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Foraging height levels and the risk of gastro-intestinal tract parasitic infections of wild ungulates in an African savannah eco-system

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Summary

Grazing herbivores mainly feed at low feeding height levels, while browsers select food items above ground level. Previous studies on gastrointestinal tract (GIT) nematode parasite burdens of African ungulates have suggested that browsing species hereby minimise the risk of infection with parasites. Here, we investigated the influence of feeding height levels on the pasture larval contamination level (PCL) in a natural African savannah eco-system in Queen Elizabeth National Park, western Uganda. The prevalence and mean abundance of infectious GIT nematode larvae on the pasture were used as measures of pasture contamination. Vegetation samples were examined following standard larval isolation, concentration and counting techniques. We found the feeding height level to be significantly related to the occurrence of infectious GIT nematode larvae, and the contamination was highest at low feeding levels. There was no statistically significant seasonal variation in the prevalence or mean abundance of the contamination of pastures with nematode larvae.

Key words: African ungulates; bushbuck; GIT nematode larvae; pasture contamination; Uganda

Introduction

Grazing herbivores feed on lower vegetation close to the ground, while browsers selectively pick their food items from higher vegetation levels (Owen-Smith, 1992). In two field surveys of GIT parasite infection of wild herbivore hosts in the savannah habitats of the Queen Elizabeth National Park, Uganda, Woodford (1976) and Apio (2003) Apio *et al*.., 2006a) provided data on the faecal egg output of parasitic gastro-intestinal tract (GIT) nematodes. Woodford's (1976) study focused on a number of primarily grazing artiodactyls, namely buffalo *Syncerus caffer* (mean 335 strongyle eggs per gram faeces (EPG), $N = 2$), waterbuck *Kobus ellipsiprymnus defassa* (638 EPG, $N = 2$), Uganda kob *Kobus kob thomasi* (918 EPG, $N = 2$) and topi *Damaliscus lunatus jimela* (922 EPG, $N = 4$). By contrast, Apio (2003), Apio *et al*., 2006a) investigated a browsing species, the bushbuck *Tragelaphus scriptus* (6.3 EPG, $N = 59$). Although these studies may not be directly comparable due to methodological differences, there appears to be a clear trend of grazers showing higher degrees of infestation with GIT nematodes than the browsing species, suggesting that browsing minimizes the risk of parasitic nematode infections.

GIT parasites, which are acquired through the process of foraging, represent one of the most pervasive challenges to the survival and reproductive capacities of their herbivore hosts (Coop *et al*., 1982). In studies on pasture contamination levels (PCL) of range-lands in temperate climates, Angus (1978) and Gibson (1966) found most free-living larval stages of GIT nematodes near the ground, probably due to the lethal effects of the environmental conditions on the survival of the infectious stages of parasites at higher heights (e.g., lower humidity, stronger exposure to sunlight). On the contrary, studies on PCL in the wild are scarce, and even more so for eco-systems outside the temperate climates.

In this study, we investigated PCL in a central African savannah eco-system. The development and survival of infective larvae of GIT nematodes on pasture in tropical environments have been reported to be primarily affected by the seasonal climatic changes between the dry and the wet season (Banks *et al*., 1990; Bekele *et al*., 1992; Chartier, 1991; Chiejina & Fakae, 1984; Dinnik & Dinnik, 1961; Onyali *et al*., 1990). The effect of the vegetation height on larval availability in tropical climates, on the other hand, has so far barely been studied. Therefore, our main goal was to determine whether there are differences in PCL between different feeding heights in our study area, Queen

Elizabeth National Park. Following previous studies, we also asked if the change between the dry and the wet season has an effect on the larval availability of pasture, with a stronger pasture contamination during the wet season (Banks *et al*., 1990; Dinnik & Dinnik, 1961; Onyali *et al*., 1990).

