contact with the ground were collected. Samples were transported in a cool box to the field laboratory, where they were preserved in 10% formalin until further analysis.

We used a modified fecal sedimentation technique for qualitative assessment of helminth egg presence (Sloss and Kemp, 1978). Briefly, fecal pellets of ungulates were gently mashed by a pestle. Three grams of the dung was mixed with 45 ml of distilled water, stirred, strained and the sediment left to stand for 30 min. The supernatant was

decanted out and the dung re-suspended with 45 ml of water. Decanting and re-suspension of the sediment was repeated 2–3 times until the suspension was clear. From each sample sediment, 3 glass slide preparations were made and examined at 100× magnification under digital light microscope (Leica, DM500). Images of the helminth eggs were taken and their dimensions determined by microscope imaging software (Leica, LAS EZ 2.0).

Except for strongyle-type eggs, morphological distinct features such as shape, size and color were used to identify eggs to genus level (Foreyt, 2001). We used the term strongyles to refer to all morphologically indistinguishable strongyle-type eggs from nematodes of the Order Strongylida. Common examples of nematodes with strongyle-type eggs include *Haemonchus* spp., *Oesophagostomum* spp., *Cooperia* spp., and *Bunostomum* spp. The genus *Strongylus* also produces strongyle-type eggs, but were not classed with other strongyles because they are equine-specific nematodes (Kilani et al., 2010).

2.3. Interspecific association surveys

Observations of interspecific association patterns were recorded between March 17 and August 2, 2011 ($N=2143$ observations). We recorded the proximity of each species to others while driving pre-determined road transects through OPC. Routes were approximately 100 km in length, covered approximately 115 km² each, utilized the existing road network within OPC, and traversed all habitat types (Fig. 1). Transects were designed so the majority of OPC was surveyed once every three days. To quantify the extent to which each species aggregated with other species, we defined "association strength" as the percentage of observations that two species were observed within 50 m of each other relative to the total number of times those species were observed.

Table 1
 Prevalence of helminth parasites by host species^a.

	Buffalo	Cattle	Eland	Giraffe	Hartebeest	Impala	Th. Gazelle	Zebra	Overall
Strongyle-type	0.2	0.21	0.5	0.02	0.79	0.94	0.37	0.06	0.249
Trichostrongylus	0	0	0.17	0.04	0.21	0.22	0.32	0.17	0.108
Trichuris	0	0	0	0.05	0.21	0	0.05	0	0.042
Paramphistomum	0.33	0	0	0	0	0	0	0	0.023
Skrjabinema	0	0	0	0	0	0	0.47	0	0.042
Strongyloides	0	0	0	0	0.29	0.22	0.26	0	0.061
Unidentified ova	0	0.07	0.06	0	0	0	0	0	0.01
Strongylus	0	0	0	0	0	0	0	1	0.085
Overall prevalence	0.47	0.29	0.72	0.09	0.79	0.94	0.84	1	0.446
<i>n</i>	15	14	18	97	14	18	19	18	213
Richness – <i>Indiv</i>	1.14	1	1	1.22	1.91	1.47	1.75	1.22	1.39
Richness – <i>Species</i>	2	2	3	3	4	3	5	3	8

^a Overall prevalence of each parasite is listed in the final column. For each host species, the final rows list overall prevalence of all helminthes, number of fecal samples examined (*n*), average number of helminth species per individual (Richness – *Indiv.*), and number of helminth species found in the host species (Richness – *Species*).

2.4. Statistics

Prevalence was defined as the proportion of individuals that were positive for a specific helminth taxon. We measured the extent to which each pair of host species shared parasite taxa using the Jaccard index. The Jaccard index is defined as the number of shared parasite taxa divided by the total number of taxa found in both host species combined. Strongyles were excluded from parasite sharing analyses because, unlike the other genera documented in this ecosystem, strongyles represent a broader taxonomic grouping of helminths. Although strongyles were found in all host species, sharing strongyle-type nematodes was a relatively meaningless metric of transmission potential between host species because we lacked genus-level specificity for strongyles. This made their inclusion in the parasite sharing calculations neither informative nor appropriate. Hence, they were not used in the calculation of the Jaccard index or subsequent regression analyses.

