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SEASONAL AND DEMOGRAPHIC FACTORS INFLUENCING GASTROINTESTINAL PARASITISM IN UNGULATES OF ETOSHA NATIONAL PARK

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ABSTRACT: Host-parasite dynamics can be strongly affected by seasonality and age-related host immune responses. We investigated how observed variation in the prevalence and intensity of parasite egg or oocyst shedding in four co-occurring ungulate species may reflect underlying seasonal variation in transmission and host immunity. This study was conducted July 2005–October 2006 in Etosha National Park, Namibia, using indices of parasitism recorded from 1,022 fecal samples collected from plains zebra (*Equus quagga*), springbok (*Antidorcas marsupialis*), blue wildebeest (*Connochaetes taurinus*), and gemsbok (*Oryx gazella*). The presence and intensity of strongyle nematodes, *Strongyloides* spp. and *Eimeria* spp. parasites, were strongly seasonal for most host-parasite combinations, with more hosts infected in the wet season than the dry season. Strongyle intensity in zebra was significantly lower in juveniles than adults, and in springbok hosts, *Eimeria* spp. intensity was significantly greater in juveniles than adults. These results provide evidence that acquired immunity is less protective against strongyle nematodes than *Eimeria* spp. infections. The seasonal patterns in parasitism further indicate that the long dry season may limit development and survival of parasite stages in the environment and, as a result, host contact and parasite transmission.

Key words: *Antidorcas marsupialis*, *Connochaetes taurinus*, *Eimeria*, *Equus quagga*, *Oryx gazella*, parasite intensity, parasite prevalence, Strongylida.

INTRODUCTION

Host-parasite dynamics can be strongly affected by seasonality and age-related host immune responses (Cattadori et al., 2005; Altizer et al., 2006; Cornell et al., 2008). Seasonal environmental changes can influence transmission rates of gastrointestinal parasites by affecting the development and survival of parasites in the environment and host contact with infectious free-living parasites (Stromberg, 1997). Synchrony in host parturition concentrates young at times of resource abundance (Sinclair et al., 2000) adding a seasonal pulse of susceptible, immunologically naïve hosts to the population (Altizer et al., 2006). Host immunity may also vary seasonally in relation to changes in reproduction, stress, nutrition, and photoperiod (Martin et al., 2008).

We focus on two groups of directly transmitted, orally ingested parasites, the strongyle nematodes (Nematoda: Strongylida; hereafter "strongyle nematodes") and *Eimeria* spp. coccidia (Apicomplexa: Eimeriidae). Both of these parasite groups are generally pathogenic and responsible for widespread production losses in livestock (Bowman, 2003). Strongyles are often generalist with respect to hosts, able to infect multiple phylogenetically close host species (Zaffaroni et al., 2000; Matthee et al., 2004), whereas *Eimeria* tend to specialize on a single host species (Fayer, 1980). Hosts can acquire protective immunity that is specific to a particular *Eimeria* species (Yun et al., 2000). In contrast, host immune responses against gastrointestinal nematodes are more effective in preventing establishment of invading larval stages than in clearing adult nematode burdens. Once established, these relatively long-lived parasites are able to successfully evade the host's immune system by modulating and regulating the immune response in their favor (Hayes et al., 2004; Maizels et al., 2004).

Seasonal changes in humidity and temperature have a strong effect on the development and survival of parasites in the environment. In a generalized life cycle for strongyle nematodes, eggs excreted with feces undergo early-stage larval development in the fecal pellets, after which the infectious third-stage larvae migrate onto vegetation, seeking foraging hosts. Development to the third-stage larva is dependent on temperature and humidity, with increasing temperature and humidity generally associated with faster development and more eggs developing, but with upper and lower thresholds for both factors (O'Connor et al., 2006). First- and second-stage larvae are highly susceptible to desiccation (Nielsen et al., 2007), and although third-stage larvae have a cuticle to protect against desiccation, their movement requires a continuous film of moisture on the vegetation (O'Connor et al., 2006). The survival of third-stage larvae is greatly reduced in tropical conditions where larvae are exposed to high temperatures or prolonged dry periods (Banks et al., 1990; O'Connor et al., 2006; Nielsen et al., 2007). After ingestion, third-stage strongyle larvae encyst in the mucosal wall of the gut, develop into fourth-stage larvae, and excyst into the lumen or mucosal epithelium and develop into adult nematodes. There is variation from this generalized life cycle depending on the species of strongyle. For example, the third- and fourth-stage larvae of *Strongylus* spp. in equids migrate through host tissue before returning to the gut and reaching maturity (Anderson, 2000).