Materials and Methods

We collected data on the Mweya peninsula and adjoining areas north of the Kazinga channel in Queen Elizabeth National Park, western Uganda (0°10` to 0°12`S; 29°52` to 29°54`E). The study area (approximately 8.7 km²) comprises *Sporobolus pyramidalis*-grassland with scattered *Capparis tomentosa* / *Euphorbia candelabra* thicket clumps (Lock, 1977; Zandri & Viskanic, 1992). The climate is equatorial, with little annual fluctuations in temperature (wet season [Sept. – Dec. and March – May], mean (±SD) night temperature: 19.9 ± 1.3°C, daytime: 30.0 ± 2.4°C; dry season [Jun. – Aug. and Jan. – Feb.], night temperature: 20.1 ± 1.9°C, daytime: 31.3 ± 3.0°C). Rainfall was determined on a daily basis using a rain gauge. Our study was carried out in 2001, when the mean annual rainfall was 680 mm. Daily rainfall showed pronounced differences between the wet (3.2 ± 7.1 mm) and dry season (0.5 ± 2.4 mm). The relative air humidity was slightly higher during the wet season (morning: 85.1 ± 5.8 %, noon: 74.3 ± 10.3 %, evening: 76.0 ± 7.6 %) than during the dry season (morning: 75.6 ± 8.3 %, noon: 62.3 ± 11.1 %, evening: 58.3 ± 16.7 %).

The sampling plots were placed haphazardly throughout the study area. Herbage cut included all edible parts of plants from non-woody herbs, woody herbs and leaves of shrubs. Based on the feeding habits of grazing and browsing species in the study area (Field, 1968, 1972; Okiria, 1977; Apio, 2003; Cerling & Viehl, 2004; Apio & Wronski 2005), we distinguished two feeding height levels as: ground level (< 20 cm) and above ground level (> 20 cm). Each sample plot along a thicket fringe consisted of a set of nine single sub-samples (a square of 900 cm²) placed either at the basis of a thicket or above 20 cm but not higher than 1.5 m. Herbage of sub-samples from the same height-level were lumped together for each plot. In the case of grassland plots, herbage was cut within a circle of 20 m diameter (modified after Hansen and Perry, 1990). From the centre, a rope was stretched along four directions to ensure systematic sampling (Apio *et al*., 2006b). Two sub-samples were collected along each direction. Together with the area in the centre, a total of nine sub-samples (900 cm²) were collected for each plot. Also in grassland plots, herbage was collected from above ground level, such as woody and non-woody herbs. Browsers (i.e., bushbuck) are known to feed on such herbage above ground level in grasslands (Apio & Wronski 2005; Haschick & Kerley, 1997; Okiria, 1977; Smits, 1986). Herbage from the nine sub-samples was lumped together for each height level. We collected herbage during two sessions during the wet season (March 1st – 16th (33 samples) and May 3rd – 27th (33 samples)) and twice during the dry season (June 30th – July 23rd (33 samples) and August 18th – 30th (32 samples)). Plant material was collected between 6.00 and 9.30 a.m., because the highest numbers of free-living nematode larvae ("L3") have been reported for the early morning hours (Soulsby, 1968).

Isolation, concentration and counts of infective larvae in pasture samples followed procedures described by Hansen and Perry (1990) and the Ministry of Agriculture, Fisheries and Food, UK (1971). Larval identification was conducted according to keys and drawings provided by Angus (1978), Bürger and Stoye (1968), Soulsby (1968) and the Ministry of Agriculture, Fisheries and Food, UK (1971). Only gastro-intestinal tract nematode genera which are known to infect ungulates in the study area were included in the investigation (Woodford, 1976; Table 1). Differentiation from saprophytic species was enabled by iodine staining (Hansen & Perry 1990; Ministry of Agriculture, Fisheries and Food, UK 1971). Afterwards each herbage sample was dried and weighed.

In total, 131 vegetation samples were analysed. In a first approach, we used the prevalence of L3 on the herbage for a logistic regression ($R^2 = 0.10$, log likelihood = -81.78, intercept log likelihood = -90.62), in which "season" (dry (reference level), or wet) and "feeding height level" (above 20 cm (reference level), or ground level) were included as separating factors. We also calculated the mean larval abundance (pasture contamination level [L3/kg dry herbage]). Data were transformed to achieve normality following the equation: $y' = \log((y + 0.5)*10)$ and were analysed using a two-way ANOVA. Since the interaction term 'season' x 'feeding height' had no statistically significant effect ($F_{1,127} = 1.21$, $p = 0.27$), only the main effects were analysed.