We hypothesized that host species frequently found together in mixed-species aggregations would be more likely to share the same parasites. To test this hypothesis, we performed multiple-regression quadratic assignment procedures (MR-QAP), a method of matrix regression that calculates *p*-values through permutation techniques (Krackhardt, 1988; Dekker et al., 2007). We used MR-QAP instead of traditional regression because these data violate the assumption of independence; the unit of analysis was a pair of species, and each species appeared in multiple pairs. The MR-QAP method avoids interdependency issues arising from relational data by performing a matrix regression where *p*-values are based on 1000 random permutations of the order of the rows and columns (Krackhardt, 1988; Dekker et al., 2007). Here, the outcome variable was the Jaccard index for parasite sharing. Covariates included association strength between the pair of species and whether the pair shared the same dietary niche (0/1).

3. Results

The prevalence of observed helminth parasites for each host species in Ol Pejeta Conservancy is summarized in

Table 1 and Fig. 2. This survey identified seven different helminth taxa present within this ungulate community. An unidentified double-walled ova measuring 55.7 × 34.2 μm (Fig. 3) was also detected in cattle and eland. Overall, the prevalence of helminth infection was 44.6%, and the majority of infected individuals were infected by one to two different taxa. Strongyle-type nematodes were found in the greatest number of host species and nearly 25% of

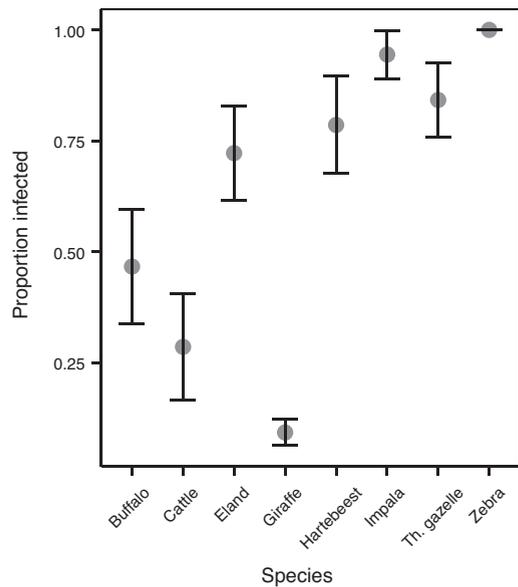


Fig. 2. Bar chart of the prevalence (±SE) of helminth infections by species.



Fig. 3. Unidentified ova found in cattle and eland at OPC in Kenya. Magnification 400x; scale 50 μm.

Table 2

Proportion of parasite taxa shared between each pair of species (Jaccard index). All taxa included in the parasite sharing calculation represent genera. Strongyle-type nematodes were not included in the calculation because they represent a much larger taxonomic grouping. Hence, sharing strongyles may not be indicative of transmission risk between two species (see Section 2). When strongyles were included, no two species had a non-zero Jaccard index.

	Giraffe	Eland	Th. Gazelle	Impala	Hartebeest	Cow	Buffalo
Giraffe							
Eland	0.33						
Th. gazelle	0.5	0.2					
Impala	0.33	0.33	0.5				
Hartebeest	0.67	0.25	0.75	0.67			
Cow	0	0.5	0	0	0		
Buffalo	0	0	0	0	0	0	
Zebra	0.33	0.33	0.2	0.33	0.25	0	0

samples were infected with strongyles. After strongyles, *Trichostrongylus* spp. was observed in the greatest range of host species (six species), and were observed in approximately 10% of all samples (Table 1). Three helminth taxa were found in only one host species (*Paramphistomum* spp. in buffalo, *Skrjabinema* spp. in Thomson's gazelle, and *Strongylus* spp. in zebra).