When sporulated *Eimeria* oocysts are ingested by a host, the sporozoites excyst and enter epithelial cells of the small intestine, initiating an asexual reproductive cycle and infecting new host cells in each cycle (Fayer, 1980). A sexual phase also occurs in the epithelial cells producing the unsporulated oocyst, which is excreted in fecal matter. In the environment, sporulation of oocysts is enhanced by warm temperatures and humidity, and moisture is the key limiting factor in the survival of sporulated oocysts in the environment (Fayer, 1980).

In this study we examine seasonal, age-, and sex-related variation in gastrointestinal parasite prevalence and propagule-shedding intensity in an assemblage of four herbivorous mammals utilizing a shared habitat in Etosha National Park, Namibia. We use "propagule" as a generic term for the reproductive output of a parasite released into the environment, including eggs from nematodes and oocysts from coccidia. We define "prevalence" as the proportion of individuals examined that are shedding parasite propagules in feces and "intensity" as the estimated number of parasite propagules shed per gram of feces by infected individuals. Prevalence is an estimate of how common a parasite is in a host population at a particular period and intensity is an estimate of an individual's ability to control infection given that parasites are present and actively reproducing. Both prevalence and average intensity measures are needed to estimate propagule input into the environment, an essential step toward understanding seasonal variation in host-parasite contact and transmission rates.

We expected to see a strong relationship between parasite prevalence or intensity and season. In a subtropical, semiarid environment, humidity may be the limiting factor for *Eimeria* or strongyle transmission, as dry conditions restrict development and reduce survival of propagules in the environment and prevent larval movement (Fayer, 1980; Banks et al., 1990; O'Connor et al., 2006; Nielsen et al., 2007). If acquired immunity limits parasitism in hosts, we expected to see a reduction in parasite prevalence or intensity with host age, because immunity modulates infection in the most highly parasitized individuals and reduces susceptibility of older hosts (Woolhouse, 1992). As an acquired immune response

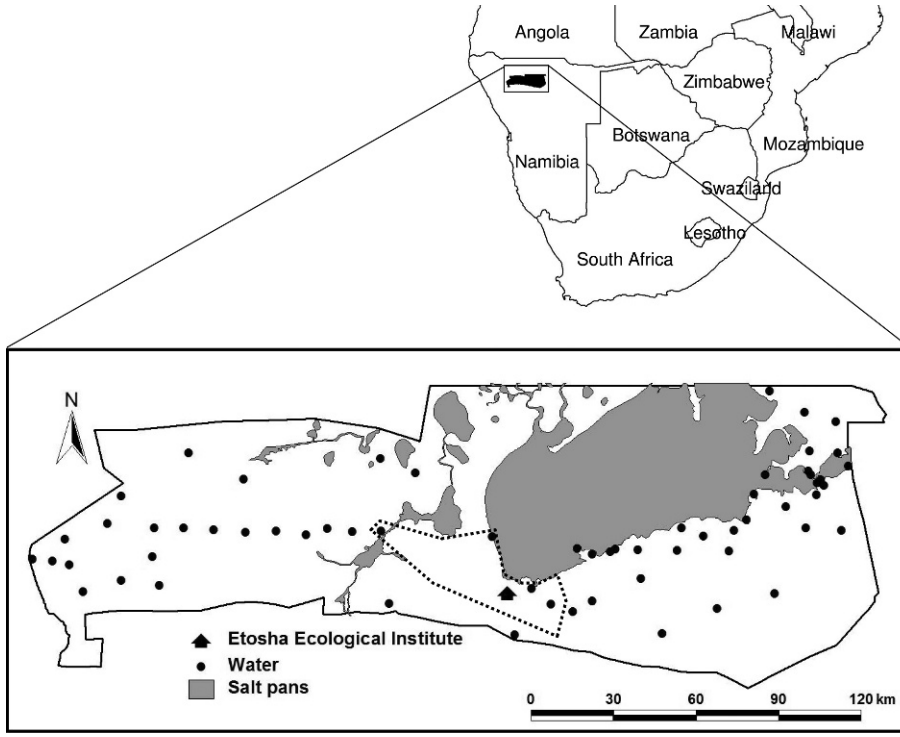

FIGURE 1. Etosha National Park, northern Namibia. Perennial watering points (springs or boreholes) are shown with black circles. Study area, located around the Etosha Ecological Institute, is outlined with dotted line.