Tab. 1. The pasture contamination level of GIT parasitic nematode larvae (L3) (mean (±SE) abundance per kilogram pasture). *Cooperia* spp. were not detected in this study

	above 20 cm		below 20 cm	
	wet season	dry season	wet season	dry season
Bunostomum	0.20 ± 0.20	0.04 ± 0.04	123.52 ± 92.30	0.56 ± 0.56
Cooperia	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Trichstrongylus	0.00 ± 0.00	0.00 ± 0.00	25.21 ± 22.74	14.76 ± 10.26
Strongyloides	0.00 ± 0.00	0.00 ± 0.00	4.55 ± 3.15	8.26 ± 8.26
Ostertagia	7.81 ± 7.57	0.65 ± 0.65	75.22 ± 68.05	6.76 ± 4.30
Haemonchus	1.90 ± 1.28	0.38 ± 0.34	387.79 ± 247.46	17.13 ± 7.45

Results

There was no statistically significant influence of the factor 'season' (wet or dry) on the prevalence of GIT nematode larvae on the pasture ($\chi^2 = 0.10$, $c = 1.12$, $p = 0.76$). On the contrary, the factor 'feeding height' had a significant effect on the prevalence of L3 larvae on the herbage ($\chi^2 = 15.93$, $c = 5.08$, $p < 0.0001$). We also found no statistically significant effect of the factor 'season' on the pasture contamination level (PCL; $F_{1,128} = 0.70$, $p = 0.41$), but again there was a significant effect of the feeding height level on the pasture contamination ($F_{1,128} = 47.27$, $p < 0.0001$; Fig. 1).

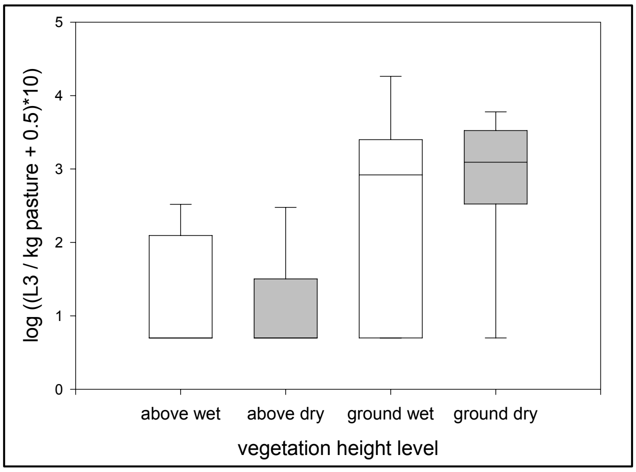

Fig. 1. Pasture contamination level (PCL) of herbage above ground level (left) and at ground level (right) during the wet season (white plots) and dry season (shaded plots) in Queen Elizabeth National Park, Uganda. Vegetation height levels were chosen to account for differences in feeding heights between grazing (ground level) and browsing ungulates (above ground level). Non-parametric boxplots, showing the median (middle line), the interquartile range (box) and the 5 and 95 % values (whiskers). Note that median values are zero above ground level

Discussion

In our study, infection risk of herbivores was determined as the GIT parasitic nematode larval intensity (PCL) and the prevalence of larvae on pasture in a natural savannah habitat carrying a pure game stocking. Several investigations on the ecology of nematode larvae in temperate areas have focused on seasonal variation in the availability of GIT nematode larvae on the pasture of domestic herbivores (Brunsdon, 1970; Donald *et al.*, 1978; Evans, 1974; Gibbs, 1967; Ollerenshaw & Smith, 1969; Southcott *et al.*, 1976), or on the effect of vegetation height on pasture contamination (Angus, 1978; Gibson, 1966). Moreover, a number of studies have concentrated on the climatic (seasonal) variation in pasture contamination in tropical ecosystems carrying pure domestic stocks (Banks *et al.*, 1990; Bekele *et al.*, 1992; Cheijina & Fakae, 1984; Chartier, 1991; Dinnik & Dinnik, 1961; Kabasa, 1999; Onyali *et al.*, 1990), or a mixed cattle/game stocking (Ocaido, 1995). Data on the contamination of latrines from a tropical (long-term) conserved area with only wild herbivores have been presented by Ezenwa (2004). A possible effect of feeding height levels and sea-sons on pasture contamination in natural tropic grassland environments with a pure game stocking, however, was investigated here for the first time.