Host species in the OPC ungulate community exhibited extensive sharing of parasite taxa (Table 2 and Fig. 4b). Our analysis revealed that the number of parasite taxa shared by two host species was positively correlated with the association strength between the hosts ($\beta = 3.39$, $p = 0.03$, Fig. 4a and b). Sharing the same foraging niche did not significantly influence the likelihood of sharing parasites ($\beta = -0.13$, $p > 0.05$). Although strongyle-nematodes were found in all host species, they were not included in the calculation of the Jaccard index because sharing strongyles may not be a meaningful indicator of transmission potential between two host species. Unlike other parasites included in this analysis, strongyles do not represent a single genus, but rather a broader phylogenetic group. For this reason, strongyles were excluded in the parasite sharing analysis. Even when strongyles were included, their inclusion did not alter the relationship between association strength and parasite sharing ($\beta = 2.50$, $p = 0.024$) beyond increasing the model intercept as a consequence of the fact that all host species shared at least one parasite taxa (strongyles).

4. Discussion

Free-ranging ungulates in OPC exhibited moderate to high rates of infection, and nearly half of all samples harbored at least one species of helminth (Table 1). Overall, zebra experienced the highest frequency of infection, with no individuals found to be helminth-free (Fig. 2). High levels of infection in zebra were primarily driven by *Strongylus* spp. This genus is also among the primary nematodes driving high prevalence observed in other populations of plains zebra in the region (Wambwa et al., 2004), though *Trichostrongylus* appears to be more common in sympatric Grevy's zebra, *E. grevyi* (Muoria et al., 2005). High overall prevalence was also observed in eland, hartebeest, impala, and Thomson's gazelle. Despite a higher sampling effort for giraffe, parasite richness was no higher than in other species, and prevalence was starkly lower (<10% of individuals infected). This pattern

likely reflects the fact that forage contamination by infective stages of helminths is minimal at higher foraging heights (Apio et al., 2006), and it has been suggested that giraffes mainly acquire helminth infections from water-holes (Krecek et al., 1990). In Namibia, the most prevalent parasites in giraffe (*Parabronema skrjabini*, *Skrjabinema* spp., *Haemonchus mitchelli* and *Echinococcus* spp.) differed from those identified in our study (Krecek et al., 1990).

Similar to other African herbivore communities (Ocaido et al., 2004), the most prevalent helminth genus was *Trichostrongylus*, which was found in nearly 11% of all fecal samples tested. High prevalence was driven in part by the fact that this genus was found in the widest range of hosts (six host species in comparison to a maximum of three hosts for other parasite genera). It is also better able to survive in dry conditions than other genera (Anderson and Levine, 1968), which may account for its high prevalence in central Kenya's semi-arid climate. Chronic infection by *Trichostrongylus* is associated with trichostrongylidosis, which can lead to poor body condition and potential economic losses for livestock owners and may reduce fitness in wildlife (Horak et al., 1968; Hudson, 1986). Although no cattle were found to be infected by *Trichostrongylus*, we cannot conclude that this parasite is absent in OPC cattle based on these data. Given that *Trichostrongylus* occurs in cattle within other African wildlife–livestock ranging systems (Ocaido et al., 2004; Kabaka et al., 2013), it may be that *Trichostrongylus* occurs at low prevalence within OPC cattle and was not detected in this study. Taken together, this suggests that there is a substantial risk of transmission of *Trichostrongylus* from wildlife to cattle in OPC.

Cattle were infected by relatively few of the parasites found in wildlife, which differs from results of other studies (Waruiru et al., 2000). The only taxa detected in cattle were strongyle-type helminths and an unidentified spirurid-type egg that was also prevalent in eland (Fig. 3). Less than 30% of bovid parasite taxa found in wild OPC ungulates were also found in cattle. In contrast, over 80% of parasite taxa found among wild bovids in the vicinity of Lake Mburo National Park, Uganda were also found in cattle (Ocaido et al., 2004). The low parasite richness exhibited by OPC cattle may have been related to the fact that prevalence (~30%) was lower than observed in some, but not all, studies of east African cattle (Waruiru et al., 2000; Ocaido et al., 2004; Swai et al., 2006; Kabaka et al., 2013). In addition, sampling in our study only spanned one rainfall season, potentially