against *Eimeria* spp. is observed in other host species (Yun et al., 2000), we predicted that juvenile hosts would have greater *Eimeria* spp. presence and oocyst shedding intensity than adult hosts. In contrast, host-acquired immunity is less effective at controlling strongyle nematode infections (Hayes et al., 2004; Maizels et al., 2004), and therefore we predicted that strongyle presence and intensity would increase with host age. If differences in parasite prevalence or intensity occur by host sex, we expected males to have higher parasitism than females, a pattern often found in other host-parasite systems (Poulin, 1996; Zuk and McKean, 1996).

MATERIALS AND METHODS

Study site

Etosha National Park is a 22,915 km^2 reserve in northern Namibia between 18°30′–19°30′S and 14°15′–17°10′E (Fig. 1). Etosha contains a 4,760 km^2 salt pan, remnant of a palaeolake (Hipondoka et al., 2006). The only perennial water comes from point water sources, including boreholes and artesian or contact springs (Auer, 1997). The mean annual rainfall (±standard deviation) at Okaukuejo station in the center of the park was 384±139 mm from 1934 to 2006. Rainfall is strongly seasonal and unimodal, with most rain falling between November and April, and peak rainfall in January and February (Fig. 2). Although the rainfall season can begin as early as September, rainfall sufficient to facilitate significant grass growth generally occurs in January or February (du Plessis, 2001). Beyond rainfall, precipitation in the form of dew does occur in immeasurable amounts (<0.1 mm) for up to 4 wk after cessation of the rains (Berry, 1980). The mean monthly temperatures range from lows of 25 C maximum and 6 C minimum in June and July to highs of 34–35 C maximum in October–December and minimums of around 18 C November–February (Fig. 2).

The vegetation in Etosha is classified as arid savanna (Huntley, 1982). The focal area for this study was the Okaukuejo plains (Fig. 1)

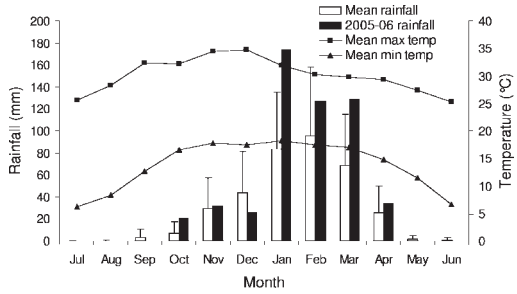

FIGURE 2. Mean monthly rainfall and temperature minima and maxima from Okaukuejo station in central Etosha National Park, Namibia. Rainfall values include the mean and standard deviation of monthly rainfall records from July 1953 to June 2008, and the monthly values recorded for the rainfall year (July 2005–June 2006) during this study. Temperature data are averages of daily minimum and maximum recordings, 1974–1978 (Berry, 1980).

that surround the Etosha pan and comprise extensively grazed, short grassland, and dwarf shrub savanna. The dominant grasses are *Enneapogon desvauxii*, *Aristida adscensionis*, and *Eragrostis nindensis*, and the dominant dwarf shrubs are *Leucosphaera bainesii*, *Cyathula hereroensis*, *Monechma tonsum*, *Monechma genistifolium*, and *Petalidium englerianum* (le Roux et al., 1988). This extensive grassland habitat is flanked by mopane (*Colophospermum mopane*) treeveld, but includes stands of woody plants, including *Acacia nebrownii*, *Acacia tortilis*, *Acacia mellifera*, *Acacia reficiens*, *Catophractes alexandri*, *Aloe littoralis*, and *Albizia anthelmintica* (le Roux et al., 1988).