In our study, we found more nematode larvae at ground level than above 20 cm height. GIT nematode larvae originate from faeces, which accumulate on the ground. It is therefore straightforward to expect most L3 stages to be found near the source of their dispersal, i.e. at ground level. However, Hippopotamus (*Hippopotamus amphibius*) are very abundant in the study area. The latter are known to "spray" their faeces onto the vegetation rather than just dropping them. This may explain why we also found a certain number of larvae also above ground level.

The survival and dispersion of GIT nematode larvae on pasture have been described to be affected by temperature and - most importantly - by sufficient humidity on the vegetation (i.e., water film or water droplets; Krecek *et al.*, 1995). Above ground level, wind and sunlight increase the evaporation of droplets, so that nematode larvae desiccate faster (Angus, 1978; Gibson, 1966; Michel, 1976). Given that moisture is known to affect GIT nematode larvae, our finding that both the larval prevalence and intensity (PCL) was not significantly affected by seasons was unexpected. Several factors, which are not mutually exclusive, may explain the lack of seasonal variation in our study. For example, all samples were collected in the morning, when humidity on the pasture is highest. Most importantly, however, we found pronounced seasonal variation in daily rainfall, but variation in the relative humidity was far less pronounced; hence, microclimatic conditions on the pasture likely show little seasonal variation in the study area.

The extend to which the macroclimate affects the microclimatic conditions on the herbage depends on the nature and state of the herbage. If the herbage is dense and tall, it will be more effective in reducing variation in humidity, temperature or light intensity than if it is thin or short (Michel & Ollerenshaw, 1963). Since the Mweya peninsula is known to be overgrazed (Lock, 1985), grassland vegetation is predominantly short and thin. Therefore, even changes in the abiotic conditions in the course of the day (such as daily variation in temperature) will immediately have a strong influence on the microclimatic conditions at higher vegetation heights. Possibly, conditions for nematode larvae therefore remain favourable for a longer period only in the lower parts of the vegetation independent of seasonal variation in rainfall.

In summary, we found the contamination of pasture with parasitic nematode larvae to be higher at low feeding levels, but no seasonality in pasture contamination was detected. Our study provides direct evidence that grazing ungulates in the study area (e.g., buffalo) have a higher risk of infection with GIT nematode larvae than browsing species (e.g., bushbuck).

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References

ANGUS, M. D. (1978): *Veterinary Helminthology.* William Heinemann Medical Books Ltd., London

APIO, A. (2003): *Foraging behaviour and gastrointestinal tract parasitic infections of the bushbuck (Tragelaphus scriptus) in Queen Elizabeth National Park, western Uganda*. MSc. Thesis, Mbarara University of Science and Technology, Uganda

APIO, A., WRONSKI, T. (2005): Foraging behaviour and diet composition of bushbuck (*Tragelaphus scriptus*) in Queen Elizabeth National Park, Uganda. *Afr. J. Ecol.*, 43: 1 – 8

APIO, A., PLATH, M., WRONSKI, T. (2006a): Patterns of gastrointestinal parasitic infections in the bushbuck *Tragelaphus scriptus* from the Queen Elisabeth National Park, Uganda. *J. Helminthol.*, 80: 213-218

APIO, A., PLATH, M., WRONSKI, T. (2006b): Localised defecation sites: a tactic to avoid re-infection by gastrointestinal tract parasites in bushbuck (*Tragelaphus scriptus*)? *J. Ethol.*, 24: 85 – 90

BANKS, D. J., SINGH, R., BARGER, I. A., PRATRAP, B., LE JAMBRE, L. F. (1990): Development and survival of infective larvae of *Haemonchus contortus* and *Trichostrongylus colubriformis* on pasture in a tropical environment. *Int. J. Parasitol.*, 20: 155 – 160

