Journal of Helminthology (2006) **80**, 213–218 DOI: 10.1076/JOH2006343

Patterns of gastrointestinal parasitic infections in the bushbuck *Tragelaphus scriptus* from the Queen Elizabeth National Park, Uganda

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Abstract

Seasonal, host sex and age-related variations in helminth egg and coccidian oocyst counts were investigated in a naturally infected wild bushbuck (*Tragelaphus scriptus*) population in Queen Elizabeth National Park, western Uganda from April 2000 to February 2002. The prevalence and mean intensity quantified as the number of eggs and oocysts per gram of faeces were taken as a measure of parasite burdens. Host sex and age-related differences in prevalence values were not found but the overall prevalence of *Eimeria* sp. was significantly higher during the rainy season, and peak counts were recorded either during or soon after a peak rainfall. A similar trend was observed for *Moniezia* spp., although the results were marginally not significant. There were also no significant differences in mean intensity values, relative to host sex, age or season.

Introduction

Wild animals can harbour heavy parasite burdens but in many cases no symptoms of disease are observed. This could be indicative of the balance between the host and parasites, which has been achieved as a result of their co-evolution (e.g. Sachs & Sachs, 1968; Carius *et al.*, 2001; Legendre *et al.*, 2002). However, a number of factors, including growth, senility, changes in climatic conditions, malnutrition, concurrent infection with other pathogens, pregnancy and lactation, conditions that result in general stress, can disrupt this balance (Crofton, 1957; Woodford, 1976; Dunn, 1978).

For domestic sheep and cattle it has been shown that host sex, age and season are factors that affect the outcome of infections with gastrointestinal tract parasites (Crofton, 1957; Michel, 1976; Dunn, 1978; Armour, 1980). Sub-clinical parasite loads in wild ungulates have been largely neglected (Gunn & Irvine, 2003), but a few authors have described the effects of season, host sex and age on internal parasite burdens (Halvorsen, 1986; Halvorsen *et al.*, 1999; Irvine *et al.*, 2000). However, such studies have so far only been carried out on wild herbivores in the Arctic. Studies on gastrointestinal tract parasitism in African ungulates have focused so far on qualitative and taxonomic investigations (Mönnig, 1933; Liang-Sheng, 1956; Dinnik *et al.*, 1963; Dinnik & Sachs, 1968; Round, 1968; Boomker *et al.*, 1984), while data on the effect of various environmental parameters on the prevalence and intensity of parasite infections are scarce or absent. For example, only a few studies have provided data on gastrointestinal tract parasite species infecting bushbuck (*Tragelaphus scriptus*; Pullan *et al.*, 1971; Boomker *et al.*, 1984, 1987).

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In the present study, the influence of season, age and sex on the infection of bushbuck (host) with gastrointestinal tract parasites (helminths and a protozoan) in the Queen Elizabeth National Park, Uganda was investigated. Most notably, variation in parasite loads in this species has not yet been studied continuously within one population over an extended period of time. As demonstrated for domestic ungulates, we predicted an increase in parasite burdens (egg and oocyst output) during the wet season, that subadults and juveniles would harbour higher parasite loads than adults and males would show higher egg and oocyst output than females (Crofton, 1957; Michel, 1976; Dunn, 1978; Armour, 1980).

Materials and methods

Study site

The field study was carried out in the Queen Elizabeth National Park (0°10′S to 0°12′S, 29°52′E to 29°54′E), south-western Uganda between April 2000 and February 2002. This area (Mweya peninsula and adjacent mainland), covers approximately 8.7 km^2 and comprises a *Sporobolus pyramidalis* grassland with scattered *Capparis tomentosa/Euphorbia candelabra* thicket clumps (Lock, 1977; Zandri & Viskanic, 1992). The mean annual rainfall during the investigation was 655 mm, with a mean annual temperature of 25.3°C. Wet seasons extend from March to May and from September to December (more than 45 mm rainfall per month). The topography, geology and soil of the park have previously been described by Spinage (1968). Bushbuck populations in the study area experience little human disturbance, and flight distances are low. This made it possible to observe bushbuck at close range and collect fresh faecal samples soon after defecation. Age determination followed criteria described by Simpson (1973) and Wronski (2004).

Faecal collection

A total of 303 faecal droppings obtained from randomly encountered bushbuck were collected soon after defecation. The number of pellets per faecal dropping varied between 12 and 390 and droppings weighed between 3 and 154 g. Faecal samples were collected regardless of the time of the day, at least twice a week over a period of two years, and were either processed directly after collection or preserved in 3% formalin. Only fresh samples were used for the isolation of protozoan oocysts. Preservation in formalin may strongly affect the number of nematode eggs recovered (Foreyt, 1986). However, for statistical analyses, the prevalence of eggs (present or absent in a sample) was used as a (binary) dependent variable (see below). Therefore, potential differences in the absolute number of eggs recovered do not affect the outcome of this analysis. All counts of samples which did contain nematode eggs, however, were done from fresh samples, so that different preservation methods did not affect the outcome of our comparison of parasite intensities (see below).