Host species

We focused on four species of herbivores that commonly utilize the grassland and dwarf shrub savanna habitats of Etosha. These species are springbok (*Antidorcas marsupialis*), plains zebra (*Equus quagga*, previously *Equus burchelli*), gemsbok (*Oryx gazella*), and blue wildebeest (*Connochaetes taurinus*). Park-wide population estimates (with 95% confidence intervals all rounded to the nearest 100) for these species in 2005 were 15,600 (13,200–17,900) for springbok, 13,000 (10,900–15,000) for zebra, 5,700 (5,000–6,400) for gemsbok, and 4,200 (3,000–5,500) for wildebeest (Namibian Ministry of the Environment and Tourism, unpubl. aerial survey data). Zebra are nonruminants in the family Equidae, and the other species are ruminants in the family Bovidae. Zebra and wildebeest are mainly grazers with a diet composed of 92% and 90% grass, respectively (Sponheimer et al., 2003; Codron et al., 2007). Springbok and gemsbok consume a mix of browse and grass, although the diet of gemsbok has far more grass than the diet of springbok, with 81% vs. 23% grass in the diet, respectively (Sponheimer et al., 2003; Codron et al., 2007). The timing of parturition in Etosha is strongly seasonal in wildebeest and springbok (birth peaks occurring in January), somewhat seasonal in zebra (births mostly occurring between December and April), and largely aseasonal in gemsbok, where births occur throughout the year with peak activity in April–December (Gasaway et al., 1996).

Sample collection

Gastrointestinal parasitism was evaluated from examination of fecal material collected between July 2005 and October 2006, for a total of 1,022 fecal samples for parasitological analysis from the four ungulate species. Collecting periods were July–August 2005 and February–October 2006. We collected 403 samples from zebra, 384 from springbok, 133 from wildebeest, and 102 from gemsbok. Fecal collection was focused in the first week of each month, with our aim a target of 40 samples/month from each host species. We collected an average of 37 samples/month from zebra and 35 samples/month from springbok. Gemsbok and wildebeest have lower population sizes than zebra and springbok, and sampling these species was difficult. As a consequence we collected an average of 12 samples/month from wildebeest and 9 samples/month from gemsbok.

Each month we spread the sampling effort across the study area, in order to collect a representative sample of hosts and to avoid resampling of individuals. In the collecting period of each month, we drove all the roads and visited a different water hole each day without repetition, as much as possible, searching for animals to sample. Within this sampling regime, we observed all individuals of our study species that were within approximately 100 m of the road. We only collected feces between 7:00 AM and 1:00 PM to reduce potential bias introduced through daily variation in parasite-shedding rates (Ezenwa, 2003; Villanúa et al., 2006). Although group size is a common factor associated with parasitism, the effect of group size is greatest for host-specific parasites and for host species living in stable groups (Ezenwa, 2004). In Etosha animals often congregate in large associations around water or moving toward water, making group sizes variable and difficult to define. We

therefore did not include group size as a factor in our study.

The age and sex composition of each host population changes throughout the year with seasonal birth pulses and likely through varied effects of predators or disease on the different age classes or sexes, and we did not have prior data on these factors to support stratified sampling by age or sex. Therefore we assumed that rates of defecation would not vary among age classes and that the individuals sampled would be roughly in proportion to the population age structure. We also assumed that there was an approximate 1:1 sex ratio, and if we collected few individuals from a particular sex within an age class, we targeted sampling to collect equivalent numbers between the sexes within each age class. As three of the study species sexually segregate into breeding and bachelor herds, attention to sex distribution was important when sampling different group types. There are limitations to this sampling regime, but it was the least biased approach that we could take without prior data on population composition and dynamics of the study species.

We used binoculars to watch individuals defecate, recorded the locations of feces, and then collected a homogenized subsample of the feces within 10 min of deposition. For each fecal sample collected we recorded the date, time, species, sex, and age of the defecator. Age was assessed in three categories: juveniles were <1 yr, yearlings 1–2 yr, and adults 2+ yr old. Age and sex were determined via horn growth and morphology and genitalia for springbok (Rautenbach, 1971), wildebeest (Atwell, 1980), and gemsbok (Dieckmann, 1980). Zebra age and sex were assessed based on relative size, pelage, and genitalia (Smuts, 1975, 1976).

Parasitological analysis

Fecal samples were evaluated for GI parasites within 48 hr of collection using a modification of the McMaster method for fecal egg counts (Food and Agriculture Organization, 2005), a commonly used noninvasive method for quantifying parasitism (Bowman, 2003). Four grams of homogenized fresh fecal matter was combined with 56 ml of a saturated salt (NaCl) solution (specific gravity 1.2), large plant debris were removed via a tea strainer, and a separate homogenized aliquot of the filtrate was added to each chamber on a McMaster slide. The slide was left to stand 5 min to allow the eggs and oocysts to float to the surface. The number of eggs or oocysts observed in the two chambers using a compound microscope was added together and multiplied by 50 to calculate the number of eggs or oocysts per gram of feces.