BEKELE, T., WOLDEAB, T., LAHLOU-KASSI, A., SHERINGTON, J. (1992): Factors affecting morbidity and mortality on-farm and on station in the Ethiopian highland sheep. *Acta Trop.*, 52: 99 – 109

BRUNSDON, R. V. (1970): The spring rise phenomenon: seasonal changes in the worms burdens of breeding ewes and the availability of pasture infection. *New Zeal. Vet. J.*, 18: 47 – 54

BÜRGER, H. J., STOYE, M. (1968): *Parasitologische Diagnostik* (Teil II), Eizählung und Larvendifferenzierung. Therapogen Praxisdienst 3

CERLING, T. E., VIEHL, K. (2004): Seasonal diet changes of the forest hog *(Hylochoerus meinertzhageni* Thomas) based on the carbon isotopic composition of hair. *Afr. J. Ecol.*, 42: 88 – 92

COOP, R. L., SYKES, A. R., ANGUS, K. W. (1982): The effect of three levels of intake of *Ostertagia circumcincta* larvae on growth rate, food intake and body composition of growing lambs. *J. Agr. Sci.*, 98: 247 – 255

CHARTIER, C. (1991): Développement et survie d'Haemonchus contortus d'origine ovine sur parcelle a Bunia (Ituri, Zaire). *Revue d'Elevage et de Médecine Vétérinaire des pays Tropicaux*, 44: 169 – 174

CHIEJINA, S. N., FAKAE, B. B. (1984): Development and survival of infective larvae of gastrointestinal nematode parasites of cattle on pasture in eastern Nigeria. *Res. Vet. Sci.*, 37: 148 – 153

DINNIK, J. A., DINNIK, N. N. (1961): Observations on the longevity of *Haemonchus contortus* larvae in the Kenya highlands. *Bull. Epizootic Dis. Afr.*, 9: 193 – 208

DONALD, A. D., MORLEY, F. H. W., WALLER, P. J., AXELSON, A., DONELLY, J. R. (1978): Availability to grazing sheep of gastrointestinal nematode infection arising from summer contamination of pastures. *Austr. J. Agr. Res.*, 29: 189 – 204

EVANS, A. A. F. (1974): The effect of climate on plant and soil nematodes. In TAYLOR, A. E. R., MULLER, R. (Eds): *Effects of metereological factors upon parasites*. Symposia of 12th British Society for Parasitology. Blackwell Scientific Publications, Oxford, London, pp. 53 – 77

EZENWA, V. O. (2004): Selective defecation and selective foraging: Antiparasite behavior in wild ungulates. *Ethology*, 110: 851 – 862

FIELD, C. R. (1968): A comparative study of the food habits of some wild ungulates in the Queen Elizabeth National Park, Uganda preliminary report. *Symposium of the Zoological Society London*, 21: 135 – 151

FIELD, C. R. (1972): The food habits of wild ungulates in Uganda by analysis of stomach contents. *E. Afr. Wildl., J.*, 10: 17 – 42

GIBBS, H. C. (1967): Some factors involved in the spring rise phenomenon in sheep. In Soulsby, E. J. L. (Ed): *Veterinary Medical Review "The reaction of the host to parasitism".* Proceedings of the Third International Conference of the World Association for Advances in Veterinary Parasitology, pp. 169 173

GIBSON, T. E. (1966): The ecology of the infective larvae of *Trichostrongylus colubriformis*. in SOULSBY, E. J. L. (Ed): *Biology of Parasites.* Academic Press, London, pp. 2 – 13, 354

HASCHICK, S. L., KERLEY, G. I. H. (1997): Factors influencing forage preferences of bushbuck and boer goats for subtropical thicket plants. *Afr. J. Range Forage Sci.*, 14: 49

– 55

HANSEN, J., PERRY, B. (1990): *The epidemiology, diagnosis and control of gastro-intestinal parasites of ruminants in Africa. A handbook*. International Laboratory for Research on Animal Diseases, Nairobi