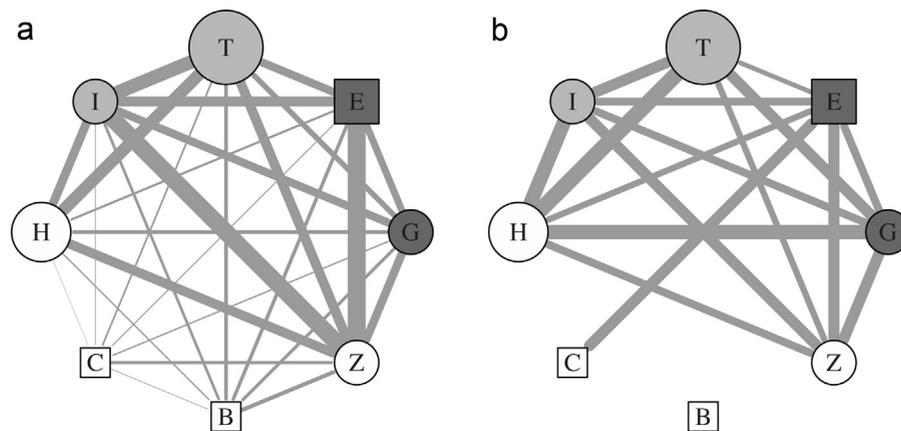


Fig. 4. Representation of (a) patterns of association and (b) parasite sharing among hosts. Host species are represented as nodes (B = Buffalo, C = Cattle, H = Hartebeest, I = Impala, T = Thomson's gazelle, E = Eland, G = Giraffe, Z = Plains Zebra). Square nodes represent species of sub-family Bovinae. Shading indicates feeding niche (dark gray = browser, light gray = intermediate feeder, white = grazer). The thickness of lines drawn between nodes correlates with the extent to which pairs (a) share parasite taxa or (b) are found together in mixed species aggregations.

reducing the diversity of taxa observed given that shedding rates of some helminths are temporally variable (Ocaido et al., 2004). Also, our laboratory methods focused on the identification of helminth eggs. Utilization of methods focusing on identification of larval or adult parasitic stages would have allowed some of the observed strongyle-type eggs to be speciated, thus increasing apparent diversity.

Hartebeest appear to be the primary reservoir of *Trichuris* spp. in OPC. Approximately 20% of hartebeest were infected, while only incidental infections occurred in other species and it was entirely absent in cattle (Table 1). The sub-species of hartebeest found in OPC (*A. buselaphus jacksonii*) is endangered and the population in OPC has been declining for unknown reasons (OPC Ecological Monitoring Department, unpublished data). While we have no conclusive evidence that declines in OPC are related to parasitism, it may be important to note that hartebeest were among the most parasitized host species, and individual parasite richness was higher in hartebeest than in any other species examined (Table 1). Two helminths found at moderately high prevalence in OPC hartebeest (*Trichuris* and *Strongyloides*) were not present in hartebeest in nearby Mpala Ranch (Ezenwa, 2003). However, we cannot distinguish between whether high parasite prevalence is a cause or a symptom of population declines. Gastrointestinal parasites have been shown to reduce host fecundity and survival in free-ranging ungulates, suggesting that they have the ability to play a role in regulating populations (Gulland, 1992; Stein et al., 2002), but more research would be necessary to link parasitism to hartebeest declines.

While *Paramphistomum* spp. eggs are typically found in a wide range of ungulates (Dunn, 1978; Ocaido et al., 2004), this trematode was only found in buffalo in OPC. *Paramphistomum* spp. requires an intermediate aquatic or amphibious gastropod host to complete its life cycle (Kilani et al., 2010), and requires a wet environment with more standing water than offered by the semi-arid ecosystem of OPC. Unlike the smaller-bodied species in this study, buffalo frequently wallow for thermoregulation (Ayeni, 1975) and are often found grazing in marshy habitats within OPC.

Grazing in marshy areas likely increases their exposure to water-borne parasites such as *Paramphistomum* spp. (Penzhorn, 2000).