Fecal egg counts provide a nonlethal means for estimating relative nematode burdens among hosts (Stear et al., 1995; Seivwright et al., 2004), although the relationship between the fecal egg count and the actual nematode burden in the host is generally unknown, particularly for wildlife species (Wilson et al., 2001). Fecal egg or oocyst counts provide an accurate measurement of how the input of parasite propagules into the environment varies in relation to factors of interest. In a prior study we assessed the influence of variation in fecal water content on fecal egg counts (Turner et al., 2010) because fecal water content can vary substantially between seasons, particularly for ruminants. Although fecal water content varied significantly between seasons and among age classes, it had no effect on model outputs of seasonal and age-related patterns in strongyle intensity (Turner et al., 2010).

Fecal flotation techniques are best for recovery of nematode and cestode eggs and protozoan cysts from feces, but fail to recover trematode eggs or nematode larvae (Bowman, 2003). The parasite groups observed in this study included nematodes in the order Strongylida and the genus *Strongyloides*, coccidia in the genus *Eimeria*, and cestodes in the family Anoplocephalidae. The strongyle nematodes, *Eimeria* spp., and cestodes are orally ingested, with direct transmission for the nematodes and *Eimeria* spp. and via accidental ingestion of the intermediate arthropod host for the anoplocephalids (Bowman, 2003). *Strongyloides* spp. are facultative parasites that are transmitted through ingestion of milk, transplacentally, or through penetration of host skin (Anderson, 2000). Although little is known about the effects these parasites have on wild hosts, *Strongyloides* spp. and anoplocephalid infections are often asymptomatic in domestic animals. The strongyle nematodes and coccidia are pathogenic and responsible for widespread production losses in livestock (Bowman, 2003).

We chose to be conservative in our assignment of the observed parasite eggs or oocysts to taxonomic groupings, to avoid identification errors. We therefore did not attempt to differentiate the strongyle nematode eggs. We also did not distinguish cestode eggs beyond the level of family Anoplocephalidae, although equids are commonly infected by *Anoplocephala* spp. and ruminants by *Moniezia* spp. We observed a variety of *Eimeria*

oocysts in this study but did not distinguish beyond genus because the oocysts did not match any of the published records of *Eimeria* from these host species and appear to be undescribed species (Turner, 2009).

Although we kept the strongyle nematode grouping at the order Strongylida, strongyles of ruminant hosts are generally those of the family Trichostrongylidae, whereas strongyles of equid hosts are generally the family Strongylidae. In our study system, Krecek et al. (1987) necropsied plains zebra and recovered 14 species of strongyles from seven genera. The most abundant nematodes recovered were the small strongyles, Cyathostominae, although the large strongyles (mainly *Craterostomum acuticaudatum*) were also present in all hosts examined (Krecek et al., 1987). We are not aware of any studies conducted in Etosha on parasites of the other host species, but studies in other systems demonstrate that the diversity of strongyle parasites in springbok, wildebeest, and gemsbok is diverse and overlapping (Round, 1968; Horak et al., 1982; Horak et al., 1983; De Villiers et al., 1985; Boomker et al., 1986; Boomker et al., 2000).

Data analysis

We quantified parasitism based on the presence or absence of parasites in individual hosts and the intensity of parasite propagule counts. Our definitions for prevalence—the proportion of individuals examined who were infected—and intensity—the estimated number of parasite propagules from infected individuals only—are as defined by Margolis et al. (1982). Peaks in parasite shedding lag behind rainfall peaks by 1–2 mo (Turner, 2009), so we defined the seasons based on peak periods in parasitism and not rainfall. Therefore, for this study the wet season was January–May, and the dry season was June–October.

Statistical analyses of parasite presence were done using logistic regression with season, age, and sex as independent variables. Analyses of parasite intensity were done using generalized linear models with a negative binomial error distribution and log link function and season, age, and sex as independent variables. Because of low numbers of juvenile or yearling wildebeest and gemsbok sampled, we combined these two categories and evaluated age patterns in parasite prevalence with a two-class distinction. We did not analyze parasite intensity for these species because the sample size of infected individuals was deemed too low for statistical examination of the counts in positive individuals. For parasite intensity estimates, we reported the mean and standard error of the $\log_{10}$-transformed counts. Where parasite prevalences were reported, we included 95% binomial confidence intervals based on the sample sizes examined. Statistical analyses and confidence intervals were computed using the MASS and epitools packages in R 2.7.0 (R Development Core Team, 2008).