Isolation, identification and counts of eggs and oocysts

Diverting from Hansen & Perry's (1990) egg counting technique, five grams of faeces were crushed, mixed with 70 ml of 40% 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 and oocysts were identified and counted under a microscope. Counts of each egg or oocyst type from both chambers were summed and multiplied by the factor 50 to calculate the number of eggs and oocysts per gram of faeces (Hansen & Perry, 1990; Zajac, 1994).

The identification of helminth eggs and protozoan oocysts was carried out using keys provided by Barth (1967), Soulsby (1968), Georgi (1990) and Zajac (1994). A list of helminth parasites from the gastrointestinal tract of wild herbivores in the Queen Elizabeth National Park by Woodford (1976) also aided identification. There was a mixed infection by nematodes laying strongyle eggs, the eggs of which were likely produced by species belonging to one of the following families: Trichostrongylidae, Trichonematidae or Ancylostomatidae (e.g. *Haemonchus vegliae*, *Ashworthius pattoni* and *Cooperia* spp.). These parasite types have already been reported for bushbuck from the Queen Elizabeth National Park (Woodford, 1976). Furthermore, *Haemonchus bedfordi*, *Haemonchus contortus*, *Trichostrongylus colubriformis* and *Oesophagostomum columbianum* were reported from other wild bovids in the Queen Elizabeth National Park (Woodford, 1976) and these nematode species parasitize bushbuck in other parts of Africa (Round, 1968; Boomker *et al.*, 1984, 1986, 1987). Therefore, these species were considered potential nematode parasites when strongyle eggs were found in bushbuck in the Queen Elizabeth National Park. Apart from strongyle nematodes, eggs of *Strongyloides* sp. (Rhabditidae) and *Moniezia benedeni* and *Moniezia expansa* (Anoplocephalidae, Cestoda) were counted together with the oocysts of the protozoan, *Eimeria* sp. (Eimeridae, Coccidia, Sporozoa), morphologically resembling *Eimeria bovis* in cattle.

Statistical analyses

In total, 303 faecal samples were analysed. Comparably few animals were infected with either type of parasites (figs 1, 2). Therefore, the prevalence of eggs or oocysts in the faeces (present or absent in the sample) was used for statistical analyses to test the effect of season, and host age and sex on parasite loads. 'Season' (dry (reference level) or wet), 'sex' (female (reference level) or male) and 'age' (adult (reference level) or subadult) were used as factors for logistic regressions for the three parasite types (*Eimeria* sp.: $R^2 = 0.039$, log likelihood $= -78.23$; *Moniezia* spp.: $R^2 = 0.058$, log likelihood $= -53.45$; strongyle nematodes: $R^2 = 0.012$, log likelihood $= -46.72$).

We asked whether those factors which had an effect on the prevalence of certain parasites also influence the intensity of these parasite types. For example, if the factor 'season' had an effect on prevalence values, we tested whether this is also reflected by a greater intensity of this parasite among the infected animals. For this, the mean intensity (mean number of parasite intensities (count per g) for all infected animals)