Buffalo are considered to play a significant role in disease epidemiology at the wildlife–livestock interface, especially in the maintenance, amplification and spread of several economically important diseases, such as foot and mouth disease, bovine tuberculosis, bovine brucellosis and theileriosis (Kock, 2005; Michel and Bengis, 2012). They also harbor diverse enteric helminthes and protozoa (Penzhorn, 2000; Taylor et al., 2013). However, buffalo stand out among OPC ungulates in that they were the only host species that did not share any parasite taxa with other host species beyond strongyles (Fig. 4b). Strongyle-type eggs are produced by a rich group of nematodes that infect multiple wild and domestic hosts. Without the inclusion of strongyle genera, it is difficult to fully account for the potential role of buffalo in the dissemination of helminths in this system. However, our results suggest that buffalo at OPC may play a limited role in the spread of the other helminths observed in this study. This parallels results from a study on *Escherichia coli* transmission patterns in OPC (VanderWaal et al., 2014b), which showed that buffalo tended to share few genotypes of this fecal–oral bacterium with other ungulate species.

Host species frequently found together in mixed-species aggregations were significantly more likely to share the same parasites (Figs. 3–4). Indeed, species pairs observed associating in >7.5% of observations (maximum 14.2%) shared nearly half their parasite taxa on average, while the maximum association strength among pairs with no shared parasite taxa beyond strongyles was 3.2%. Even though the list of helminth genera identified could have been greatly enhanced by differentiating strongyle-type nematode eggs to the genus level, our metric of parasite sharing serves as a useful indicator for demonstrating relative differences in parasite sharing across species with varying levels of spatiotemporal contact. It seems reasonable that other helminth genera with similar transmission modes, such as strongyles, would be similarly

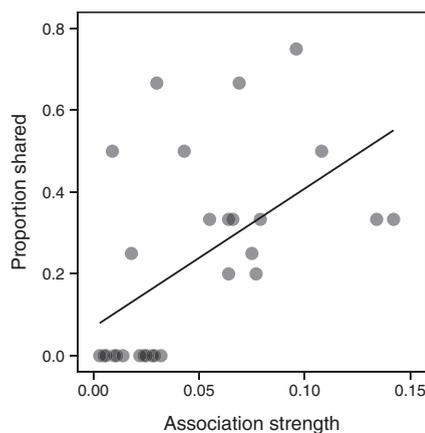


Fig. 5. Effect of association strength between species on parasites shared.

influenced by interspecific contact. Because helminths are environmentally transmitted, the importance of association in determining parasite sharing patterns likely arose from similarity in habitat and space use. Species associating more frequently, and consequently utilizing the same space, were more likely to share helminth taxa (Fig. 5). Similarly, interspecific association patterns were correlated with cross-species transmission of *E. coli* (VanderWaal et al., 2014b). In addition, Ezenwa (2003) showed that parasite richness per individual was higher in areas utilized by a greater number of ungulate species, suggesting a strong role of habitat overlap in facilitating cross-species transmission of parasites. Thus, spatial contact patterns, which are mediated in part by mixed-species aggregations, are crucial for understanding the risk of transmission among ungulate species.

This study provides meaningful data about helminth infection dynamics at the wildlife–livestock interface. Such data is critical for minimizing transmission risk for cattle, enhancing wildlife conservation efforts at a local level, and providing baselines to which we can measure the impacts of anthropogenic and climate change. Livestock losses to disease are approximately twice as high as those to predation, and disease accounts for 81% of cattle mortality in some districts of Kenya (Mizutani et al., 2005). Tolerance of livestock owners toward wildlife is intimately linked to the perceived economic costs, especially in areas such as East Africa where pastoralism dominates. Thus, uncertainties about disease threats posed by wildlife can seriously erode the good will of livestock stakeholders toward conservation if wildlife are perceived, correctly or erroneously, as a source of disease (Simonetti, 1995; Cleaveland et al., 2005). In this study, we show that there likely are substantial opportunities for cross-species transmission of helminth parasites, and that variation in levels of heterospecific contact should be considered when assessing the risk of helminth infections for a single host population. From a livestock management perspective, avoiding close proximity between cattle herds and wildlife may minimize the sharing of helminth taxa across the wildlife–livestock interface. While interspecific transmission of helminths may ultimately be the consequence of shared space use, our results suggest that mixed-species aggregations play a

role in determining levels of parasite sharing, or at least are a useful proxy for estimating helminth transmission risk.

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