RESULTS

Parasite prevalence in the plains ungulates

We observed four types of parasites: strongyle nematodes, *Strongyloides* spp. nematodes, coccidia in *Eimeria* spp., and Anoplocephalid cestodes. The prevalence of Anoplocephalid cestodes was below 5% for all host species (prevalence and 95% CI: zebra, 4% [2–6%]; springbok, 2% [1–3%]; wildebeest 3% [1–8%]; gemsbok 0% [0–4%]), so these parasites were not considered for statistical analyses. We also did not statistically analyze *Strongyloides* spp. in zebra or wildebeest because of low prevalence, and we found no *Eimeria* spp. in zebra.

The presence of strongyles, *Strongyloides* spp., and *Eimeria* spp. parasites was strongly seasonal for most host-parasite combinations, with more hosts infected in the wet season than the dry seasons (Table 1). Unlike the bovid species, zebra showed no statistical difference between seasons in the occurrence of strongyle nematodes, and very high prevalence (>98%) in both seasons (Fig. 3). Springbok showed high prevalence (>89%) in the wet season for the three parasite types considered and large differences in prevalence between wet and dry seasons (Fig. 3).

Eimeria spp. occurred significantly more in younger animals than adults for gemsbok and wildebeest but not springbok (Table 1). We detected no significant age-related patterns in strongyle presence in the three bovid species (Table 1). Strongyle prevalence in zebra was very high at 98.5%. Of the six zebra that were negative for strongyles, five were juveniles, and one was an adult female. *Strongyloides* spp. presence in springbok was significantly

TABLE 1. Relationships between parasite presence or intensity and season, host age, and sex for four host species in Etosha National Park, Namibia, July 2005–October 2006.

				Season (wet)[a]		Age (yearling)[b]		Age (adult)[b]		Sex (male)[c]	
Host species	Data type	Parasite type	*n*	β(SE)	*P*	β(SE)	*P*	β(SE)	*P*	β(SE)	*P*
Zebra	Intensity	Strongyles	367	0.58(0.07)	***	0.27(0.13)	*	0.22(0.10)	*	0.13(0.07)	ns
Springbok	Presence	Strongyles	377	3.3(0.6)	***	0.32(0.39)	ns	0.28(0.30)	ns	0.53(0.25)	*
	Intensity	Strongyles	267	1.3(0.1)	***	−0.39(0.20)	ns	−0.05(0.16)	ns	−0.24(0.13)	ns
	Presence	*Strongyloides*	377	3.5(0.4)	***	−0.25(0.41)	ns	−0.62(0.31)	*	0.39(0.27)	ns
	Intensity	*Strongyloides*	170	1.3(0.2)	***	−1.4(0.2)	***	−1.1(0.2)	***	0.02(0.16)	ns
	Presence	*Eimeria*	377	3.4(0.4)	***	−0.08(0.39)	ns	−0.38(0.25)	ns	−0.002(0.249)	ns
	Intensity	*Eimeria*	200	2.4(0.2)	***	−1.2(0.3)	***	−1.0(0.3)	***	−0.14(0.21)	ns
Wildebeest	Presence	Strongyles	90	2.6(0.8)	**			0.58(0.77)	ns	−0.66(0.50)	ns
	Presence	*Eimeria*	90	0.28(0.54)	ns			−2.0(0.7)	**	−0.68(0.50)	ns
Gemsbok	Presence	Strongyles	90	2.3(0.5)	***			−1.1(1.2)	ns	0.45(0.58)	ns
	Presence	*Strongyloides*	90	3.2(1.1)	**			−0.77(1.01)	ns	1.5(0.65)	*
	Presence	*Eimeria*	90	−0.77(0.55)	ns			−2.5(0.9)	**	−0.07(0.58)	ns

[a] Positive β estimates for season implies these parasite values (presence or intensity) are higher in wet than dry season.

[b] Each age class was contrasted against the youngest age class; a positive β value for age implies that parasitism is higher in the age class tested (yearlings or adults) than in juveniles.

[c] A positive β value implies that parasitism is higher in males than in females. Because of low sample size of positive individuals, we did not assess intensity for gemsbok or wildebeest, and we grouped juveniles and yearlings into one age class for assessing presence relationships.