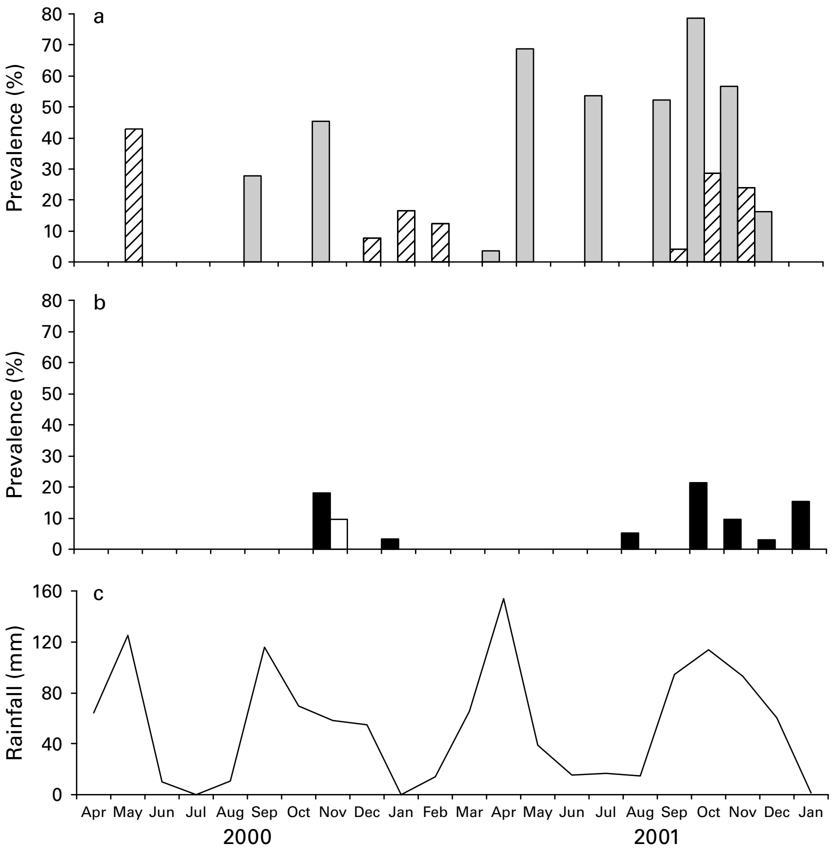

Fig. 1. Seasonal changes in the prevalence (%) of (a) *Eimeria* sp. (▨) and *Moniezia* spp. (▩) and (b) *Strongyloides* sp. (□) and strongyle nematodes (■) in a free ranging bushbuck population from the Queen Elizabeth National Park, Uganda from April 2000 to February 2002. Data were collected continuously, hence, zero values indicate that no parasites were found. Rainfall data (c).

was calculated and compared between wet and dry seasons using non-parametric Mann-Whitney *U*-tests.

Results

Nematode eggs of *Strongyloides* sp. were present in only one sample (an adult male during the wet season with 50 eggs per g faeces). Therefore, only the data for *Eimeria* sp., *Moniezia* spp. and strongyle gastrointestinal tract nematodes were analysed. *Eimeria* sp. and *Moniezia* spp. were the dominant parasites in the bushbuck population. Both were more prevalent during the wet season (fig. 1a). The factor 'season' had a statistically significant influence on the occurrence of *Eimeria* sp., while there was a marginally non-significant effect in *Moniezia* spp. (table 1). Again, strongyle nematodes were more frequent during the wet season (fig. 1b), but no statistically significant seasonal effect was found. However, this parasite type was much less frequent than the other two, so that such a negative finding must be interpreted with caution. There was no statistically significant effect of both host sex and age on either type of parasites (table 1).

The mean intensity of *Eimeria* sp. did not significantly differ between the dry (mean ± SE = 2118.33 ± 1718.98 oocysts per g) and wet seasons (1755.88 ± 859.34 oocysts per g; $T = 59.5$, $P = 0.40$, $n_{dry} = 6$, $n_{wet} = 17$; fig. 2). Likewise, there was no significant difference in the mean intensity of *Moniezia* spp. eggs between the dry (436.36 ± 110.59 eggs per g) and wet seasons (433.33 ± 142.4 eggs per g; $T = 24.5$, $P = 0.82$, $n_{dry} = 3$, $n_{wet} = 11$) nor did the mean intensity of eggs of strongyle nematodes differ between seasons (dry: 70 ± 12.25 eggs per g; wet: 64.29 ± 9.22 eggs per g; $T = 34.5$, $P = 0.76$, $n_{dry} = 5$, $n_{wet} = 7$).

Discussion

The effect of season, host sex and age on the prevalence and intensity of gastrointestinal tract parasitic infections in a wild bushbuck population was analysed and small R^2 values of logistic regressions indicate that regressions explain observed variations only to some extent. For example, the immune status of the bushbuck population may show periodic variation (e.g. Koelle & Pascual, 2004; Koelle *et al.*, 2005), but this factor was not included in the investigation. The prevalence of *Eimeria* sp. was significantly higher in the wet than in the dry season. The same was true for *Moniezia* spp. but

https://doi.org/10.1079/JOH2006343 Published online by Cambridge University Press

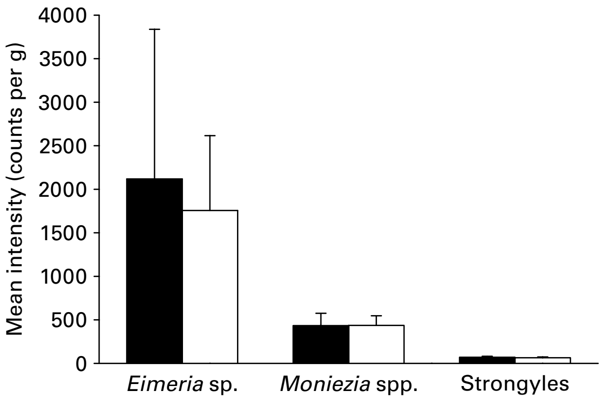

Fig. 2. Seasonal differences (■, dry season; □, wet season) in the mean intensity (± SE) of *Eimeria* sp. (oocysts per g), *Moniezia* spp. and strongyle nematodes (eggs per g) in the faeces of a free ranging bushbuck population from the Queen Elizabeth National Park, Uganda from April 2000 to February 2002.

statistical results were marginally non-significant (table 1). This is in accordance with our predictions. Moisture is known as a major factor enhancing the development, survival and transmission of the infective stages of these parasites (Michel, 1976; Dunn, 1978; Armour, 1980). Moreover, it has been shown that adult female worms release their eggs preferentially when environmental parameters are optimal for the successful survival and development of the eggs (Dunn, 1978; Armour, 1980). The observed periodicity in helminth infections has already been described for European helminths (e.g. *Ostertagia*, Armour, 1980).