KABASA, J. D. (1999): *The nutritional ecology and effects of browse polyphenols in goats of the Ankole range land ecosystem in Uganda*. PhD dissertation, Georg-August-University-Goettingen, Germany

KRECEK, R. C., HARTMAN, R., GROENEVELD, H. T., THORNE, A. (1995): Microclimatic effect on vertical migration of *Haemonchus contortus* and *Haemonchus placei* third-stage larvae on irrigated Kikuyu pasture. *Onderstepoort J. Vet.*, 62: 117 – 122

LOCK, J. M. (1977): The vegetation of the Rwenzori National Park, Uganda. *Bot. Jahrb. Syst*., 98: 372 – 148

LOCK, J. M. (1985): Recent changes in the vegetation of Queen Elizabeth National Park, Uganda. *Afr. J. Ecol.*, 23: 63 – 65

MICHEL, J. F. (1976): The epdemiology and control of some nematode infections in grazing animals. *Adv. Parasit*., 14: 355 – 397

MICHEAL, J. F., OLLERENSHAW, C.B. (1963): Helminth diseases of grazing animals. In WORDEN, A. N. *et al*. (Eds.): *Animal Health, Production and Pasture*. Longmans Green, London, pp. 445 – 457

MINISTRY OF AGRICULTURE, FISHERIES AND FOOD, UK (1971): Manual of Veterinary parasitological laboratory technique. *Technical Bulletin* No. 18. Her majesty's stationnary office, London, United Kingdom

OCAIDO, M. (1995): *Effects of diseases on developing mixed game and livestock ranching around Lake Mburu National Park, Uganda*. MSc. thesis, Makerere University, Kampala, Uganda

OKIRIA, R. (1977): *The behaviour and ecology of the bushbuck (Tragelaphus scriptus Pallas) in Rwenzori National Park, Uganda*. MSc thesis, University of Moscow

OLLERENSHAW, C. B., SMITH, L. P. (1969): Meteriological factors and forecast of helminth disease. In DAVES, B. (Ed): *Advances in Parasitology*. Academic Press, London, New York, pp. 283 – 323

ONYALI, I. O., ONWULIRI, C. O. E., AJAYI, J. A. (1990): Development and survival of *Haemonchus contortus* larvae on pasture at Vom, Plateau State, Nigeria. *Vet. Res. Com.*, 14: 211 – 216

OWEN-SMITH, N. (1992): Grazers and Browsers: ecological and social contrasts among African ruminants. In SPITZ, F., JANEAU, G., GONZALEZ, G., AULAGNIER S. (Eds): 'ongules /Ungulates 91': Proceedings of the International Symposium 'ongules / Ungulates 91', Toulouse - France, September 2 – 6, 1991. Societe Francaise Pour L'etude Et La Protection Des Mammiferes, Paris and Institut De Recherche Sur Les Grands Mammiferes, Toulouse, pp. 175 –181

SMITS, C. M. M. (1986): Diet composition and habitat use of the West African bushbuck *Tragelaphus scriptus scriptus* (Pallas, 1776) during the first half of the dry season. *S. Afr. J. Zool.*, 21: 89 – 94

SOULSBY, E. J. L. (1968) *Helminths, Arthropods and Protozoa of domestic animals*. Bailliere, Tindall and Cassell Ltd., London

SOUTHCOTT, W. H., MAJOR, G. W., BARGER, I. A. (1976): Seasonal pasture contamination and availability of nematodes for grazing sheep. *Austr. J. Agr. Res.*, 27: 277 – 289

WOODFORD, M. H. (1976): *A survey of parasitic infestation of wild herbivores and their predators in the Rwenzori National Park, Uganda*. Report to the Uganda Institute of Ecology, Rwenzori National Park, Kasese, Uganda

ZANDRI, E., VISKANIC, P. (1992): *Vegetation and Mapping in the Queen Elizabeth National Park, Kyambura Game Reserve and Kigezi Game Reserve*. Uganda National Parks Technical Assistance to the Uganda Institute of Ecology, Agriconsulting, Italy. (Commission of the European Communities, EDF Project 6100.037.42.031)

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