*** $P<0.001$, ** $P<0.01$, * $P<0.05$, ns = nonsignificant.

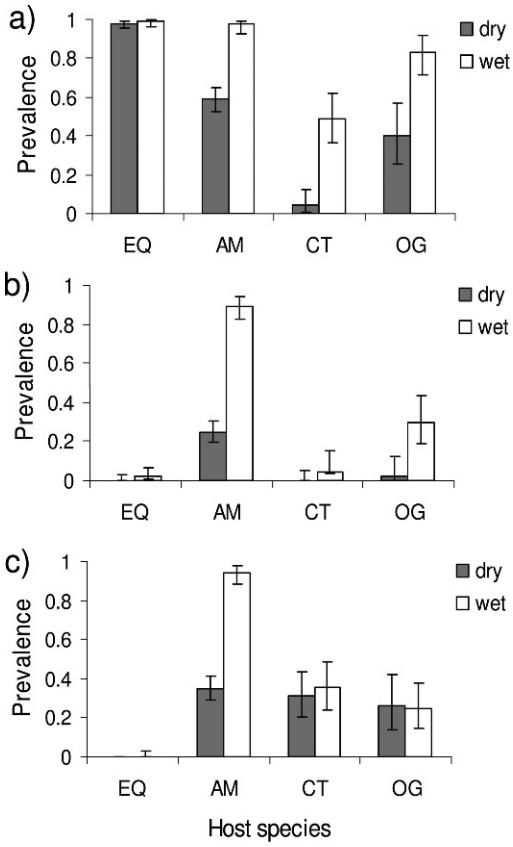

FIGURE 3. Seasonal differences in parasite prevalence in the four host species for (a) strongyle nematodes, (b) *Strongyloides* spp., and (c) *Eimeria* spp., Etosha National Park, Namibia, July 2005–October 2006. Host species abbreviations used are EQ = zebra (*Equus quagga*), AM = springbok (*Antidorcas marsupialis*), CT = wildebeest (*Connochaetes taurinus*), and OG = gemsbok (*Oryx gazella*). Prevalences are shown with 95% confidence intervals based on sample sizes. Even with a recorded prevalence of zero, we included a confidence interval of the prevalence estimate because we cannot with certainty confirm the absence of the parasite in the entire host population based on a subsample.

lower in adults than juveniles, and we found no significant difference between age classes in gemsbok (Table 1).

Strongyle presence was significantly higher in male than female springbok (prevalence and 95% CI: males=75% [68–81%], females=68% [61–75%]; Table 1). *Strongyloides* spp. was significantly more prevalent in male than female

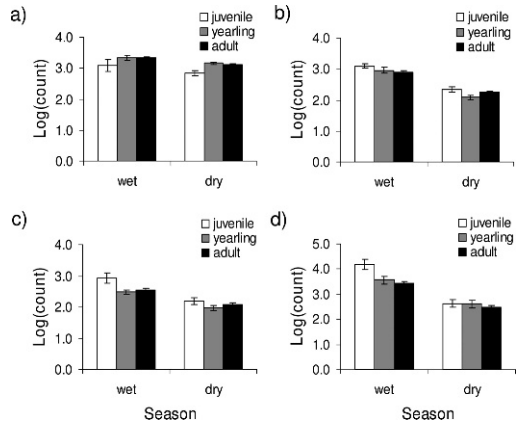

FIGURE 4. Parasite intensity by age class and season for (a) strongyle nematodes in zebra, (b) strongyle nematodes in springbok, (c) *Strongyloides* spp. in springbok, and (d) *Eimeria* spp. in springbok, Etosha National Park, Namibia, July 2005–October 2006. The mean and standard error of the log(counts) of parasite propagules for positive individuals are presented.

gemsbok (*Strongyloides* prevalence and 95% CI: males=32% [16–52%], females=15% [7–26%]; Table 1). There were no statistically significant patterns with sex observed for any other host-parasite combinations.

Parasite intensity in zebra and springbok

Parasite intensities in springbok and zebra were significantly higher in the wet season than the dry season for all parasite types examined (Table 1; Fig. 4). Strongyle intensity in zebra was significantly lower in juveniles than in yearlings or adults (Table 1; Fig. 4). In springbok, however, there were no statistically significant patterns in strongyle intensity with host age. The intensities of both *Eimeria* spp. and *Strongyloides* spp. infections in springbok were significantly higher in juveniles than yearlings or adults (Table 1; Fig. 4). There were no significant patterns in parasite intensity by host sex for any host-parasite combinations.