The principal environmental factors controlling parasite population increase are temperature and humidity, particularly the microclimate (Armour, 1980). Rowcliffe & Ollerenshaw (1960) developed a model to predict the prevalence of fascioliasis in domestic sheep, based on microclimatic observations in Great Britain. For African wild ungulates such data are not yet available. Therefore, assessing what microclimatic factors influence pasture nematode larval availability and infection rates would be worthwhile in the Queen Elizabeth National Park.

Table 1. Logistic regressions on the prevalence of oocysts of *Eimeria* sp. and eggs of *Moniezia* spp. and strongyle nematodes in the faeces of free-ranging bushbuck *Tragelaphus scriptus* in the Queen Elizabeth National Park, Uganda from April 2000 to February 2002. Season (dry (reference level) or wet), sex (reference level: female) and age (adult (reference level) or subadult) were treated as separating factors.

Parasite type		Coefficient	X^2	P
Eimeria sp.	Season	1.01	4.98	0.026*
	Sex	− 0.39	0.77	0.38
	Age	0.16	0.07	0.79
Moniezia spp.	Season	1.26	3.61	0.057**
	Sex	0.30	0.27	0.61
	Age	0.77	1.51	0.22
Strongyle nematodes	Season	0.52	0.66	0.42
	Sex	0.32	0.29	0.63
	Age	0.18	0.05	0.81

Significant $^*P < 0.05$; $^{**}P < 0.1$.

Only a few animals were infected with strongyle and rhabditoid (*Strongyloides* sp.) nematodes, whereas *Eimeria* spp. and *Moniezia* sp. were the most frequently occurring parasites. While *Eimeria* spp. are transmitted through water and (wet) soil, the risk of infection with strongyle and *Strongyloides* nematodes is lower, since infectious larval stages are ingested during foraging. *Moniezia* (Cestoda) produce eggs in the gut of their definitive host (e.g. bushbuck). In faeces, oncospheres hatch, and develop in mites as intermediate hosts (Soulsby, 1968; Dunn, 1978). Moisture is likely to positively influence the survival of free-living oncospheres.

Bushbuck from the Queen Elizabeth National Park preferentially browse and forage along thicket fringes and in open grassland, and perennial woody herbs are preferentially eaten. In both cases, bushbuck forage at a level above ground where the contamination of pasture with infective strongyle nematode larvae was found to be very low (Apio, 2003). This minimizes the probability of ingesting infective stages of strongyle and *Strongyloides* sp. helminths during foraging. Moreover, *Eimeria* spp. produces millions of oocysts per specimen, while strongyle nematodes shed comparatively few eggs (Soulsby, 1968). Therefore, coccidian parasites may spread faster than the nematode parasites during the wet season.

The mean intensities of infection by all parasite taxa recorded during this study were low compared to those reported for other African wild herbivores (Sachs & Sachs, 1968; Woodford, 1976). One possible explanation is that bushbuck have exceptionally effective immune response mechanisms against these parasites. This might be due to the co-evolution between wild artiodactyls, in this case bushbuck, and their parasites (Sachs & Sachs, 1968). The ability of bushbuck to overcome gastrointestinal tract nematode infections and to tolerate light worm burdens has been described by various authors (Pullan *et al.*, 1971; Woodford, 1976; Mares *et al.*, 1984; Boomker *et al.*, 1984, 1986, 1987). However, a more plausible explanation for the low degree of infection is that the foraging habits of bushbuck keep the risk of infection to a minimum. The discrepancy between pronounced seasonal variation in the prevalence of gastrointestinal tract parasites and the lack of seasonality in the mean intensity of such parasites is likely to be caused by the small sample size in the present analysis of mean intensities, since only relatively few samples actually contained parasites.

The lack of variation in intensity of infection relative to host sex is surprising, because domestic ungulate males have been reported to be more susceptible to infections with gastrointestinal tract parasites than females (Dunn, 1978). This has been attributed to male hormones debilitating immune functions, thereby favouring the growth and success of parasites in their gut (Dunn, 1978). The lack of a difference in parasite burdens between the sexes of free-ranging bushbuck clearly warrants future research.

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(Accepted 19 January 2006)

https://doi.org/10.1079/JOH2006343 Published online by Cambridge University Press