DISCUSSION

The seasonal patterns in parasitism indicate that the long dry season may limit

development and survival of parasite stages in the environment and, as a result, host contact and parasite transmission. We also found evidence of strong protective immunity against *Eimeria* spp. and *Strongyloides* spp., and a weaker immune response against strongyle nematodes.

The observed seasonal differences in parasite prevalence and intensity suggest a strong reduction in parasite transmission in dry seasons, from both environmental and host immune mechanisms. First, humidity is required for successful development and survival of parasite stages and movement of larval nematodes in the environment (Fayer, 1980; Banks et al., 1990; O'Connor et al., 2006; Nielsen et al., 2007). Rainfall may be the main constraining factor affecting parasite dynamics in semiarid systems by severely limiting transmission (Chiejina et al., 1989). In a semiarid area of Mauritania, Jacquiet et al. (1995) found that young goats born during the dry season were free from GI nematode infections until the following rainy season, indicating a lack of transmission. The rainfall and temperature patterns in Etosha may limit parasite transmission for up to 6 mo of the year. Increased parasitism in the wet season may be due to a resumption of parasite transmission, or parasite activity in the case of arrested strongyle larvae. Additionally, the pulse of newborn immunologically naïve hosts during the wet season increases the number of susceptible hosts.

Second, during the dry season hosts are shedding far fewer parasite propagules into the environment than during the wet season, leading to strong seasonal differences in the amount of potentially infectious material input to the environment. Factors that may reduce propagule-shedding rates include host immune response or, for nematodes, density-dependent effects reducing individual nematode fecundity. Immune responses against adult nematodes can include constraints on adult nematode size, which reduces fecundity (Rowe et al., 2008), loss of the vulvar flap in female nematodes, or expulsion of adult nematodes (Balic et al., 2000).

Examination of how parasitism changes with host age can provide insight into the existence of host-acquired immunity and age-dependent variation in host exposure (Woolhouse, 1992). The relatively coarse assessment of host age, particularly for the adult age class, limits the scope of our analysis of the age structure; however, the comparison of juveniles to adults provides insight into the potential for acquired immunity in this system. In springbok hosts, *Eimeria* spp. prevalence was not significantly related to host age, but *Eimeria* spp. intensity was significantly greater in juveniles than adults. This implies that contact with sporulated oocysts may be similar for each age class, but that juvenile hosts have not yet acquired an immune response to control the intensity of their *Eimeria* spp. infections, as have the older age classes. Strongyle intensity in zebra was significantly lower in juveniles than adults, and there was no significant age pattern in strongyle intensity in springbok. This indicates, as we expected, that acquired immunity is less protective against strongyle nematodes than *Eimeria* spp. infections. Adult nematodes are relatively long-lived, and once an adult strongyle population or community is established, the host may not clear the worm burden easily (Hayes et al., 2004; Maizels et al., 2004).

Sex differences in parasite prevalence or intensity are observed commonly, with males of many species exhibiting higher parasitism than females (Poulin, 1996). A sex bias in parasitism may be due to ecologic, behavioral, or physiologic differences between males and females (Zuk and McKean, 1996). The only sex differences in parasitism observed were in the prevalences of strongyle nematodes in springbok and *Strongyloides* spp. in gemsbok, with males of each species significantly more likely to have the parasite than

females. We did not observe sex differences in the prevalence or intensity of *Eimeria* infections, but this could be because of the strong age-related patterns where *Eimeria* infections are concentrated in juvenile hosts, the age class least likely to show variation between the sexes.

In contrast to the bovid species, zebra strongyle infections retained a high prevalence across seasons and had a much smaller effect size in the seasonal differences in strongyle intensity. This marked variation in the seasonality of strongyle parasitism among host species could be a result of differences in the longevity of strongyle nematodes infecting equid versus bovid hosts, or host species differences in parasite contact, susceptibility, or immune function, or a combination of factors. Zebra and the bovid species vary in their digestive physiology, feeding ecology, body size, and population density, factors that may affect rates of contact with parasites in the environment. Further research into host ecology, immune function, and parasite diversity would be required to distinguish which of these factors contribute to the observed interspecific differences in strongyle parasitism.

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